PATCH OCCUPANCY AND POPULATION DENSITY OF THE CREVICE SPINY LIZARD (*SCELOPORUS POINSETTII*) IN THE CENTRAL MINERAL REGION OF TEXAS

by

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My accomplishments are shared with those who support me. I would like to thank my family. My mother, Susan Jenkerson, and my father, Terrill Jenkerson, have provided me every opportunity and underpin my success. I would like to thank the immutable Cathleen Mackinnon, an abiding force in my life. In addition, my grandparents, Robert and Rosemary Seale, and Carol Gallagher deserve distinction as my perpetual and unbidden advocates.

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ABSTRACT

Occupancy is a state variable that can be used as a response variable to assess the suitability of habitats (Larson 2014). In this project, I compared crevice spiny lizard (*Sceloporus poinsettii*) distributions of occurrence to variables relevant to a local rock habitat (patch) and a landscape (extent) scale. In addition, I investigated the influence of habitat size on crevice spiny lizard density. When detection of an animal is imperfect, occupancy modeling becomes critical, providing a detection estimate that will serve as a correction factor for a less biased estimation of true occupancy (Royle et al. 2005). Herpetofaunal species within a landscape are strongly associated with the amount and availability of suitable habitat as well as numerous characteristics of the habitat. The goals of my research were to (1) determine the relative influences of local habitat and extent landscape variables on crevice spiny lizard occupancy of monadnock features present within the Llano Uplift area of the Central Mineral Region of Texas and to (2) determine population density using mark-recapture based population estimates. I estimated site occupancy of crevice spiny lizards using presence-absence surveys conducted from June to September 2015. I recorded survey-specific covariates, which are known or are suspected to influence the probability of detection. In addition, I measured habitat variables and calculated indices which are known or suspected to influence lizard occupancy at local rock habitat scale (habitat size, percent cover vegetation, ground cover complexity, number of refuges, and refuge quality) and at extent landscape scale (percent

cover vegetation, ground cover complexity, aspect, roughness, and burn interval). For the estimation of lizard density, I conducted a series of mark-recapture surveys at 3 sites that differed in size but were similar with respect to other habitat characteristics. To estimate lizard density, I captured and marked 46 adult crevice spiny lizards using ®Floytag T-bar anchor tags. Average lizard density across sites was 1.41/100 m^2 (SE = 0.023, n = 46). For the assessment of occupancy, 350 lizards were detected on 69 surveys (n = 19 sites) over one field season. I used single-season occupancy models in the program PRESENCE to estimate effects of environmental and habitat variables on probability of detection (p) and occupancy (ψ). Multimodel information-theoretic approach suggests that at a local rock scale, crevice spiny lizard occupancy may be more closely related to refuge quality. At an extent landscape scale, most parsimonious models suggest that geographic aspect is most influential to occupancy. These results indicate that patterns of occurrence may be tied closely to characteristics most immediately affecting the ability to thermo-regulate and find cover. In addition, extent landscape may also play a role in microhabitat suitability and thus quantification of suitable habitat without consideration of landscape context is unlikely to be sufficient for the assessment of species distribution. Lizard density decreased with increasing site size, indicating that habitat size may not be positively correlated with habitat suitability for the crevice spiny lizard.

I. INTRODUCTION

Human presence and activities can influence species occupancy, abundance, or persistence within a landscape (Gibbons et al. 2000). Habitat heterogeneity may have a large influence on species distribution, and human activities can positively or negatively change landscape heterogeneity (August 1983). Studies concerning reptile and amphibian habitat relationships are relatively few in number (Stuart et al. 2004; Larson 2014) despite the prevalence and importance of herpetofauna in ecological settings. Accordingly, studies which seek to understand the relationships between species occupancy and habitat attributes are becoming more relevant.

The presence of a herpetofaunal species within a landscape is strongly associated with the amount and availability of suitable habitat and the persistence of that species may be associated with numerous characteristics of the microhabitat (Smith 1996). Habitat occupancy is likely influenced by different variables and is scale dependent. Therefore, both characteristics of the local habitat and the extent landscape should be considered when evaluating these influences (Blevins and With 2011). For saxicolous (rock-dwelling) lizards, habitat occupancy may be influenced by vegetation composition, rock composition or morphology, amount of rock cover, or geographic aspect (Fischer et al. 2004; Jellinek et al. 2004). For instance, landscapes with predominately southerly facing slopes receive more direct sunlight in the Northern Hemisphere, potentially increasing opportunities to bask. These lizard species may select microhabitat based on rock size, rock slope, thermal properties, the width of crevices, or the prevalence of vertical surfaces (Schlesinger and Shine 1994; Ridenour 2002; Eifler et al. 2007).

At larger landscape scales, fire elicits an array of responses in lizard species (Russell et al. 1999; Schrey et al. 2011). Fire can influence species richness, alter dispersal and movement, and affect local abundance (Mushinsky 1985; Griffiths and Christian 1996; Templeton et al. 2001). Specifically, it is well documented that fire directly and indirectly affects abundance and species composition of plants and insects (Duchesne 1994; Kim and Holt 2012). While some lizard species may not directly utilize vegetation for primary cover (e.g., saxicolous lizards are relegated to areas of minimal vegetative cover), vegetation may be an important component in diet and foraging cover (Ballinger et al. 1977). Concurrently, fire may alter both foraging cover and forage availability surrounding lizard habitat, and thus may play a role in habitat suitability. Fire frequency can also affect the thermoregulatory opportunities of terrestrial ectotherms by altering the amount of canopy cover in the habitat. Consequently it is relevant to investigate the influence of fire and vegetation on lizard occupancy within surrounding habitat (Elzer et al. 2013).

The higher extinction rates of small populations are often linked with both demographic and environmental stochasticities wherein smaller populations are more vulnerable to chance variation (Reed et al. 2003). Size of lizard populations within microhabitats (patches) can be used as tools to assess the persistence of a species, as habitat size can constrain population size (Hokit and Branch 2003). While stochastic processes are relevant to persistence, habitat size has been shown to influence abundance and survival of local populations and may also have an impact on habitat quality and species demography (Thomas 1994, Hokit and Branch 2003). Such deterministic effects on demography may often define patch occupancy and abundance patterns seen in amphibians and reptiles independent of stochasticities (Groombridge 1992; Thomas 1994). For most species, however, the associations between habitat size and demography are largely unknown (Hokit and Branch 2003).

The crevice spiny lizard (*Sceloporus poinsettii*) is well suited for studying the effects of relevant habitat parameters on lizard occupancy. The crevice spiny lizard prefers semi-arid habitats, is abundant, diurnal, does not migrate, and is an important food web component as both predator and prey (Pianka 1986). Within the Llano Uplift region of Texas, crevice spiny lizards are restricted to habitats composed of local rock outcrops of limestone or granite (Bartlett and Bartlett 1999). Because they are closely associated with rocks and seek shelter in crevices, their distribution and abundance are likely controlled by morphological aspects of the rock terrain as well as by the extent landscape (Degenhardt et al. 1996). My main objectives for this study were to (1) determine the relative influences of local habitat and extent landscape variables on crevice spiny lizard occupancy of monadnock features (granite outcrops) present within the Llano Uplift area of the Central Mineral Region of Texas, to (2) determine population densities using mark-recapture models, and to (3) investigate the influence of habitat size on density.

II. METHODS

Study Site

My project was conducted over one field season (June - August) in 2015 at the Mason Mountain Wildlife Management Area (Mason Mountain WMA), located 9 km north of Mason, Texas (30.8449°N, 99.2134°W). Mason Mountain WMA (2,145-ha) is owned and managed by the Texas Parks and Wildlife Department and supports research concerning the ecology of the Central Mineral Region and its application to wildlife management on private lands. Mason Mountain WMA is located in the northwestern portion of the Llano Uplift with elevations ranging from 518 to 621 m. Temperatures range from an average high of 36 °C in July to an average low of 3 °C in January and the average annual precipitation is 63.5 cm (Rhoades 2010). Crevice spiny lizard habitat is naturally fragmented within Mason Mountain WMA and can be visualized as a nested hierarchy of rock habitats involving granitic monadnocks interspersed within rangeland typical of the Llano Uplift area. The granite outcrops display characteristic morphology and weathering patterns which create differences in habitat size, number and size of crevices, slope, aspect, and soil moisture, and thus variation in habitat suitability (Wiens et al. 2013). The surrounding rangeland supports mixed oak (*Quercus spp.*) and whitebrush (*Aloysia gratissima*) woodlands, and grasslands with grama grasses (*Bouteloua spp.*), love grasses (*Eragrostis spp.*), little bluestem (*Schizachyrium scoparium*), and silver bluestem (*Bothriochloa saccharoides*). Additionally, areas of suitable crevice spiny lizard rock habitat are surrounded by rangeland that has been subjected to varied burn treatments. While some are managed in a fashion similar to historical disturbance regimes of the Llano uplift (mean fire interval = 3 to 4 yr;

Stambaugh et al. 2014), others are atypical in time interval across suitable crevice spiny lizard rock habitat. Time since fire (TSF) ranges from 1 to 6 yr with a burn interval ranging from 2 to 11 yr.

Field Methods

Count Surveys

To evaluate local habitat characteristics contributing to lizard occupancy, I conducted a multi-site occupancy study. I selected survey sites from an array of granite outcroppings of variable area from a digitized land cover layer (National Agriculture Imagery Program, acquired 2014 at a spatial resolution of 1 m) using ArcGIS version 10.3 (ESRI, Redlands California, USA). I estimated site area using ArcGIS, as well as the area calculating function of a handheld GPS unit (Garmin GPSMAP 64s). I used hand-held GPS area calculations when boundary lines on satellite images were occluded by vegetation or landscape. I defined locally isolated habitat as those non-contiguous granite monadnocks separated by a distance of at least 15m, a distance similar to that used in studies of other rock-dwelling lizards (Ridenour 2002; Whitaker 1996). From available isolated sites, I took 20 random samples from 5 habitat size categories (0-1.4, 1.4-2.8, 2.8-4.2, 4.2-5.6, and 5.6-7 ha). This sampling structure allowed for replicates within the 5 habitat size treatments (Fig. 1).

I sampled crevice spiny lizard populations during the peak activity season (June – August), conducting surveys between 0800 and 1800 hrs during clement weather conditions when lizards are most likely to be visible, e.g. sunny days with adequate basking temperatures (average = 34.2°C, SD = 3.93) and low wind speeds (average = 4.7

m/s, SD = 2.57, n = 19 days). I conducted weekly surveys throughout the study interval (between 3 and 6 surveys per site) to estimate true detection rate, or the rate at which non-detection of a species is characteristic of true absence (Mackenzie et al. 2002). I conducted count surveys by slowly and systematically walking the length of each granite outcrop until the entire site had been scanned (n = 19 rock outcrops; one site was later removed due to accessibility issues). Lizard presence (occupancy) and location (UTM coordinates) for all adult and sub-adult (<95 mm SVL for males and <85 mm SVL for females) crevice spiny lizards on each outcrop were recorded using a handheld GPS unit (Ballinger 1973). In addition, I recorded date, time of day, survey time, percent cloud cover, air temperature and wind speed (measured with a Kestrel 3000 Pocket Weather Meter), and rock temperature (measured with an EXTECH Fluke 62 Mini IR thermometer), for each survey. These variables were subsequently included as detection variables (Table 1) in models exploring factors affecting lizard detectability.

Local Rock Habitat and 15 m Buffer Measures

For the purposes of assessing habitat occupancy, I surveyed a sample of locally isolated rock habitats (patches) within the Mason Mountain WMA. To determine which habitat parameters influence crevice spiny lizard occupancy, I measured 10 variables representing factors that are either known or suspected to influence habitat suitability (Blevins and With 2011). These variables represent hypotheses evaluated using a multi-model selection procedure (Table 2; Burnham 2003), including descriptors of the fine-scale rock habitat (measured within site boundaries) and the extent landscape.

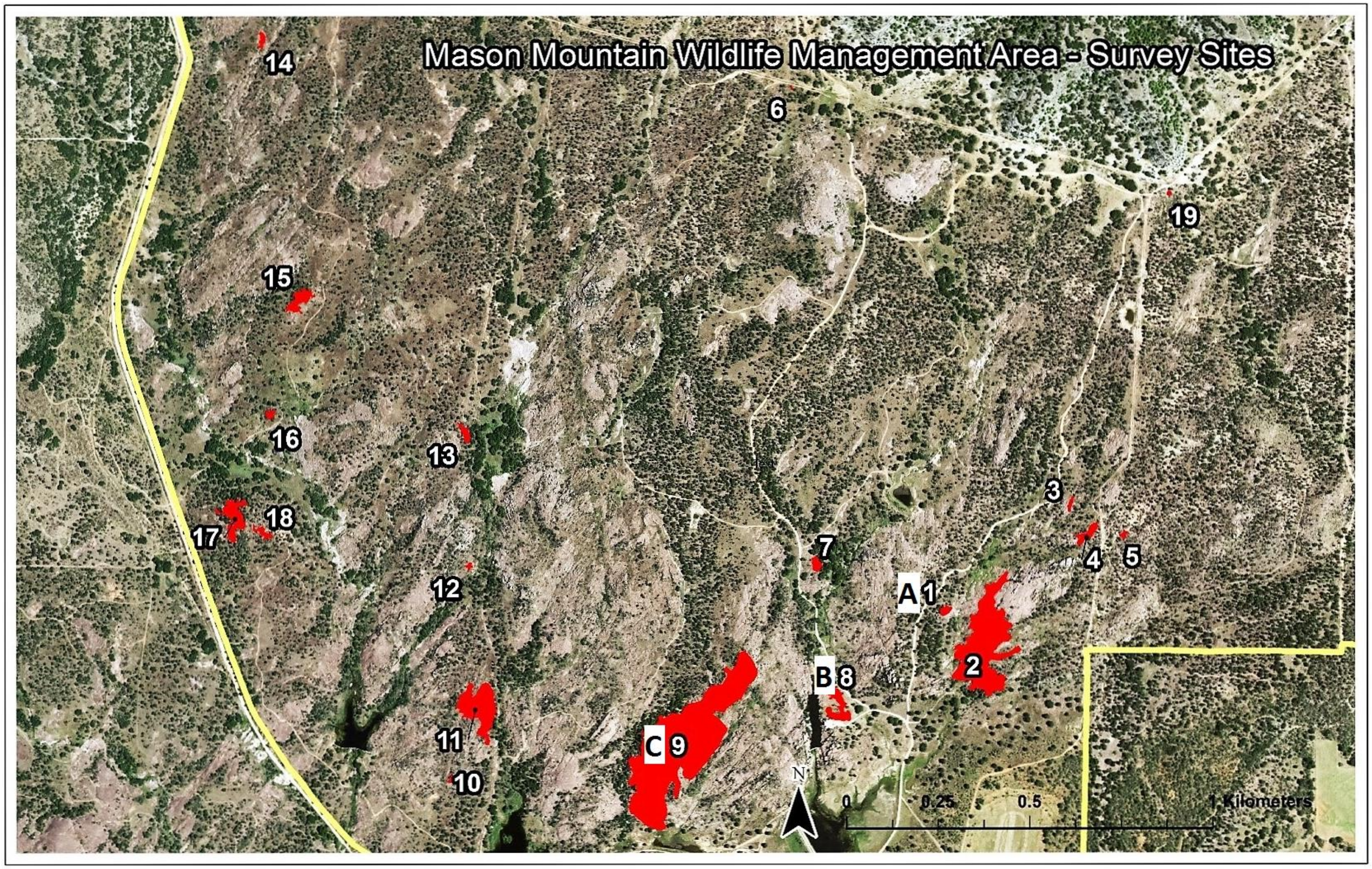

Figure 1. Map of Survey Sites Used for Presence – Absence Surveys, for the Measurement of Relevant Habitat Variables (n = 19 Sites) and for Mark – Recapture Surveys (n = 3 Sites; A, B, and C).

Table 1. Variables Used in Models for Determining Factors Affecting Detection Probabilities of the Crevice Spiny Lizard at Mason Mountain Wildlife Management Area, Texas.

Detection variable	Variable type	Description
Constant	None	Detection assumed constant, no detection variable applied
Date	Continuous	Date of each survey recorded as Julian day
Start time	Continuous	Start time of each survey
Air temperature	Continuous	Air temperature (°C) during each survey
Rock temperature	Continuous	Temperature of granite outcrop (°C) during each survey
Wind	Continuous	Wind speed (m/s) during each survey
Cloud cover	Ordinal	% cloud cover during each survey organized by cover class (1-4)
Weather (Rock, Air, and Wind)	Continuous	Additive combination of variables associated with overall weather conditions during surveys

In order to estimate the effects of habitat characteristics within the extent landscape on occupancy, I measured variables within a 15 m buffer area around each site. To quantify variables within the local rock habitat and the 15 m buffer areas, I used the line intercept method across all sites. At 100 m intervals, I positioned intercepts perpendicular to a line covering the length of each site in order to completely assess each site. At site boundaries, I extended line intercepts an additional 15 m to assess attributes within the buffer areas (Fig. 2; number of transects per site ≥ 4).

To quantify crevice-refuge quality, I devised an ordinal scale for assessing the relative crevice width, length, and depth at each site, adapting the approach used by

Howard and Hailey (1999). The ordinal scales for width, length, and depth ranged from 1 to 3 and were based on mean lizard height (1 cm), snout-vent length (10 cm), and width of body (5 cm), respectively. I assumed that crevices ranging between 1 cm and 5 cm in width represented optimum conditions for crevice spiny lizard habitation with decreasing suitability as width increased ($1 = x > 10$ cm, $2 = 5 \text{ cm} < x \leq 10$ cm, and $3 = 1 \text{ cm} < x \leq 5$ cm). For length and depth, I assumed that after minimum sizes were reached, crevice suitability increased with size [depth = 1 ($x \leq 5$ cm), 2 ($5 \text{ cm} < x \leq 10$ cm), and 3 ($x > 10$ cm); length = 1 ($x \leq 10$ cm), 2 ($10 \text{ cm} < x \leq 30$ cm), and 3 ($x > 30$ cm)]. Width, length, and depth assessments were added together to create an overall refuge quality estimate (3-9). Along transects laid for the purpose of estimating habitat variables, I recorded any crevice meeting the minimum requirements (i.e. width, length, and depth great enough to provide refuge) of this ordinal scale in order to quantify refuge quality as well as refuge amount (refuge/m). I also assessed percent cover by vegetation and ground cover complexity along the intercept for both the local rock habitat and the 15 m buffer area around each site. Ground cover complexity was based on all available ground cover types (8 classes = solid granite, gravel granite, dirt, grass, forb, tree, cactus, and leaf litter). Cover classes constituting at least 5% of the ground cover were included in ground cover complexity estimates (ranging from 0 to 8). I devised ground cover complexity categories to assess the amount of heterogeneity within sites consisting of predominately rock cover.

In addition, I obtained variables measured within the 15 m buffer area (including site area) from an analysis of a digital elevation model (DEM, National Elevation Dataset, acquired 2013 at a spatial resolution of 10 m) of the Mason Mountain WMA in ArcGIS. I calculated aspect because of its potential influence on microclimate, particularly temperature, which can affect the presence of saxicolous lizards (Corbalán 2013). Because crevice spiny lizards at the Mason Mountain WMA inhabit areas that could be considered rugged (rocky or steep), I calculated terrain irregularity (roughness) by dividing surface area by planimetric area (Jenness 2004). Fire regime (time-since-fire) was included as a 15 m buffer area variable as it may not directly affect rock outcrop characteristics (wherein sites are largely without vegetation).

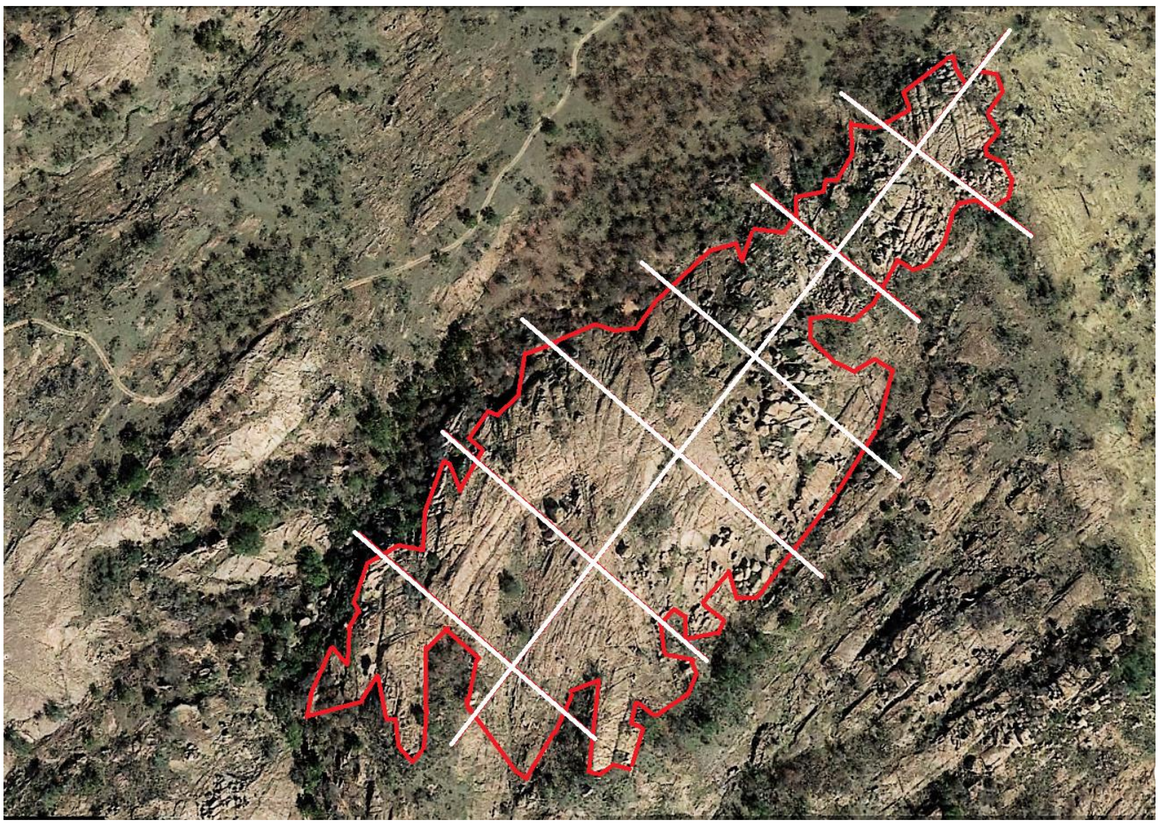

Figure 2. Diagram Depicting Transect Placement for Each Site for the Assessment of Habitat Variables. Perpendicular Transects Were Run at 50 m Intervals Along Main Transect Extending the Length of Each Site. In Addition, Transects Intersecting Boundary Lines Were Extended an Additional 15 m for Assessment of Habitat within a 15 m Buffer Area.

Table 2. Variables Measured within Site Boundaries (Local Rock Habitat) and within a 15 m Buffer Area (Extent Landscape) to be Used for Modeling Crevice Spiny Lizard Occupancy.

Variable	Variable type	Description
Local rock habitat		
Habitat size	Continuous	Per site area, estimated using GPS area calculation
% cover vegetation	Continuous	% ground cover vegetation within site estimated by line intercept method
Ground cover complexity	Ordinal	Number of ground cover types within site, estimated by line intercept method (8 classes: solid granite, gravel granite, dirt, grass, forb, tree, cactus, and leaf litter)
Number of refuges	Continuous	Number of crevices large enough for lizard cover based on minimum snout vent length, estimated by line intercept method
Refuge quality	Ordinal	Additive combination of width, depth, and length of crevice (3-9) estimated for each crevice intercepting transect
15 m buffer area		
Roughness	Continuous	Measure of topographic change (terrain irregularity)
Aspect	Continuous	Mean aspect per site, measured in degrees from north
% cover vegetation	Continuous	% vegetation cover measured within 15m buffer area, estimated by line intercept method
Ground cover complexity	Ordinal	Number of ground cover types within site, estimated by line intercept method (8 classes: solid granite, gravel granite, dirt, grass, forb, tree, cactus, and leaf litter)
Burn interval	Ordinal	Burn treatment interval (TSF)

Mark-Recapture Surveys

I captured and marked adult crevice spiny lizards to estimate lizard density at my study sites. I restricted capture efforts to three locally isolated granite outcrops ranging in size from approximately 300 to 71,000 m^2. I captured visually detected crevice spiny lizards during the peak activity season (June – September) using a pole-noose (Bertram and Cogger 1971). I measured snout-vent length, total length, weight, and cloacal temperature and marked all lizards caught with a uniquely numbered and colored Floy® fine fabric T-Bar anchor fish tags (Floy® Tag, Inc., Seattle Washington, www.floytag.com; model FF-94). I inserted individual tags subcutaneously and dorso-laterally behind the front leg using a Floy® Mark II fine fabric tagging gun. After injection, I applied a small amount of cyanoacrylate adhesive on the injection site in order to improve tag retention and reduce risk of infection. Before release, I also marked each lizard with a unique toe-clip (Tinkle 1967; Perry et al. 2011). Recapture surveys were conducted by slowly and systematically walking the length of each granite outcrop with binoculars and recording the presence of tagged and untagged individuals. Presence of a tagged lizard within a recapture survey represented a recapture. In order to calculate per site density estimates, I estimated population size ($\widehat{N}$) using the Schnabel Method (Schnabel 1938). This method treats multiple samples as a series of Petersen samples, calculating a population estimate as a weighted average of multiple mark-recapture events (Krebs 1999). The Schnabel method employs the following equation:

$$\widehat{N} = \frac{\Sigma_t\ (C_t M_t)}{\Sigma_t\ R_t}$$

Where C_t = the total number of individuals caught in sample t, M_t = the number of marked individuals in the population just before sample t is taken, and R_t = the number of individuals already marked when caught in sample t.

Model Development and Analysis

Occupancy modeling is a statistical tool developed to estimate population parameters and investigate the influence of habitat variables on those parameters (Mackenzie et al. 2002). These models use repeat count data that incorporate detection probabilities and do not require identification or capture of individual animals (Mackenzie et al. 2002; Lee et al. 2011). I estimated site occupancy (i.e., Ψ, proportion of sites occupied) using single-season occupancy models implemented in the program PRESENCE (Hines 2006) adjusted for detection probabilities (i.e., individuals may be present but go undetected; Mackenzie et al. 2006). Prior to the inclusion of variables in models, I z-standardized all variables and conducted a Pearson's product-moment correlation test using the program R version 3.2 (R Core Team 2015) to assess multicollinearity. I found no significant correlations among any of my habitat variables (all $-0.5 < r < 0.5$). Models were ranked according to Akaike Information criterion adjusted for small sample size (AICc). The model with the smallest AICc is treated as the best model, however, any model with ΔAIC <2 is considered to have support and is viewed as equally parsimonious. In addition, Akaike weight (ω_i) was calculated in order to determine the relative support for each model, which determines the probability that a given model is the best model given repeated sampling (Burnham 2003).

Because changes in counts between surveys and sites may be a product of changes in detectability and not habitat qualities, I evaluated survey specific covariates which appeared to affect detectability of crevice spiny lizards (Mackenzie 2002). Factors which might affect lizard visibility and therefore bias estimates of detection rates included variables associated with the weather (air temperature, rock temperature, wind speed, and percent cloud cover), and temporal variations (Julian date and time of survey). I created models using one each of those factors affecting lizard detectability and subsequently included those variables significantly influential to lizard detection in my models for occupancy (Blevins and With 2011). In addition to models including survey specific covariates (n = 7 models), I ran two predefined models in PRESENCE: (1) with detection probability constant across surveys, and (2) with variable detection probability among surveys.

Using an information-theoretic approach (Burnham 2003), I applied multimodel selection and statistical inference to establish which model(s) best explained the relationship between crevice spiny occupancy and measured habitat parameters for both the local rock habitat and the extent landscape. In order to explore all possible combinations of variables, models in my analysis were selected using a full AIC approach for rock habitat variables (n = 32 models; Appendix 1) and boundary habitat variables (n = 32 models; Appendix 2) separately. I investigated a total of 64 candidate models within 2 AIC selection tables.

III. RESULTS

Count Surveys and Habitat Measurements

The average area of outcrops in my study was 0.72 ha (SD = 1.68, n = 19 outcrops). I recorded 350 lizards over one field season (n = 69 surveys), with a total of 319 (91.4%) adults and 31 (8.6%) sub adults. Sixteen of the 19 sites had at least one lizard detection (naïve proportion of sites occupied = 0.84), with a mean count per site surveyed of 5.07 lizards (SD = 8.11). For the quantification of certain habitat variables, I employed line-intercept method (5,059.6 m total transect distance). Percent vegetative cover within sites ranged from 7.5% to 53.6% with a mean of 29.3% (SD = 12.7). Percent vegetative cover measured within the 15 m boundary habitat, ranged from 39.0% to 100.0% with a mean of 72.2% (SD = 16.8). At the local rock habitat scale, ground cover complexity varied from 2 to 4, with a mean value of 3.06 (SD = 0.9). Ground cover complexity within the 15 m buffer averaged 2.4% greater than within site estimates and ranged from 1 to 6 with a mean of 3.41 (SD = 1.3). To assess refuge quality and amount, I recorded 252 crevices meeting minimum requirements for habitation along transects. Of these, 31.0% were vertical refuges and 69.1% were horizontal refuge. Refuge number (refuges/m) ranged from 0 (no crevices intercepting line) to 0.4 refuges/m with a mean of 0.16 refuges/m (SD = 0.10). Mean refuge quality across sites was 7.92 (SD = 0.64).

Site Occupancy

Among single-season models assessing the influence of time specific covariates (detection probabilities) on site occupancy there were 2 competing models (Table 3; ΔAICc < 2). Detection probability correlated negatively with temperature within the survey period (β = -0.907, *SE* = 0.483). This model generated detection probability estimates ranging from 59.55% (*SE* = 15.67%) to 99.30% (*SE* = 1.34%) across all surveys. The competing model (ΔAICc = 1.74) assumed detection probabilities constant across surveys and estimated a detection probability of 83.01% (*SE* = 4.99%) across all surveys. Consequently, I included air temperature as a factor influencing probability of detection in all models exploring the effect of habitat variables on lizard occupancy. Within the local rock habitat scale, there were two competing models: (1) occupancy expressed as a logit-link function of refuge quality with detection probability corrected for temperature, and (2) constant occupancy with detection probability corrected for temperature (ΔAICc = 1.12; Table 4). Refuge quality was positively correlated with lizard occupancy (β = 1.257, *SE* = 0.980) and generated site occupancy estimates that ranged from ψ = 0.063 (*SE* = 0.213) to ψ = 0.959 (*SE* = 0.051). In addition, I used a two sample student's t-test to determine if there were significant differences in refuge quality between occupied and unoccupied sites. Mean refuge quality was significantly different between occupied and unoccupied sites (t = 4.231, df = 18, $P < 0.001$). Within the 15 m buffer, there was only one supported model, occupancy expressed as a logit-link function of aspect with detection probability corrected for temperature (ω_i = 0.277; Table 4). Aspect was positively correlated with lizard occupancy (β = 2.782, *SE* = 1.559) and generated site occupancy estimates ranging from ψ = 0.216 (*SE* = 0.241) to ψ = 1.00 (*SE* = 0.0003). In addition, I used a two sample student's t-test to determine significant differences in aspect between occupied and unoccupied sites. Mean aspect was significantly different between occupied and unoccupied sites (t = -15.361, df = 18, P <

0.001). Mean aspect among occupied sites was 193.86° (SD = 54.08, a value which corresponds to a southerly aspect.

Mark-Recapture Surveys

A total of 46 crevice spiny lizard species were marked using T-Bar anchor tags between 27 June and 5 September 2015 (Table 5). Tagged lizard snout-vent length ranged from 7.3 (sub-adult) to 11.5 cm. A total of 20 individuals were visually assessed as recaptured across the 3 sites. On 5 occasions, individuals were physically recaptured and identified as recaptured more than 3 weeks after marking. On one occasion, a crevice spiny lizard was shown to be originally tagged 7 weeks prior to recapture. There was no evidence of tag loss as all new captures lacked the identifiable toe-clip linked to the initial capture event. Average lizard density across sites was 1.41/100 m^2 (SE = 0.023, n = 46). Lizard density decreased considerably with site size (Fig. 2).

Table 3. Probability of Occupancy (ψ) Expressed as a Logit Function of Time Specific Covariates (Detection Variables) with Corresponding Standard Errors and Upper and Lower 95% Confidence Intervals and Relevant ΔAICc and AICc Weight (ω_i) Values. Naïve Probability of Occupancy across All Sites = 0.8421 (n = 19 Sites). All Parameters Estimated Using Single-Season Occupancy Models (Mackenzie et al. 2002).

Detection Model	Ψ	SE	95% CI	Δ AICc	ω_i	No. Parameters
Ψ(.),p(air temperature)	0.850	0.085	0.607 - 0.954	0.00	0.432	3
Ψ (.),p(.)	0.846	0.084	0.608 - 0.951	1.74	0.181	2
Ψ (.),p(rock temperature)	0.849	0.085	0.607 - 0.953	2.11	0.150	3
Ψ (.),p(start time)	0.848	0.085	0.607 - 0.953	3.45	0.077	3
Ψ (.),p(Julian date)	0.846	0.084	0.608 - 0.951	4.26	0.051	3
Ψ (.),p(wind speed)	0.847	0.084	0.608 - 0.951	4.48	0.046	3
Ψ (.),p(cloud cover)	0.846	0.084	0.608 - 0.951	4.53	0.045	3
Ψ (.),p(temperature + rock temperature + cloud cover)	0.850	0.085	0.606 - 0.954	6.69	0.015	5
Ψ (.),p(1)	0.847	0.084	0.608 - 0.952	16.01	0.000	7

Table 4. Parameter Estimates (β) and Standard Errors of Top Models ($\omega_i \leq 2$) for Site Specific Covariates (Local Rock and 15 m Buffer Variables) with Corresponding ΔAICc and AICc Weight (ω_i) Values. All Parameters Estimated Using Single-Season Occupancy Models.

Model	β_1[SE]	Δ AICc	ω_i	No. Parameters
Local rock habitat				
Ψ (refuge quality),p(air temperature)	1.256 [0.981]	0.00	0.348	4
Ψ (.),p(air temperature)	-0.907* [0.483]	1.12	0.199	3
15 m buffer area				
Ψ (aspect),p(air temperature)	2.782 [1.559]	0.00	0.277	4

***β** estimate for detection variable (temperature)

Table 5. Mark-Recapture Data and Estimated Population Sizes ($\widehat{N}$), Standard Errors and Densities (Lizards/100 m^2) for 3 Sites at the Mason Mountain Wildlife Management Area.

Site	Site Area (m^2)	Captures	Recaptures	$\widehat{N} \pm$ SE	Lizard Density (lizards/100 m^2)
A	287	3	4	7.5 ± 0.067	2.607
B	3727	15	10	47.5 ± 0.0070	1.276
C	71149	27	8	242.6 ± 0.0015	0.341

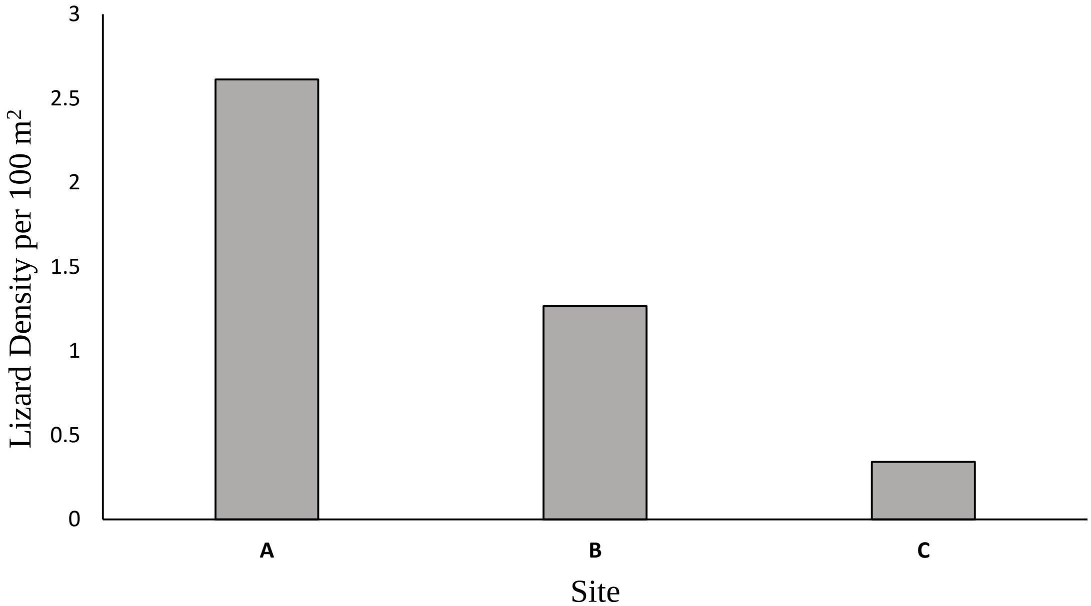

Figure 3. Crevice Spiny Lizard Density Estimates for 3 Sites (A = 287 m^2, B = 3727 m^2, and, C = 71,149 m^2) Calculated Using the Schnabel Method (Schnabel 1938).

IV. DISCUSSION

A major research agenda in ecology involves understanding the influence of habitat structure on the distribution of a species (Turner et al. 2001). The spatial structure of resources within a habitat will likely influence patterns of habitat occupancy at both a local rock habitat and extent landscape scale (Wiens et al. 2013). However, the relative effects of local habitat variables and the surrounding landscape on lizard occupancy will vary among species (Collinge 2009). The results of my study suggest that crevice spiny lizard patterns of occurrence are most likely driven by habitat characteristics most closely related to thermoregulatory opportunities and cover. This further suggests that local habitats that are otherwise suitable for lizard occupancy may be thermally unsuitable, depending on thermal properties of the environment. Because saxicolous lizard species are invariably dependent on the availability of rock habitat, it is not surprising that characteristics of monadnocks influence occupancy. For saxicolous lizards, elements of the rock habitat including, rock morphology, rock height, and amount of rock cover are typically found to be determinants of species distribution (Ruby 1986). These attributes present basking opportunities in addition to providing protection from predation. For the crevice spiny lizard, habitats with higher refuge quality and more southerly aspects may provide optimum conditions for escape from predation and thermoregulatory control.

Environmental temperature is a major factor regulating the activity of ectotherms and active basking in the sun by many lizards is a significant mechanism for thermoregulation (Cowles and Bogert 1944; Lara-Reséndiz et al. 2014). Lizards of the genus *Sceloporus* are relatively precise thermoregulators, reaching optimum body temperatures by basking early in the day, and maintaining this preferred body temperature throughout the day within narrow limits (Fitzpatrick et al. 1978; Ferguson et al. 2014). Negative correlations in my data between lizard counts and temperature may be due to morning surveys with optimum basking temperatures having higher lizard activity (basking rates) than later afternoon surveys (wherein lizards may seek refuge from the sun after optimum body temperatures have been reached).

Through thermoregulation, ectotherms sustain body temperatures that encourage higher levels of biochemical activity, locomotor performance, and physiological function (Adolph 1990). Because thermal microclimates vary spatially, the thermal environment often constrains patterns of habitat use among many herpetofaunal species (Adolph 1990; Martín and Salvador 1997). Previous studies suggest that rocks are fundamental habitat components for saxicolous lizards in satisfying the combined requirements of basking and refuge (Barlett and Gates 1967). The presence of crevices is a useful feature of rocky habitats, allowing lizards to attend to the demands of avoiding predation while participating in other activities (i.e., basking or foraging; Lima and Dill 1990). In addition, the quality of refuge sites may differ as the thermal properties of the refuges themselves may vary (Huey et al. 1989). Consequently, refuge quality may have a profound impact on thermoregulatory activity and therefore may be an important factor directing crevice spiny lizard site occupancy and distributions of occurrence.

Slopes with southerly aspects located within the Northern Hemisphere experience more direct sunlight throughout the day. Accordingly, habitats presenting greater amounts of southerly aspect should provide greater opportunity for thermoregulation and thus lizard occupancy. My research suggests that the relevance of aspect is more closely tied to thermoregulatory benefits than to its effect on vegetation composition even though floristic composition of a habitat can be highly influenced by both geology and aspect and characteristics of the vegetation have a large influence on structuring reptile communities (Kitchener et al. 1980; Jellinek et al. 2004). However, within both the local rock habitat and extent landscape, there were no competitive models which included any floristic parameters (e.g., % vegetation, ground cover complexity, or time-since-fire). It would follow that vegetative parameters are not likely constraining the distribution of the crevice spiny lizard to the extent of rock attributes.

Site area varied greatly ($\bar{x}$ = 8.21 ha, SD = 1.68), however, habitat size was not a significant predictor of occupancy. Crevice spiny lizard presence at Mason Mountain WMA was recorded on isolated rock habitats as small as approximately 9 m^2 and as large as 7 ha. Habitat size was not related to the presence of crevice spiny lizards within the range of studied habitat sizes. This indicates that habitat suitability (or habitat quality) may be a more important factor constraining lizard occurrence than habitat size. I conclude that vegetative elements, including percent cover, ground cover complexity, and fire regime, do not seem to be confining the distribution of crevice spiny lizards. Patterns of occurrence are instead associated with the prevalence and quality of both basking opportunities and refuge from predators.

The processes underlying the association between patch size and crevice spiny lizard demography are largely unknown. Research on other species indicates that patch size may directly affect population persistence through a number of mechanisms related to population size (Hokit and Branch 2003). My data suggest that for the crevice spiny lizard, density decreases with increasing patch size. It is known that density may not always be positively correlated with habitat suitability, it is therefore difficult to determine the influence habitat size has on habitat suitability (Van Horne 1983). Distribution may be in part structured by territoriality. Being that the crevice spiny lizard is closely tied to areas within the margins of rock habitat, it may be that habitat size restricts within site distribution. Higher densities may increase instances of territoriality, with larger areas providing more space to spread out within a finite boundary. The biotic and abiotic changes associated with patch edges are recognized as being able to impact amphibians and reptiles (deMaynadier and Hunter 1998; Schlaepfer and Gavin 2001). If the crevice spiny lizard is dependent on the edge between rock habitat and surrounding rangeland, differences in density estimates may be an artifact of an increasing edge (perimeter) to surface area ratio. This is because smaller sites will have more edge per unit area than larger sites, a fact which may inherently decrease density estimates for species tied to edge habitats when the entire site is considered in calculations. While habitat amount and quality is undisputedly relevant to species conservation, it is difficult to delineate their relative effects on species demography. In the case of the crevice spiny lizard, patch size appears to have less of an influence on patch occupancy than density, suggesting a species whose density may be tied to more intricate relationships with the environment as compared to its occupancy.

APPENDIX SECTION

Appendix 1. Model selection design for 5 local rock habitat variables measured at the Mason Mountain Wildlife Management Area, exploring all combinations. (n = 31 models)

	Variable				
Model No.	Habitat Size	% Cover Vegetation	Ground Cover Complexity	Number of Refuges	Refuge Quality
1	Constant				
2	X	X	X	X	X
3	X	X	X	X	
4	X	X	X		X
5	X	X		X	X
6	X		X	X	X
7		X	X	X	X
8	X	X	X		
9		X	X	X	
10			X	X	X
11	X			X	X
12	X	X			X
13	X		X	X	
14		X		X	X
15	X		X		X
16	X	X		X	
17		X	X		X
18	X	X			
19		X	X		
20			X	X	
21				X	X
22	X		X		
23		X		X	
24			X		X
25	X			X	
26		X			X
27	X				X
28	X				
29		X			
30			X		
31				X	

32					X

Appendix 2. Model selection design for 5, 15 m buffer area variables measured at the Mason Mountain Wildlife Management Area, exploring all combinations. (n = 31 models)

	Variable				
Model No.	Aspect	Roughness	% Cover vegetation	Ground Cover Complexity	Burn Interval
1	Constant				
2	X	X	X	X	X
3	X	X	X	X	
4	X	X	X		X
5	X	X		X	X
6	X		X	X	X
7		X	X	X	X
8	X	X	X		
9		X	X	X	
10			X	X	X
11	X			X	X
12	X	X			X
13	X		X	X	
14		X		X	X
15	X		X		X
16	X	X		X	
17		X	X		X
18	X	X			
19		X	X		
20			X	X	
21				X	X
22	X		X		
23		X		X	
24			X		X
25	X			X	
26		X			X
27	X				X
28	X				
29		X			
30			X		
31				X	
32					X

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