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RESEARCH ARTICLE

Landscape context matters: local habitat and landscape effects on the abundance and patch occupancy of collared lizards in managed grasslands

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Abstract The distribution and abundance of a species may be simultaneously influenced by both local-scale habitat features and the broader patch and landscape contexts in which these populations occur. Different factors may influence patch occupancy (presence–absence) versus local abundance (number of individuals within patches), and at different scales, and thus ideally both occupancy and abundance should be investigated, especially in studies that seek to understand the consequences of land management on species persistence. Our study evaluated the relative influences of variables associated with the local habitat patch, hillside (patch context), and landscape context on patch occupancy and abundance of the collared lizard (*Crotaphytus collaris*) within tallgrass prairie managed under different fire and grazing regimes in the northern Flint Hills of Kansas, USA. Using a multi-model information-theoretic approach that accounted for detection bias, we found that collared lizard abundance and occupancy was influenced by factors measured at both the local habitat and landscape scales. At a local scale, collared lizard abundance was greatest on large rock ledges that had lots of crevices, high vegetation complexity, and were located higher up on the hillslope. At the landscape scale, collared lizard abundance and occupancy were both higher in watersheds that were burned frequently (1–2 year intervals). Interestingly, grazing only had a significant effect on occupancy and abundance within less frequently burned (4-year burn interval) watersheds. Our results suggest that, in addition to the obvious habitat needs of this species (availability of suitable rock habitat), land-management practices have the potential to influence collared lizard presence and abundance in the grasslands of the Flint Hills. Thus, mapping the availability of suitable habitat is unlikely to be sufficient for evaluating species distributions and persistence in such cases without consideration of landscape management and disturbance history.

Keywords Land management · Grazing · Fire · Crotaphytus collaris · Flint Hills · Tallgrass prairie · Habitat suitability

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Introduction

Wildlife populations must contend with 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 (Gibbons et al. 2000; Fahrig 2007).

Environmental characteristics of both the local habitat patch and of the surrounding landscape context can be important determinants of habitat occupancy and abundance of species (Pearson 1993; Wiens et al. 1993; Ricketts 2001; Thomas et al. 2001; Driscoll 2007), 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 (either positive or negative), may vary across the geographic range of a species or in different landscape contexts (Fielding and Haworth 1995; McAlpine et al. 2008; Mateo-Tomás and Olea 2009). Thus, studies of species occupancy-abundance patterns should consider how local patch attributes, as well as the broader patch or landscape context, ultimately influence species' occurrence and persistence (Wiens 1997). Because different factors may influence population size versus species presence (patch occupancy), it is important to assess habitat effects on both abundance and occurrence, especially if these two measures of species distribution are influenced by different factors at different scales (e.g., if occurrence is affected more by landscape context, such as the amount or fragmentation of habitat, but abundance is more sensitive to local habitat features).

In particular, studies assessing the influence of landscape factors on species occurrence and abundance are needed to identify the effects of anthropogenic land use or habitat management on amphibians and reptiles (Gardner et al. 2007). 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 (Vié et al. 2009). For lizards, habitat occupancy and abundance may be variously influenced by characteristics such as vegetation composition, rock composition or morphology, amount of rock cover, or geographic aspect (Fischer et al. 2004; Jellinek et al. 2004). Rock-dwelling lizards, for example, select habitat based on local features such as rock size, shape, thermal properties or the width of crevices (Schlesinger and Shine 1994; Howard and Hailey 1999; Shah et al. 2004). However, landscape-scale factors, such as the spatial configuration of habitat within the landscape (Mazerolle and Villard 1999) or type of land management (James 2003; Castellano and Valone 2006; Wilgers et al. 2006) may also influence the presence and abundance of lizards at a local scale. Suitable habitat in one landscape context may be wholly unsuitable in another.

The Collared Lizard (*Crotaphytus collaris*) is an ideal species in which to examine the effects of local habitat 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 the rock habitat as well as of the surrounding tallgrass prairie landscape (Fitch 1956). Collared lizard habitat can be conceptualized as a nested hierarchy of habitat involving rock outcrops (patches), which are aligned along the ridges of hillsides (patch context), which in turn are located within the context of managed rangeland (landscape context). In terms of rock habitat, several different limestone layers provide outcrops at distinctive topographic positions along hillsides of the Flint Hills. These different geologic layers display characteristic weathering patterns, which create variation in rock morphology, and thus habitat suitability, for collared lizards (Smith 1991). Hillsides themselves may differ in characteristics such as slope, aspect or soil moisture, such that rock layers of a given type may occur within very different patch contexts, which may have implications for collared lizard occupancy or abundance. Additionally, hillsides in the Flint Hills are typically situated within some sort of managed landscape context, representing different fire and grazing regimes.

Most of the Flint Hills region is managed for cattle production, with widespread grazing and annual burning commonly occurring (up to 70% of grasslands are burned in a given year; With et al. 2008). 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 habitat 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). Although other studies have examined the influence of burning on habitat occupancy by collared lizards and found a positive effect (Templeton et al. 2001; Brisson et al. 2003), these studies were conducted in rocky glades within the forests of 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 hillside 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). The KPBS (3,487-ha) is a member of the National Science Foundation's Long-Term Ecological Research network, and supports research on the effects of grazing, fire and climatic variability on the structure and function of tallgrass prairie. Vegetation at KPBS primarily consists of native grasses such as big and little bluestems (*Andropogon gerardii*, *Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). Woody species such as roughleaf dogwood (*Cornus drummondii*) and Eastern redcedar (*Juniperus virginiana*) are also present and locally abundant, especially in watersheds that are rarely burned. 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 throughout the year, from −2.7°C (January) to 26.6°C (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 3- to 4-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 (the rate at which nondetection of a species is indicative of true absence, MacKenzie et al. 2002). Because the collared lizard is 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 that could potentially support collared lizard populations (Fig. 1). The watersheds we surveyed included grazed (by bison) and ungrazed treatments subjected to annual, biennial, or 4-year burn frequencies, and each treatment type had at least two watershed replicates (Table 1). Nearly half of the experimental watersheds that contained suitable collared lizard habitat were either burned annually or grazed (7/16 = 44% each).

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 (i.e., rock outcrop; $n = 247$ patches) using a hand-held GPS unit (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, rock outcrop temperature, ambient temperature, and windspeed during each survey and included these as detection variables (Table 2) in our models estimating detection probability (described below). 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. We also tested for a trap effect at outcrops where lizards (marked or unmarked) were sighted.

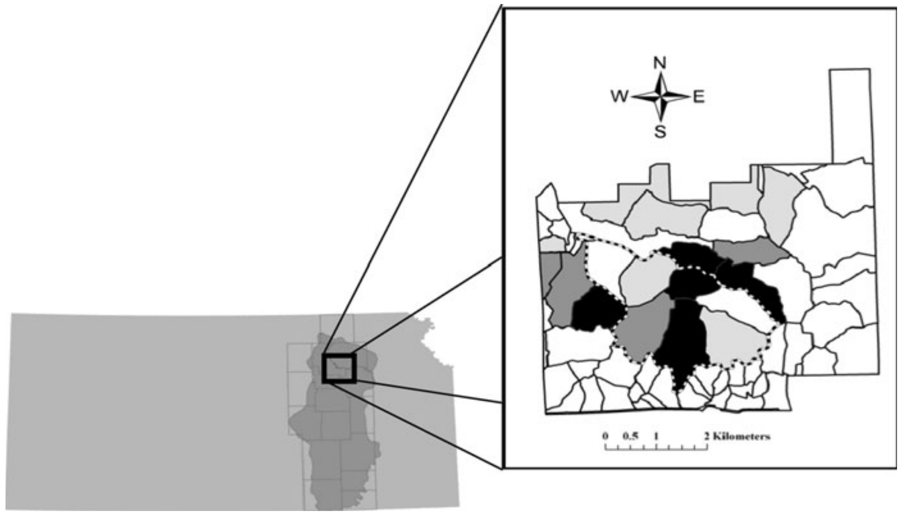


Fig. 1 Map of study site in the Flint Hills of Kansas (*darker gray* in left image of the state of Kansas). *Inset*: rock outcrops were surveyed for collared lizards in experimental watersheds (*shaded polygons*) at the Konza Prairie Biological Station in Riley County, Kansas. Watersheds under different burn treatments are indicated by intensity of shading (*light gray* annual, *dark gray* biennial, *black* 4-year). Watersheds enclosed by the fence (*dashed line*) are grazed by bison

Table 1 Number of surveyed 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)

Local habitat, hillside, and landscape measures

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 in studies of other rock-dwelling lizards (Whitaker 1996). The average length of rock outcrops in our study landscape was 583 m (±41 m SE, $n = 247$ outcrops). To evaluate which habitat factors—and at what scales—influenced collared lizard abundance and the probability that a rock outcrop was occupied, we measured 16 variables (Table 3) at each point where lizards were sighted. These variables were either known or suspected to influence habitat suitability for collared lizards, and thus represent different hypotheses that we evaluated using a multi-model selection procedure (described below). These variables include descriptors of the local rock habitat (patch), the hillside in which the rock outcrop is embedded (patch context), and the landscape context (the watershed in which the hillside is located, involving a particular burning and grazing treatment).

To describe rock habitat (local patch), we devised an ordinal scale that categorized the relative amount of rock cover, number of refuges, vegetation complexity, and relative height of the rock ledge (Table 3), 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 that could potentially provide refuge, ranged from no refuges (0) to many crevices and/or much loose rock of adequate size for cover (4). Vegetation complexity ranged from little complexity (grass = 1) to greater complexity (shrub patches = 2, dense shrub and tree cover = 3, and gallery forest = 4).

In addition, we obtained variables from an analysis of a Quickbird (GeoEye) satellite image of the KPBS (acquired 13 August 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 vegetation classes: grass and tree/shrub. We also quantified aspect, topographic wetness, and terrain irregularity from a 2-m digital elevation model (DEM) of the KPBS (Fig. 2) in ArcGIS version 9.3 (ESRI, Redlands, California, USA). We calculated aspect because of its potential influence on outcrop

Table 2 Variables used in models for determining factors affecting the probability of detecting collared lizards during surveys at the Konza Prairie Biological Station, Kansas

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	Average ambient temperature (°C) measured over 10 s during each survey
Wind	Continuous	Average windspeed (m/s) measured over 10 s 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 were previously sighted
Weather (Rock, Air, and Wind)	Continuous	Additive combination of variables describing overall weather conditions during surveys

Table 3 Variables for modeling habitat occupancy and abundance of collared lizards at the Konza Prairie Biological Station, Kansas. Asterisk indicates variable measured at three buffer sizes (5-, 60-, and 120-m)

Variable name	Variable type	Abbreviation	Description
Burn interval	Ordinal	burn	Burn treatment interval (1, 2, or 4 years)
Grazing treatment	Categorical	graze	Grazing treatment (grazed or ungrazed)
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	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)
Vegetation complexity	Ordinal	vegindex	Relative amount of grass, shrub, or tree cover (1–4)
Vegetation complexity	Categorical	vegcat	Presence of grass, shrub, or tree cover
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

microclimate, specifically temperature, which can affect the presence of collared lizards (Fitch 1956). We 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 (Beven and Kirkby 1979; Theobald 2007), 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 (Fitch 1956; McGuire 1996), we also calculated terrain irregularity (roughness) using a surface area ratio method by dividing surface area by planimetric area (Jenness 2004; Walters 2007). For each of these variables, we calculated either the percent (vegetation composition) or average and coefficient of variation (aspect, wetness, and roughness) at each lizard location within a buffer with a radius of 5 m. Variables measured within the 5-m buffer were thus considered representative of the local rock habitat, as a circle with a radius of 5 m mainly encompassed the rock outcrop. These geospatial variables were also measured at the hillside scale using buffers with radii of 60 and 120 m. The size of these buffered areas corresponds to longer movements within an individual's territory (60 m) and movements among territories (120 m).

Landscape variables refer to burning and grazing treatments, which are applied at a watershed scale at the KPBS (Fig. 1). Given the experimental landscape design of the KPBS, we were able to explore the interaction between grazing and burn interval, as well as parse out their relative influence, on collared lizard occupancy and abundance.

Beyond those locations where lizards were sighted, we also included a subset of randomly selected points within seemingly suitable outcrops (i.e., those that met our definition of "patch"; see above) where lizards were never detected ($n = 178$ of the 247 outcrops surveyed), and derived the same habitat measures at these points as for our lizard sites. Thus, our models are not based on presence-only data, but also include presence-absence data, which should enhance our ability to correlate collared lizard occupancy and abundance with measured habitat variables.

Prior to their inclusion in models, we *z*-standardized variables and conducted correlation analysis using SAS version 9.1 (SAS Institute, Cary, North Carolina). We found no significant correlations between any of our habitat variables (all $-0.7 < r < 0.7$).

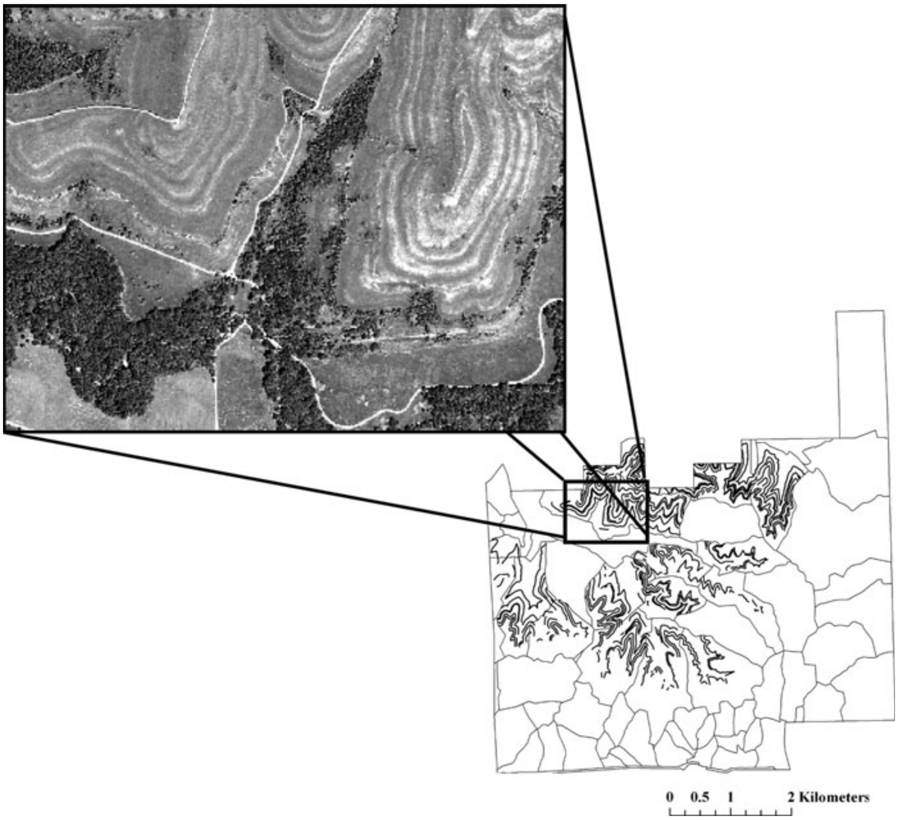
Model development and analysis

Because the 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), we first needed to evaluate what factors appeared to influence our ability to detect collared lizards (Table 2). For ectotherms, visibility and therefore detection probability are often dependent on variable temporal and environmental conditions such as temperature and humidity (Pough et al. 2003). 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; Kacoliris et al. 2009; Kéry et al. 2009).

Newer modeling methods based on multiple surveys for occupancy and repeat counts for abundance provide a method to simultaneously 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; Royle and Young 2008; Wenger and Freeman 2008). We thus developed and evaluated models of lizard abundance and detection based on maximum likelihood estimation of generalized linear models using the Royle repeated-count method (Royle 2004) implemented in the software PRESENCE version 2.4 (MacKenzie et al. 2002). As part of our model development, we identified factors affecting the probability of detection by constructing models with one of each detection variable (Table 2), and subsequently included those variables influencing probability of detection in our models for abundance (Table 4).

Adopting an information-theoretic approach (Burnham and Anderson 2002), we used multi-model selection and statistical inference to evaluate which model(s) best explained the relationship between our habitat variables and collared lizard occupancy and abundance. Rather than test all possible combinations of variables to identify a single best model, we developed a set of candidate models a priori that were constructed to evaluate which specific habitat variable(s), representing a nested hierarchy of scales (local habitat, hillside, and landscape), most influenced lizard occupancy and abundance (Table 3). Given our a priori expectation regarding the importance of landscape context on the occupancy patterns of collared lizards, and the experimental landscape in which this study was conducted, all models in our final analysis contained landscape variables (burn treatment, grazing treatment, and their interaction). We also constructed three models that contained multiple variables measured within 5-, 60- or 120-m buffers (Table 4). For the 5-m model, we included the

Fig. 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. Rock outcrops in this image are digitized from a contour-line data layer developed from a 2-m digital elevation model (see text)



number of refuges, height of the rock ledge, amount of rock cover, vegetation complexity, and watershed treatment. For the 60- and 120-m models (hillside scale), we included roughness, aspect, topographic wetness, percent shrub, and watershed treatment. Thus, we examined a total of 36 candidate models (Table 4, Supplementary Table 1).

Models were run using the logit link function with the assumption of a Poisson distribution of abundances and were ranked according to Akaike Information Criterion adjusted for small sample size (AIC_c). The model with the smallest AIC_c is considered the best model, although any model with ΔAIC <2 is considered to have strong support and is viewed as equally parsimonious. We also calculated Akaike weight (w_i) to determine the relative support for each model, which gives the probability that a given model is likely the best model upon repeated sampling (Burnham and Anderson 2002).

Because we included landscape context in each model (Table 4), we conducted additional analyses to determine the relative influence of burn and grazing treatments 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. Because some model estimates fell between 0 and 1, we calculated a threshold for determining if sites were occupied by minimizing the difference between sensitivity (i.e., the percentage of sites correctly classified as occupied by the model) and specificity (i.e., percentage of sites correctly classified as unoccupied by the model) (Cantor et al. 1999; Liu et al. 2005). Outcrops were considered occupied if abundance estimates were greater than or equal to the threshold value. We then 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), identified according to the criteria above, to examine the relative influence of burning and grazing treatment on abundance and patch occupancy. We determined total lizard abundance over all

Table 4 Design of models developed to identify factors influencing lizard abundance (and thus occupancy) at rock outcrops at Konza Prairie Biological Station, Kansas

Model	Detection	Abundance				
		None (Constant)	Landscape context[a]	Local rock habitat[b]	Hillside context[c]	Scale[d]
1	X	X				
2	X		X			
3	X		X			
4	X		X			
5	X		X			
6	X		X	X		
7	X		X	X		
8	X		X	X		
9	X		X	X		
10	X		X	X		
11	X		X	X		
12	X		X	X		
13	X		X	X		
14	X		X	X		
15	X		X	X		
16	X		X	X		
17	X		X	X		
18	X		X	X		
19	X		X	X		
20	X		X	X		X
21	X		X		X	
22	X		X		X	
23	X		X		X	
24	X		X		X	
25	X		X		X	
26	X		X		X	
27	X		X		X	
28	X		X		X	X
29	X		X		X	
30	X		X		X	
31	X		X		X	
32	X		X		X	
33	X		X		X	
34	X		X		X	
35	X		X		X	
36	X		X		X	X

Headings indicate the type of variables included in each model (cf. Supplementary Table 1)

[a] Landscape (watershed) context models include either burn frequency (B; $n = 1$), grazing (G; $n = 1$), their additive effect (B + G; $n = 1$), their interaction (B * G; $n = 1$), or the full-factorial (B + G + B * G; $n = 32$)

[b] Each local habitat model includes one of the variables presented in Table 3 ($n = 14$ models)

[c] Each hillside model ($n = 14$) includes one of the hillside characteristics presented in Table 3, which were assayed at two broader scales (60 m and 120 m), resulting in 7 models at each of these two scales (e.g., wet60 or wet120)

[d] Each "scale" model includes habitat or landscape variables measured by either the 5-, 60- or 120 m buffer ($n = 3$ buffer "scale" models)

surveyed watersheds by summing the abundance estimates for each rock outcrop from the model output. We compared any other variables that emerged 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 χ^2 tests of independence to determine the influence of burning and grazing treatments on habitat occupancy.

Results

Surveys

We recorded 501 lizard sightings during 2 years of study (2008 = 341; 2009 = 160). Of these, 250 (49.9%) were first sightings (i.e., lizards that were observed during the first survey of that outcrop or unmarked lizards of a sex or age not previously observed at that outcrop), 80 (16.0%) were repeat sightings of marked individuals (several individuals were resighted on multiple occasions), and 171 (34.1%) were of unmarked lizards. A small number of marked lizards were later resighted without marks (8 of 45 resighted lizards; 18%), but were identifiable as recaptures due to the presence of a small scar at the site of marking. 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 1). Within these 11 watersheds, the percentage of outcrops on which we detected lizards varied from 6 to 100%, with an average of 40% ± 7% SE ($n = 196$ outcrops). The majority of our sightings occurred in annually burned, ungrazed treatments (54%, $n = 501$ sightings), which represented 31% of the watersheds surveyed. 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 two models (year and survey) highly supported. The probability of detection was higher in the first year (41% ± 1% SE) than the second (22% ± 1% SE), and higher during the first survey of each year (2008: 44% ± 12% SE, 2009: 25% ± 12% SE) than during the second (2008: 38% ± 12% SE, 2009: 20% ± 12% SE). Among our set of abundance models, the 5-m model (which contained multiple local habitat variables) was the only candidate (AIC weight = 1) and included both local habitat characteristics (number of refuges: $\beta = 0.66 \pm 0.07$ SE; height of rock ledge: $\beta = 0.45 \pm 0.06$ SE; amount of rock cover: $\beta = 0.18 \pm 0.08$ SE; vegetation complexity: $\beta = 0.11 \pm 0.06$) and landscape context (burn interval: $\beta = 32.68 \pm 0.20$ SE; grazing treatment: $\beta = 32.54 \pm 0.16$; burning/grazing interaction: $\beta = -32.72 \pm 0.29$). Model prediction for average abundance at outcrops was 1.14 ± 0.19 SE lizards, with a maximum outcrop abundance of 22 and a KPBS total abundance of 282 (95% CI = 258–593). To convert our outcrop abundance estimates to occupancy estimates, we minimized the difference between sensitivity (69.7%) and specificity (90.6%) at a threshold equal to one. Using this threshold, the model predicted 33% occupancy at the rock outcrops we surveyed, somewhat larger than the naïve occupancy estimate of 28%. The model estimates for lizard abundance predicted an abundance >1 at only one outcrop in a watershed where lizards were never observed (N4D), suggesting a high accuracy for this model. The average estimates for habitat variables present in the top model were significantly higher in occupied than unoccupied outcrops ($t_{115} = 14.57$, $P < 0.001$), suggesting that they have similar effects on both occupancy and abundance.

Two of the 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 4 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. Only burning had a significant effect on the estimated average abundance ($F_{5,\ 241} = 4.43$, $P = 0.01$, ANOVA) or occupancy ($\chi^2_{2,\ 6} = 15.57$, $P < 0.001$) of collared lizards (Fig. 3). Among burn treatments, average abundance of collared lizards was significantly different only between annually and 4-year burned watersheds ($P < 0.05$, Tukey test). Examination of χ^2 adjusted residuals also indicated that habitat occupancy of collared lizards is different for 4-year burned watersheds (adjusted residuals >|2|). Although neither the ANOVA nor the χ^2 test found a significant overall effect of grazing, occupancy (and therefore abundance) differed between 4-year burned, grazed and ungrazed watersheds (Fig. 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 ($t_{50} = 1.87$, $P = 0.03$) and occupancy ($z = 2.06$, $P = 0.02$) were significantly different between the two treatments, indicating an effect of grazing on abundance and occupancy in 4-year burned watersheds.

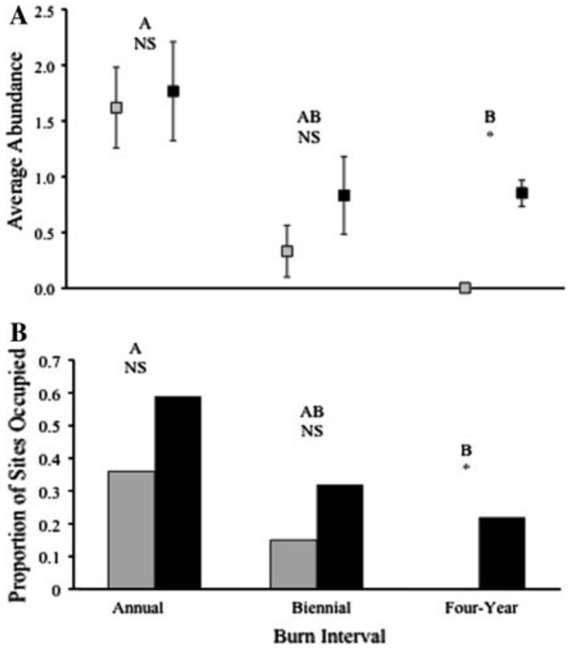


Fig. 3 Average abundance (**a**) and proportion of rock outcrops occupied (**b**) by collared lizards in managed tallgrass prairie as a function of burning interval and grazing treatment, based on model estimates. *Light gray* indicates ungrazed watersheds; *black* indicates grazed watersheds. Columns with the same letter are not significantly different ($P > 0.05$) for abundance (Tukey test) or occupancy (χ^2 test) based on a comparison of *burning 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*

Discussion

Understanding the effects of landscape structure 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 local habitat 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 (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 rock habitat characteristics (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 (Ruby 1986; Whitaker 1996). Refuges are an especially important habitat feature for collared lizards, because they provide protection from predators and are used as hibernacula during the winter (Fitch 1956). We also found that ledges higher above the hillslope or that have 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 the occupancy and abundance of collared lizards. More complex vegetation structure, such as from shrubs or trees, increased the likelihood of patch occupancy and the average abundance of collared lizards. In open grassland, some 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 contrast, collared lizard populations in Missouri Ozark glades are negatively impacted by tree cover or thick understory vegetation, but then these lizards occupy small rocky openings in what is otherwise forest, which is therefore a very different sort of landscape context than the predominantly tallgrass prairie system we studied (Templeton et al. 2001; Brisson et al. 2003). Further, our measure of vegetation complexity (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 rock outcrops appear to afford the associated vegetation some protection from fire (Weisberg et al. 2008). Nevertheless, these contrasting results regarding the effect of woody vegetation on collared lizards in different systems underscores once again that local habitat effects on abundance or patch occupancy may change in different landscape contexts.

In addition to the effects of local habitat characteristics, we found that landscape context also influenced patch occupancy and abundance of collared lizards in tallgrass prairie. We found a positive effect of burning, although the effect was significant only between annually burned and 4-year burned watersheds. Other studies have found both positive (Wilgers and Horne 2006; Cano and Leynaud 2010; Hellgren et al. 2010) and negative (Russell et al. 1999; Wilgers et al. 2006) effects of burning on lizards. These opposing effects are presumably due to differences in direct mortality rates and the effect of fire on vegetation (Russell et al. 1999). In the Missouri glades ecosystem within the eastern portion of the collared lizard's range, fire has also been shown to have a positive influence on occupancy patterns, allowing dispersal of individuals among rocky glades (Templeton et al. 2001).

Although two local habitat 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, these measures were likely biased by watershed treatment. Dense vegetation or litter that was not removed by fire or grazing likely obscured rock habitat and thus reduced our ability to assay these variables. Indeed, we did assess less rock cover and fewer refuges in watersheds that were burned less frequently or were ungrazed. However, it is highly unlikely that collared lizards would use ledges covered by litter or dense vegetation in any case because they require open rock habitat for basking (Fitch 1956). 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 4-year burned, grazed watersheds relative to 4-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 (4- or 20-year intervals) (Vinton et al. 1993), and bare ground is known to increase the abundance of xerically adapted lizards (Mushinsky 1985), by improving the suitability of habitat for lizards (Hellgren et al. 2010). Additionally, grazing may improve other habitat features. Jones (1981) found that sit-and-wait foraging lizards (like the collared lizard) had a significantly higher abundance in desert grassland when land was heavily grazed rather than lightly grazed by cattle, due to an increase in the amount of downed wood.

While many studies have noted that intense grazing may have a negative impact on lizard abundance, survival, richness, or community composition (Jones 1981; James 2003; Castellano and Valone 2006; Hellgren et al. 2010), bison graze at a more moderate intensity at KPBS, with a smaller herd size grazing year round than most cattle-grazed rangeland within the region (Hartnett et al. 1996; Towne et al. 2005). As such, bison grazing creates a more heterogeneous, structurally complex grassland than prairie heavily grazed by cattle in the Flint Hills (Knapp et al. 1999). Structural heterogeneity in vegetation produced by bison grazing (though not by burning) directly influences grasshopper densities, which may be more than twice as high in grazed watersheds compared to ungrazed areas (Joern 2004). With a higher density of prey, 4-year burned, grazed watersheds might be able to support collared lizards while 4-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$100 m; unpubl. data). However, we can provide some anecdotal evidence that the absence of collared lizards in 4-year burned, ungrazed treatments was apparently not due to dispersal limitation. Collared lizards were frequently observed in an annually burned, grazed watershed (N1A) at a rock ledge in close proximity ($\sim$10 m) to rock habitat in an adjacent 4-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 4-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 collard 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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