

INFLUENCE OF LANDSCAPE CONTEXT ON PATTERNS OF OCCUPANCY,  
ABUNDANCE, AND GENE FLOW AMONG COLLARED LIZARDS IN THE FLINT HILLS  
OF KANSAS

by

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B.A., BEREA COLLEGE, 2007

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Division of Biology  
College of Arts and Sciences

KANSAS STATE UNIVERSITY  
Manhattan, Kansas

2010

Approved by:

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## Abstract

Organisms exist within complex landscapes, and landscape features may influence multiple aspects of a species' distribution within the landscape, including patch occupancy, abundance within patches, and population genetic diversity at a local or regional scale. We took two approaches to identify the relative importance of landscape context for populations of the Eastern Collared Lizard (*Crotaphytus collaris collaris*) in the northern Flint Hills of Kansas. First, we conducted surveys at limestone outcrops in experimental watersheds managed under different burning and grazing practices. Habitat occupancy and lizard abundance were estimated by constructing models that incorporated aspects of the environment at multiple scales. Both abundance and occupancy were higher on rock ledges that had more crevices, greater complexity in vegetation, covered a larger area, and were more prominent than available habitat. Abundance and occupancy were also higher in watersheds that were burned frequently (1–2 year intervals), but grazing only had a significant effect in less frequently burned (four–year burn interval) watersheds. Our second approach was to measure genetic diversity and population genetic differentiation and relate these measures to differences in landscape context. We sampled collared lizard DNA at four locations (sample sites < 45 km apart) and analyzed trends in 10 polymorphic microsatellite loci. We found evidence for low genetic variability and moderate population differentiation among our sample sites relative to estimates reported in the literature at the core of the species' range. Differences in migration rates and ancestry among sampling locations also appear to correspond to differences in landscape resistance based on land cover and rock availability. Thus, it appears that habitat management may influence the suitability of

habitat patches at the local scale, and that differences in land cover and rock availability may influence the connectivity of populations at the landscape scale.

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## Acknowledgements

This thesis was an entirely collaborative work and reflects not only my own efforts, but also the effort and support of many. I would like to thank my advisor, Kimberly With, for her numerous contributions to this thesis and for offering me the opportunity to work in the Laboratory for Landscape and Conservation Ecology. In addition, by sharing her passion for ornithology with me, she has inspired a wonderful new interest. I would also like to thank my committee members, Eva Horne and Samantha Wisely, for their review and support of this thesis. I thank Eva Horne for her project support, for including me in various herping opportunities, and for her friendship over the last three years. I thank Samantha Wisely for seeing potential in my project from the start and allowing me to conduct my genetic research in her Conservation and Molecular Ecology Lab, and for her provision of a lab technician in the fall of 2009. I also thank her for including me in her journal club and in lab activities, and providing me with unique opportunities, including the chance to survey black-footed ferrets in western Kansas.

I thank Page Klug for her contributions to this project, including collection of samples and help with fieldwork, lab work, analyses, and writing. I would also like to thank her for her friendship, from my first summer as her REU student, where I gained an appreciation of the beautiful Midwest and the tallgrass prairie in particular, to our eventful birding and cross-country trips. I thank Jodi Whittier and Adam Skibbe for their technical assistance, particularly working with GIS, as their educational and technical support enabled much of my analysis. I thank Craig Paukert for graciously providing field equipment, and Jennifer Nemeč, who provided several collared lizard samples and assisted me with lab work. I thank Jack Oviatt for

taking the time to teach me Konza geology. I thank members of the Kansas Herpetological Society, Ben Mulhern, and many other volunteers who assisted with sample collection. I thank the staff of the Konza Prairie Biological Station for their on-site assistance. Annie Baker and Valerie Wright kindly contributed to sightings of marked lizards and the inclusion of Konza Prairie Biological Station docents in these efforts. John Harrington, Page Klug, and Tom Prebyl kindly provided access to data layers used in spatial analyses. I thank members of the Conservation and Molecular Ecology Lab, past and present, with whom I have worked for their generous assistance, as well as the many other graduate students and faculty members, too numerous to list here, who have contributed assistance to this project and shared their friendship with me. Finally, I would like to thank my husband, Jimmie, and Beau the dog, for their constant support, friendship, and understanding, and my parents and sister for their constant support and encouragement.

This project was supported by funding from Kimberly With, a graduate teaching assistantship awarded by the Division of Biology at Kansas State University, a grant awarded to Kimberly With, Page Klug, and Samantha Wisely through the Ecological Genomics Institute at Kansas State University, a University Small Research Grant at Kansas State University, the Dean E. Metter Memorial Award provided by the Society for the Study of Amphibians and Reptiles, the Institute for Grassland Studies at Kansas State University, and the Konza Prairie NSF-LTER program. This work was conducted in compliance with Kansas State University IACUC protocol #2297 and Kansas Department of Wildlife and Parks collecting permits SC-078-2008 and SC-045-2009.

## **CHAPTER 1 - Introduction**

Habitat patches and corridors exist in a heterogeneous mosaic that can influence patterns of species' distribution or processes such as dispersal and gene flow through the landscape (Taylor et al 1993; Forman 1995). This "landscape context" may be important for the suitability of habitat patches for focal species, where differences in the surrounding microclimate, food availability, and predation are hypothesized to either decrease or increase patch suitability (Saunders et al 1991; Dunford and Freemark 2004; Sisk et al 1997; Sergio and Newton 2003). Landscape context may also influence the connectivity of habitat patches or landscapes through differences in landscape or matrix resistance, which can have important effects on patch occupancy (Ricketts 2001; Chardon et al 2003; Verbeylen et al 2003) or gene flow (Clark et al 1999; Coulon et al 2006; McRae et al 2008).

Landscape context may thus play an important role in population processes, even though local habitat characteristics appear to be the primary determinant of population distributions (Collinge 2009). The ultimate response of populations to landscape context depends on both a species' characteristics and on the landscape in which it resides or has evolved, and individual species responses to different landscape contexts will likely vary (With et al 1997; With and King 1999; Fahrig 2007; Darvill et al 2010), which may be one reason landscape context does not appear to play a greater role in population processes (Collinge 2009). Because of species' differences in habitat requirements or dispersal ability, some organisms may be more sensitive to natural habitat conversion, fragmentation, or degradation, which are considered the primary threat to species and populations worldwide (Vitousek et al 1997; Millennium Ecosystem Assessment 2005).

Nearly 85% of temperate grasslands has now been lost (70% since 1950; Millennium Ecosystem Assessment 2005). Amidst these broad-scale changes, the Flint Hills ecoregion of Kansas stands out. This region contains the largest contiguous tract of tallgrass prairie (over 2 million ha) remaining in North America (Knapp and Seastedt 1998). Because of its complex topography, where shallow soils with alternating limestone and shale layers form bench-like rock outcroppings along hill slopes (Smith 1991; Oviatt 1998), the Flint Hills region has avoided conversion to row-crop agriculture in favor of cattle ranching, which has developed into an economically important enterprise (With et al 2008). Maintenance of tallgrass prairie habitat is dependent on both climatic factors and disturbance in the form of burning and grazing, which together create a heterogeneous prairie landscape (Anderson 2006; Glenn et al 1992).

Because of their effects on landscape structure, burning and grazing can influence the presence, survival, recruitment, and abundance of species, including plants (Hartnett and Fay 1998; Briggs et al 2002a,b), insects (Joern 2004; Jonas and Joern 2007), mammals (Clark and Kaufman 1990), birds (With et al 2008; Zimmerman 1992), and reptiles (Cavitt 2000; Wilgers and Horne 2006; Wilgers et al 2006). Because much of the Flint Hills landscape is now actively managed for cattle, current land management favors intensive early stocking coupled with annual burning, which together can create homogeneous landscapes dominated by select number of forage species (Fuhlendorf and Engle 2001; With et al 2008). Additionally, certain types of land management, such as infrequent burning or the active planting of trees, have also contributed to shrub encroachment and forest expansion in the region (Briggs et al 2002a,b; Briggs et al 2005). Although most of the Flint Hills tallgrass prairie habitat has remained unplowed, and little exurban expansion has occurred over the majority of the region, land management has the potential to alter landscape context at a regional scale.

The Eastern Collared Lizard (*Crotaphytus collaris collaris*) is a crotaphytid lizard whose range extends into the northern Flint Hills. Much is known about its distribution and phylogeny (McGuire 1996; McGuire et al 2007), ecology (Fitch 1956; Husak and McCoy 2000), behavior (Baird et al 2007; Yedlin and Ferguson 1973; Greenberg 1945; Husak and Fox 2003), and population genetics (Hutchison and Templeton 1999; Hutchison 2003; Yoshioka 1996). It is highly dependent on the presence of rock habitat (Fitch 1956), and the limestone escarpments at upland sites in the Flint Hills provide collared lizards with habitat amidst a tallgrass prairie matrix.

Rock habitat in the region is morphologically diverse, with differences in the amount of bedrock exposure, shape or thickness, or the topographic position along hillsides. Outcrops are generally restricted to upland sites, and thus not uniformly distributed throughout the region (Smith 1991; Oviatt 1998). Additionally, rock habitat has been constructed along lakes or dam faces in the region for bank stabilization, which also provides variability in the distribution and suitability of this resource. Some urban expansion has occurred in the northern Flint Hills, particularly in lowland areas and along the Kansas River (the cities of Manhattan and Junction City). The presence of these urban centers and lowland areas associated with the Kansas River, which do not provide the necessary rock habitat and less open grassland, may limit collared lizard population distribution and gene flow in the area. At the eastern periphery of the collared lizard range in the Missouri Ozarks, forest expansion has decreased the connectivity of rock habitat patches and influenced patch occupancy and gene flow (Templeton et al 2001; Brisson et al 2003).

The major goal of this study was to identify the role of landscape context in structuring collared lizard populations in the Flint Hills landscape at the northern periphery of their range.

Specifically, we took two approaches to evaluate the role of landscape context on collared lizard populations, and these approaches are described in chapters two and three of this thesis. As discussed in Chapter 2, we surveyed rock habitat patches at the Konza Prairie Biological Station in Riley County, Kansas, to identify the relative effects of local habitat characteristics and landscape context (including different burning and grazing regimes) on patch occupancy and species abundance in habitat patches. Occupancy and abundance was modeled using an approach analogous to mark–recapture models, and variables concerning rock habitat, vegetation, hillside, or management treatment were incorporated into the model to identify their importance for determining occupancy and abundance in habitat patches. As discussed in Chapter 3, we evaluated the influence of range position (central versus peripheral populations) and landscape context (rock availability) or connectivity (land cover) on genetic diversity and population genetic differentiation at four sampling locations in the Flint Hills. We specifically assessed how landscape connectivity compares to patterns of gene flow and population genetic differentiation. Also, because landscape context (including topographical complexity, abundance of limestone rock habitat, and matrix composition) differs markedly in the Flint Hills as compared to populations located in Missouri, Oklahoma, and Texas, we discuss how these factors might influence population genetics at a landscape scale. The final chapter of this thesis, Chapter 4, is a summary of our findings and implications for future research.

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## **CHAPTER 2 - Landscape context matters: local vs. landscape effects on abundance and patch occupancy of collared lizards in managed grasslands**

Emilie Blevins and Kimberly A. With

### **Abstract**

Both local habitat and landscape characteristics have the potential to influence species distribution and abundance, and identification of their relative effects is useful for understanding the consequences of land management. Our study examined the influences of local vs. landscape characteristics on habitat occupancy and abundance of the Eastern Collared Lizard (*Crotaphytus collaris collaris*). We conducted surveys at limestone outcrops in experimental watersheds managed under different burning and grazing practices in the Flint Hills of Kansas. Habitat occupancy and lizard abundance were estimated by constructing models that incorporated aspects of the environment at multiple scales. Collared lizard abundance and occupancy was higher on rock ledges that had more crevices, greater complexity in vegetation, covered a larger area, and were higher above slope, than unoccupied habitat. Collared lizard abundance and occupancy was also higher in watersheds that were burned frequently (1–2 year intervals), but grazing only had a significant effect on occupancy and abundance in less frequently burned (four–year burn interval) watersheds. Our results suggest that, in addition to rock habitat, land management practices have the potential to influence collared lizard presence and abundance in the Flint Hills. Our study also highlights the importance of taking a multi–scale approach when modeling species abundance and distribution.

## Introduction

Populations of plants, animals, and other organisms currently must contend within increasingly human–modified landscapes, which has important consequences for the connectivity and suitability of native habitats that, in turn, may influence the patch occupancy, abundance and persistence of species in those habitats (Fahrig 2007; Gibbons et al 2000). Environmental characteristics of both the local habitat patch (e.g., patch quality) and of the surrounding landscape (e.g., the land–use context of the habitat patch) can be important determinants of habitat occupancy and abundance of species (Wiens et al 1993; Thomas et al 2001; Driscoll 2007; Ricketts 2001; Pearson 1993), though the relative importance of patch versus landscape characteristics varies among taxa (Collinge 2009). Additionally, the habitat characteristics affecting occupancy and abundance of a species, as well as the nature of their influence (e.g., positive or negative), may vary across the geographic range of a species (Fielding and Haworth 1995; McAlpine et al 2008; Mateo–Tomas and Olea 2009). For example, Bamford et al (2009) found that models relating nest occurrence of two species of African vultures (*Gyps africanus* and *Aegyptius tracheliotos*) to local habitat and landscape variables were not transferable across regions due to differences in landscape characteristics such as topography and soil, which in turn influenced the type of vegetation available for nesting. Thus, studies of species occupancy patterns should consider landscape context (the broader landscape in which patches are embedded) as well as landscape heterogeneity (the range of habitat types in which the species occurs) (Wiens 1997).

Habitat loss, fragmentation and degradation are the most critical threats to the diversity of amphibians and reptiles (Gardner et al 2007), which are at higher risk of extinction worldwide than either birds or mammals (Vie et al 2009). In particular, studies assessing the influence of alterations to the landscape (i.e., habitat degradation or fragmentation) are needed to identify the

effects of anthropogenic land use or habitat management on amphibians and reptiles (Gardner et al 2007). For lizards, habitat occupancy and abundance may be variously influenced by patch characteristics such as vegetation composition, rock composition or morphology, amount of rock cover, or geographic aspect (Jellinek et al 2004; Fischer et al 2004). Rock-dwelling lizards, for example, select habitat based on features such as rock size, shape, thermal properties or width of crevices (Shah et al 2004; Schlesinger and Shine 1994; Howard and Hailey 1999). Landscape-scale factors, such as the spatial configuration of habitat within the landscape (Mazerolle and Villard 1999) or type of land management, may also influence the presence and abundance of lizards at a local scale (Castellano and Valone 2006; James 2003; Wilgers et al 2006).

The Eastern Collared Lizard (*Crotaphytus collaris collaris*) is an ideal species in which to examine the effects of local versus landscape factors on habitat occupancy and abundance. In the Flint Hills region of Kansas, which contains the largest remaining tracts of tallgrass prairie in North America (Knapp and Seastedt 1998), collared lizards are restricted to limestone outcrops along hillsides. Their patterns of occurrence and abundance are likely influenced by characteristics of their rock habitat as well as of the surrounding tallgrass prairie landscape (Fitch 1956). Along hillsides, several different limestone layers provide outcrops at distinctive topographic positions and display characteristic weathering patterns, providing variation in limestone rock morphology (Smith 1991). These hillsides may also differ in characteristics such as slope, aspect or soil moisture. At the landscape scale, most of the region is managed for cattle production, with widespread grazing and annual burning occurring over much of the Flint Hills (up to 70% of the region is burned in a given year; With et al 2008). Though fire and grazing are important disturbances for the maintenance of tallgrass prairie habitat, current management is applied over shorter intervals and at greater intensities than the historical disturbance regime of

periodic, local fires that permitted “rest–rotational” grazing by native ungulates such as bison (*Bison bison*; Collins and Gibson 1990; Fuhlendorf and Engle 2001). Conversely, fire suppression in some areas of the Flint Hills, especially near urban centers, has promoted woody invasion by species such as Eastern red cedar (*Juniperus virginiana*), which can enhance the establishment of other woody species (Briggs et al 2002a). Because burning and grazing (or lack thereof) have the potential to alter vegetation structure (Gibson and Hulbert 1987; Towne et al 2005), land–management practices could influence patch occupancy and abundance of collared lizards either by altering the suitability of rock habitat (through changes to associated vegetation at rock outcrops) or by affecting dispersal and thus colonization of rock habitat (Brisson et al 2003). Other studies have examined the influence of burning on patch occupancy by collared lizards and found a positive effect (Templeton et al 2001; Brisson et al 2003), but these studies were conducted in rocky glades within the Missouri Ozarks, which is a very different landscape context from the predominantly prairie landscape of the Flint Hills. Our main objectives in this study were thus to (1) model collared lizard occupancy and abundance at a landscape scale, and (2) determine the relative influences of local habitat and landscape variables on the abundance and habitat occupancy of collared lizards in different landscape management contexts.

## Methods

### *Study site*

Our study was conducted over two field seasons (May–July) in 2008 and 2009 at the Konza Prairie Biological Station (KPBS), located 10 km south of Manhattan, Kansas (39°05' N, 96°35' W). This 3,487-ha field station, a member of the National Science Foundation’s Long–Term Ecological Research (NSF–LTER) network, is managed by Kansas State University’s Division of Biology. Vegetation at KPBS primarily consists of native grasses such as big and

little bluestems (*Andropogon gerardii*, *Schizachyrium scoparium*), indiagrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), which can grow over 2 m in height each year. Woody species such as roughleaf dogwood (*Cornus drummondii*) and Eastern red cedar (*Juniperus virginiana*) are also present and locally abundant. Topography is hilly, with both lowland and upland prairie. Most (75%) of the annual precipitation falls during the growing season, and average monthly temperature varies considerably, from  $-2.7$  °C in January to  $26.6$  °C in July (Bark 1987). The KPBS is divided into 55 experimental watersheds that are managed under different grazing and burning regimes. Although some watersheds are managed in a fashion similar to the Flint Hills historical disturbance regime (bison-grazed with a three- to four-year burn frequency), others are more typical of current rangeland management practices in the Flint Hills (burned and grazed annually by either bison or cattle), while still others are long-term unburned sites (both grazed and ungrazed).

## ***Field methods***

### ***Surveys***

We conducted two surveys each season to allow estimation of true detection rate (i.e., the rate at which nondetection of a species is indicative of true absence, MacKenzie et al 2002). Because collared lizards are a rock-dwelling species that establishes and defends territories during the breeding season (April—July), we conducted our surveys by slowly and systematically walking the length of each limestone outcrop on the ridgetops and hillsides. We restricted our surveys to the 16 experimental watersheds known to provide rock habitat (i.e., watersheds that could potentially support collared lizard populations). The watersheds we surveyed included grazed (by bison) and ungrazed treatments subjected to annual, biennial, or four-year burn frequencies (Figure 2.1), and each treatment type had at least two watershed



replicates (Table 2.1). Nearly half of the experimental watersheds that contained suitable collared lizard habitat were either burned annually or grazed ( $7/16 = 44\%$  each). The unique experimental design of the KPBS thus afforded us with the opportunity to assess the influence of different land-management practices on the habitat occupancy and abundance of collared lizards.

For the purposes of estimating habitat occupancy and abundance, we defined habitat patches as individual rock outcroppings that were separated by at least 15 m along a single geological layer, a distance similar to that used for other rock-dwelling lizards (Whitaker 1996). Average length of rock outcrops measured 583 m ( $\pm 41$  SE). We conducted our surveys between 0800 and 1800 during clement weather when lizards were most likely to be visible [i.e., sunny days with temperatures  $> 16$  °C (average =  $30.4$  °C +  $0.11$  SE) and low wind (average =  $1.8$  m/s +  $0.04$  SE),  $n = 122$  days]. Surveys were conducted from mid-May to mid-July and took 67 days to complete in 2008 and 55 in 2009. We recorded the presence (occupancy) and location (UTM coordinates) of all adult or subadult ( $< 71$  mm snout-vent length; Sexton et al 1992) collared lizards on each patch ( $n = 247$ ) using a hand-held GPS unit (Garmin; accuracy  $< 8$  m). We captured and marked adults using a unique color combination of beads affixed to the base of the tail to permit individual identification (Fisher and Muth 1989). We also recorded the date, time of day, temperature of the rock outcrop, ambient temperature, and windspeed during each survey of a patch (rock outcrop) and included these as survey-specific covariates in our models estimating detection probability (described later). We recorded the presence of a marked lizard at an outcrop to account for a potential “trap” effect, in case marked lizards were more (or less) likely to be observed on subsequent surveys, which could bias our occupancy and abundance estimates.

### ***Local vs. landscape habitat measures***

To evaluate which habitat factors influenced collared lizard abundance and the probability that a rock outcrop was occupied, we measured 16 habitat features across a range of scales that encompassed both local and landscape measures (Table 2.2). At the local patch scale, we recorded characteristics of rock outcrops at the exact location where lizards were sighted. We developed an ordinal scale to categorize the relative amount of rock cover, number of refuges, vegetation complexity, and relative height of the rock ledge (Table 2.2), following the approach adopted by Howard and Hailey (1999) for several rock-dwelling lizards. Rock cover indicated the relative amount of rock habitat ranging from only a few scattered rocks (0) to several exposed ledges or large blocks of rock (3). Number of refuges, indicating the relative amount of loose rock around the rock ledge or crevices within the ledge potentially providing refuge, ranged from no refuges (0) to many crevices and/or much loose rock of adequate size for cover (4). Vegetation complexity ranged categorically from grass (1) to shrub patches (2), dense shrub and tree (3), or gallery forest (4). Because collared lizards do not saturate all available habitat, and to increase our ability to predict habitat occupancy and abundance, we measured these same local-scale habitat features at a number of randomly chosen points within seemingly suitable patches (e.g., rock outcrops) where no lizards were ever detected.

At the landscape scale, we characterized the landscape context of each patch in terms of the surrounding habitat composition and topographic characteristics of the hillside for each rock outcrop (i.e., habitat patch). We first digitized the location of individual habitat patches using a contour-line data layer developed from a 2 m digital elevation model (DEM) of the KPBS in ArcGIS version 9.3 (ESRI, Redlands, California, USA) (Figure 2.2). From the DEM, we calculated several variables to quantify hillside characteristics. First, aspect was calculated because of its potential influence on outcrop microclimate, specifically temperature, which can

affect the presence of collared lizards (Fitch 1956). We then calculated topographic wetness, an indicator of soil moisture conditions (xeric–mesic) based on altitude and aspect, using the Landscape Connectivity and Pattern (LCap) metrics toolbox for ArcGIS (Theobald 2007; Beven and Kirkby 1979), because drier habitats are typically preferred by collared lizards (Fitch 1956). Because collared lizards inhabit rugged habitat in the central and southwestern portion of their range (McGuire 1996; Fitch 1956), we also calculated terrain irregularity (roughness) using a surface area/surface ratio method (Jenness 2004; Walters 2007).

To characterize the habitat surrounding each patch (relative amount of grass and woody cover), we used a Quickbird (GeoEye) satellite image of the KPBS that was acquired August 13, 2007 at a spatial resolution of 0.6 m. Using the Environment for Visualizing Images (ENVI) version 4.3 (ITT Visual Information Solutions), we developed a classification map for KPBS at a 2 m resolution composed of two habitat classes: grass and tree/shrub. To characterize landscape context in a biologically relevant manner, we buffered patches at three scales by measuring habitat variables at three different radii around our lizard and random points. These buffers were intended to capture different scales potentially relevant to lizard movement based on our observed movements by marked lizards, corresponding to short movements within an individual lizard's territory (5 m), longer movements within a territory (60 m), and movements among territories (120 m). Within these buffers, we calculated the mean and coefficient of variation of hillside characteristics at each location and then averaged for all points along an outcrop. For the classification layer, we calculated the area of each habitat class and recorded the percentage (percent grass vs. woody cover).

### *Statistical analysis*

Estimation of habitat occupancy and abundance may be subject to detection bias if the probability of detecting a species when it is actually present is  $< 1$  (MacKenzie et al 2002; Royle 2004). For ectotherms, visibility and therefore detection probability are often dependent on variable temporal and environmental conditions such as temperature and humidity (Pough et al 2004). Despite these concerns, many herpetological field studies have not incorporated imperfect detection of species when measuring occupancy or abundance (Mazerolle et al 2007), although more recent publications suggest this trend is changing (Royle and Young 2008; Kery et al 2009; Kacolis et al 2009). Newer modeling methods based on multiple surveys for occupancy and repeat counts for abundance provide a method to account for a detection probability of  $< 1$  and have been used for surveys of many taxa, including lizards (MacKenzie et al 2002; Royle and Nichols 2003; Hood and Dinsmore 2007; Wenger and Freeman 2008; Royle and Young 2008).

We developed and evaluated models of lizard abundance and detection using the Royle repeated-count method (Royle 2004) implemented in the software PRESENCE version 2.4 (MacKenzie et al 2002). To incorporate model uncertainty when estimating probability of detection (parameter  $p$ ), we first constructed a set of 30 models using three different sets of abundance covariates and ten different sets of detection covariates (Table 2.3). The detection covariate(s) present in any candidate model from this set were retained for our final set of abundance models. Prior to inclusion of site-specific variables in models, we conducted correlation analysis using SAS version 9.1 (SAS Institute, Cary, North Carolina) and found no significant correlations ( $-0.7 < r < 0.7$ ) among our habitat variables.

Because rock habitat patches occur within the context of watershed burning and grazing treatments in our system, each model in our set contained a single local or topographic landscape variable in addition to our watershed treatment variables (burn treatment, graze treatment, and

their interaction) and the best detection covariate(s). We included watershed treatment variables because preliminary analysis comparing models with or without their inclusion showed better model fit when watershed treatment variables were included (Appendix A). We also developed three “scale” models, which contained several covariates collected at a single scale (5, 60, or 120m). We constructed three additional models, one with only an additive effect of burning and grazing (no local or topographic variables) on abundance, the second with only the additive and interactive treatment effects on abundance, and the third with no covariates on abundance. Thus, we examined 30 habitat models with a single local or landscape variable plus watershed treatment variables, 3 scale models, and 3 treatment models, totaling 36 candidate models (Appendix B). Variables were *z*-standardized, and models were run using the logit link function and fit using maximum likelihood estimation. We used Akaike Information Criterion adjusted for small sample size ( $AIC_c$ ) and Akaike weight ( $w_i$ ) to determine the best model(s) and indicate the relative support for each model (Burnham and Anderson 2002).

Because we included burn treatment, graze treatment, and their interactive effect in each model, we conducted additional analyses to determine the relative influence of each of these variables on patch occupancy and abundance. We first conducted a multivariate analysis of variance (MANOVA) to identify habitat differences among watersheds under the six treatment types. We also conducted a full-factorial analysis of variance (ANOVA) and a post hoc Tukey’s HSD test on model estimates of abundance from our top model(s) to examine the relative influences of burn and graze treatment. We calculated the total lizard abundance over all 16 watersheds we surveyed by summing the abundance estimates from the model output. Because we also wanted to calculate the number of outcrops occupied in our surveyed watersheds, but some abundance estimates fell between 0 and 1, we calculated occupancy estimates over a range

of values for abundance  $< 1$  (range: 0.5, 0.75, 0.95). Outcrops were considered occupied if abundance estimates were  $\geq$  cutoff values. We compared variables other than watershed treatment that were also present in the top model(s) between occupied and unoccupied outcrops using a student's t-test to identify their influence on patch occupancy, and we conducted chi-square tests of independence to determine the influence of burn or graze treatment on habitat occupancy over the range of cutoff values.

## Results

### *Surveys*

We recorded 501 lizard sightings during two years of study (2008 = 341; 2009 = 160). Of these, 250 (49.9%) were first sightings, 80 (16.0%) were repeat sightings of marked individuals, and 171 (34.1%) were of unmarked lizards. Of our 250 first sightings, 158 (63.2%) were adults and 92 (36.8%) were subadults. We detected collared lizards in the same 11 watersheds (of the 16 we surveyed) in both 2008 and 2009 (Table 2.1). Within these 11 watersheds, the percentage of outcrops on which we detected lizards varied from 6 to 100%, with an average of  $40\% \pm 7\%$  SE ( $n = 196$  outcrops). The majority of our sightings occurred in annually burned, ungrazed treatments (54%,  $n = 501$  sightings). For all 16 watersheds surveyed, we detected lizards at 28% of outcrops (our naïve occupancy estimate uncorrected for detection bias).

### *Model comparison*

Detection probability varied among years and surveys, with detection probability higher in the first year ( $41\% \pm 1\%$  SE) than the second ( $22\% \pm 1\%$  SE), and higher during the first survey of each year (2008:  $44\% \pm 12\%$  SE, 2009:  $25\% \pm 12\%$  SE) than during the second (2008:  $38\% \pm 12\%$  SE, 2009:  $20\% \pm 12\%$  SE). Among our set of 36 abundance models, the 5-m scale model was the only candidate (AIC weight = 1) and included both local habitat characteristics

and watershed treatment type (Table 2.4). Average abundance at outcrops was  $1.39 \pm 0.18$  SE lizards, with a maximum outcrop abundance of 22 and a KPBS total abundance of 346 (95% CI = 315–737). Expected occupancy based on the abundance estimates generated by this model varied according to our cutoff values (0.50: 51%, 0.75: 38%, 0.95: 33%). The model estimates for lizard abundance predicted an abundance  $> 0.5$  at several outcrops in two watersheds where lizards were never observed (N4D and K2A). The average scores for habitat variables present in the top model (Table 2.4) were significantly higher in occupied than unoccupied outcrops for all cutoff values (cutoff: 0.5,  $t_{221} = 16.93$ ,  $p < 0.001$ ; 0.75,  $t_{154} = 17.87$ ,  $p < 0.001$ ; 0.95,  $t_{130} = 17.94$ ,  $p < 0.001$ ), suggesting that they have similar effects on both occupancy and abundance.

Two of the habitat variables important to collared lizards according to our models exhibited significant differences among watersheds. Watersheds that were either burned biennially and ungrazed or burned every four years (grazed or not) had significantly less exposed rock cover ( $F_{5, 241} = 3.86$ ,  $p = 0.002$ ; MANOVA) and fewer refuges ( $F_{5, 241} = 3.15$ ,  $p = 0.009$ ; MANOVA) than other watersheds (Table 2.5). Only burning had a statistically significant effect on the estimated average abundance ( $F_{2, 241} = 4.15$ ,  $p = 0.017$ , ANOVA) or occupancy ( $X^2_{2, 6} = 16.29$ ,  $p < 0.003$ ) of collared lizards (Figure 2.3). Among burn treatments, average abundance of collared lizards was significantly different only between annually and four-year burned watersheds ( $p < 0.05$ , Tukey test). Examination of chi-square adjusted residuals indicated the same for patch occupancy of collared lizards over the full range of cutoffs (adjusted residuals for both annually and four-year burned watersheds  $> |2|$ ). Although neither the ANOVA nor the chi-square test found a significant overall effect of grazing, occupancy (and therefore abundance) differed between four-year burned, grazed and ungrazed watersheds (Figure 2.3). Thus, we also tested for differences in average abundance and occupancy between these two treatments using a

student's t-test (average abundance) and a z-test for proportions (occupancy). Both average abundance ( $t_{48} = 5.96$ ,  $p < 0.001$ ) and occupancy ( $z_{48} = 2.14$ ,  $p < 0.01$ ) were significantly different between the two treatments, indicating an effect of grazing on abundance and occupancy in four-year burned watersheds.

## Discussion

Understanding the effect of spatial pattern on the distribution and abundance of organisms is a major research agenda in landscape ecology (Turner et al 2001). Spatial structure in the distribution of resources or habitat (i.e., patchiness) exists simultaneously across a range of scales, and factors at both patch and landscape scales will likely influence local population sizes and patterns of habitat occupancy, thus contributing to the spatial structure and dynamics of populations at broader spatial scales (i.e., metapopulation dynamics; Wiens 1997; With 2004). However, the relative degree to which local habitat variables and landscape context influence the abundance and distribution of organisms will ultimately vary among species (Collinge 2009). The results of our study suggest that habitat occupancy and abundance of collared lizards was affected both by local patch (rock habitat) characteristics (i.e., number of refuges, rock height, and amount of rock cover) and landscape context (land management). As all members of the genus *Crotaphytus* (except *C. reticulatus*) are dependent upon the presence of rock habitat (McGuire 1996), it is perhaps unsurprising that characteristics of rock outcrops might influence occupancy or abundance of *C. collaris*. Rock habitat characteristics such as rock morphology, rock height, and amount of rock cover are commonly found to be important aspects of the habitat for rock-dwelling lizards (Whitaker 1996; Ruby 1986). Refuges are an especially important habitat feature for collared lizards, because they provide protection from predators and serve as hibernacula (Fitch 1956). Ledges higher above the hillslope or with greater rock cover are also



important features of the local habitat patch, which might provide greater variability in substrate temperatures and therefore more opportunities for thermoregulatory control (Angert et al 2002).

Vegetation within the immediate (5 m) vicinity of rock habitat also appeared to positively influence collared lizards, where more complex vegetation structure, such as from shrubs or trees, increased likelihood of patch occupancy and the average abundance of collared lizards. In open grassland, the presence of limited tree or shrub cover at rock outcrops may provide thermoregulatory benefits (shade cover) or protection from aerial predators (Fitch 1956; Wilgers and Horne 2007). In comparison, collared lizard populations in the Missouri Ozark glade habitat occur within relatively small rocky glades, some of which are surrounded by forest, and are negatively impacted by tree cover or thick understory vegetation (Brisson et al 2003; Templeton et al 2001). However, our measure of vegetation complexity (i.e., grassy vs. woody cover) accounts for the presence but not density of vegetation at rock outcrops. In fact, we found no correlation between watershed burn treatment (frequency of fire) and our measure of vegetation complexity at rock outcrops because the rock outcrops appear to afford the associated vegetation some protection from fire (Weisberg et al 2008).

In addition to habitat patch characteristics, landscape context also appears to influence patch occupancy and abundance. We found a positive effect of burning, although the effect was significant only between annually burned and four-year burned watersheds. Although two habitat patch characteristics in the top model—number of refuges and amount of rock cover—were also significantly different among watersheds under different burning or grazing treatments (Table 2.5), this may also have been a result of watershed treatment. Dense vegetation or litter not removed by fire or grazing likely obscured rock habitat and reduced our ability to assay these variables. Indeed, we assessed less rock cover and fewer refuges in watersheds that were less

frequently burned or ungrazed. However, collared lizards are unlikely to use ledges covered by litter or dense vegetation because they require open rock habitat for basking (Fitch 1956), and thus our measure of refuge number and amount of rock cover likely coincides with the perception of such outcrops by collared lizards. Grazing also appears to have a positive effect on the likelihood of patch occupancy and average collared lizard abundance for four-year burned, grazed watersheds relative to four-year burned, ungrazed watersheds. The proportion of bare ground is greater in grazed than in ungrazed watersheds, regardless of whether such watersheds are burned frequently (annual or biennial intervals) or infrequently (four- or twenty-year intervals) (Vinton et al 1993), and bare ground is known to increase the abundance of xerically adapted lizards (Mushinsky 1985), by potentially improving the suitability of habitat for lizards (Hellgren et al 2010). Jones (1981) found that sit-and-wait foraging lizards (like the collared lizard) had a significantly higher abundance in desert grassland and other vegetation communities when land was heavily grazed rather than lightly grazed by cattle, due to changes in vegetation structure.

While many studies have noted that intense grazing may have a negative impact on lizard abundance, survival, richness, or community composition (James 2003; Hellgren et al 2010; Jones 1981; Castellano and Valone 2006), bison graze at a moderate intensity at KPBS, with a smaller herd size grazing year round, than many cattle ranches within the region (Towne et al 2005; Hartnett et al 1996). At our site, bison may be creating patches of higher quality vegetation either through grazing or structural disturbance in four-year burned, grazed watersheds relative to their ungrazed counterparts. Furthermore, structural heterogeneity in vegetation produced by grazing (though not burning) directly influences grasshopper densities, which may be more than twice as high in grazed watersheds compared to ungrazed (Joern 2004). With a higher density of

prey, four-year burned, grazed watersheds might be able to support collared lizards while four-year burned, ungrazed watersheds could not.

Although habitat occupancy in different landscape contexts is often attributed to differential movement through the matrix or other landscape elements (Collinge 2009), we believe that land management is instead influencing occupancy and abundance of collared lizards through variation in habitat suitability. We were not able to compare movement frequency or dispersal distance for marked lizards among different watershed treatment types because we observed so few dispersal or long-distance movements (100% of recorded movements  $\leq 1,000$  m, 74%  $\leq 100$  m; unpubl. data). However, we can provide some anecdotal evidence that the absence of collared lizards in four-year burned, ungrazed treatments was apparently not due to dispersal limitation. Collared lizards were frequently observed in an annually burned, grazed watershed (N1A) at a rock ledge in close proximity ( $\sim 10$  m) to rock habitat in an adjacent four-year burned, ungrazed watershed (K4A). A gravel road also ran between both watersheds, and as we have observed collared lizards on these roads, we speculate that they are able to use them as dispersal corridors to move among watersheds. These observations, though anecdotal, suggest that collared lizards have access to rock habitat in four-year burned, ungrazed watersheds, and thus their absence from these watersheds is due less to dispersal limitation than to a lack of suitable habitat (e.g., rock ledges were covered by dense vegetation in these watersheds).

Limestone rock outcrops in the Flint Hills represent relatively static habitat for collared lizards. However, the landscape in which this habitat occurs is now subject to extensive human modification that has shifted the historical grazing and fire regime to the extremes, resulting in either complete fire suppression and no grazing around urban centers, or annual burning and uniform grazing throughout much of the Flint Hills (Fuhlendorf and Engle 2001; With et al

2008). Although rock features at the local habitat scale were important, landscape context—created by different management practices—was also a major factor affecting the abundance of collared lizards. Despite the positive effect of frequent fire (annual burns) on the occurrence and abundance of collared lizards at the KPBS, we note that both burning and grazing now occur with greater intensity throughout much of the Flint Hills, which is managed predominantly for cattle. Thus, it is unclear whether current management practices involving intensive cattle grazing and annual burning would be as beneficial to collared lizard populations elsewhere in the Flint Hills. Although additional work is necessary to identify the exact mechanisms by which grazing and burning influence collared lizards, our results highlight the importance of examining both local habitat characteristics and the landscape context in which these patches are embedded when examining the effects of spatial pattern on the abundance and habitat occupancy of a species.

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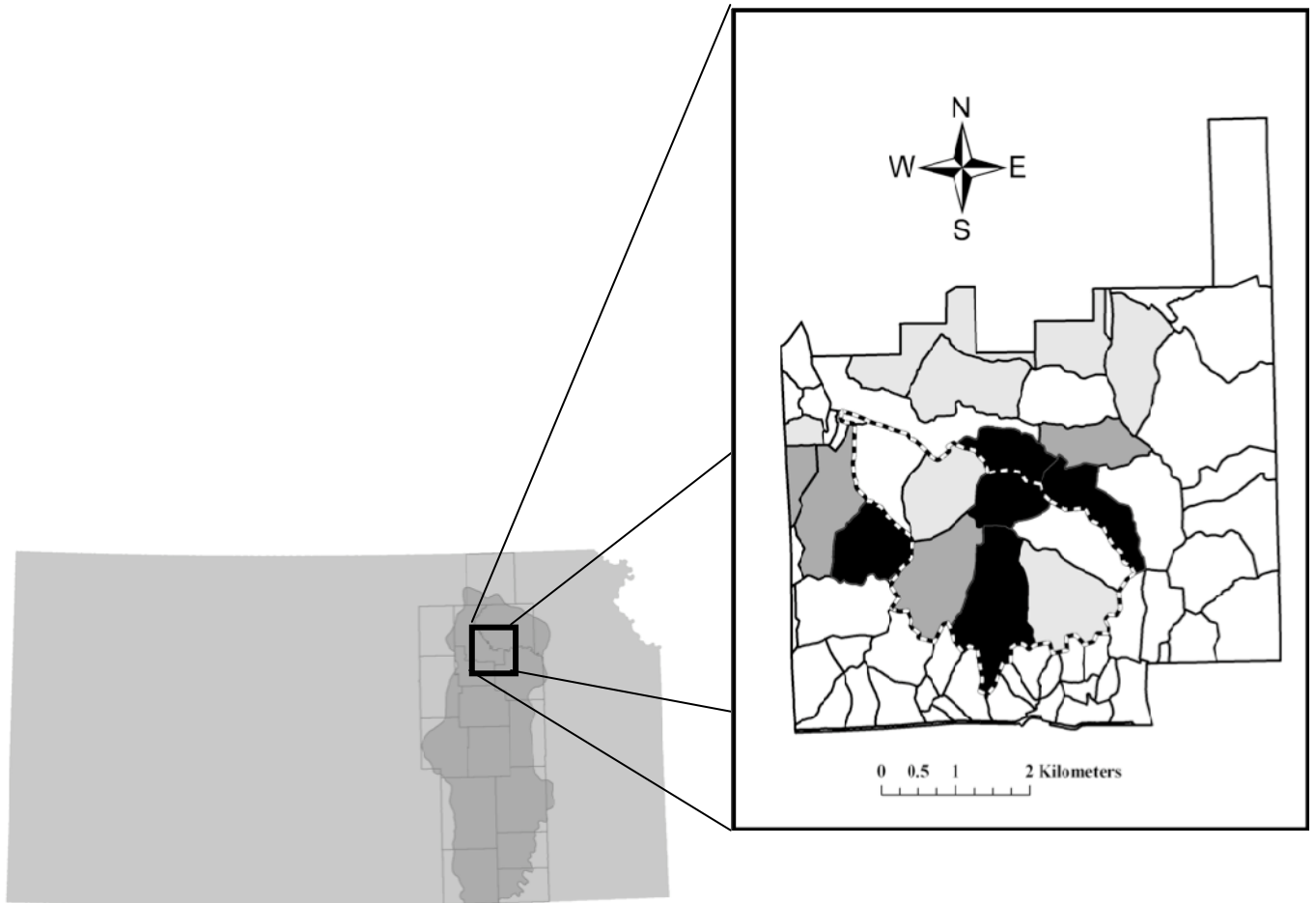
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## Figures and Tables



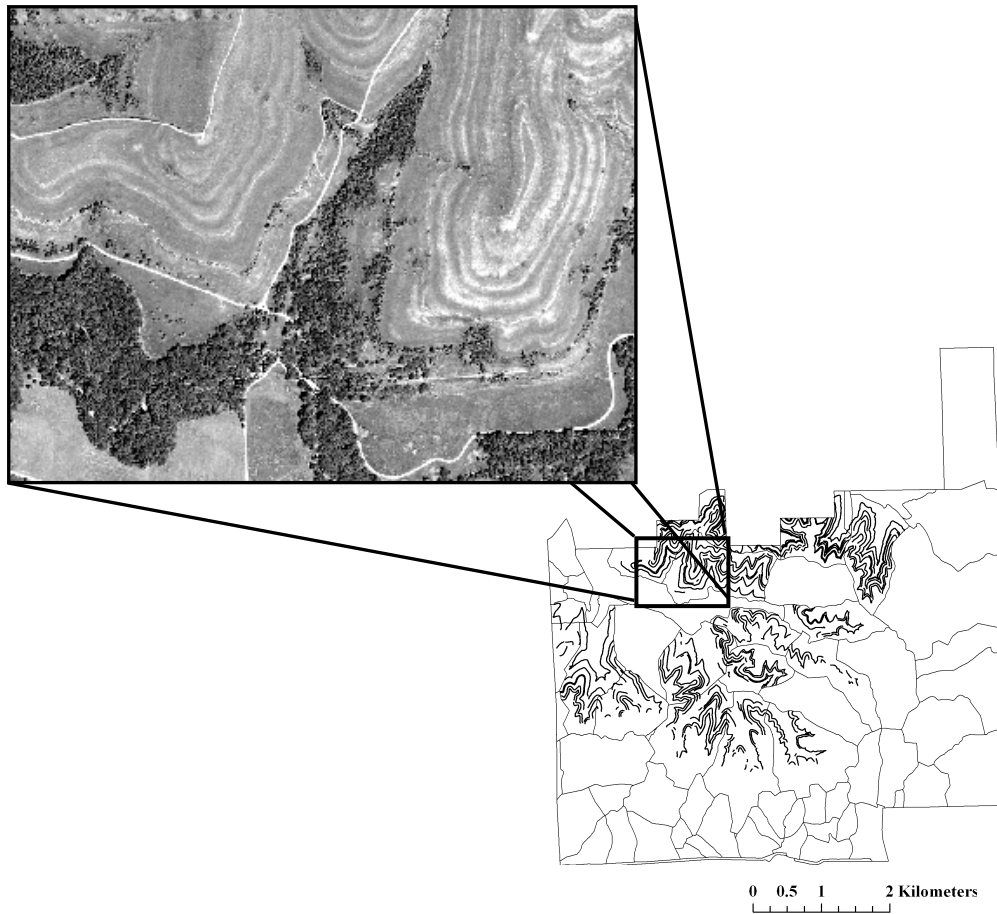
**Figure 2.1** Map of study site in the Flint Hills of Kansas (darker gray in left image of the state of Kansas). Inset: rock outcrops were surveyed for collared lizards in experimental watersheds (shaded polygons) at the Konza Prairie Biological Station in Riley County, Kansas. Watersheds under different burn treatments are indicated by intensity of shading (light gray = annual, dark gray = biennial, black = four-year). Watersheds enclosed by the fence (dashed line) are grazed by bison.

**Table 2.1 Number of watersheds with suitable collared lizard habitat versus those where collared lizards were actually detected (parentheses) within different management treatments at the Konza Prairie Biological Station in the northern Flint Hills of Kansas.**

Grazing Treatment	Burning Interval (years)		
	One	Two	Four
Grazed	2 (2)	2 (2)	3 (2)
Ungrazed	5 (5)	2 (0)	2 (0)

**Table 2.2 Local habitat and landscape variables (abbreviation in parentheses) assayed at rock outcrops for modeling habitat occupancy and abundance of collared lizards at the Konza Prairie Biological Station, Kansas. Asterisk indicates variable measured at three scales: 5, 60, and 120m.**

Variable	Variable Type	Abbreviation	Description
Burn treatment	Categorical	burn	Watershed burn treatment (1, 2 or 4-year burn frequency)
Graze treatment	Categorical	graze	Watershed grazing treatment (grazed vs. ungrazed)
Roughness	Continuous*	rough	Measure of topographic change (ruggedness)
Roughness CV	Continuous*	roughcv	Coefficient of variation in roughness measure
Wetness	Continuous*	wet	Soil moisture, derived from a topographic wetness index, indicating whether outcrop is generally xeric or mesic
Wetness CV	Continuous*	wetcv	Coefficient of variation in wetness measure
Aspect	Continuous*	asp	Converted to aspect value (AV) to indicate relative degrees northeast and southwest
Aspect CV	Continuous*	aspcv	Coefficient of variation in aspect
Shrub (%)	Continuous*	pershrub	Percentage of shrub habitat
Vegetation complexity	Categorical	vegcat	Presence of grass, shrub, or tree cover
Vegetation complexity	Ordinal	vegindex	Relative amount of grass, shrub, or tree cover (1-4)
Geology	Categorical	geology	Geologic layer where outcrop occurs (6 types of limestone layers)
Number of refuges	Ordinal	refs	Relative number of rocks or crevices large enough for lizard cover (based on minimum snout-vent length) (0-4)
Relative ledge height above slope	Ordinal	height	Relative height of rock ledge above the slope (1-3)
Perch diameter (cm)	Continuous	perch	Diameter of actual (lizard) or potential (randomly selected) perching rocks
Rock cover	Ordinal	rock	Relative amount of exposed rock (uncovered by soil; 0-3)



**Figure 2.2 Limestone rock outcrops (n = 247) were surveyed for collared lizards in 16 watersheds at Konza Prairie Biological Station. Outcrops were considered distinct if they occurred within different geologic layers and/or were separated by at least 15 m.**

**Table 2.3 Covariates used in models for determining factors affecting detection of collared lizards for modeling of habitat occupancy and abundance at the Konza Prairie Biological Station, Kansas. Each model included one of three sets of abundance covariates, with only the detection covariate changing. Abundance variables include rough5, wet60, and refs (cf. Table 2.2).**

Detection Variable	Variable Type	Description
constant	None	No detection variable applied. Detection assumed constant
date	Continuous	Date of each survey modeled as Julian day
rock temp	Continuous	Temperature of rock outcrop (°C) measured using infrared thermometer during each survey
air temp	Continuous	Ambient temperature (°) measured over ten seconds during each survey
wind	Continuous	Average windspeed (m/s) measured over ten seconds during each survey
year	Categorical	Year of survey (2008 or 2009)
survey	Categorical	First or second survey of each year
mark	Categorical	Presence of a marked lizard at the rock outcrop
trap	Categorical	Rock outcrop where lizards have been previously sighted
weather (rock, air, and wind)	Continuous	Additive combination of variables describing overall weather conditions during surveys

**Table 2.4 Top model results for habitat and landscape variables affecting collared lizard abundance in managed tallgrass prairie, which included both watershed treatments (grazing and burning) and habitat variables measured within 5m of rock outcrops.**

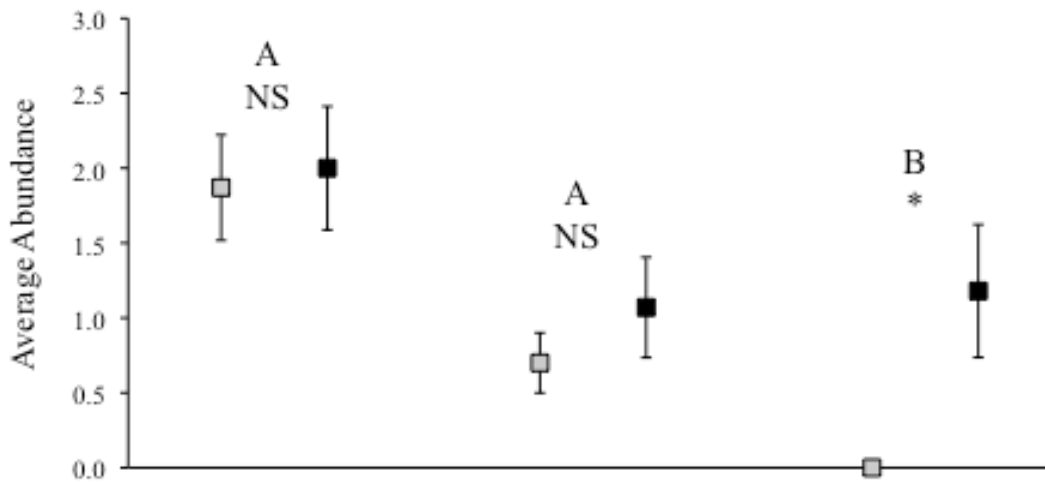
Variable	refs	height	rock	vegindex	burn	graze	burn*graze
$\beta$	0.66	0.45	0.18	0.11	32.68	32.54	-32.72
SE	-0.07	-0.06	-0.08	-0.06	-0.20	-0.16	-0.29



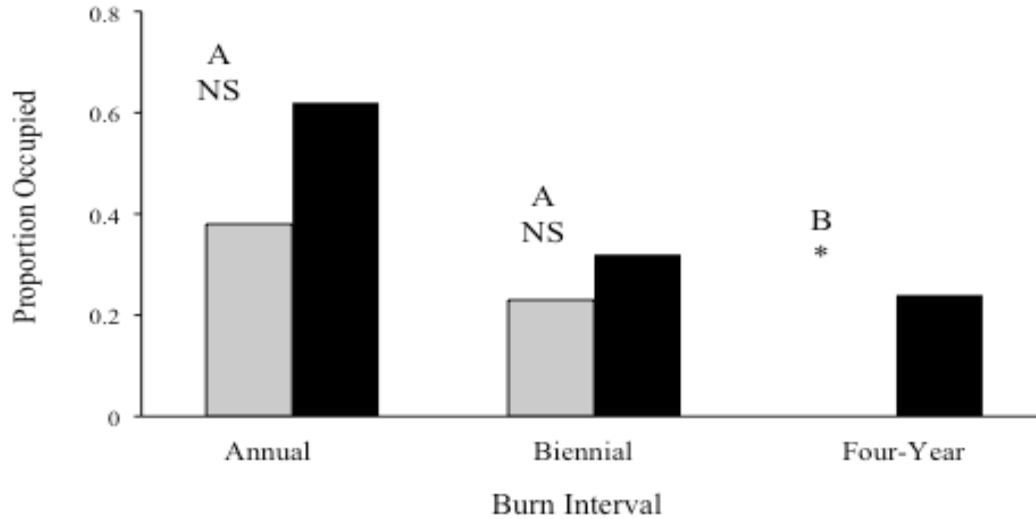
**Table 2.5 Average scores ( $\pm$  SE) for the amount of rock cover and number of refuges within management treatments at the Konza Prairie by experimental watershed type. Different letters following values under each heading (amount of rock cover or number of refuges) indicate significant differences ( $p < 0.05$ , MANOVA) across both columns and rows.**

Grazing Treatment	Burning Interval (years)		
	One	Two	Four
Amount of rock cover			
Grazed	1.5 $\pm$ 0.2 A	1.1 $\pm$ 0.3 A	1.0 $\pm$ 0.5 B
Ungrazed	1.2 $\pm$ 0.4 A	1.0 $\pm$ 0.3 B	1.0 $\pm$ 0.3 B
Number of refuges			
Grazed	1.8 $\pm$ 0.8 A	1.3 $\pm$ 0.9 A	1.1 $\pm$ 0.5 B
Ungrazed	1.3 $\pm$ 1.0 A	1.1 $\pm$ 1.1 B	0.7 $\pm$ 0.2 B

A



B



**Figure 2.3 Average abundance (A) and proportion of rock outcrops occupied (B) by collared lizards in managed tallgrass prairie as a function of burn interval and graze treatment, based on model estimates. For (B), results were comparable for all cutoff values, and we only present estimates for cutoff = 0.95 for simplicity. Light gray indicates ungrazed watersheds; black indicates grazed watersheds. Different letters indicate significant differences ( $p < 0.05$ ) for abundance (Tukey test) and occupancy (chi-square test) based on differences in burn interval. Asterisks indicate significant differences ( $p < 0.05$ ) for abundance (Student's  $t$ -test) and occupancy ( $Z$ -test) within burn treatments based on grazing treatment.**

# **CHAPTER 3 - Genetic variability and population differentiation in northern peripheral populations of the Eastern collared lizard (*Crotaphytus collaris collaris*) as a result of historical processes and landscape context**

Emilie Blevins – Samantha M. Wisely – Kimberly A. With

## **Abstract**

Populations at the periphery of a species range are expected to show reduced genetic variability within populations and increased genetic differentiation among populations compared to those at the core. However, these population characteristics may be a product of both historical processes, such as founder effects or population expansion, and the influence of landscape context on gene flow. Eastern Collared Lizards (*Crotaphytus collaris collaris*) were sampled at four locations in the northern Flint Hills of Kansas to determine the genetic variability and extent of genetic differentiation at the northern edge of their range using 10 microsatellite loci ( $n = 229$ ). We found evidence for low genetic variability (average allelic richness =  $3.37 \pm 0.23$  SE; average heterozygosity =  $0.54 \pm 0.05$  SE) and moderate population differentiation (average  $F_{ST} = 0.08 \pm 0.01$  SE) among our sample sites relative to estimates reported in the literature at the core of the species' range in Texas. We also identified differences in migration rates and ancestry among sampling locations that corresponded to differences in landscape resistance based on land cover and rock availability, which have the potential to fragment populations. Still, our results indicate the potential for heightened gene flow in the Flint Hills region, due to land cover (tallgrass prairie) that is more conducive to dispersal relative to the forested cover that has isolated collared lizard populations at the eastern periphery of their

range. Our findings signify the importance of considering landscape context when evaluating core–peripheral trends in genetic diversity and population differentiation.

## **Introduction**

Populations at the periphery of a species' range are thought to be less abundant than at the core of their range (Whittaker 1956; Hengeveld and Haeck 1982; Brown 1984). One explanation for this pattern is that populations at the periphery experience more extreme conditions, for which the species is less adapted, than do central populations (Brown 1984). The trend of decreasing abundance from the core to the periphery of a species' range may be a useful concept for many species (Brown et al 1995; but see Sagarin and Gaines 2002), especially for those with a large distribution (Murphy et al 2006). Peripheral populations are predicted to have smaller population sizes, lower levels of gene flow, reduced genetic diversity, and higher genetic differentiation than populations at the core of a species' range because of drift, selection, and founder effects (Nei et al 1975; Bush 1975; Lesica and Allendorf 1995; Eckert et al 2008; Ibrahim et al 1996; Ramakrishnan et al 2010).

A population's location at the core versus the periphery of the range is unlikely to fully account for population structure, however. Local landscape structure can have a major effect on genetic diversity and gene flow (Storfer et al 2007). Factors such as habitat fragmentation or the presence of barriers to dispersal can limit gene flow among local populations and increase population differentiation (Keyghobadi et al 2005; Cegelski et al 2003; Templeton et al 1990; Spear et al 2005). Many studies have identified characteristics of the landscape that can alter dispersal pathways and influence gene flow, which often provide better measures of connectivity than simple isolation by distance measures (Epps et al 2007; McRae 2006; Coulon et al 2006; Arnaud 2003). Incorporation of spatially explicit connectivity estimates among populations may

thus help to determine the relative effects of regional vs. local landscape factors influencing populations.

The Eastern Collared Lizard (*Crotaphytus collaris collaris*) is a useful species for making comparisons of population genetic structure between core and peripheral populations and connecting these patterns to differences in landscape characteristics (Hutchison 2003). Their distribution extends broadly throughout North America, from northern Mexico to northern Kansas and from Arizona east to Missouri. Populations within the range are subject to considerable variation in climate, rock habitat, and matrix (vegetative) cover, all of which are factors that affect the abundance and distribution of collared lizards (Fitch 1956; McGuire et al 2007; Templeton et al 2001; Chapter 2). Characteristics of collared lizard populations have been examined intensively at the northeastern edge of their range in the Missouri Ozarks, where recent (since ~1950) habitat fragmentation is likely responsible for reduced population growth rates, reduced body size, decreased seasonal activity, and decreased duration of the breeding season as compared to central populations (Sexton et al 1992). In addition, Hutchison (2003) compared central populations of collared lizards to peripheral Missouri populations and concluded that Missouri populations appear to represent “evolutionary dead ends,” given their dramatically reduced genetic variability as well as their high risk of extinction. Although Hutchison and Templeton (1999) examined genetic diversity in collared lizard populations across their range (including Kansas), they explored only the relationship between pairwise genetic ( $F_{ST}$ ) and geographic distances to identify the relative influences of gene flow and drift. A lack of sampling sites < 45 km apart precluded their ability to quantify local population genetic structure at a landscape scale, although local landscape characteristics may potentially have a great effect on gene flow and population differentiation.

Our aim was to provide a more comprehensive examination of genetic diversity and local population genetic structure at a landscape scale (sampling locations < 45 km apart) in the northern Flint Hills of Kansas, a region that contains the largest contiguous tallgrass prairie landscape remaining in North America. The characteristic limestone escarpments of the Flint Hills in Kansas may provide “dispersal avenues” for collared lizards that have been conducive to gene flow among populations in the region (Hutchison and Templeton 1999), potentially limiting the applicability of the core–peripheral model to collared lizard population genetics. However, populations of collared lizards in the Flint Hills are at the northern periphery of the collared lizard range, where there is little potential for northern expansion given a lack of suitable rock habitat north of the Flint Hills, even if climatic conditions were to become more amenable to collared lizards in the future owing to climate change. Rock habitat is patchily distributed within the Flint Hills landscape, and because collared lizards exhibit reduced seasonal activity length in the Flint Hills relative to more southern Mexico populations (Sexton et al 1992), populations appear to be less well adapted to the northern climate. Our two objectives, then, were (1) to quantify genetic diversity and variation within and among sampling locations to describe local population genetic structure of collared lizards in the northern Flint Hills (i.e., at the northern periphery of this species’ range), and (2) to quantify dispersal within and among sites with respect to landscape characteristics to assess the potential for gene flow. We consider our results within the context of core–peripheral population genetic trends, and discuss the potential for the regional differences in peripheral population genetic diversity and structure, particularly in light of differences in landscape context.

## Methods

### *Study sites*

Our study populations of collared lizards were located in the Flint Hills ecoregion of Kansas. Collared lizards have experienced multiple range expansions and contractions over the last several thousand years and have expanded into their current distribution in northern Kansas only in the last 7,000 years (McGuire et al 2007; Hutchison and Templeton 1999; Hutchison et al 1999); we therefore assume that any current genetic diversity or population genetic structure is a result of processes occurring since invasion. We collected DNA from lizards ( $n = 229$ ) at four locations (pair-wise distances between sites ranged from 10 to 35 km) to look at patterns of local genetic structure. Locations were: the Konza Prairie Biological Station (Konza Prairie) in Riley Co.; the Fort Riley Military Reservation (Fort Riley) in Riley Co.; Milford Dam in Geary Co.; and Tuttle Creek Dam in Riley/Pottawotamie Cos. (Figure 3.1).

Konza Prairie is a 3,487-ha tallgrass prairie site managed by Kansas State University's Division of Biology. Rock habitat occurs as limestone ledges outcropping along hillsides under different bison/cattle grazing and burning regimes. Konza Prairie is separated from our other sampling sites to the north by the Kansas River and some urban development including the cities of Manhattan and Junction City and the Fort Riley Army Post. Our other sites (Fort Riley, Milford Dam, and Tuttle Creek Dam) were sampled less intensively. Fort Riley is an active military site with over 28,000 ha of tallgrass prairie and gallery forest. Lizards were sampled at several locations across the site. Milford and Tuttle Creek Dams were both constructed and are managed by the U. S. Army Corps of Engineers. Construction began at Milford Dam in 1962 and at Tuttle Creek Dam in 1952. Although some natural rock ledges occur at both sites, lizards were sampled at riprap along the eastern side of Milford dam (~2 km in length) and within the

spillway and at riprap along the eastern lake edge at Tuttle Creek Dam. Upland habitat mainly separates Milford Dam from Fort Riley, while Tuttle Creek Dam is separated from Fort Riley and Milford Dam by Tuttle Creek Lake and the city of Manhattan, Kansas.

We captured individual lizards from May–August in 2008 and 2009 ( $n = 229$ ) by hand (noosing) and recorded the location (UTM coordinates), sex (adults are sexually dimorphic, with males being more brightly colored and 10–15 mm larger than females at maturity; Yedlin and Ferguson 1973, Fitch 1956), and age based on size classes (juveniles  $< 80$  mm; Sexton et al 1992) when possible. Tail tips (up to 1 cm) for DNA extraction were clipped from each lizard and stored in tubes containing DryRite for dehydration (IACUC protocol #2297). Four samples from Konza Prairie came from frozen tissue of lizards believed to have died of natural causes. The majority of our samples (77%) came from collared lizards located at Konza Prairie (adults,  $n = 113$ ; juveniles,  $n = 64$ ), with fewer from Fort Riley (adults,  $n = 14$ ; juveniles,  $n = 0$ ), Milford Dam (adults,  $n = 14$ ; juveniles,  $n = 3$ ), and Tuttle Creek Dam (adults,  $n = 20$ ; juveniles,  $n = 1$ ).

### ***Molecular methods***

We used polymorphic microsatellite markers to examine genetic diversity and population differentiation since the most recent collared lizard range expansion, because microsatellites provide relatively contemporary estimates of genetic diversity and differentiation (Selkoe and Toonen 2006). We used 10 previously published microsatellite primers specific to collared lizards: Orig6, Orig7, Orig11, Orig21, Orig 24, Orig25, Orig26, Enr3, Enr48, and N5 (Hutchison et al 2004). Loci were motifs of 2–4 nucleotide repeats with a minimum of 6 consecutive repeats. We isolated DNA from tail tips ( $< 0.5$  cm) by first immersing tail tissue in liquid nitrogen and then crushing it using a mortar and pestle and used standard proteinase K–phenol–chloroform extraction methods (Sambrook et al 1989). We amplified DNA using polymerase chain reaction



(PCR) performed in a total volume of 20  $\mu\text{L}$  containing 3  $\mu\text{L}$  of DNA, 1 U of recombinant Taq DNA polymerase, 0.20-0.25 mM dNTPs, 0.1-1.0  $\mu\text{g}/\mu\text{l}$  BSA, 0.25-0.55  $\mu\text{M}$  of each primer, 0.8-1.2 M betaine, and 2-4.5 mM  $\text{MgCl}_2$ . We added an additional 0.2-0.6  $\mu\text{M}$  of a fluorescent universal M-13 labeled primer complementary to a 5' label for the forward primer. Thermocycler profiles for all loci included a denaturation step (5 minutes, 94°C), 30 cycles of 94°C (30 seconds)/annealing temperature (45 seconds)/72°C (45 seconds), followed by 10 cycles of 94°C (30 seconds)/53°C (45 seconds)/72°C (45 seconds), ending with a 30 minute extension at 72°C. The exception to this was Orig21, for which we used the touchdown method recommended by Hutchison et al (2004). Annealing temperatures were as published in Hutchison et al (2004), with the exception of Orig7 (58.8°C) and Orig25 (54°C). We visualized products using a 3730 DNA Analyzer (Applied Biosystems). Genotypes were manually scored using GeneMarker version 1.8 (Softgenetics). Samples that failed to amplify or were ambiguous were repeated, either by PCR or DNA extraction.

### ***Statistical methods***

Because genotyping errors have the potential to bias final conclusions (Bonin et al 2004), we calculated the average per locus allelic dropout (ADO) rate (Broquet and Petit 2004). We checked our data set for errors in genotyping caused by null alleles, stuttering, and large allele dropout using the software MICROCHECKER version 2.2.3 (Van Oosterhout et al 2004). For each sampling location, we also tested for departure from Hardy–Weinberg equilibrium, calculating  $F_{IS}$  according to Weir and Cockerham (1984), and for genotypic linkage disequilibrium for each locus pair using Fisher's method (Markov chain with parameters set to default values) within GENEPOP on the web (<http://genepop.curtin.edu.au/>; Raymond and Rousset 1995). Genetic diversity was also assessed for each sample site by calculating several

diversity measures. Allelic richness was calculated using a rarefaction method accounting for differences in sample size implemented in F-STAT (Goudet 1995), and the effective number of alleles ( $n_e$ ) was calculated according to the method of Kimura and Crow (1964), where  $n_e = 1 / [\sum(x_i)^2]$ . Observed and expected heterozygosity was calculated using GENEPOP. Relatedness ( $r$ ) of individuals within each sampling location was calculated using maximum likelihood estimation implemented in the software ML-RELATE (Kalinowski et al 2006). Because reduced genetic diversity might be the result of a recent (within the last few dozen generations; Luikart et al 1998) population bottleneck (Nei et al 1975), independent of the location of a population within a species' range (core vs. periphery), we determined whether samples exhibited heterozygote excess relative to allelic richness as an indicator of a recent population bottleneck (Cornuet and Luikart 1996). We used the two-phase mutation (TPM) model available in the software BOTTLENECK version 1.2.02 (Cornuet and Luikart 1996) and assessed significance using a one-tailed Wilcoxon test. Additionally, we explicitly tested for evidence of population expansion by analyzing the distribution of allele lengths using a within-locus and an interlocus test (Reich and Goldstein 1998; Reich et al 1999) conducted using the Excel macro Kgtests (Bilgin 2007).

To identify whether high levels of genetic differentiation exist among sample sites as hypothesized for peripheral populations, we assessed genetic population structure by calculating  $F_{ST}$  (Wright 1951) for all sampling locations and conducting significance testing using F-STAT. To determine if the trends in genetic variation among samples could be partitioned along axes that also describe sampling location, we conducted a principal coordinates analysis (PCA) using the software GENALEX version 6.2 (Peakall and Smouse 2005). We also conducted an analysis of molecular variance (AMOVA) to determine the distribution of molecular variation within and

among sampling locations (Excoffier et al 1992) using this program.

Because rock habitat that likely supports collared lizards also occurs between sampling locations and may promote continuous gene flow, we assigned individuals to populations based on their multilocus genotypes using the Bayesian clustering technique implemented in program STRUCTURE version 2.1.3 (Pritchard et al 2000). Distances between sampling locations likely exceeded lizard maximum dispersal distance (345 m, Hranitz and Baird 2000; 1,000 m, pers. obs.) and we therefore used the ‘no–admixture’ model. For each value of K from one to four (for each of our sample sites), we performed 30 independent runs with 100,000 iterations and a burn–in of 100,000. The number of populations considered as the best fit to our data set was determined by the K value with the highest average log probability [ $\Pr(X|K)$ ] over the thirty runs and by examination of bar plots for predicted ancestry of samples.

To examine whether estimates of migration and dispersal correspond to our estimates of population differentiation, we quantified dispersal both among and within our sampling locations. To quantify dispersal among sampling locations, we calculated pairwise migration rates ( $m_i$ ) and  $\Theta = 4N\mu$  using the coalescent approach available in program MIGRATE–N (Beerli and Felsenstein 2001). We first used  $F_{ST}$  values to calculate  $m_i$  and  $\Theta$  using the Brownian motion method. Model–estimated values were used as starting values for three additional runs to obtain reliable parameter estimates. Parameter estimates were determined using the full migration model and default values for search parameters. We used maximum likelihood estimation, and results for the final three models were equivalent.

Because gene flow and population genetic differentiation may be influenced by landscape features, we analyzed and compared the connectivity of the four populations to patterns of gene flow and population genetic differentiation. We tested for isolation by distance (Wright 1943) by

comparing pairwise genetic ( $F_{ST} / 1 - F_{ST}$ ) with log-geographic (Euclidean) distance matrices and conducting 1,000 permutations using Mantel's test (Mantel 1967) in GENETPOP. We also compared genetic and landscape resistance (McRae 2006) distances to identify the influence of land cover configuration and rock habitat availability on population connectivity among our four sampled populations. Landscape resistance is a measure of the amount of "flow" occurring between locations within a landscape and relies on user-defined resistance values for different land-cover classes or landscape elements for focal species to predict the likelihood of movement through these elements (McRae 2006). To measure the influence of land-cover on connectivity, we used a 30-m resolution land cover map of Geary, Riley, and Pottawatomie counties based on Landsat 5 (2009) data, classified according to urban, agricultural, forest, water, and grass land cover classes (T. Prebyl and J. Harrington, unpubl. data). We reclassified the map to a 100-m resolution (due to computing constraints) and calculated resistance values to test the hypothesis that urban development, forest cover, and bodies of water such as the Tuttle Creek Lake impoundment have increased population isolation in the northern Flint Hills. Urban, forest, and water land cover classes were assigned the maximum resistance value (1,000) and all other classes were assigned a value of 1. To measure the influence of rock habitat availability on connectivity, which often occurs as thin (~5 m wide) benches ringing hillsides not captured by a 100-m resolution land cover map, we used elevation as a proxy for availability of rock habitat, where higher elevations are indicative of hillsides that potentially provide rock habitat while lower elevations are associated with drainages between hillsides or river/creek bottoms and were not considered habitat (Oviatt 1998). We reclassified a 30-m resolution digital elevation map for the state of Kansas (Gesch et al 2002) to a 100-m resolution. The lowest elevation at which collared lizards were observed at the Konza Prairie (Beattie limestone rock layer; 340 m above

sea level) was used as our resistance cutoff (elevation < 340, resistance value = 1,000; elevation > 340, resistance value = 1). We used CIRCUITSCAPE version 3.5 (McRae 2006), which utilizes graph theory to estimate conductance and resistance of network pathways and calculate resistance distances among sampled populations. We conducted 1,000 permutations on pairwise genetic ( $F_{ST}/1 - F_{ST}$ ) and log-resistance distance matrices using Mantel's test in GENETPOP.

To calculate dispersal occurring at the finest scale, within a sampling location, we performed global spatial autocorrelation analyses on samples from Konza Prairie, as this was the only sample site for which we had georeferenced locations for individuals. We first calculated pairwise geographic and genetic distance matrices among individuals and then generated the autocorrelation coefficient ( $r$ ) using GENALEX. Statistical significance was assessed by generating 999 random permutations and by performing 1,000 bootstrap trials to determine the 95% confidence interval for each. The selection of distance classes (30, 60, 100, 300, and 1,000 m) was based on observed movements of 44 uniquely marked lizards during this study (total number of re-sightings = 50; Figure 3.2) and on dispersal distances reported in literature (Hranitz and Baird 2000).

## Results

Although we documented a high rate of ADO (8%), we conducted replicate genotyping when possible to minimize the influence of allelic dropout on the results. We identified two loci, Orig11 and N5, as monomorphic and excluded them from all further analyses except tests for recent population expansion, which require inclusion of such loci (Reich et al 1999). We found evidence for the presence of a null allele, which is distinguishable from biological causes for Hardy-Weinberg disequilibrium such as the Wahlund effect (Van Oosterhout et al 2004), at a single locus (Orig7; frequency in sampling locations = 0.23–0.44, average = 0.36, SE = 0.05).

After removal of this locus, all sampling locations were found to be in Hardy–Weinberg equilibrium. We therefore calculated and applied a correction to that locus using the Van Oosterhout method available in the software MICROCHECKER for our population–level analyses. The software ML–RELATE provides a correction for the presence of null alleles, but for all other analyses requiring genotypic data, we either compared results with or without the inclusion of this locus or simply excluded it, depending upon the underlying assumptions of the analyses. The test for linkage disequilibrium indicated that only loci Orig24 and Orig25 are significantly linked in one of our four populations (Konza Prairie). Hutchison (2003) also found evidence for linkage disequilibrium at Orig24 and Orig25 (they are indeed physically linked; Hutchison et al 2004), but in only 1 of 42 populations, and concluded these loci are evolving independently.

Measures of genetic diversity were similar for Konza Prairie, Fort Riley, and Milford Dam (Table 3.1). We therefore grouped these sampling locations together and compared them to results for Tuttle Creek Dam, which had lower estimates of genetic diversity and higher inbreeding and relatedness estimates, using a two–sample t–test (data normally distributed:  $H_O$ ,  $H_E$ , and  $F_{IS}$ ) and a nonparametric two–sample Kolmogorov–Smirnov test (data non–normally distributed: allelic richness, effective number of alleles). Relatedness was compared using a z–test for two proportions. Only observed heterozygosity was significantly different between the two groups ( $p = 0.035$ ). We found evidence for a recent population bottleneck in only one sample location (Tuttle Creek Dam,  $p = 0.04$ ; all other sampling locations,  $p > 0.05$ ). With the exclusion of this site, we found evidence for recent population expansion [within locus ( $k$ ) test,  $p = 0.04$ ]. The interlocus ( $g$ ) test for population expansion was not significant (significance assessed based on Table 1, Reich et al 1999); however, other studies have found similar results,

suggesting decreased power of the test when mutation rates among loci are variable (i.e., data sets that, like ours, contain dinucleotide, trinucleotide, and tetranucleotide microsatellite loci; Donnelly et al 2001).

Modest genetic differentiation was evident among sites, with  $F_{ST}$  values ranging from 0.05 to 0.13 (average including Tuttle Creek Dam =  $0.08 \pm 0.01$  SE; average excluding Tuttle Creek Dam =  $0.05 \pm 0.00$  SE). All pairwise estimates except between Fort Riley and Milford Dam were significantly  $> 0$  after Bonferroni adjustment (Table 3.2). The PCA returned six principal coordinates with eigenvalues  $> 1$ , with the first three explaining 59% of the variation in genotypes. However, a plot of the first two coordinates indicates this method was unable to fully discriminate between each of our sampling locations, as indicated by the large amount of overlap among all individuals, with the exception of Tuttle Creek Dam, which separated from Konza Prairie along coordinate one (Figure 3.3). The AMOVA revealed that the majority (86%) of the molecular variance occurred within populations rather than among populations, but results from Bayesian genetic clustering indicated that the number of clusters ( $K$ ) = 2 had the highest average likelihood. Examination of ancestry estimates revealed that Fort Riley and Milford Dam samples derived most (84%) of their ancestry from cluster 1, while both Konza Prairie and Tuttle Creek Dam samples derived roughly half (Konza Prairie = 60%, Tuttle Creek Dam = 49%) of their ancestry from cluster 2 (Figure 3.4).

Estimated migration rates differed among sampling locations (Table 3.3) and indicate gene flow has occurred (average  $Nm$  per generation =  $1.56 \pm 0.47$  SE). The highest number of migrants is predicted from Tuttle Creek Dam to all other sites (average  $Nm$  per generation =  $3.76 \pm 0.53$  SE) and between Milford Dam and Fort Riley (average  $Nm$  per generation =  $1.73 \pm 0.10$  SE). We did not find evidence for isolation by distance ( $p = 0.08$ ), nor did we find evidence for

isolation by resistance (land cover,  $p = 0.12$ ; rock availability,  $p = 0.23$ ). However, resistance values generated by each analysis (Table 3.4) follow a pattern similar to several other analyses, and are discussed further below. Neither positive nor negative spatial autocorrelation was evident in the four smallest distance classes ( $< 1$  km). However, results for spatial autocorrelation analysis at the 1-km distance class demonstrate positive correlation in distance class 1 (0-1 km) and negative correlation in distance classes 4 and 5 (3-5km) (Figure 3.5).

## Discussion

Our results support the hypothesis that peripheral populations within a species' distribution should have reduced genetic variability and increased population differentiation relative to core populations at the center of the range (Eckert et al 2008; but see Gaston 2003, Table 2). We observed low genetic diversity within several collared lizard populations sampled in the northern Flint Hills at the range periphery. Our estimates of allelic diversity were intermediate between estimates for central populations in Texas and peripheral populations in the southwestern Ozarks (Hutchison 2003). We identified two loci (Orig11 and N5) that were monomorphic for all four sampling locations, and thus lacked any genetic variation. Hutchison (2003) found core–peripheral trends in monomorphism among collared lizard populations, with peripheral populations in the northeastern Ozarks having significantly more monomorphic loci than core populations in central Texas, which had none.

We found no evidence for lower genetic diversity resulting from a recent population bottleneck at three of our sampling sites. Rather, with the exclusion of Tuttle Creek Dam, our results support the hypothesis of a recent range expansion for collared lizards (Hutchison et al 1999). Hutchison and Templeton (1999) speculated that collared lizard populations have not been present within the Kansas region long enough ( $\sim 7,000$  ybp) to have attained drift–migration



equilibrium conditions, a conclusion also supported by the lack of evidence for isolation by distance (both our study and theirs) or isolation by resistance (our study). Populations that have been founded by a small, genetically homogeneous group in an area where the species has recently extended its distribution may appear genetically similar and indicate high rates of gene flow that are not actually occurring (Ibrahim et al 1996; Pogson et al 2001; Duvernell et al 2008). This has been suggested for species that have recently expanded into habitat that was formerly unsuitable due to the presence of glaciers (Larson et al 1984; Highton 1995).

Indeed, several of our results suggest that gene flow is overestimated. For example, the AMOVA results indicated that the majority of molecular variance for samples occurs within rather than among sampling locations, and the PCA was unable to clearly partition samples into groups based on sampling sites. Bayesian clustering analysis also indicated a mixed ancestry for many individuals from different sampling locations. Still, our estimates of population genetic structure provide evidence that population genetic differentiation is occurring among some sites, consistent with expectations of a core–peripheral trend of increasing population structure (pairwise estimates of  $F_{ST}$  were significant between all but two sites), though we did not observe the high levels of differentiation characteristic of peripheral Missouri populations (southwestern Ozarks, average  $F_{ST} = 0.14$ ; northeastern Ozarks,  $F_{ST} = 0.34$ ; Hutchison and Templeton 1999) over the same distance (< 45 km). Our average  $F_{ST}$  (0.08 with Tuttle Creek Dam, 0.05 without) appears intermediate between Missouri peripheral and Texas central ( $F_{ST} = 0.02$ ; Hutchison and Templeton 1999) populations.

Several additional trends were evident in our results. First, multiple lines of evidence indicate that two of our study sites, Fort Riley and Milford Dam, display high rates of gene flow (nonsignificant pairwise  $F_{ST}$ , shared ancestry in cluster 1, and 1–2 migrants exchanged per

generation). We are not able to determine whether these estimates indicate ongoing levels of gene flow or are also a result of a past founder effect, but analyses of landscape context indicate that gene flow is likely to occur as these sites were connected by areas predicted to have very little resistance to dispersal (Table 3.4). Second, although migration estimates and Bayesian cluster results suggest Tuttle Creek Dam experienced high rates of gene flow with other sites, this site also exhibited significantly reduced genetic diversity and high estimates of inbreeding and relatedness relative to other sites. Evidence for a recent population bottleneck at this site, coupled with a low sample size for these tests (number of samples with complete genotype = 6), likely impaired our ability to derive robust estimates of migration rates or ancestry. Our detection of a genetic bottleneck may correspond to a large flooding event in 1993 that scoured the dam's spillway and raised the lake level, covering rock habitat and eroding the spillway where we collected our samples.

Although we did not find evidence for isolation by resistance based on land cover or rock availability, the highest average landscape resistance estimates for each analysis were between Tuttle Creek Dam and all other sites, with resistance estimates between Konza Prairie and all other sites also high (Table 3.4; Figure 3.6). These resistance estimates correspond well with our estimates of population differentiation and migration rates (with the exception of Tuttle Creek Dam, see above). Thus, it seems that the genetic differences we observed between these sites are related to landscape characteristics such as rock availability and land cover. Rock habitat is a naturally patchy resource in the Flint Hills, which is dependent on natural hillside soil erosion or the construction of rock piles. Using spatial autocorrelation analysis, we identified restricted gene flow, with a positive correlation between genetic and geographic distance occurring over fine spatial scales (0-1 km) at the Konza Prairie, a site with ample rock habitat. We detected

significantly negative correlation at greater distances (3-5 km), which may reflect a spatial limit to this population. These results are consistent with our observations of movements by marked lizards at the Konza Prairie (100% of recorded movements  $\leq 1,000$  m, with 74%  $\leq 100$  m; Fig. 3.2). Similar within-population movements have also been reported for central populations in Oklahoma, with lizards dispersing  $\sim 200$  m but not more than 350 m among rock ledges, with no evidence of population genetic substructure (Hranitz and Baird 2000). We also observed what appears to be a single long-distance dispersal event (1,000 m) by a male having reached sexual maturity, the point at which collared lizards most often disperse (Fitch 1956).

Our results indicate that local landscape characteristics may be influencing the population genetics of collared lizards in the Flint Hills of Kansas. We are thus able to make several comparisons between northern Flint Hills and Missouri Ozark peripheral populations based on our estimates of genetic diversity, population genetic differentiation, and landscape resistance. Missouri peripheral populations exist in rock habitat within an unsuitable oak-hickory forest matrix, where dispersal and gene flow are highly restricted over short distances (as little as 50 m apart; Brisson et al 2003; Hutchison and Templeton 1999; Templeton et al 2001). In comparison, rock habitat patches in the Flint Hills of Kansas occur in a tallgrass prairie matrix, where fire and grazing have maintained the grassland and prevented the expansion of closed-canopy forest, both historically as well as at present (Freeman 1998; Hartnett and Fay 1998).

We are able to draw several conclusions based on our results. First, the genetic diversity and population genetic structure of collared lizards in the Kansas Flint Hills appear in part to support the core-peripheral trend commonly reported for other taxa (Eckert et al 2008), and this “edge” effect is most likely a result of founder effects coupled with population expansion into habitat previously unsuitable due to climatic factors. Second, barriers such as urban

development, bodies of water, and forested cover are likely influencing gene flow among some sites, even though dispersal and gene flow appear to occur readily among rock habitat patches within sites. Future genetic diversity and population differentiation among our sampling sites may be dependent on alterations to current land cover in the form of urbanization or forest expansion within tallgrass prairie habitat may fragment grassland patches. We conclude that our results show evidence for core–peripheral trends in genetic diversity and population differentiation, but that local population differences and differences between populations in peripheral regions are also influenced by landscape context.

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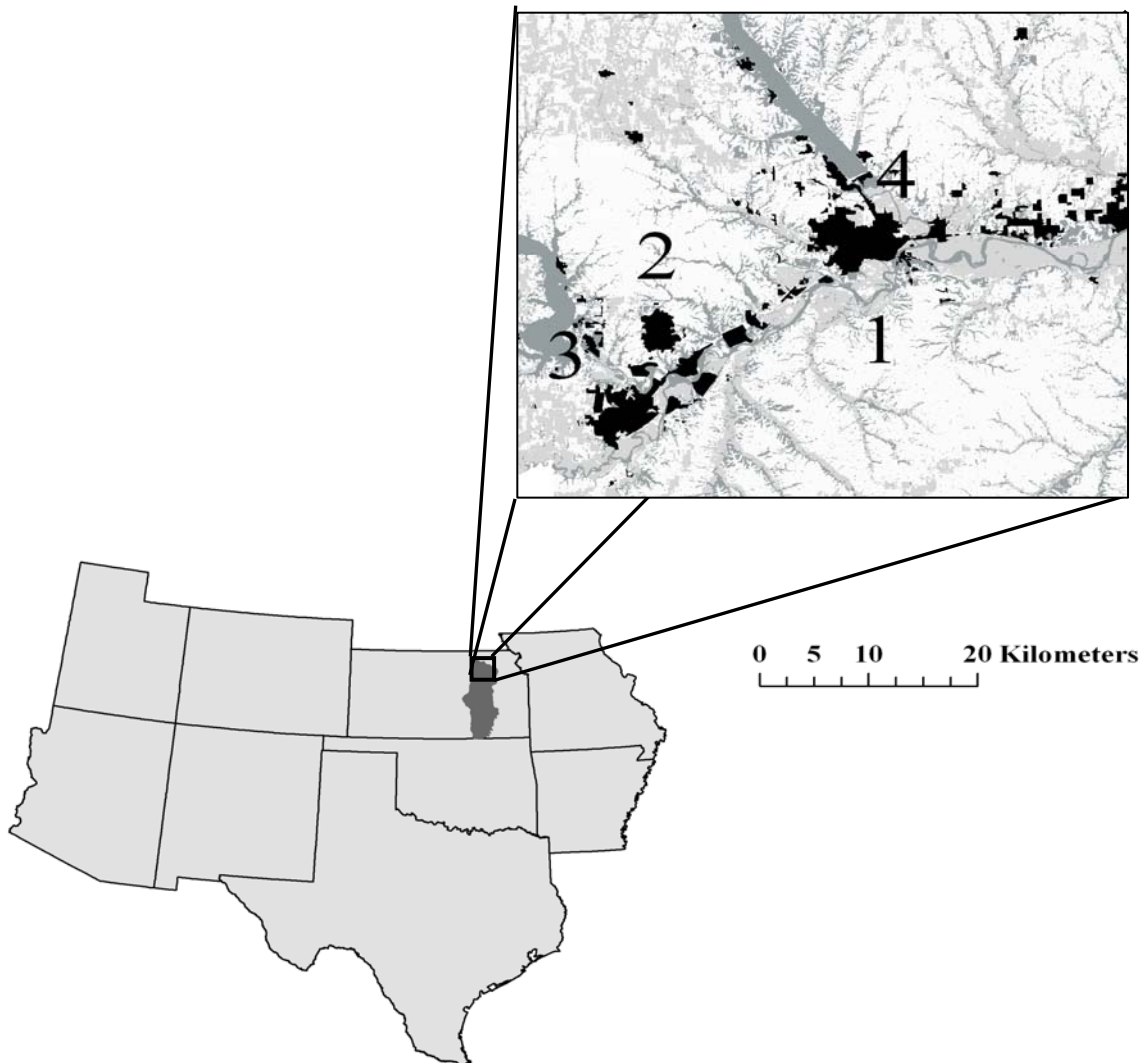
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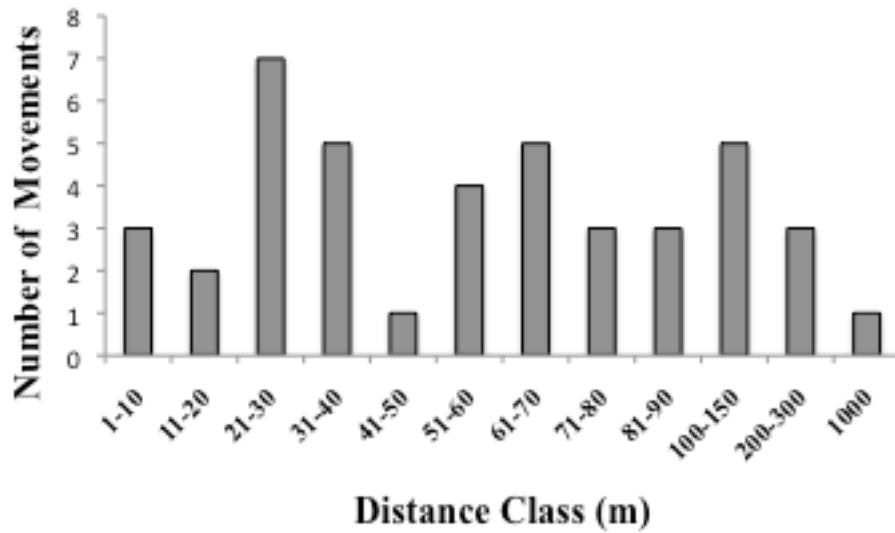
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## Figures and Tables



**Figure 3.1** The Eastern Collared Lizard's (*Crotaphytus collaris collaris*) range extends broadly through the mid- and southwestern United States. Sampling locations for this study (inset) occur along the northern periphery of the range in the Flint Hills, Kansas (dark gray, state map). Numbers correspond to this study's sample sites (inset; 1. Konza Prairie with boundary outline, 2. Fort Riley, 3. Milford Dam, and 4. Tuttle Creek Dam). Inset colors indicate land cover class (white = prairie or agriculture, light gray = forest, dark gray = water, black = urban development).



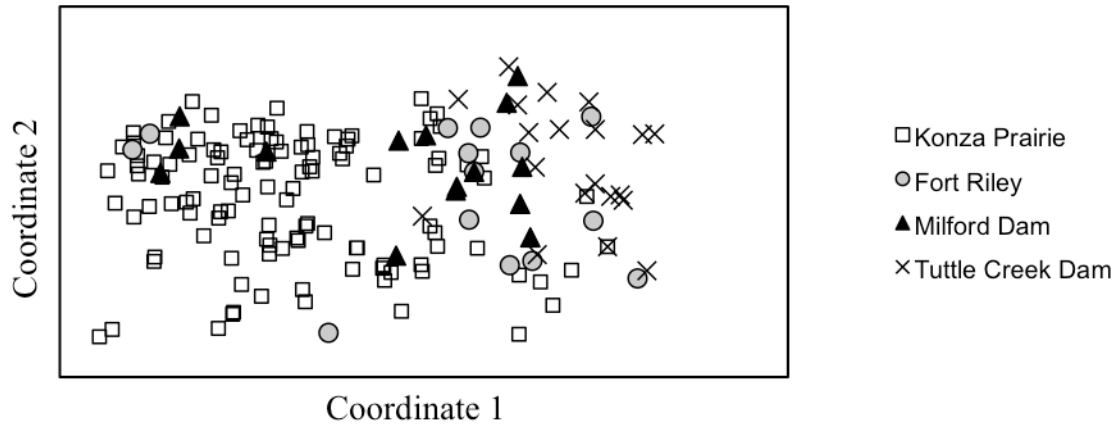
**Figure 3.2** Frequency distribution of distances moved by collared lizards based on resighting of marked individuals (n = 50).

**Table 3.1 Average ( $\pm$  SE) allelic richness adjusted by sample size (AR), effective number of alleles ( $N_e$ ), average observed and expected heterozygosity, inbreeding coefficient ( $F_{IS}$ ), and relatedness ( $r$ ) of four sampling locations for adult collared lizards (sample sizes: Konza Prairie,  $n = 113$ ; Fort Riley,  $n = 14$ ; Milford Dam,  $n = 14$ ; and Tuttle Creek Dam,  $n = 20$ ) using eight microsatellite DNA loci.**

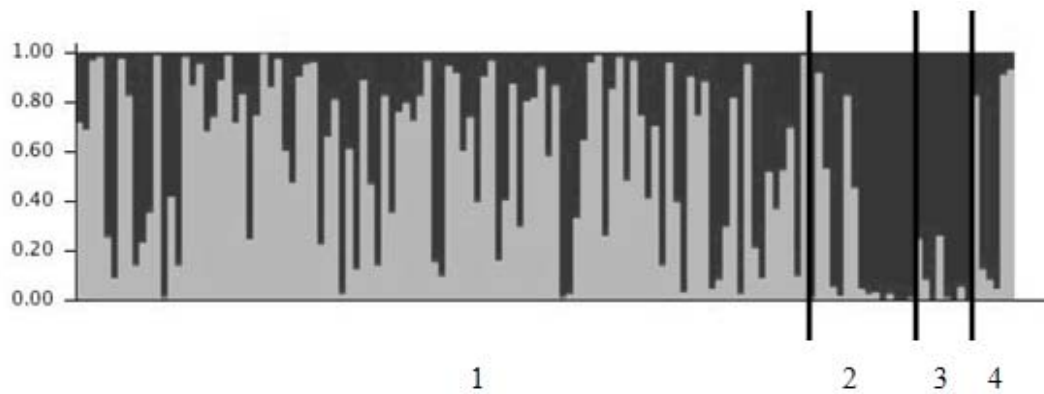
Population	AR	$N_e$	$H_O$	$H_E$	$F_{IS}$	$r$
Konza Prairie	3.63	2.91	0.59	0.57	-0.03	0.11
Fort Riley	3.64	2.85	0.57	0.57	0.01	0.09
Milford Dam	3.49	2.65	0.58	0.56	-0.04	0.10
Tuttle Creek Dam	2.70	2.08	0.40	0.45	0.11	0.15
Average	3.37	2.62	0.54	0.54	0.01	0.11
SE	0.23	0.19	0.05	0.03	0.03	0.01

**Table 3.2 Pairwise comparisons of genetic distance between four sampling locations for adult collared lizards (for sample sizes, see Table 3.1) based on eight microsatellite DNA loci. Significant ( $P < 0.05$  after Bonferroni correction) differences are indicated by asterisks.**

Population	Konza Prairie	Fort Riley	Milford Dam
Konza Prairie	-		
Fort Riley	0.06*	-	
Milford Dam	0.05*	0.05	-
Tuttle Creek Dam	0.09*	0.09*	0.13*



**Figure 3.3 Plot of results from principle coordinates analysis conducted on DNA samples from adult collared lizards collected at four sampling locations in northeastern Kansas (for sample sizes, see Table 3.1).**



**Figure 3.4 Results from Bayesian cluster analysis conducted on adult collared lizard DNA samples using program Structure. Ancestry estimates (percentage of ancestry from each predicted cluster) are displayed for each sample along the y-axis and are separated by sampling location (1. Konza Prairie, 2. Fort Riley, 3. Milford Dam, and 4. Tuttle Creek Dam). Estimates are shown for the highest likelihood run, where number of clusters ( $K$ ) = 2. Only samples providing complete genotypes were included (sample sizes: Konza Prairie,  $n = 103$ ; Fort Riley,  $n = 14$ ; Milford Dam,  $n = 9$ ; Tuttle Creek Dam,  $n = 6$ ).**

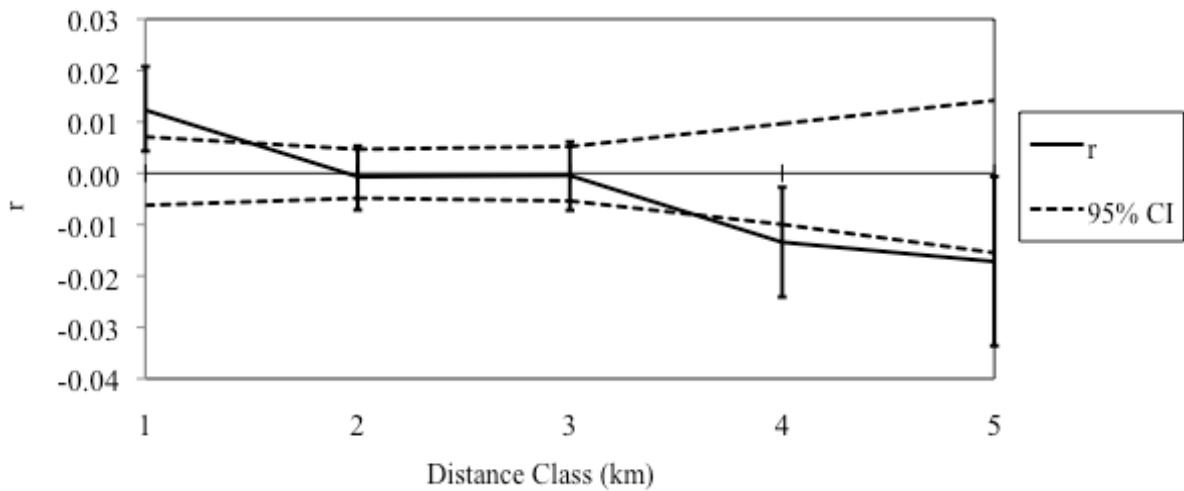
**Table 3.3 Estimates of theta ( $4N\mu$ ) and number of migrants per generation ( $Nm = \Theta M$ ,  $M = mi/\mu$ ) in program MIGRATE. Estimates are based on DNA samples from adult collared lizards at four sampling locations in northeastern Kansas using eight microsatellites (for sample sizes, see Table 3.1).**

Population	$\Theta$	Nm			
		1, x	2, x	3, x	4, x
Konza Prairie	3.08	-	0.52	1.11	5.39
Fort Riley	3.10	0.50	-	1.98	4.12
Milford Dam	0.91	0.00	1.48	-	1.77
Tuttle Creek Dam	0.21	0.71	0.52	0.55	-

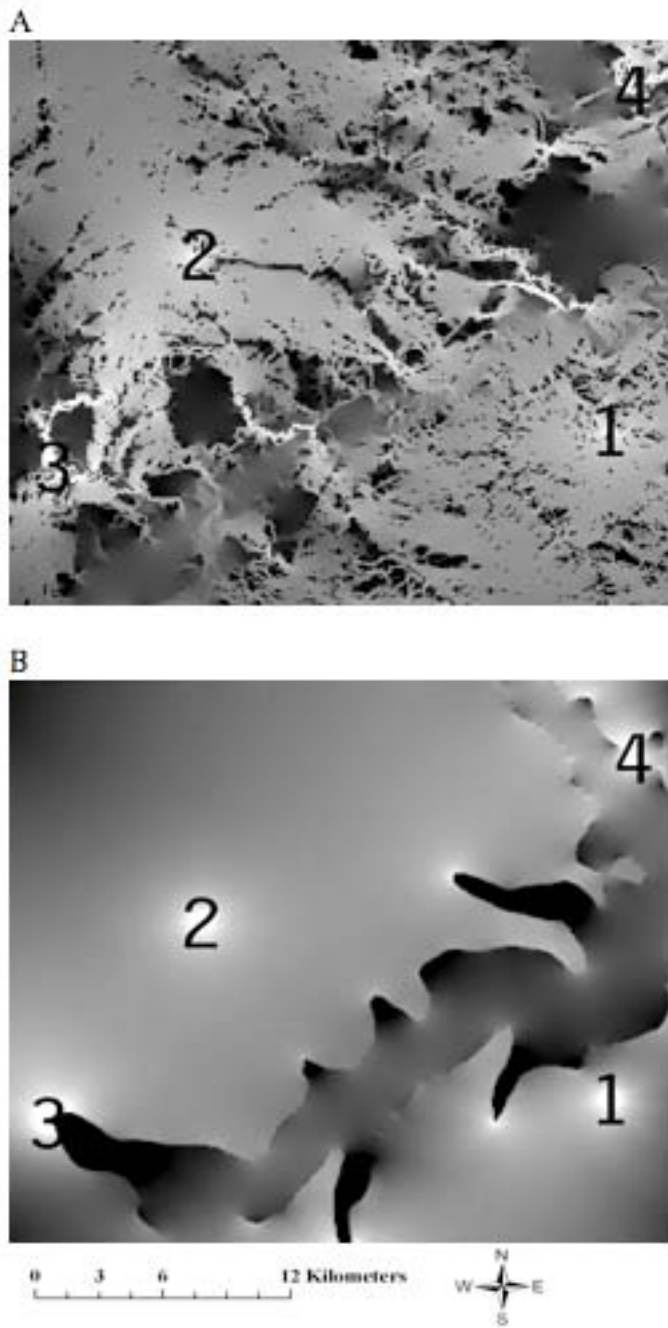
**Table 3.4 Pairwise estimates of landscape resistance values for land cover (lower diagonal) and rock availability (upper diagonal) among four collared lizard sampling locations in the Flint Hills, Kansas.**

	Konza Prairie	Fort Riley	Milford Dam	Tuttle Creek Dam
Konza Prairie	-	44.14	44.40	402.27
Fort Riley	7.55	-	1.23	364.29
Milford Dam	9.95	3.93	-	364.77
Tuttle Creek Dam	9.24	13.02	15.49	-





**Figure 3.5 Results from spatial autocorrelation analysis conducted on collared lizard DNA samples collected at Konza Prairie (n = 177) grouped into distance classes of 1 km (i.e., distance class 1 indicates the correlation between genetic and geographic distance for samples collected between 0 and 1 km). Bootstrapped 95% error bars in black.**



**Figure 3.6 Resistance maps of (A) land cover and (B) elevation (as a proxy for rock availability) for four collared lizard sample locations in the northern Flint Hills of Kansas. Sampling locations include: 1. Konza Prairie, 2. Fort Riley, 3. Milford Dam, and 4. Tuttle Creek Dam. Higher resistance values are indicated by darker shades, with black having the highest and white the lowest resistances.**

## CHAPTER 4 - Conclusion

Complex processes often influence the spatial patterns of resources or organisms within the landscape. We examined the influence of multiple aspects of the environment, including local habitat characteristics, land management, and land cover on collared lizard populations in the northern Flint Hills of Kansas, taking several approaches, including surveys of patch occupancy and abundance and genetic analysis of populations. The results presented in Chapter 2 suggest that patch occupancy and lizard abundance are dependent both on the presence of suitable habitat and the type of land management implemented, where, in addition to several rock characteristics, land management such as frequent burning and grazing by bison increase the likelihood of patch occupancy and lizard abundance. The results presented in Chapter 3 concerning the population genetics of collared lizards indicate that historical processes have had enduring effects on the genetic variability of these populations (i.e., populations still display the effects of past expansion and bottlenecks following the post-glacial invasion of the region). We also found evidence that gene flow among populations is influenced by land cover and the availability of rock habitat, which create landscapes containing areas that vary in resistance to dispersing lizards.

Together, these studies support the idea that landscape context may have a significant effect on collared lizard populations. In the Flint Hills of Kansas, where disturbances such as fire and grazing have historically been vital to the maintenance of tallgrass prairie (Anderson 2006), land-management practices that alter nutrient cycles and soil chemistry (Knapp et al 1998; Blair et al 1998) and vegetation composition and structure (Fuhlendorf and Engle 2001; Gibson and Hulburt 1987) have the potential to influence many other organisms. The effects of land

management, however, may not be limited to upland prairie sites, because urban development and tree planting also occur in lowland areas, and these practices may fragment grassland patches (Briggs et al 2002b; Briggs et al 2005).

In the Missouri Ozarks, collared lizards have been negatively impacted by fire suppression and woody expansion. In areas of fire suppression, collared lizards have decreased body size (Brisson et al 2003; Sexton et al 1992), reduced growth rates, and decreased seasonal activity length (Sexton et al 1992). In addition, dispersal among habitat patches, and subsequently gene flow, is highly limited, with populations showing extreme differentiation and overall reduced genetic variability (Templeton et al 2001; Templeton et al 1990; Hutchison and Templeton 1999; Hutchison 2003). Fire appears to increase the quality and size of habitat patches and increase the frequency of dispersal among habitat patches by thinning understory cover, allowing for gene flow through enhanced dispersal, as well as colonization of empty habitat patches (Brisson et al 2003; Templeton et al 2001).

Expansion of woody habitat in the Flint Hills is the result of complex interactions between disturbances (fire and grazing) and human influence (fire suppression, landscape fragmentation, and tree planting) (Briggs et al 2002b). At one of our study sites, the Konza Prairie Biological Station, woody cover increased in less-frequently burned watersheds (four-year interval) by 29% from 1983–2000 (Briggs et al 2005). The pattern of gene flow among our study sites appears to correspond to differences in land cover and availability of rock habitat. Because gene flow among collared lizard populations appears to be influenced by the presence of urban cover, forest cover, and rock habitat, changes to the landscape, namely in the form of urban or forest expansion, may result in increased fragmentation of collared lizard populations. We therefore recommend the use of prescribed burns that limit woody expansion and the use of

moderate grazing in areas subject to infrequent burns, to maintain the suitability of rock patches and genetic variability for collared lizards in the region.

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## Appendix A - Preliminary models developed for comparison of collared lizard occupancy and abundance

### Figures and Tables

**Table A.1 Preliminary models developed for comparison of collared lizard occupancy and abundance, with and without watershed treatment variables. For simplicity, we show only models with survey (S) as the detection covariate except for the top model, which shows the effect of year (Y). Variable names are given in Table 2. Watershed treatment variables are shortened to B (burn) and G (graze).**

Model	Abundance	<i>p</i>	AICc	$\Delta$ AICc	Weight	Likelihood	K
1	5m scale+B+G+B*G	Y	1152.06	0.00	0.55	1.00	13
2	5m scale+B+G+B*G	S	1152.46	0.40	0.45	0.82	15
3	5m scale	S	1168.04	15.98	0	0	14
4	roughcv5+B+G+B*G	S	1300.72	148.66	0	0	11
5	refs+B+G+B*G	S	1319.92	167.86	0	0	11
6	refs	S	1332.26	180.20	0	0	6
7	roughcv5	S	1361.84	209.78	0	0	6
8	height+B+G+B*G	S	1383.71	231.65	0	0	11
9	height	S	1444.44	292.38	0	0	6
10	rock+B+G+B*G	S	1468.25	316.19	0	0	11
11	rock	S	1499.11	347.05	0	0	6
12	wetcv5+B+G+B*G	S	1514.98	362.92	0	0	11
13	vegcat+B+G+B*G	S	1543.17	391.11	0	0	12
14	wetcv5	S	1545.90	393.84	0	0	6
15	aspcv120+B+G+B*G	S	1552.19	400.13	0	0	12
16	geology+B+G+B*G	S	1571.79	419.73	0	0	15
17	vegindex+B+G+B*G	S	1572.59	420.53	0	0	11
18	aspcv5+B+G+B*G	S	1586.49	434.43	0	0	11
19	perch+B+G+B*G	S	1605.32	453.26	0	0	11
20	roughcv60+B+G+B*G	S	1606.65	454.59	0	0	11
21	aspcv60+B+G+B*G	S	1607.63	455.57	0	0	11
22	rough5+B+G+B*G	S	1610.70	458.64	0	0	11
23	vegcat	S	1612.93	460.87	0	0	7
24	wetcv60+B+G+B*G	S	1614.87	462.81	0	0	11
25	60m scale+B+G+B*G	S	1615.09	463.03	0	0	14
26	wet5+B+G+B*G	S	1619.70	467.64	0	0	11
27	geology	S	1619.94	467.88	0	0	10

28	120m scale+B+G+B*G	S	1621.76	469.70	0	0	14
29	pershrub120+B+G+B*G	S	1625.19	473.13	0	0	11
30	pershrub5+B+G+B*G	S	1625.89	473.83	0	0	11
31	roughcv120+B+G+B*G	S	1626.42	474.36	0	0	11
32	pershrub60+B+G+B*G	S	1627.96	475.90	0	0	11
33	wet60+B+G+B*G	S	1628.90	476.84	0	0	11
34	wetcv120+B+G+B*G	S	1629.90	477.84	0	0	11
35	asp5+B+G+B*G	S	1632.15	480.09	0	0	11
36	rough120+B+G+B*G	S	1632.86	480.80	0	0	11
37	B+G+B*G	S	1633.78	481.72	0	0	10
38	wet120+B+G+B*G	S	1635.62	483.56	0	0	11
39	asp60+B+G+B*G	S	1635.76	483.70	0	0	11
40	veginde	S	1635.77	483.71	0	0	6
41	rough60+B+G+B*G	S	1635.83	483.77	0	0	11
42	asp120+B+G+B*G	S	1635.92	483.86	0	0	11
43	aspcv5	S	1641.92	489.86	0	0	6
44	roughcv60	S	1652.85	500.79	0	0	6
45	B+G	S	1656.26	504.20	0	0	8
46	B	S	1659.57	507.51	0	0	7
47	rough5	S	1661.66	509.60	0	0	6
48	aspcv60	S	1662.45	510.39	0	0	6
49	perch	S	1663.09	511.03	0	0	6
50	wetcv60	S	1669.85	517.79	0	0	6
51	wet5	S	1671.42	519.36	0	0	6
52	roughcv120	S	1676.65	524.59	0	0	6
53	wet60	S	1680.30	528.24	0	0	6
54	60m scale	S	1680.58	528.52	0	0	9
55	wetcv120	S	1681.17	529.11	0	0	6
56	pershrub5	S	1682.85	530.79	0	0	6
57	120m scale	S	1684.30	532.24	0	0	9
58	none	S	1686.39	534.33	0	0	5
59	wet120	S	1686.41	534.35	0	0	6
60	asp5	S	1686.70	534.64	0	0	6
61	pershrub120	S	1686.88	534.82	0	0	6
62	rough120	S	1686.98	534.92	0	0	6
63	pershrub60	S	1687.10	535.04	0	0	6
64	asp120	S	1688.35	536.29	0	0	6
65	aspcv120	S	1688.36	536.30	0	0	6
66	rough60	S	1688.38	536.32	0	0	6
67	G	S	1688.43	536.37	0	0	6
68	asp60	S	1688.47	536.41	0	0	6



## Appendix B - Final models developed for the estimation of collared lizard occupancy and abundance

### Figures and Tables

**Table B.1 Models developed for the estimation of collared lizard occupancy and abundance. For simplicity, we show only models with survey as the detection covariate except for the top model, which shows the effect of year. Variable names are given in Table 2. Watershed treatment variables are shortened to B (burn) and G (graze).**

Model	Abundance	$p$	AICc	$\Delta$ AICc	Weight	Likelihood	K
1	5m scale+B+G+B*G	Y	1152.06	0.00	0.55	1	12
2	5m scale+B+G+B*G	S	1152.46	0.40	0.45	0.82	14
3	roughcv5+B+G+B*G	S	1300.72	148.66	0	0	11
4	refs+B+G+B*G	S	1319.92	167.86	0	0	11
5	height+B+G+B*G	S	1383.71	231.65	0	0	11
6	rock+B+G+B*G	S	1468.25	316.19	0	0	11
7	wetcv5+B+G+B*G	S	1514.98	362.92	0	0	11
8	vegcat+B+G+B*G	S	1543.17	391.11	0	0	12
9	aspcv120+B+G+B*G	S	1552.19	400.13	0	0	12
10	geology+B+G+B*G	S	1571.79	419.73	0	0	15
11	vegindex+B+G+B*G	S	1572.59	420.53	0	0	11
12	aspcv5+B+G+B*G	S	1586.49	434.43	0	0	11
13	perch+B+G+B*G	S	1605.32	453.26	0	0	11
14	roughcv60+B+G+B*G	S	1606.65	454.59	0	0	11
15	aspcv60+B+G+B*G	S	1607.63	455.57	0	0	11
16	rough5+B+G+B*G	S	1610.70	458.64	0	0	11
17	wetcv60+B+G+B*G	S	1614.87	462.81	0	0	11
18	60m scale+B+G+B*G	S	1615.09	463.03	0	0	14
19	wet5+B+G+B*G	S	1619.70	467.64	0	0	11
20	120m scale+B+G+B*G	S	1621.76	469.7	0	0	14
21	pershrub120+B+G+B*G	S	1625.19	473.13	0	0	11
22	pershrub5+B+G+B*G	S	1625.89	473.83	0	0	11
23	roughcv120+B+G+B*G	S	1626.42	474.36	0	0	11
24	pershrub60+B+G+B*G	S	1627.96	475.9	0	0	11
25	wet60+B+G+B*G	S	1628.90	476.84	0	0	11
26	wetcv120+B+G+B*G	S	1629.90	477.84	0	0	11
27	asp5+B+G+B*G	S	1632.15	480.09	0	0	11
28	rough120+B+G+B*G	S	1632.86	480.8	0	0	11
29	B+G+B*G	S	1633.78	481.72	0	0	10
30	wet120+B+G+B*G	S	1635.62	483.56	0	0	11

31	asp60+B+G+B*G	S	1635.76	483.7	0	0	11
32	rough60+B+G+B*G	S	1635.83	483.77	0	0	11
33	asp120+B+G+B*G	S	1635.92	483.86	0	0	11
34	B+G	S	1656.26	504.2	0	0	8
35	B	S	1659.57	507.51	0	0	7
36	none	S	1686.39	534.33	0	0	5
37	G	S	1688.43	536.37	0	0	6

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