

EASTERN DIAMONDBACK RATTLESNAKES: USING OCCUPANCY AND POPULATION MODELS TO
DIRECT MANAGEMENT

by

KEVIN MICHAEL STOHLGREN

(Under the Direction of John C. Maerz)

ABSTRACT

Eastern diamondback rattlesnakes (*Crotalus adamanteus*) are declining throughout their range. We used occupancy and population models to help direct future management objectives. Our occupancy analysis on Georgia's barrier islands indicated that the influence of habitat composition varied with scale. The area of maritime forest negatively influenced occupancy rates at the 500- and 1000-m spatial scale, while the area of secondary dune habitat positively influenced occupancy rates at the 1000-m spatial scale. Landscape composition did not appear to influence occupancy rates at the 250-m spatial scale. Coastal management for eastern diamondback rattlesnakes should focus on protecting large tracts of secondary dune habitat. Our stage-based population models indicated that population growth was most sensitive to changes in adult survival rate. Management strategies for eastern diamondback rattlesnakes should aim to increase adult survival rate by reducing anthropogenic threats such as road mortality, collection for rattlesnake roundups, and malicious killings.

INDEX WORDS: Eastern diamondback rattlesnake, *Crotalus adamanteus*, occupancy, detection, population, modeling, matrix model, Leftkovitch

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DEDICATION

I would like to dedicate this thesis to my parents, Mike and Karen. Thank you for all of your love and encouragement, and for supporting my crazy obsession with “creepy crawlies”.

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CHAPTER 1

INTRODUCTION

One of the most prevalent causes for species declines is the degradation, fragmentation, and loss of habitat (Alford and Richards 1999; Gibbons et al. 2000; Brown et al. 2005). The longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States is one of the most imperiled habitats in the world, with possibly less than three percent of its historic distribution remaining intact (Noss et al. 1995; Outcalt and Sheffield 1996; U.S. Fish and Wildlife Service 2003). The loss of this ecosystem is primarily due to the conversion to agriculture and forestry plantations, as well as development (Means and Grow 1985; Noss 1988). The longleaf pine ecosystem also suffers from the removal of fire from the landscape (Outcalt and Wade 2004; Van Lear et al 2005). A fire climax community, the longleaf pine ecosystem relies on frequent, low intensity fires to maintain an open pine canopy with a high diversity of ground cover (Means and Grow 1985; Noss 1988). The removal of fire allows the succession of oaks (*Quercus spp.*), which eventually shade out young pine trees and much of the native ground cover, such as wiregrass (*Aristida stricta*). The decline in this ecosystem has been followed by declines in many fauna that are endemic to this ecosystem, including red-cockaded woodpeckers (*Picoides borealis*), gopher tortoise (*Gopherus polyphemus*), gopher frogs (*Lithobates capito*), striped newts (*Notophthalmus perstriatus*), Florida pine snakes (*Pituophis melanoleucus*), and eastern

diamondback rattlesnakes (*Crotalus adamanteus*; hereafter referred to as Eastern diamondbacks)(Gibbons et al. 2000; Trani-Griep 2002; Rudolph et al. 2004).

Eastern diamondbacks historically ranged throughout much of the Coastal Plain from eastern Louisiana to southeastern North Carolina, and south through all of Florida, following closely the range of the longleaf pine ecosystem (Martin and Means 2000; Waldron et al. 2006; Waldron et al. 2008; Hoss et al. 2010). Like the longleaf pine ecosystem, eastern diamondbacks have declined throughout much their native range, possibly being extirpated from Louisiana, listed as state endangered in North Carolina, and considered rare or uncommon in Mississippi, Alabama and South Carolina (Timmerman 1995; Martin and Means 2000; Timmerman and Martin 2003). Declines in this species have prompted its proposal to be listed as a threatened species under the Endangered Species Act, and its status is currently being reviewed by the US Fish and Wildlife Service (U.S. Fish and Wildlife Service 2012).

Identifying important conservation areas is an essential step in any conservation efforts for a declining species (Gibbons et al. 2000). These are areas that meet all of the requirements for the species of interest, and protection of these areas will help to ensure the species persistence. The barrier islands on the coast of Georgia are one of these important conservation areas for eastern diamondbacks (Means 1994). While Georgia's barrier islands don't contain the longleaf pine ecosystems found on the mainland, these rattlesnakes are commonly found in the secondary dune systems, which have a similar habitat structure of an open canopy with dense ground cover (Means 1994).

In order to develop effective management strategies for eastern diamondbacks on Georgia's barrier islands, it is important to first understand the influence landscape

composition has on where they occur. One commonly used method to examine this relationship is occupancy modeling. Occupancy modeling allows to you estimate a species use of an area as a function of the surrounding landscape (MacKenzie et al. 2002). These occupancy models can be of great use in setting up management strategies such as identifying critical habitat, developing protected areas, and monitoring imperiled species (MacKenzie et al. 2003; De Wan et al. 2009; Durso et al. 2011).

Another set of useful tools in developing conservation strategies are population models (Crowder et al. 1994; Heppell and Crowder 196; Lo et al. 1995; Enneson and Litzgus 2008). Population models allow you to use a species' life history parameters, such as birth rate and survival, to estimate a population growth rate. From these models you can also identify which parameters have the greatest influence on the population growth rate. Identifying these important parameters allows you to target conservation strategies where they will have the greatest impact, saving time and money (Lo et al. 1995).

The first objective of this thesis is to identify the landscape-level influences on eastern diamondback occupancy on Georgia's barrier islands. In chapter 2 we use an occupancy modeling approach to identify the important landscape factors and use the results to make recommendations for management and future research. The second objective of this thesis is to identify the most important life history parameters for eastern diamondback population growth. In chapter 3 we build stage-based population models to estimate population growth rate. We also run sensitivity and elasticity analyses to determine which parameters have the greatest contribution our models, and lastly, make recommendations as to how this model can be used to develop management strategies. We believe that the results of this research will

provide information that can be used to help conserve this rapidly declining species as well as provide a framework for future research on eastern diamondbacks at other locations.

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Chapter 2

EASTERN DIAMONDBACK RATTLESNAKE OCCUPANCY OF SECONDARY DUNE HABITAT ON THE GEORGIA COAST

Introduction

With increasing human population, the loss, alteration, and degradation of natural areas is of great conservation concern. This change in landscape composition poses a significant threat to biological communities as it destroys and fragments habitat, increases road density, and brings humans into greater contact with wildlife (Alford and Richards 1999; Gibbons et al. 2000; Brown et al. 2005; De Wan et al. 2009). These threats are often cited as the cause for species declines, yet the influence of landscape composition is not known for most species (Tigas et al. 2002; Graham 2002).

The coast of Georgia is roughly 100 miles long and lined by fourteen major barrier islands and numerous smaller islands. It is relatively undisturbed with only three of the barrier islands (Jekyll, St. Simon's, and Tybee Islands) being heavily developed and connected to the mainland via causeways. On ten of these islands, there is some amount of protection of natural areas by federal, state, or private landowners and one third of all the remaining salt marsh on the Atlantic Coast is in Georgia (Seabrook 2006). Despite this protection, coastal Georgia is under threat of development activities, with a projected 51% increase in population from the year 2000 to the year 2030 (Coastal Georgia Regional Development Center 2006). It is essential

to understand the influence of habitat composition on the fauna of this region in order to develop effective conservation strategies.

Eastern diamondback rattlesnakes (*Crotalus adamanteus*; hereafter referred to as Eastern diamondbacks), which occur throughout much of the Coastal Plain of the southeastern United States, are currently facing rapid population declines (Martin and Means 2000). These declines have mainly been attributed to anthropogenic factors, such as habitat loss and fragmentation, fire suppression, malicious killing by humans, and road mortality (Timmerman 1995; Martin and Means 2000; Timmerman and Martin 2003; Steen et al. 2007). Changes in land use that bring people into closer contact with rattlesnakes amplify these threats. Despite these declines, healthy populations of eastern diamondbacks remain on many of the barrier islands on the coast of Georgia (Means *in press*).

The range of eastern diamondbacks is strongly associated with the historic range of the longleaf pine and wiregrass ecosystem (Martin and Means 2000; Waldron et al. 2006; Waldron et al. 2008; Hoss et al. 2010). While the longleaf pine and wiregrass habitat does not occur on the Georgia barrier islands, eastern diamondbacks occupy habitats with a similar structure of dense ground cover and an open canopy. The secondary dune systems of the barrier islands are early successional habitats that consist of dense grasses, such as muhley grass (*Muhlenbergia capillaries*), that are interspersed with patches of shrubby trees like wax myrtle (*Myrica cerifera*)(Means 1994). These dunes systems have high densities of marsh rabbits (*Sylvilagus palustris*), cotton rats (*Sigmodon hispidus*), and other small mammals, which are prey for eastern diamondbacks, and also provide suitable cover from predators (Means 1994; Timmerman 1995; Martin and Means 2000). While these snakes likely use all available habitats

to some extent, secondary dune systems have the highest use and likely comprise the most important habitat for eastern diamondbacks on the barrier islands (Means *in press*).

One commonly used measure of population status in wildlife studies is occupancy, or the proportion of sites or area occupied. The occupancy modeling framework of MacKenzie et al. (2002) allows researchers to estimate the proportion of sites occupied as a function of site-level covariates. These site occupancy estimates are often used in prioritizing areas for conservation efforts, monitoring populations over time, and metapopulation studies (MacKenzie et al. 2003; De Wan et al. 2009; Durso et al. 2011). However, estimates of site occupancy will be underestimated if a species was present at a site but failed to be detected (i.e. detection is <1), as is often the case with highly cryptic species or species with secretive life histories (MacKenzie et al. 2002; MacKenzie et al. 2003; Mazerolle et al. 2007).

Recent developments in occupancy modeling allow the incorporation of detection probability for a species where detection is imperfect (MacKenzie et al. 2002). Estimating detection probability requires repeat surveys of each sampling site to account for individuals that were present but not detected. These repeat surveys must be completed in a short time span to assure population closure of the survey area. That is, the occupancy status (occupied or unoccupied) of the survey area must remain constant during the sampling period (MacKenzie et al. 2002; MacKenzie et al. 2003). Detection probability can also be modeled with survey-level covariates such as weather, time of day, season, and observer, which may vary with each secondary sampling period (MacKenzie et al. 2003). Incorporating detection probability into habitat use models is essential for cryptic and secretive species to give unbiased predictions of where a species may occur in the landscape (De Wan et al. 2009).

Another important consideration when conducting ecological studies is spatial scale. The degree to which landscape features influence a species may not be consistent across scales, therefore, the scale at which a study is conducted may have a significant impact on the patterns seen in the results (Wiens 1989). For example, eastern diamondbacks have long been known to be associated with the longleaf pine forest, but habitat heterogeneity has been shown to be important at finer scales (Hoss et al. 2010; Steen et al. 2012). Studies conducted at a large scale may fail to pick up the importance of heterogeneity, whereas finer scale studies may fail to recognize the importance of the longleaf pine forest.

The objective of this study was to use an occupancy modeling framework to identify the habitat features and associated spatial scales that influence eastern diamondback populations in early successional dune habitats on Georgia's barrier islands. We did this by using a random sampling design to select survey sites in secondary dune habitat where we conducted repeated surveys, and then estimated the probability of detection and occupancy rate of eastern diamondbacks. We then examined the influence of the surrounding habitat on occupancy rates at multiple spatial scales.

Methods

Study Area

The field portion of this study was conducted on ten of the barrier islands on the coast of Georgia, USA (Fig. 2.1). Three of these islands (Jekyll, St. Simon's, and Tybee) are connected to the mainland via causeways and have been developed, while the other seven have little to

no development and are only accessible by boat (Blackbeard, Cumberland, Little Cumberland, Little St. Simon's, Ossabaw, Sapelo, and Wassaw).

Site Selection

Within the ten study islands, we used a geographic information system (GIS) to identify secondary dune habitats (interdune swale and southern hairgrass land cover types) from the land cover shapefile (Georgia Department of Natural Resources 2010). Hawth's Analysis Tools (Beyer 2004) within ArcGIS 9.x (ESRI, Redlands, CA) was used to generate random sampling locations within the secondary dune habitats. The sampling locations were placed a minimum of 500 m apart to insure spatial independence. We then placed 1 ha square survey plots around each point (Fig 2.2). The shapes of the plots were adjusted to fit within the secondary dune habitat when needed.

Sampling methodology

Area constrained visual encounter surveys (VES) were conducted at all sampling locations. Each survey was conducted by thoroughly searching in a grid pattern, transecting the plot and then moving approximately 5 meters and then transecting back the other direction. We used a GPS unit to navigate each sampling plot. During the survey, vegetation was probed, cover objects were turned (and replaced), and a light was shined into any holes or burrows. This was continued until the entire plot was covered. At the end of each survey the plot was assigned a 1 or a 0, if an eastern diamondback was detected or not detected, respectively (MacKenzie et al. 2002). We also recorded sampling covariates associated with each survey

including date, time of day, temperature, and cloud cover. The number of snakes encountered during each VES was also recorded. Each plot was surveyed using this methodology for three consecutive days to minimize movement out of the survey area, although we had no reason to believe that movement out of a survey area would be nonrandom, allowing us to relax the assumption of population closure (MacKenzie et al. 2006) Surveys were conducted during three distinct periods, fall (September through November) 2011, spring (February through April) 2012, and fall 2012. Surveys were conducted only when the air temp was above 16° C. This is when eastern diamondbacks are most active and most likely to be on the surface (Means 1985; Timmerman and Martin 2003). During each sampling period, a new set of sampling plots were surveyed.

Model Development

To estimate detection (p) and occupancy (ψ) rates, we analyzed the detection/non-detection data using Program PRESENCE 3.1 (<http://www.mbr-pwrc.usgs.gov/software/presence.html>). PRESENCE uses information on detection probability and likelihood-based log-linear models to estimate occupancy of a site by a species and also allows you to model detection and occupancy as a function of survey level and site level covariates (MacKenzie et al. 2003). Survey data from all three sampling seasons were aggregated and run using the single-season model.

Data collected during each survey was used to model detection rate. These survey covariates included AIRT (mean air temperature during the survey), CLOUD (mean percent cloud cover during the survey), TIME (median time during the survey), and DAY (day of the

survey where January 1 = 1). From these covariates we developed seven competing models that represented hypothesized influences on eastern diamondback detection rates (Table 2.1). We included a null model $\{\psi(\cdot)p(\cdot)\}$ to determine if these covariates explained detection rates better than a model that assumed a constant detection rate across all surveys. The best supported detection model was then applied to all models representing eastern diamondback occupancy rate.

To assess the impact of landscape composition and spatial scale on eastern diamondback occupancy rate, we first used a GIS to condense our land cover data into structural categories, as habitat structure has been shown to be more important to snakes than habitat composition (Reinert 2001; Vitt 2001). We then delineated 250-, 500-, and 1000-m radius buffers from the center of each survey plot (Fig 2.3). These buffer sizes have been used in previous studies examining landscape level influences on eastern diamondback rattlesnakes (Hoss et al. 2010; Steen et al. 2012). We calculated the area of four of the structural categories, DUNES (secondary dunes), FOREST (maritime forest), MARSH/WETLAND (all marsh and wetlands), DEV (developed), within each of the buffer sizes. We used these variables to create a series of models that reflect hypothesized influences on eastern diamondback occupancy (Table 2.2) to ensure that our results are biologically meaningful and not the result of spurious statistical correlations (Burnham and Anderson 2002).

All survey and site covariates were standardized to mean = 0 and standard deviation = 1 prior to analysis to facilitate model convergence (MacKenzie et al. 2006). We then assessed collinearity among the survey and site covariates using Spearman rank correlations. None of our variables were highly correlated ($r \geq 0.60$).

We ranked our models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c , Burnham and Anderson 2002) to determine the models and associated covariates that have the strongest support based on our data. Models less than two AIC_c units from the top ranked model were considered to have equal support as the top model. We assessed the fit of the global model $\{\psi(\text{Dunes+Forest+Marsh+Dev}) p(\text{AIRT+CLOUD})\}$ for each spatial scale by comparing the observed Pearson's chi-square statistic to the expected chi-square statistic generated with 10,000 bootstraps (MacKenzie and Bailey 2004).

Results

We detected eastern diamondbacks on 20 of 156 surveys (12.8%) and at 13 of 52 sites for a naïve (i.e., uncorrected) occupancy rate of 25.0%.

The best supported model for eastern diamondback detection rate contained AIRT and CLOUD and had moderately high support ($w = .6301$, Table 2.3). Detection rate estimates for AIRT (Fig. 2.4) and CLOUD (Fig. 2.5) were negative, indicating that detection rate decreases with increasing air temperature and cloud cover. Incorporating AIRT and CLOUD parameters increased our overall occupancy rate estimate to 37.4% (95% confidence interval 0.2051 - 0.5809), an increase of 12.4% over the naïve occupancy rate. The model that included only CLOUD had equal support ($\Delta AIC_c = 1.51$) and the parameter estimate was also negative. The null model representing constant detection rate $\{\psi(\cdot)\}$ was $\Delta AIC_c \geq 5$ from the top model. As both of the top models included the CLOUD covariate, we choose to include AIRT+CLOUD detection parameters in our occupancy analysis as that model had high support.

In our occupancy analysis at the 250-m spatial scale, five models had equal support (Table 2.4), including the null model representing constant occupancy $\{\psi(\cdot)\}$. This indicates that none of the variables at this scale had an effect on occupancy rate. At the 500-m scale, the FOREST model was the top performing model ($w = 0.5087$, Table 2.5) and was better than the null model ($w = 107.09, \Delta AIC_c = 4.10$), indicating that the area of forest habitat is influencing occupancy rates. The estimated effect of FOREST at 500-m was negative, indicating that occupancy rates decrease with increasing maritime forest habitat (Fig. 2.6). At the 1000-m scale, three models comprised over 60% of the AIC weight (Table 2.6), FOREST, DUNES, and FOREST+DUNES. The null model was $\Delta AIC_c = 2.76$ from the top model at this spatial scale. Occupancy estimates for FOREST were negative (Fig. 2.7) and the estimates for DUNES were positive (Fig. 2.8). This indicates that occupancy rates increase with increasing secondary dune habitat and decreasing maritime forest habitat at this spatial scale.

No lack of model fit was found at any spatial scale when we compared the observed the Pearson's chi-square statistic from the global model at each spatial scale, to the expected chi-square statistic generated with 10,000 bootstraps (250-m: $p \geq 0.3281, \hat{c} \leq 1.1397$; 500-m: $p \geq 0.3365, \hat{c} \leq 1.1146$; 1000-m: $p \geq 0.3516, \hat{c} \leq 1.0914$).

Discussion

Detection rate in our study was strongly influenced by the covariates reflecting air temperature and cloud cover, with detection rate decreasing as temperature and cloud cover increase. Eastern diamondbacks, like all snakes, are ectothermic. Meaning their body temperature is determined by heat obtained from the environment. Snakes can control their

body temperature behaviorally, within the limits provided by the environment (Peterson et al. 1993). On cool, sunny days, snakes will utilize radiant heat from the sun to increase their body temperature through basking. When it is cloudy, snakes are not able to obtain radiant heat from the sun and so are less likely to expose themselves in the open. Likewise, as the ambient air temperature increases, snakes are able to maintain their body temperature without basking, and may even seek shelter in cooler areas if the temperature gets too high. These conditions make detecting a snake more difficult, whereas snakes that are basking are more likely to be observed as they are at least partially exposed to the sun.

The influence of landscape variables in our occupancy models appears to increase with increasing scale, as maritime forest and secondary dunes were related to eastern diamondback occupancy at the larger spatial scales but there was no relationship detected at the 250-m scale. Eastern diamondbacks are capable of moving long distances and may have home ranges greater than 80 ha (Waldron et al. 2006). Regardless, the results of this study show that landscape-level factors may have an influence on occupancy at scales even larger than the home range of an individual. This indicates that landscape composition has a greater impact on eastern diamondback populations at larger scales, rather than fine scales. The results of this study emphasize the need to examine the influence of spatial scale on an animal's habitat association.

Our occupancy models showed that maritime forest and secondary dune habitats had the strongest relationship to eastern diamondback occupancy rates. Parameter estimates for maritime forest were negative. Maritime forest is generally a closed canopy habitat that is not likely highly suitable for eastern diamondbacks. While they are known to use the forest to some

degree, they are likely tied to more open canopied areas or edges. Secondary dune habitat only came out as an important variable at the largest spatial scale, and occupancy estimates were positive. This suggests that large tracts of secondary dune habitat may be beneficial.

Development was not an important variable in our occupancy models at any spatial scale. We believe that development may pose a significant threat to this species on barrier islands, but did not represent enough of the landscape of our study area to influence our models. Development is relatively limited on Georgia's barrier islands, and only 2 of our 52 plots contained more than 8% developed area within any spatial scale. Even if the presence of development on the landscape itself does not result in a decreases in eastern diamondback occupancy rates, the loss of secondary dune habitat due to the construction of homes and hotels near the beach may, as our study showed occupancy rates are lower in areas with less secondary dune habitat. Studies that examine eastern diamondback ecology on islands within a more developed landscape, such as in Florida, will be extremely useful in conjunction with this study, to develop management strategies for this declining species in coastal habitats.

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Table 2.1. Description of models used to model eastern diamondback (*Crotalus adamanteus*) rattlesnake detection rates. Occupancy (psi) was held constant for all models.

Model	Hypothesis
p(AIRT)	Detection rate decreases with increasing temperature
P(CLOUD)	Detection rate decreases with increasing cloud cover
p(TIME)	Detection rate decreases throughout the day
p(DAY)	Detection rate increases throughout the year
p(.)	Detection rate is constant across all surveys
p(AIRT+CLOUD)	Detection rate decreases with increasing temperature and cloud cover
p(AIRT+TIME)	Detection rate decreases with increasing temperature and throughout the day

Table 2.2. Description of models used to model eastern diamondback rattlesnake (*Crotalus adamanteus*) occupancy rates and their hypothesized relationship. AIRT+CLOUD covariates were included in detection (p) for all models.

Model	Hypothesis
psi(DUNES)	Probability of occupancy increases with area of dune habitat
psi(DEV)	Probability of occupancy decreases with area of developed land
psi(FOREST)	Probability of occupancy decreases with area of maritime forest
psi(MARSH/WETLAND)	Probability of occupancy decreases with distance to marsh or wetland
psi(.)	Probability of occupancy is constant across all sites
psi(DUNES+FOREST)	Probability of occupancy increases as a function of increased dune habitat and decreased maritime forest
psi(DUNES+MARSH/WETLAND)	Probability of occupancy increases with area of dune and marsh or wetland habitat
psi(DUNES+DEV)	Probability of occupancy increases with quality of dune habitat
psi(DUNES+FOREST+MARSH/WETLAND+DEV)	Probability of occupancy increases with quality of habitat the surrounding landscape

Table 2.3. Model selection results for eastern diamondback rattlesnake (*Crotalus adamanteus*) detection rates. ΔAIC_c represents the change in AIC_c , w = model weight, K = number of parameters in the model, $-2\text{Log}(L)$ = the negative 2 log likelihood. Occupancy was held constant $\{\psi(\cdot)\}$ for all models.

Model	AIC_c	ΔAIC_c	w	K	$-2\text{Log}(L)$
p(AIRT+CLOUD)*	107.09	0.00	0.6301	4	98.24
p(CLOUD)*	108.60	1.51	0.2961	3	102.10
P(.)	112.46	5.37	0.0412	2	108.22
p(AIRT)	113.59	6.50	0.0244	3	107.09
p(DAY)	113.70	6.61	0.0231	3	107.20
p(TIME)	114.17	7.08	0.0183	3	107.67
p(AIRT+TIME)	115.83	8.74	0.0080	4	106.98

* indicates top ranking models ($\Delta AIC_c \leq 2.0$)

Table 2.4. Model selection results for eastern diamondback rattlesnake (*Crotalus adamanteus*)

occupancy rates at the 250-m spatial scale. ΔAIC_c represents the change in AIC_c , w = model weight, K = number of parameters in the model, $-2\text{Log}(L)$ = the negative 2 log likelihood.

AIRT+CLOUD covariates were included in detection (p) for all models.

Model	AIC_c	ΔAIC_c	w	K	$-2\text{Log}(L)$
psi(FOREST)*	106.78	0.00	0.2531	5	94.48
psi(.)*	107.09	0.31	0.2168	4	98.24
psi(DUNES)*	108.08	1.30	0.1321	5	96.78
psi(DEV)*	108.58	1.80	0.1029	5	97.28
psi(MARSH/WETLAND)*	108.65	1.87	0.0994	5	97.35
psi(DUNES+FOREST)	109.20	2.42	0.0755	6	95.33
psi(DUNES+MARSH/WETLAND)	109.66	2.88	0.0600	6	95.79
psi(DUNES+DEV)	110.01	3.23	0.0503	6	96.14
psi(DUNES+FOREST+MARSH/WETLAND+DEV)	113.25	6.47	0.0100	8	93.90

* indicates top ranking models ($\Delta AIC_c \leq 2.0$)

Table 2.5. Model selection results for eastern diamondback rattlesnake (*Crotalus adamanteus*)

occupancy rates at the 500-m spatial scale. ΔAIC_c represents the change in AIC_c , w = model weight, K = number of parameters in the model, $-2\text{Log}(L)$ = the negative 2 log likelihood.

AIRT+CLOUD covariates were included in detection (p) for all models.

Model	AIC_c	ΔAIC_c	w	K	$-2\text{Log}(L)$
psi(FOREST)*	102.99	0.00	0.508	5	91.69
psi(DUNES+FOREST)	105.05	2.06	0.181	6	91.18
psi(DUNES)	107.08	4.09	0.058	5	95.7
psi(.)	107.09	4.10	0.065	4	98.24
psi(DEV)	108.02	5.03	0.041	5	96.72
psi(MARSH/WETLAND)	108.12	5.13	0.039	5	96.82
psi(DUNES+MARSH/WETLAND)	108.15	5.16	0.038	6	94.28
psi(DUNES+FOREST+MARSH/WETLAND+DEV)	108.59	5.59	0.031	8	89.23
psi(DUNES+DEV)	108.75	5.76	0.028	6	94.88

* indicates top ranking model ($\Delta AIC_c \leq 2.0$)

Table 2.6. Model selection results for eastern diamondback rattlesnake (*Crotalus adamanteus*)

occupancy rates at the 1000-m spatial scale. ΔAIC_c represents the change in AIC_c , w = model weight, K = number of parameters in the model, $-2\text{Log}(L)$ = the negative 2 log likelihood.

AIRT+CLOUD covariates were included in detection (p) for all models.

Model	AIC_c	ΔAIC_c	w	K	$-2\text{Log}(L)$
psi(FOREST)*	104.33	0.00	0.2565	5	93.03
psi(DUNES)*	104.63	0.30	0.2208	5	93.33
psi(DUNES+FOREST)*	104.84	0.51	0.1988	6	90.97
psi(DUNES+MARSH/WETLAND)	106.62	2.29	0.0816	6	92.75
psi(DUNES+DEV)	106.72	2.39	0.0777	6	92.85
psi(.)	107.09	2.76	0.0645	4	98.24
psi(MARSH/WETLAND)	108.15	3.82	0.0380	5	96.85
psi(DEV)	108.15	3.82	0.0380	5	96.85
psi(DUNES+FOREST+MARSH/WETLAND+DEV)	109.06	4.73	0.0239	8	89.71

* indicates top ranking models ($\Delta AIC_c \leq 2.0$)

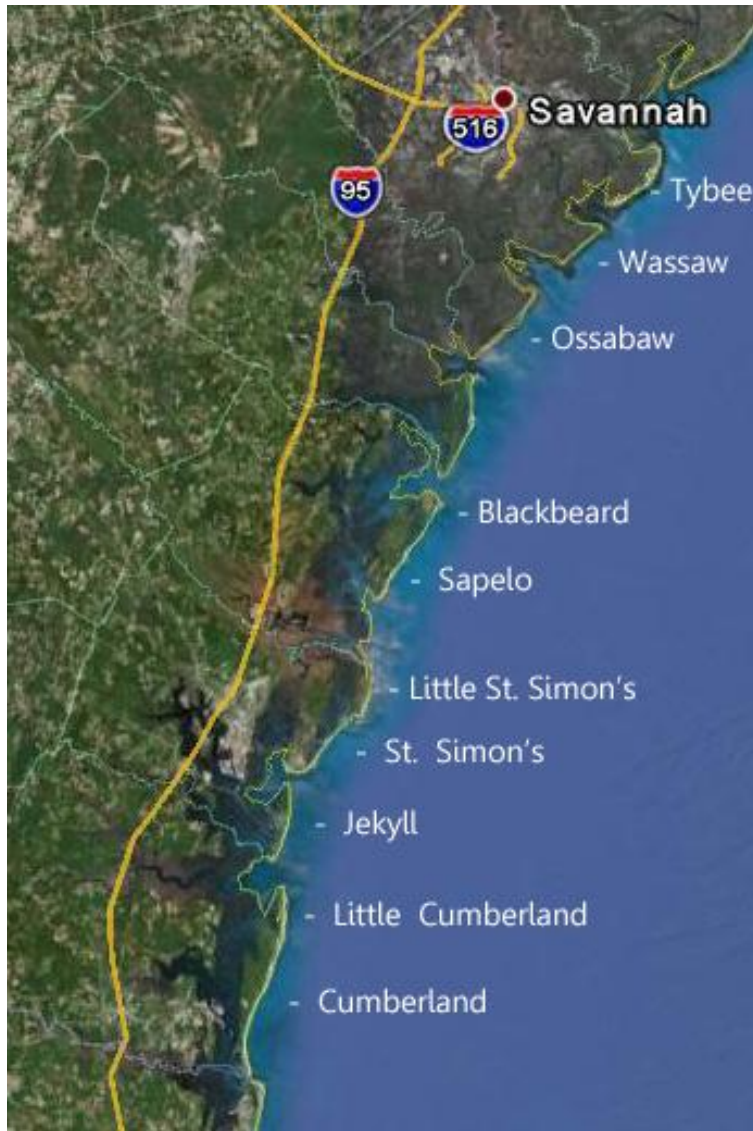


Figure 2.1. Map of the ten study islands on the coast of Georgia, USA where occupancy surveys for eastern diamondback rattlesnakes (*Crotalus adamanteus*) were conducted.

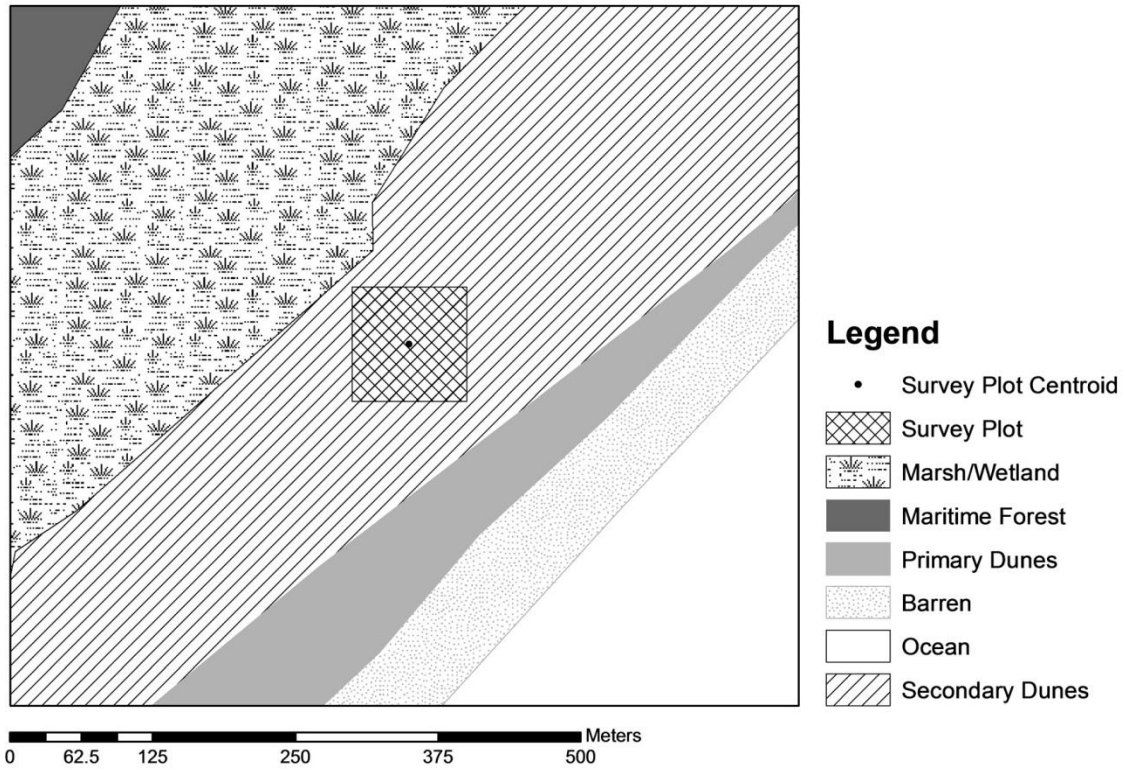


Figure 2.2. A 1-ha survey plot in secondary dune habitat on a Georgia, USA Barrier Island. Plots were surveyed on three consecutive days to determine presence or apparent absence of eastern diamondback rattlesnakes (*Crotalus adamanteus*), which was used to analyze detection and occupancy rates in secondary dune habitat.

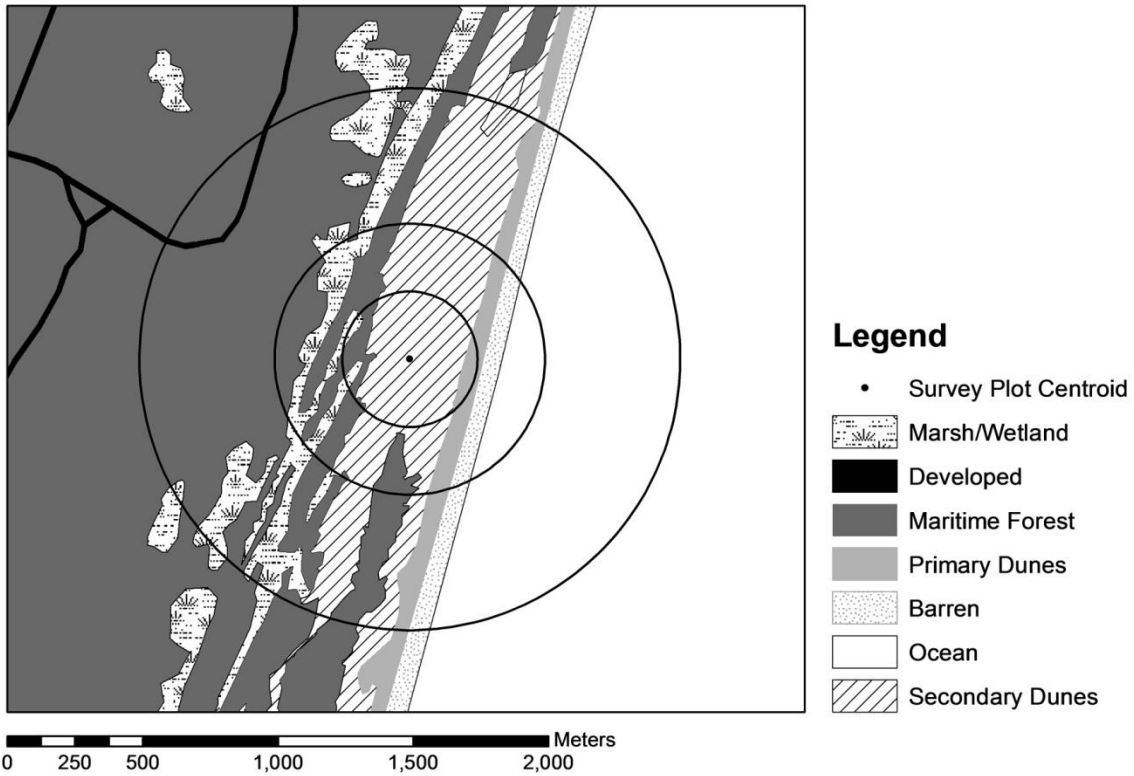


Figure 2.3. A survey plot centroid in secondary dune habitat, with buffers of 250-, 500-, and 1000-m radii. The area of each structural habitat type within each buffer was calculated and used to analyze the relationship between habitat, landscape scale, and eastern diamondback rattlesnake (*Crotalus adamanteus*) occupancy.

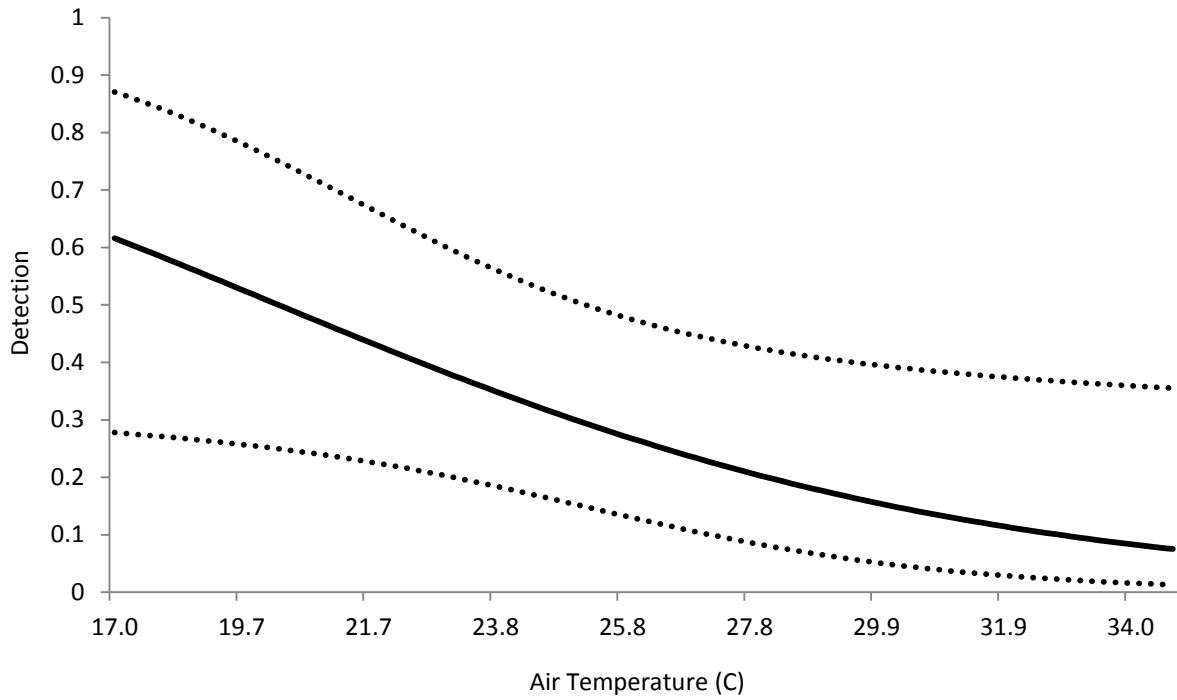


Figure 2.4. The relationship between eastern diamondback rattlesnake (*Crotalus adamanteus*) detection rates and average air temperature during each survey. The dotted lines indicate the upper and lower 95% confidence intervals.

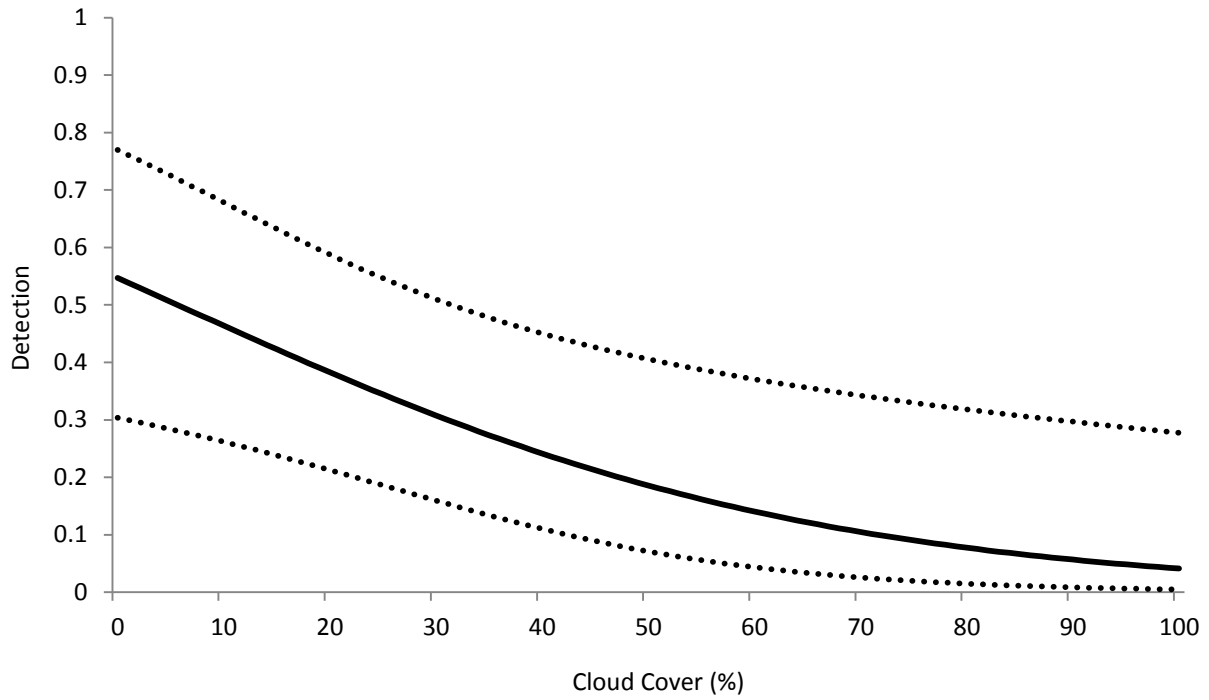


Figure 2.5. The relationship between eastern diamondback rattlesnake (*Crotalus adamanteus*) detection rates and average cloud cover (%) during each survey. The dotted lines indicate the upper and lower 95% confidence intervals.

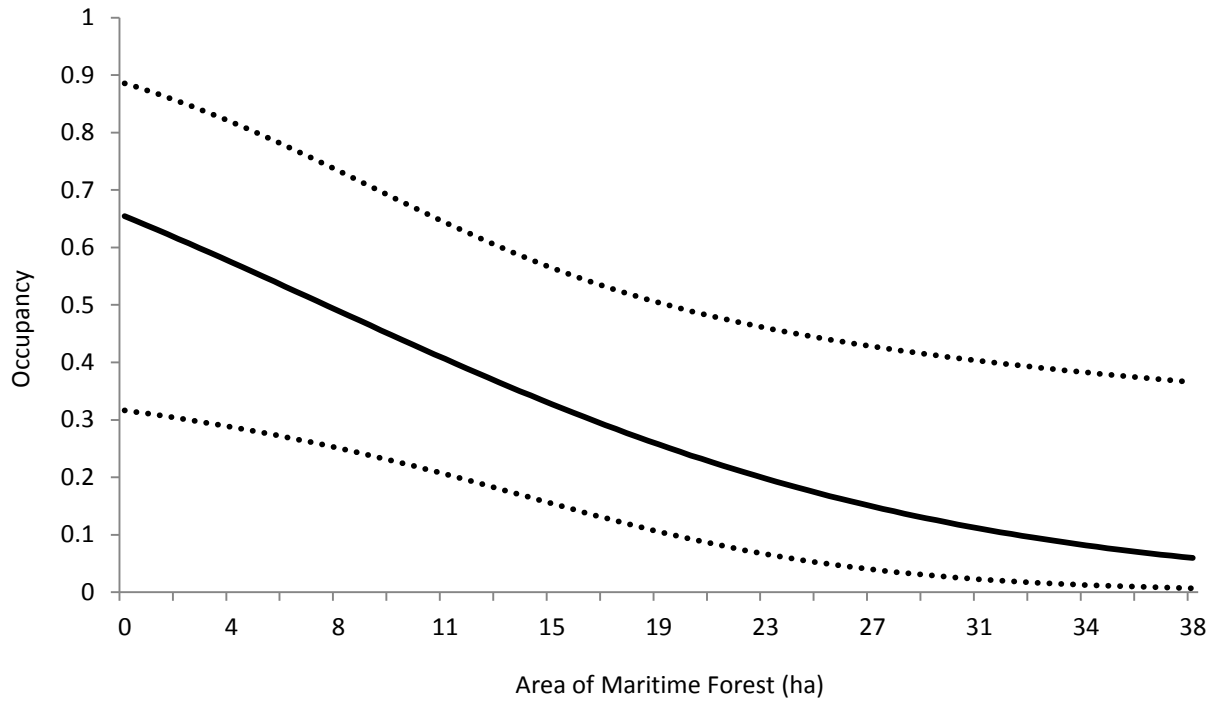


Figure 2.6. The relationship between eastern diamondback rattlesnake (*Crotalus adamanteus*) occupancy rates and area of maritime forest within a 500-m buffer of survey plot. The dotted lines indicate the upper and lower 95% confidence intervals.

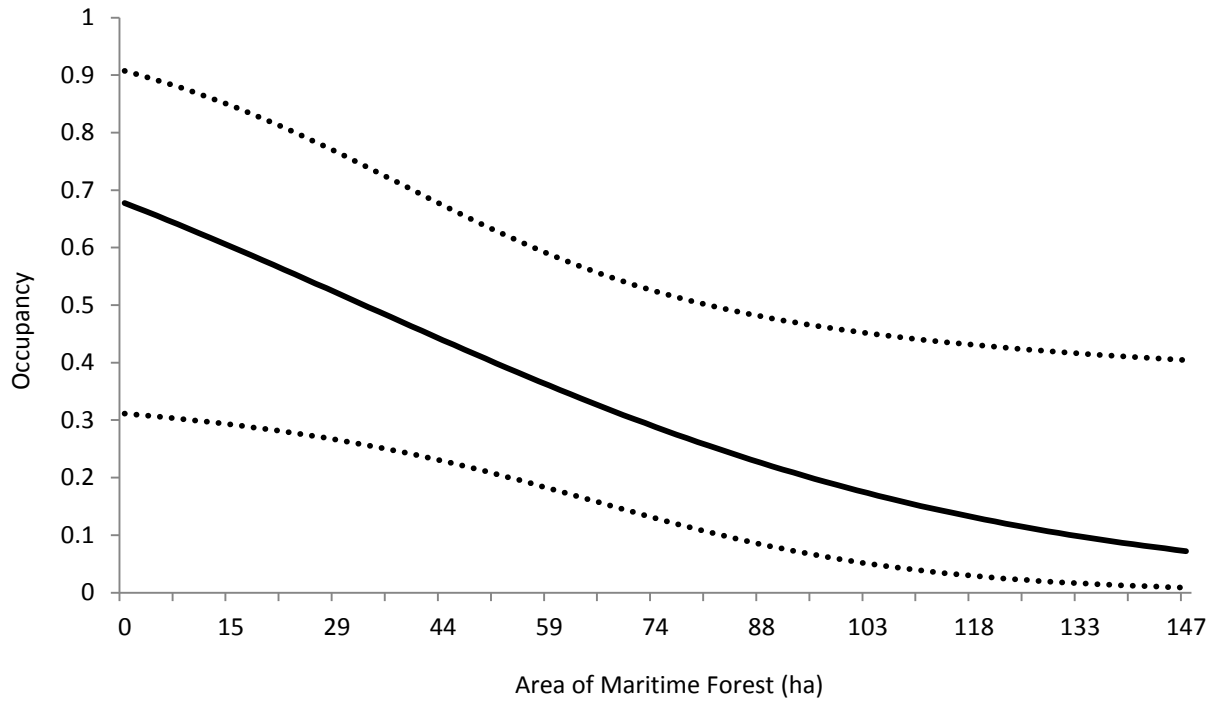


Figure 2.7. The relationship between eastern diamondback rattlesnake (*Crotalus adamanteus*) occupancy rates and area of maritime forest within a 1000-m buffer of survey plot. The dotted lines indicate the upper and lower 95% confidence intervals.

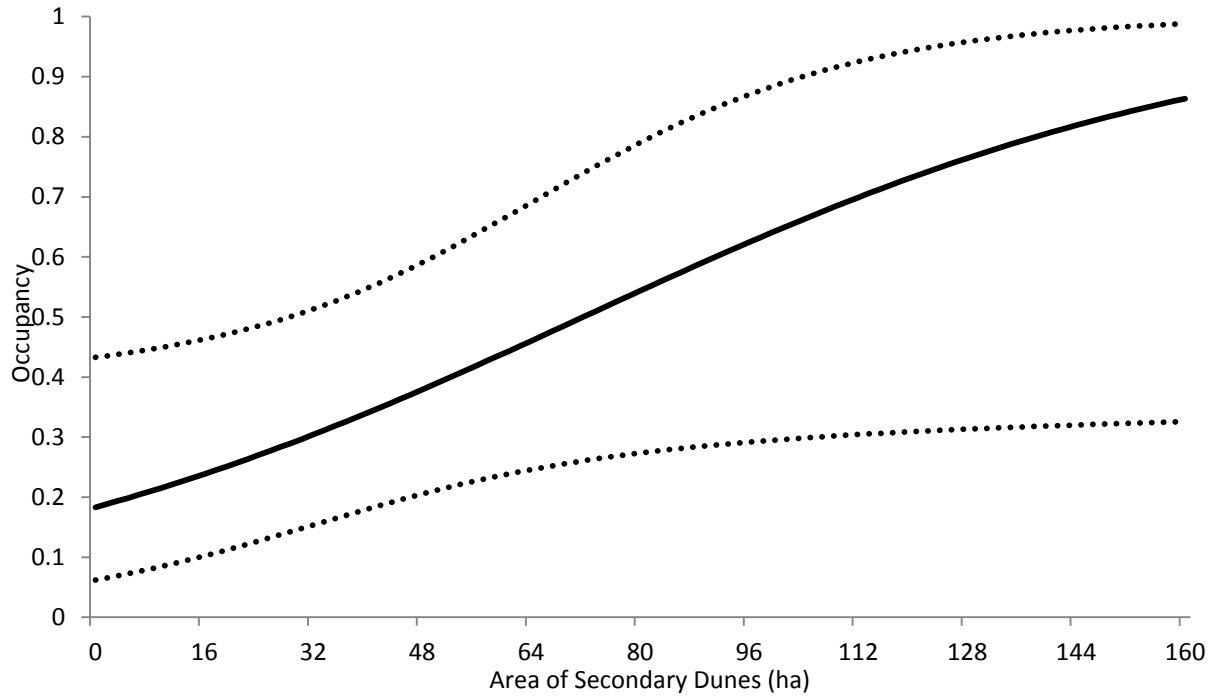


Figure 2.8. The relationship between eastern diamondback rattlesnake (*Crotalus adamanteus*) occupancy rates and area of secondary dunes within a 1000-m buffer of survey plot. The dotted lines indicate the upper and lower 95% confidence intervals.

CHAPTER 3

A STAGE-BASED MATRIX MODEL OF EASTERN DIAMONDBACK RATTLESNAKES

Introduction

Monitoring population trends is an important goal of most management efforts for wildlife. One way to obtain these trends is to directly sample the population to calculate abundance estimates over time (Stenseth et al. 1997). While this may be effective for species that are highly abundant or easily encountered, this is not the case for species that are secretive, rare or declining, or long-lived. When dealing with these types of species, data on population abundance is typically lacking, making the use of models essential (Starfield and Bleloch 1986; Carroll 1992). Models are by design, abstractions of reality, but they allow managers to make predictions about how populations will react to threats and management efforts (Congdon et al. 1993; Morris and Doak 2002; Enneson and Litzgus 2008). One of the most common models used in conservation efforts are population growth models.

Population growth models are useful in assessing the status and informing the management of threatened and endangered species (Crowder et al. 1994, Heppell and Crowder 1996, Lo et al. 1995, Enneson and Litzgus 2008). Age and stage structured matrix models use estimates of survival and fecundity rates to determine estimate the rate of population growth (Leslie 1945, Lefkovitch, 1965, Crouse et al. 1987, Smith et al. 1992, Lo et al. 1995, Pertierra et al. 1997). Typically, matrix models are deterministic, and by their nature simplified abstractions

of population dynamics intended to compare the effects of changes in demographic rates on the instantaneous rate of population growth. Nonetheless, matrix models can be useful in conservation and management by identifying the relative responsiveness of population growth to changes in specific demographic rates [elasticity] (Crowder et al. 1994, Heppell et al. 1996, Merrill et al. 2003). Elasticity analyses can be used to identify or rank threats to different life stages, and to compare the relative effectiveness of independent or combined management actions (Lo et al. 1995). Further, matrix models can accommodate analyses of the influence of stochastic variation in demographic rates, which may be useful for species where demographic rates exhibit naturally high variability or where few estimates of demographic rates are available.

Eastern diamondback rattlesnake (*Crotalus adamanteus*; hereafter referred to as Eastern diamondback) population sizes are declining throughout the species' range, and in 2012 the species was publicly petitioned for listing as a threatened species under the endangered species act (Gibbons et al 2000; Martin and Means 2000; U.S. Fish and Wildlife Service 2012). Eastern diamondbacks occur throughout most of the Coastal Plain of the southeastern United States. They occur in a variety of habitats including swamp forests, xeric hammocks, tropical hammocks, oak scrub, temperate hardwood forests, salt marsh, and coastal dunes, but they are most often associated with open canopy pine savannas (Timmerman and Martin 1995; Martin and Means 2000; Timmerman and Martin 2003; Waldron et al. 2006; Waldron et al. 2008; Hoss et al. 2010). Eastern diamondback population declines are attributed primarily to habitat loss, specifically, the extensive loss of longleaf pine-wire grass savannahs to intensive agroforestry and agriculture. Remnant habitats are fragmented and often degraded due to the suppression

of fire (Steen et al. 2007), and are now threatened by increasing residential and commercial development, particularly in coastal portions of the species' range. Eastern diamondback population declines are exacerbated by overharvesting and malicious killing, and road mortality (Timmerman 1995, Martin and Means 2000, Antonio 2003, Timmerman and Martin 2003). Because of the varied threats to eastern diamondbacks, variable management strategies will be needed to conserve and restore the species.

The objectives of this study were to (1) review published estimates of demographic rates for eastern diamondbacks, (2) construct a stage-based population matrix model from published estimates to determine whether those estimates predict a stable, increasing, or decreasing population growth rate, and (3) to compare the elasticity of different stage-specific demographic rates as they relate to specific threats and management actions. We identify areas of research needed to improve population models and inform management recommendations that should have the greatest impact on conserving and restoring eastern diamondback populations.

Methods

Literature Review of Demographic Estimates

Demographic estimates for eastern diamondbacks are scarce in the published literature. Timmerman and Martin (2003) found a survival rate of 0.33 for neonate eastern diamondbacks, and a survival rate of 0.77 for females every year after. Waldron et al. (2013) found an annual survival rate for adults of 0.82.

Female eastern diamondbacks reach sexual maturity at approximately one meter in length. Growth rate varies with latitude, with snakes in the southern portion of the range growing faster, therefore reaching maturity at an earlier age. Timmerman and Martin (2003) estimated that females from Florida likely reach maturity at 4 years of age, but females at the northern extent of their range in the Carolinas may take 7 to 8 years to reach maturity. Waldron et al. (2013) estimated that females at their study site on the coast of South Carolina reach sexual maturity at approximately 7 years of age.

Reported clutch sizes of eastern diamondback rattlesnakes in the wild range from 6 to 32. Kain (1995) reported an average of 14 (11-19) from four females in southern Mississippi, Ernst (1992) reported an average of 12.8 (6-21) from 28 clutches, and Antonio (2003) reported a clutch sizes of 9 and 19 from Florida. The combined average clutch size from these sources is 13. Sex is genetically determined in eastern diamondbacks and while there are no published data on sex ratio at birth, the sex ratio of adults appears to be 1:1 (Timmerman and Martin 2003).

Eastern diamondbacks only breed every 2 to 4 years. Like age at maturity, breeding interval appears to vary with latitude, with rattlesnakes in the southern portion of the range breeding more frequently than those at the northern portion of the range. Breeding frequency appears to be dependent on food availability and the length of the active season (Antonio 2003; Timmerman and Martin 2003).

Model Parameters

Data used in estimating baseline model parameters were synthesized from our literature review. We calculated fecundity rate of the adult stage (F_3) as the birth rate (B) multiplied by the survival rate of adults (P_3). Birth rate was calculated as the product of the average number of offspring per clutch, the percent of female offspring per clutch (because only females are included in the model), and the breeding interval of females (number years between breeding events) (Ebert 1999). Fecundity rates for Stages 1 and 2 were 0, as these represent the portion of the population that has not yet reached sexual maturity.

To calculate the probability of surviving and transitioning to the next stage (G_i) and the probability of surviving and remaining in the same stage (P_i), we followed the methods from Ebert (1999). We first calculated the fraction ready to leave a stage (f) using the following equation:

$$f = \frac{(1 - p)p^{y-1}}{1 - p^y}$$

Where p is the survival rate and y is the number of years in a stage. The probability of surviving and transition from one stage to the next (G) is the fraction ready to leave (f) multiplied by the survival rate (p):

$$G = fp \text{ or } p \left(\frac{(1 - p)p^{y-1}}{1 - p^y} \right)$$

The probability of surviving and staying in a stage, P , was calculated using the following equation:

$$P = p \left(1 - \frac{(1 - p)p^{y-1}}{1 - p^y} \right)$$

Model Development

To examine the growth rate of eastern diamondback populations we used a female-only, stage-based population matrix (A) consisting of three stages with the following parameterization:

$$A = \begin{pmatrix} 0 & 0 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{pmatrix}$$

P_i was the probability of an individual in stage i surviving and remaining in the same stage, G_i was the probability of an individual in stage i surviving and transitioning into the next stage, and F_i was the fecundity of individuals in stage i (Lefkovich 1965, Morris and Doak 2002).

To account for the different estimates of age at first reproduction that appears to be related to latitude, we built two models. Model 1 represents an age at first reproduction of 4 years and model 2 represents an age at first reproduction of 7 years. In both models stage 1 was the neonate stage, lasting 1 year. Stage 2 was the subadult stage and lasted 3 years for model 1 and 6 years for model 2. Stage 3 represents reproductive adults. We did not include a maximum age for stage 3.

Models were used to project the population from time t to time $t+1$ using the equation:

$$n(t + 1) = A \cdot n(t)$$

where n is a population vector that takes the form:

$$n_t = \begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}$$

where N_i is the number of individuals in stage i at time t . The projection was carried out to time $t = 100$ years to ensure the population would reach a stable-stage distribution. The population growth rate (λ) is calculated as the dominant value of the matrix.

In building these models we made several assumptions. First, we assumed density-independence. Second, we assumed population closure, that is, there was no immigration or emigration. Lastly, we assumed that there was no stochasticity in the fecundity (F) or survival rates (G, P) due to environmental or demographic variability. While these assumptions undoubtedly do not hold true in wild populations, they allow for mathematical simplicity and interpretable results.

Sensitivity and Elasticity

We performed a sensitivity analysis to examine the sensitivity of population growth rate (λ) to changes in the matrix parameters (de Kroon et al. 1986, Ebert 1999). The sensitivity (S_{ij}) of an element in the projection matrix (A) is given by the equation:

$$S_{ij} = \frac{v_i w_j}{\langle w, v \rangle}$$

where S_{ij} is the (i, j) element of the sensitivity matrix, v_i is the i th element of the reproductive vector (v) and is the dominant left eigenvector, w_j is the j th element of stable-stage distribution vector (w) and is the dominant right eigenvector, and $\langle w, v \rangle$ is the product of the w and v vectors, which is a single number referred to as the scalar (Morris and Doak, 2002).

The issue with sensitivity is that different elements of the matrix, such as fecundity and survival rates, contribute differently to λ (Ebert 1999). Elasticity analysis is used to calculate the proportional sensitivity of λ to changes in the matrix parameter and allows us to compare

parameters that are not in the same units or on the same scale. We used the following equation to calculate elasticity:

$$E_{ij} = \frac{A_{ij}}{\lambda} \cdot \frac{v_i w_j}{\langle w, v \rangle}$$

where E_{ij} is the (i, j) element of the elasticity matrix, A_{ij} is the (i, j) element of the stage-based matrix, λ is the dominant eigenvalue (de Kroon et al. 1986).

To examine how changes in the survival rates will influence λ , we independently altered the survival rate of each stage (neonate, subadult, and adult) by -10, -5, +5, and +10%. We then calculated the percent change in λ from each of the baseline models.

Results

Model Parameters

The survival rate parameters for eastern diamondbacks included in our models were 0.33 for neonates and 0.82 for both subadults and adults. With the average clutch size for eastern diamondback rattlesnakes reported in the literature of 13, a 1:1 sex ratio (0.50 females), and an average breeding interval of 3 years (0.33 clutches per female per year), we estimated a birth rate (B) of 2.145 and a fecundity rate (F) for adults of 1.76.

The stage, stage duration, survival, fraction leaving a stage (f), fraction staying in a stage, probability of surviving and remaining in a stage (P), and probability of surviving and transitioning to the next stage (G) for model 1 are given in table 3.1, and for model 2 are given in table 3.2.

The initial population vector (n) was based off published stage distribution data of 41% neonates, 19% subadults, and 40% adults (Timmerman and Martin 2003) and took the form:

$$n_1 = \begin{pmatrix} 41 \\ 19 \\ 40 \end{pmatrix}$$

This represents an initial population of 100 females.

Model 1

The projection matrix (A) for model 1 took the form:

$$A = \begin{pmatrix} 0 & 0 & 1.76 \\ 0.33 & 0.60 & 0 \\ 0 & 0.22 & 0.82 \end{pmatrix}$$

The mean population growth rate (λ) from this projection matrix was $\lambda = 1.07$ (Fig 3.1).

The following stable-stage distribution (w) was calculated from the projection matrix:

$$w = \begin{pmatrix} 0.43 \\ 0.30 \\ 0.26 \end{pmatrix}$$

These values indicate that when the population reaches a stable-stage distribution 43% of the individuals in the population were neonates, 30% are subadults, and 26% are adults.

The following vector of reproductive values (v) was calculated from the projection matrix:

$$v = (1 \quad 3.29 \quad 8.03)$$

These values indicate that the average subadult will contribute 3.29 times more to the population growth rate than an average neonate will and the average adult will contribute 8.03 times more to the population growth rate than the average neonate will.

The following matrix of sensitivities (S) was calculated from the stage-classified projection matrix (A):

$$S = \begin{pmatrix} 0.120 & 0.088 & 0.073 \\ 0.395 & 0.290 & 0.241 \\ 0.965 & 0.708 & 0.590 \end{pmatrix}$$

Each element in the sensitivity matrix (S) represents the sensitivity of λ to changes in the corresponding parameter in the projection matrix (A)(Ebert 1999). Of the elements in the sensitivity matrix that correspond to parameters in the projection matrix, sensitivity was highest for the proportion of subadults surviving and transitioning to adults (G_2), followed by adult survival (P_3), and then the proportion of neonates surviving and transitioning to subadults (G_1). Sensitivity was lowest for fecundity of adults (F_3).

The following matrix of elasticity (E) was calculated from the projection matrix (A):

$$E = \begin{pmatrix} 0 & 0 & 0.120 \\ 0.122 & .162 & 0 \\ 0 & 0.146 & 0.451 \end{pmatrix}$$

Each element in the elasticity matrix (E) represents the proportional sensitivity of λ to changes in the corresponding parameters in the projection matrix (A). The elasticity value was highest for adult survival (P_3).

Model 2

The projection matrix (A) for model 2 took the form:

$$A = \begin{pmatrix} 0 & 0 & 1.76 \\ 0.33 & 0.74 & 0 \\ 0 & 0.08 & 0.82 \end{pmatrix}$$

The mean population growth rate (λ) from this projection matrix was $\lambda = 0.998$ (Fig 3.2).

The following stable-stage distribution (w) was calculated from the projection matrix:

$$w = \begin{pmatrix} 0.35 \\ 0.45 \\ 0.20 \end{pmatrix}$$

These values indicate that when the population reaches a stable-stage distribution 35% of the individuals in the population are neonates, 45% are subadults, and 20% are adults.

The following vector of reproductive values (v) was calculated from the projection matrix:

$$v = (1 \quad 2.76 \quad 10.95)$$

These values indicate that the average subadult will contribute 2.76 times more to the population than an average neonate will and the average adult will contribute 10.95 times more to the population than the average neonate will.

The following matrix of sensitivities (S) was calculated from the stage-classified projection matrix (A):

$$S = \begin{pmatrix} 0.087 & 0.138 & 0.049 \\ 0.239 & 0.380 & 0.134 \\ 0.949 & 1.509 & 0.533 \end{pmatrix}$$

Each element in the sensitivity matrix (S) represents the sensitivity of λ to changes in the corresponding parameter in the projection matrix (A) (Ebert 1999). Of the elements in the sensitivity matrix that correspond to parameters in the projection matrix, sensitivity was highest for the proportion of subadults surviving and transitioning to adults (G_2), followed by adult survival (P_3), and then the proportion of subadults surviving and remaining in the subadult stage (P_2). Sensitivity was lowest for fecundity of adults (F_3).

The following matrix of elasticity (E) was calculated from the projection matrix (A):

$$E = \begin{pmatrix} 0 & 0 & 0.086 \\ 0.079 & .283 & 0 \\ 0 & 0.119 & 0.438 \end{pmatrix}$$

Each element in the elasticity matrix (E) represents the proportional sensitivity of λ to changes in the corresponding parameters in the projection matrix (A). The elasticity value was highest for adult survival (P_3).

Estimating the impact of stage-specific survival rate on population growth

Proportional changes in adult survival resulted in greater changes to λ than did changes in survival rates of neonates and subadults (Fig 3.3). Changes to adult survival of -10, -5, +5, and +10% resulted in changes in λ of -7.63, -3.88, +3.98, and 8.05%, respectively for model 1 and -8.28, -4.34, +4.61, and 9.38%, respectively for model 2. Changes to neonate survival resulted in changes in λ of -4.45, -2.11, +1.94, and +3.73% for model 1 and -3.18, -1.51, +1.39, +2.67% for model 2. Changes to subadult survival resulted in changes in λ of -3.57, -1.81, +1.86, + 3.78% for model 1 and -4.13, -2.16, +2.36, and +4.91% for model 2.

Discussion

Our two models representing 4 and 7 years of age at first reproduction resulted in very different population growth rates. While model 2 (7 years to first reproduction) had a stable population growth rate, model 1 (4 years to first reproduction) had a rapidly increasing population growth rate. This outcome is likely unrealistic or populations in the southern portion of the species range would be rapidly increasing. If we assume that the age at first reproduction is correct for the southern portion of the species range, then this indicates that the survival or fecundity rates used in our models are not representative of eastern diamondbacks in this region.

It is important to note that our ability to explore a broader suite of models used was limited by the lack of different demographic data sets on eastern diamondbacks. The fecundity and survival parameters used in this model are averages from across the range of the species and therefore may not be representative of some local populations. This may be due to variability in habitat quality, food availability, and predation. It is important to conduct field studies to determine fecundity and survival rates of populations that are declining such as those in Mississippi and North Carolina, and on barrier islands that are being, or have already been, developed. This will allow managers to better understand the threats facing those local populations and to develop targeted management strategies.

The results of the elasticity analyses for both of our models indicated that the survival rate of adult eastern diamondbacks contributed the most to the population growth rate. The usefulness of these models depends on identifying stage-specific threats. Protecting and managing large tracts of longleaf pine habitat should be the primary method of managing eastern diamondback populations, as this will benefit all life stages. However, additional management effort may be required where stage specific threats occur. Anthropogenic factors that reduce survival likely have a disproportionate effect on the adult life stage. Rattlesnake roundups target the largest individuals, and because adults have larger home ranges and move greater distances, they are more likely to encounter roads. The results of this study indicate that these threats to adult survival have the greatest potential to negatively impact eastern diamondback population. Additionally, because fecundity is proportional to body size in female eastern diamondbacks, pressures that reduce survival of large adult eastern diamondbacks may also serve to reduce fecundity rates.

In some situations, management actions targeted to reduce adult mortality may not be able to achieve the level of increase in survival rates required to reach a stable or increasing population. Adult survival rates of eastern diamondbacks are high and increasing these rates may not always be feasible. Conversely, neonate survival is relatively low. While increasing neonate survival may not have as great an impact on population growth as increasing adult survival, it may be easier to achieve greater increases in neonate survival with targeted management actions. One of the primary causes of neonate mortality is predation and anthropogenic changes to the landscape often increase mesopredator abundance, which may decrease neonate survival rates. Management actions to reduce the abundance of mesopredators may serve to compensate for an inability to increase adult survival rates and should be considered as an additional strategy in conservation plans for eastern diamondbacks.

Management Implications

The results of our study show that management efforts for eastern diamondback rattlesnakes that target the adult stage will have the greatest impact on the population growth rate. While the most commonly management recommendation for eastern diamondback rattlesnakes is to protect large tracts of habitat, populations on protected land may decline if other factors are decreasing adult survival rate. Continued efforts to eliminate rattlesnake roundups, which target the largest snakes, or to convert them to wildlife friendly events, should be a priority of conservation efforts. Strategies should also be developed to decrease road mortalities. Reduced speed limits through areas with eastern diamondback rattlesnake populations, in particular on state and federally managed lands, will help to reduce the number

of animals accidentally run over. The most important conservation strategy however may be education outreach. Educating the people that live alongside these animals about their value to the ecosystem is going to be the only way to convince them to stop killing them.

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Table 3.1. Three-stage life history parameters for eastern diamondback rattlesnakes with an age at first reproduction of 4 years (model 1).

Stage	Description	Years in Stage	Survival	Fraction leaving	Fraction Staying	Gx	Px
1	Neonate	1	0.33	1.0	0.0	0.33	0.0
2	Subadult	3	0.82	0.27	0.73	0.22	0.60
3	Adult	-	0.82	0.0	1.0	0	0.82

* Adults remain in stage 3 for the rest of their lives.

Table 3.2. Three-stage life history parameters for eastern diamondback rattlesnakes with an age at first reproduction of 7 years (model 2).

Stage	Description	Years in Stage	Survival	Fraction leaving	Fraction Staying	Gx	Px
1	Neonate	1	0.33	1.0	0.0	0.33	0.0
2	Subadult	6	0.82	0.10	0.90	0.08	0.74
3	Adult	-	0.82	0.0	1.0	0	0.82

* Adults remain in stage 3 for the rest of their lives.

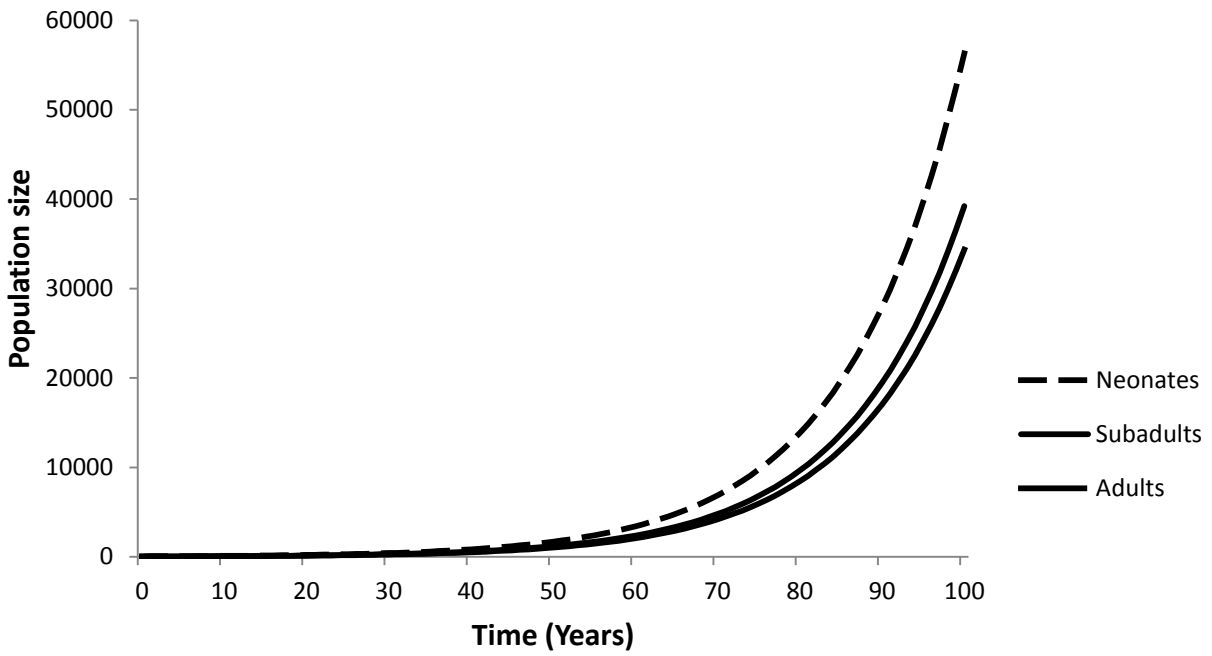


Figure 3.1. Projected population growth of three life-stages of eastern diamondback rattlesnakes with an age at first reproduction of 4 years, estimated to 100 years. Mean population growth rate of $\lambda = 1.07$.

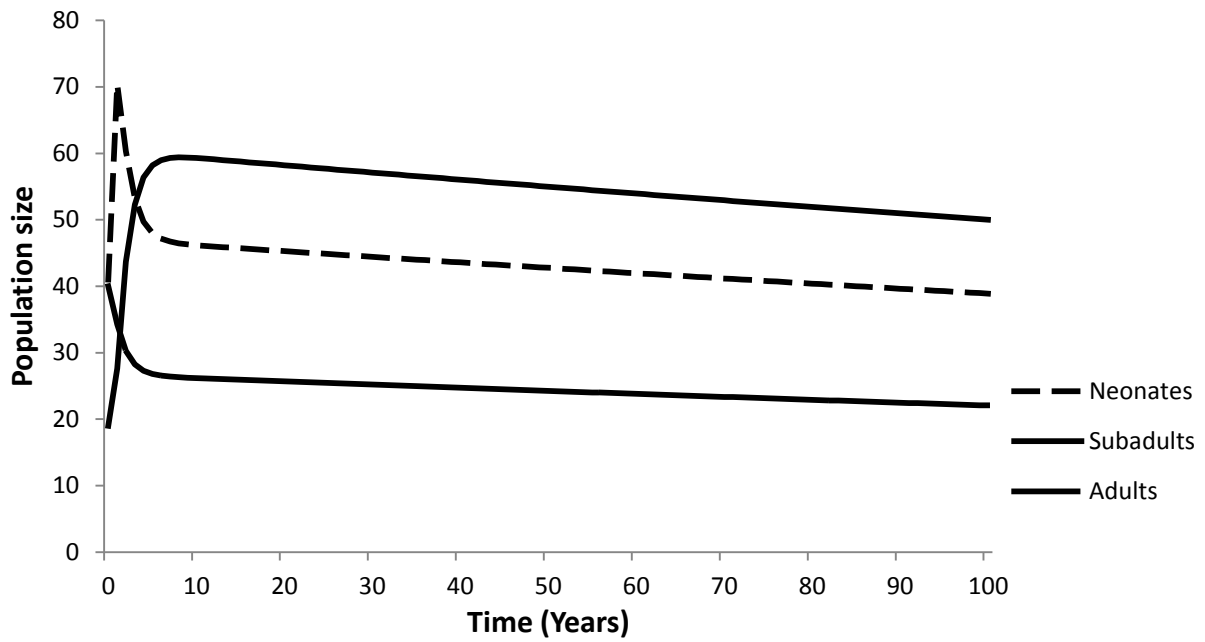


Figure 3.2. Projected population growth of three life-stages of eastern diamondback rattlesnakes with an age at first reproduction of 7 years, estimated to 100 years. Mean population growth rate of $\lambda = 0.998$.

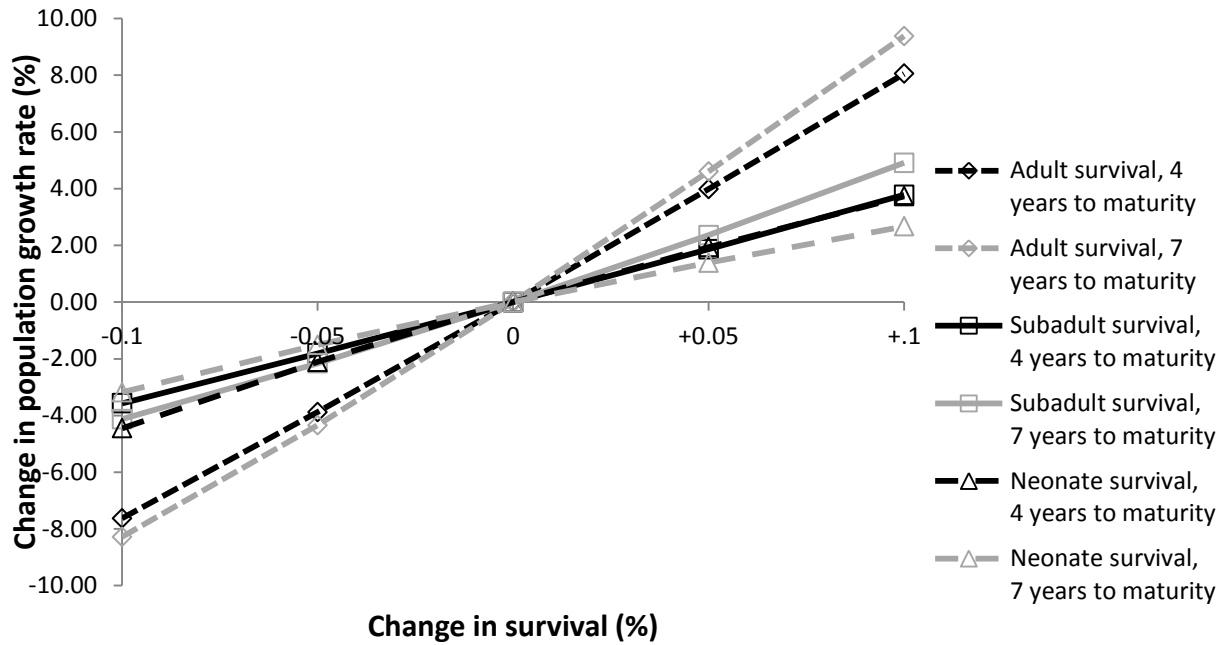


Figure 3.3. Percent change in population growth rate (λ) versus percent change in stage-specific survival rates for eastern diamondback eastern diamondback rattlesnakes.

CHAPTER 4

CONCLUSION

Eastern diamondbacks are currently facing range-wide declines, prompting the proposal to list them as a threatened species under the Endangered Species Act. The causes of their declines are primarily attributed to anthropogenic threats, such as habitat loss, road mortality, collection for rattlesnake roundups, and malicious killings. These declines provide immediacy to the need to identify the impact of these threats as well as to develop effective management strategies for this species. In this thesis we use two modeling approaches to help direct future management decisions.

In chapter two, we examined the impact of habitat composition and scale on eastern diamondback occupancy in coastal dune habitat. We conducted intensive field surveys on ten of Georgia's Barrier Islands and modeled occupancy rates as a function of landscape composition at three spatial scales. Our results indicated that the influence of habitat composition was not consistent across scales, with the area of maritime forest negatively influencing occupancy rates at the 500- and 1000-m spatial scales, and the area of secondary dunes positively influencing occupancy rates and the 1000-m spatial scale. Our analysis showed no influence of landscape composition at the 250-m spatial scale. Management efforts for eastern diamondbacks on Georgia's Barrier Islands should aim to protect large tracts of secondary dune habitat.

In chapter three, we developed a stage-based population matrix model for eastern diamondbacks based on published estimates of demographic rates. We incorporated two different ages at reproductive maturity, 4 and 7 years, to account for variability throughout the range of this species. This resulted in two different population growth rates, one that was relatively stable (7 years), and one that was increasing exponentially (4 years). The outcome of an eastern diamondback population growing this rapidly is unlikely; meaning our estimates of survival and fecundity rates must be incorrect for populations that mature at 4 years, if this estimated age of reproductive maturity is correct. Elasticity analysis of our model indicated that adult survival rate contributes the most to population growth rate of eastern diamondbacks. Mortality of adult eastern diamondbacks is primarily due to anthropogenic threats, which our model indicates could have a significant negative impact the population growth this declining species.

Future research efforts to examine how demographic rates vary geographically and temporally are essential to improving our ability to predict population growth trends in eastern diamondbacks. Research into the causes of variability in demographic rates, such as habitat quality, prey availability, predation, and intraspecific competition, will also be useful in developing future management strategies. Management efforts are in particularly need in areas where the species is known to be declining. Estimating demographic rates in these areas will allow us to create long-term monitoring projects and allow us to assess the impact that various management strategies have on the population growth rate of eastern diamondbacks.