

CONTRIBUTED PAPER

The relative contributions of habitat area, configuration, and vegetative diversity on snake and lizard presence in agricultural landscapes

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Abstract

Nearly one in five reptile species is at risk of extinction. Changes in habitat area, its configuration, and vegetation diversity could affect habitat use, but their relative importance is understudied. We assessed how these factors affected reptile presence in agricultural landscapes figure in Iowa, United States, using 695 cover boards visited 16,441 times in 2015–2020. Species-wise encounter rates ranged 0.0001–0.012. Eight of 11 species and 54.2% of individuals were species of greatest conservation need. Habitat area, configuration, and vegetation diversity influenced reptile presence similarly. Mean patch occupancy was 0.18 for common garter snake (CG, *Thamnophis sirtalis*) and 0.45 for all snakes (AS). Naïve presence was explained by effort (odds ratio [OR]_{AS} = 1.83, OR_{CG} = 1.79), vegetation diversity (OR_{AS} = 1.28, OR_{CG} = 1.28), woody cover (OR_{AS} = 1.24, OR_{CG} = 1.41), and patch size (OR_{AS} = 1.30). Large patch prairies were more likely to contain snakes than other conservation practices ($\hat{r}_{\text{encounter}} = 0.291$), and more likely to contain CG (0.098) than prairie contour strips (0.031), waterways (0.018), grass contour strips (0.016), or terraces (0.015). While we documented low overall reptile presence, their higher presence in large prairie patches underscores the importance of core nature reserves for reptile conservation.

KEYWORDS

agroecology, *Diadophis punctatus*, fragmentation, Habitat Amount Hypothesis, *Pantherophis ramspotti*, *Plestiodon septentrionalis*, reptile presence, *Thamnophis sirtalis*

1 | INTRODUCTION

Worldwide, nearly one in five reptile species is at risk of extinction from effects of habitat loss, agricultural operations, urban development, and other modifications of natural systems (Böhm et al., 2013). Consistent with this trend, North American grassland snakes appear to be

undergoing declines (Brodman et al., 2002; Busby & Parmelee, 1996; Cagle, 2008). While a systematic review of their population dynamics is lacking, the grasslands they depend on have largely been replaced by agricultural land uses (Gallant et al., 2011; Samson & Knopf, 2006; White et al., 2000; Wright & Wimberly, 2013); 71.2% of the tall-grass prairie that existed at the time of Euro-American

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colonization in the United States has been converted to cropland (White et al., 2000).

The process by which large areas of contiguous habitat, such as North America's historical tallgrass prairie, becomes fragmented occurs through five mechanisms (Fahrig, 2003): habitat loss, decreased patch size, increased patch isolation, increased number of patches, and an increase in perimeter to area ratio (i.e., "increase in edge"). In the Habitat Amount Hypothesis, Fahrig (2013) argued that reduced species richness attributed to habitat fragmentation was fundamentally due to reduced habitat area, and all other metrics of fragmentation were unnecessary. This hypothesis and related processes are still active areas of research (Fahrig, 2017; Fletcher et al., 2018).

Habitat amount on the landscape has been demonstrated to be important for grassland snakes. Pernetta (2009) found that landscape grassland percentage surrounding heath patches was among the best predictors of the presence of the smooth snake (*Coronella austriaca*) in the United Kingdom, and Kapfer et al. (2010) found that home range sizes of bullsnakes (*Pituophis catenifer sayi*) increased as the amount of habitat on the landscape decreased in Wisconsin, United States.

The effect of habitat configuration on snake occurrence or habitat preference has been investigated by several authors. For example, small nature reserves were inadequate by themselves for large-ranging snakes who must venture outside of small patches to forage or look for mates (Driscoll, 2004; Nordberg et al., 2021) and for habitat specialists restricted from immigrating due to an inability to cross the matrix between isolated patches (Pernetta et al., 2011). Importantly, Pernetta (2009) found that patch size and habitat amount on the landscape were both predictive of snake presence, demonstrating a habitat amount effect at multiple scales simultaneously. We were unable to locate any studies investigating the effect of patch number on snake occurrence or habitat preference, but edge effects have been demonstrated to be important to snake habitat use. Carfagno and Weatherhead (2006) found that forest edges were preferred by Texas rat snakes (*Pantherophis obsoletus*) and racers (*Coluber constrictor*) in some regions, but not others. Studies on grassland snake use of edge habitat are less common, but DeGregorio et al. (2011) showed that eastern massasaugas (*Sistrurus catenatus*) and eastern foxsnakes (*Pantherophis vulpinus*) were both associated with forest-grassland edge habitats using different selection techniques. Whatever the specific mechanism, the process of fragmentation is typically viewed as detrimental to habitat quality, with the resulting small, isolated patches suspected as population sinks or ecological traps (Robertson & Hutto, 2006).

Aside from habitat amount and configuration, vegetation diversity may also be an important aspect of habitat quality. Two recent studies investigated the effect vegetation diversity had on snake abundance. Glass and Eichholz (2022) found that the relative proportion of forbs to grasses was an important predictor of snake relative abundance in Illinois, US grasslands. Mizsei et al. (2020) found that directly measured vegetation Shannon diversity had a negative relationship with abundance of meadow vipers (*Vipera ursinii*) and had no effect on three species of lizards in Hungary.

Reptiles are the second most imperiled taxa in Iowa, United States, with 83% of snake species and 100% of lizard species listed as state species of greatest conservation need (Iowa Department of Natural Resources, 2015). Iowa furthermore has some of the most extensively fragmented grasslands in North America (Gallant et al., 2011; Smith, 1998; Wright & Wimberly, 2013), with very little perennial vegetation and patch sizes ranging from thousands to thousands of hectares. Previous work (Lawrence et al., 2018; Steen et al., 2012) has focused on more intact landscapes (but see Kjoos & Litvaitis, 2001; Knoot & Best, 2011) or has not investigated effects of small patches (Cagle, 2008), but Iowa landscapes provide access to a spectrum of patch sizes. Agricultural grasslands in the region are furthermore dominated by cool-season exotic plant species, with scattered patches containing high-diversity prairie reconstructions. These ranges of habitat amount, configuration, and vegetation diversity offer an opportunity to compare the relative importance of these three aspects of snake habitat quality.

A variety of perennial vegetation conservation practices have been available to farmers for decades (Appendix S4), but relatively few studies of their habitat value for reptiles have been conducted (but see Kjoos & Litvaitis, 2001; Knoot & Best, 2011). Contour or buffer strips of prairie vegetation are a more recently available conservation practice and have been demonstrated to provide multiple ecological services (Schulte et al., 2017), including bird habitat, but no assessment has been made on their quality as reptile habitat. A better understanding of how snakes and lizards utilize new and existing conservation practices may improve wildlife managers' ability to conserve these taxa.

Our goals were to compare the relative importance of habitat amount, habitat configuration, and vegetation diversity on reptile presence in agricultural landscapes and to determine relative usage of agricultural conservation practices by snakes and lizards in the Midwestern United States. We also sought to fill a gap in knowledge of the relative importance of habitat characteristics to snakes in the Midwestern US region broadly, and to

assess the relative habitat value of specific agricultural conservation practices to snakes. To accomplish these goals, we estimated reptile occupancy and presence across a range of landscape grassland amounts, configurations, and vegetative diversities in small conservation practices (0.05–8 ha), on commercial-scale corn and soy farms, and on larger grassland restorations (8.1–60 ha) designed explicitly as nature reserves. We developed multiple competing hypotheses (Chamberlin, 1890) with mechanistic predictions on how habitat amount, configuration, and vegetative diversity could affect snake habitat use (Appendix S2), meeting the call for such predictions presented by Fletcher et al. (2018). We posited that if biodiversity is affected by habitat amount on the landscape, then the occurrence rates of individual species could be similarly affected, since species occurrences summed across a community forms the higher-order measures of biodiversity.

2 | METHODS

2.1 | Study sites

Our study sites were located within 100 km of Ames, Iowa, United States (Appendix S5) on row-crop farms growing corn (*Zea mays*) and soybeans (*Glycine max*) in monocultures for commercial production, using conventional practices for the region. Study sites were opportunistically selected for presence of prairie strips, contour grass strips, or large patch grasslands and most contained multiple conservation practices (Appendix S4). We defined conservation practices as prairie if they averaged at least 15 native plant species in more than half of vegetation surveys. Prairie patches contained plant species such as big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), wild bergamot (*Monarda fistulosa*), grayhead prairie coneflower (*Ratibida pinnata*), and golden alexanders (*Zizia aurea*) and non-prairie grasslands were dominated by cool-season exotic species such as smooth brome (*Bromus inermis*), reed canary grass (*Phalaris arundinacea*), Timothy grass (*Phleum pratense*) and Kentucky bluestem (*Poa pratensis*).

Landscapes surrounding farm sites were characterized by many small, low-diversity, isolated patches such as road ditches, grassed waterways, contour grass strips, grass filter strips, and grassed terraces, and most sites contained high-diversity prairie strips ranging from 0 to 12 years in age. The land cover within 1 km of our sites averaged 63.1% row crop (28.6–84.8%), 25.2% grassland (11.1–51.1%), 7.7% woody (0.9–15.6%), 3.1% developed (1.2–6.1%), and 0.9% water (0.16–2.7%) and landscapes

had average patch sizes of 1–7 ha. The two large patch grassland sites were more internally intact with mid-high-diversity plantings of 40–60 ha, a typical size for private prairie restorations in Iowa, and were also situated in more intact landscapes with higher percentages of grassland or forest cover.

2.2 | Sampling design

All grassy areas of farms were included in stratified sampling frames to determine locations for cover board artificial cover objects. In 2015, a sampling frame consisted of all grassy areas in a crop field, within which we randomly placed 12 cover boards a minimum of 10 m apart. This resulted in unequal sampling effort per conservation practice; thus, in 2016, we switched from fields to individual conservation practices as the sampling frame and located three cover boards at least 10 m apart in each conservation practice. Conservation practices were defined by vegetation community, management history, conservation purpose (Appendix S1) and edges with non-habitat areas (crop, roads, and water bodies). Monolithic conservation practices such as full-field restorations or large filter strips were broken into equal-area sampling frames no larger than 8 ha.

We rebalanced our sites in 2017 because we lost access to one private farm (MCC) and establishment-phase mowing of prairie strips continued longer than anticipated on other farms (GUT, RHO, WHI, and WOR; Appendix S4). To compensate, we added one site (INH) that contained a large prairie strip that would not be mowed and a large site (NIR) that contained many grassed terraces, which were limited at our existing sites. We also added two large patch prairie sites (SPI and TER). The final analysis contained data from 15 sites over 6 years for a combined total of 70 site “survey-years” (years individual sites were visited). Not all sites were used in every year and survey effort varied among sites and years (Table S3).

2.3 | Field methods

Cover boards were made from 1.27 cm thick 3-ply plywood or ordinated-strand board. The large majority were 0.6 m by 1.2 m with a few boards 0.85 m by 0.85 m, but all with the same area of 0.72 m². From 2016 to 2020 cover board locations were not altered, with boards replaced in the spring every 2–4 years. Cover boards were checked opportunistically when researchers were on-site between April and November 2015–2019; all coverboards were checked weekly in 2020.

When a board was checked, all reptiles present were counted and, when possible, captured to record age, sex, total length, snout-vent length, and mass. Snakes could generally be identified to species without capture, with the exception of some garter snakes (*Thamnophis* sp.). Snakes displaying clinical symptoms of Snake Fungal Disease (Allender et al., 2015; Clark et al., 2011) were discovered at multiple sites in 2016, so starting in 2017 any gear that contacted a study animal was sanitized with 99.8% isopropyl alcohol wipes between captures and hands were sanitized with 70% ethanol liquid hand sanitizer (Purell Advanced Hand Sanitizer, GOJO Industries, Inc., Akron, Ohio, USA). This study was conducted under Institutional Animal Care and Use Committee log number 2-16-8204-J.

We collected vegetation data in August of the first year a site was used and in 2019, or the last year a site was used. We placed a 1 m² quadrat by each cover board directly next to the least trampled long edge and estimated coverages of each plant species present and repeated 5 m away in the 0°, 120°, and 240° azimuthal directions. We also measured vegetation visual obstruction (as a correlate to vegetation density) using the Robel method (Robel et al., 1970) from approximately 1 m off the ground 5 m away from four directions.

Weather data were summarized from raw data downloaded from the Automated Surface Observing System (National Weather Service, 2022). Cover board check times were matched to the nearest weather station that gathered data for that timeframe, with mean site-to-station distance of 65.5 km (standard deviation [SD] = 21.9).

2.4 | Statistical methods

All analyses were conducted in R version 4.0-4.2 (R Foundation for Statistical Computing, 2020). To compare reptile diversity among conservation practices while accounting for unequal sampling effort, we used package “Rarefy” (Thouvenai et al., 2021) to calculate a spatially explicit richness rarefaction curve (Chao et al., 2014; Chiarucci et al., 2009) where each sample was one cover board visit.

All spatial data were curated in spatial software (ArcGIS Desktop 10.1–10.5, ESRI, Redlands, CA) and spatial measurements were conducted in R with packages “landscapemetrics,” “rgeos,” and “raster” (Bivand et al., 2017; Hesselbarth et al., 2019; Hijmans et al., 2022). A categorical land cover map was hand-digitized for each site based on high-resolution National Agricultural Imagery Program aerial imagery (Farm Service Agency, 2021) and light detection and ranging imagery (Iowa LiDAR

Consortium, 2021), and verified in-person. Differing amounts of grass land cover at our study sites was controlled for using interaction effects to isolate effects of configuration from the effect of habitat area.

Patch-level detection and occupancy were estimated using a maximum-likelihood framework (MacKenzie et al., 2002) in package “unmarked” (Fiske & Chandler, 2011). Primary periods were years (2015–2020), and secondary periods were weeks within the year. Each line of data ($n = 1$) represented all cover boards (median = 3) in a single conservation practice or portion of a conservation practice larger than 8 ha for a single year (one “patch survey-year”). A detection under any board in a conservation practice counted as a detection for that patch and secondary period. Variable effort among patch survey-years was captured through inclusion of the “board_flips” covariate on detection (Table 1).

Our covariate list (Table 1) was composed of variables from our a priori list of hypotheses (Appendix S2) and additional expert opinion variables thought to be important to occupancy to reduce un-modeled variation and improve our ability to resolve the relationships outlined in our hypotheses. Expert opinion variables included confounding variables (quadrats_mowed_percent), those found to be important in similar studies (woody_cover_ppn_##_m_r) (Glass & Eichholz, 2022), or those related to potential overwintering habitat (developed_##_m_r_ppn, distance_to_water_meters). Detection covariates included effort (number of board-turns), time of year, mean temperature, cloudiness, and total precipitation. Covariates on occupancy and naïve presence included vegetation richness and density, landscape configuration, and habitat area variables. Covariates on habitat amount and configuration were measured at ecologically relevant radii based on published home ranges (Fahrig, 2017). Habitat area variables included the proportion of the landscape in grassy, woody, and developed land cover. Habitat configuration variables included patch area, patch nearest neighbor, edge density, number of patches, and interactions with grass habitat amount. For common garter snakes, we used 650 m as the radius of interest (“##_m_r”) to center on one mean home range of 5.2 ha (Macartney et al., 1988) plus one rank of neighboring 5.2 ha home ranges. We also used a 650 m radius for snakes as a group, as common garter snakes were the most frequently encountered species. The second and third most commonly encountered species, western foxsnake and prairie ringneck snake, respectively had larger and smaller home ranges.

Very low detection rate estimates led us to also estimate naïve presence for each board survey-year using a generalized linear mixed model (GLMM) in package “glmmTMB” (Brooks et al., 2017) where presence was

TABLE 1 Occupancy and presence variables considered.^a

Variable	Description	Native units	Transformations considered	Category	Selected for final model list
grassland_area_##_m_r_ppn	Proportion of a ## m radius circle in grass land cover	Proportion	Linear, log , interaction	Landscape: patch habitat area	Occupancy, presence
patch_area_veg_ha	Area of patch using vegetation communities and 3 m pixels	ha	Linear, log , interaction	Landscape: patch size	Occupancy, presence
patch_area_mean_##_m_radius	Mean area of patches within ## m	ha	Linear, log , interaction	Landscape: patch size	Neither
patch_nearest_neighbor_veg_m	Distance to nearest similar-community patch	m	Linear, log , interaction	Landscape: isolation	Occupancy, presence
mean_nearest_neighbor_m_##_m_radius	Within ## m radius, the mean distance to nearest similar-community patch	m	Linear, log , interaction	Landscape: isolation	Neither
patch_count_##_m_radius	Count of distinct patches within ## m	Count	Linear, log , interaction	Landscape: patch count	Occupancy, presence
perimeter_area_ratio_veg_m_per_sq_m	Perimeter: Area ratio of patch using vegetation community definition and 3 m pixels	m	Linear, log , interaction	Landscape: edge effects	Neither
edge_density_m_per_ha_##_m_radius	Length of edge per unit area within ## m	m/ha	Linear, log , interaction	Landscape: edge effects	Occupancy, presence
vor_final_mean	Visual obstruction around cover board measured with a Robel pole from 5 m (10–150)	cm obscured	Linear, log , interaction	Vegetation: density	Occupancy, presence
species_richness_all_5m_total	Plant species count within 5 m of cover board	Count	Linear, log , interaction	Vegetation: diversity	Occupancy, presence
<i>Expert opinion variables</i>					
quadrats_moved_percent	Percent of quadrats mowed	Percentage	Linear, log , interaction	Confounding	Neither
woody_cover_ppn_##_m_r	Proportion of a ## m radius circle in woody land cover	Proportion	Linear, quadratic, log	Life history	Occupancy, presence
developed_##_m_r_ppn	Proportion of a ## m radius circle in developed land cover	Proportion	Linear, quadratic, log	Life history	Occupancy, presence
distance_to_water_meters	Distance to nearest water land cover	m	Linear, quadratic, log , interaction	Life history	Occupancy, presence
board_flips	Number of cover board flips (visits) per year	Count	Linear , log	Detection	Occupancy, presence
time	Numerical week-of-season trend	Week-of-season	None	Detection	Occupancy
cloud_cover_percent_daily_mean	Daily mean percent cloud cover	Percent	None	Detection	Occupancy

(Continues)

TABLE 1 (Continued)

Variable	Description	Native units	Transformations considered	Category	Selected for final model list
temperature_fahrenheit_daily_mean	Daily mean temperature	Degrees Fahrenheit	None	Detection	Occupancy
coverboardID	Individual cover board	Categorical	None	Random effects	Presence
sample_unit_areaID	Individual conservation practice	Categorical	None	Random effects	Neither
site_abbreviation	Site	Categorical	None	Random effects	Presence

^aLandscape variables used 650 m radius from cover board, denoted as “##” for snakes as a functional group and common garter snakes. Bold text “transformations considered” indicates the final transformation. Interactions were included for grassland area with patch area, patch count, and edge density. Variables were selected for the final model list in the presence analysis, occupancy analysis, or neither.

modeled as a binary response variable (presence/absence). Each line of data ($n = 1$) represented the aggregated result of multiple visits to a single board over a calendar year (a “board survey-year”). Covariates on presence were the same as those in the occupancy model, including the number of times each board was visited that year (Equation S2, Appendix S3). To control for spatial autocorrelation and pseudo-replication, we included random effects for site and cover board.

For both modeling approaches, we developed a fully parameterized global model and vetted them against model assumptions (after Zuur et al., 2010, see Appendix S1), removing a small number of variables that caused the model to substantially violate model assumptions. Log transformations were used for all explanatory variables unless residuals indicated a lack-of-fit.

After vetting the preferred global model (Appendix S1), additional expert opinion variables were eliminated if they did not improve model AICc to keep the all-subsets model list within computational limits. Goodness of fit for the single-season occupancy global model was assessed with a parametric bootstrap implemented in “unmarked” (Fiske & Chandler, 2011) and the naïve presence global model was assessed as R^2_{GLMM} using the delta method ($p_{tb} > t_0$, Nakagawa et al., 2017). To compare the effect size of each variable on the parameter of interest, we exponentiated the beta parameter estimates from the global model and their 95% confidence intervals (CI) to give odds ratios (OR) to express effect size and direction (Rita & Komonen, 2008). Because all variables were centered and scaled, their effect sizes were directly comparable (Schielzeth, 2010).

To predict occupancy and presence across conservation practices and other variables of interest, we then developed a model list of all possible subsets of the global model, fit each model, and calculated an AICc value (Burnham & Anderson, 2002). To reduce the number of models and improve computation time, we then trimmed the all-subsets model list to those models comprising 95% of the cumulative AICc model. Using this model list, we predicted the parameter of interest (and associated standard error) for each model at the observed mean values for each conservation practice. We then calculated weighted averages of the predictions using AICc model weight and made predictions across the range of observed values for variables of interest.

We were able to make meaningful estimates of presence for all snakes as a functional group and for the most common species (common garter snake). Although the predictions were less informative, we also include results for western foxsnake, ringneck snake, Dekay's brown snake, and Northern prairie skink as baseline data (Appendix S5). We present 90% CI on presence estimates to improve our ability to highlight subtle relationships in

a complicated system, while acknowledging this increases the Type I error rate compared to an alpha level of 0.05, and thus interpretation of the results should be treated appropriately. Because all our sites were privately owned, we present summary statistics by site code or county to protect the owners' identity. Project raw data, formatted data, and analysis code are available at <https://doi.org/10.25380/iastate.25250839>.

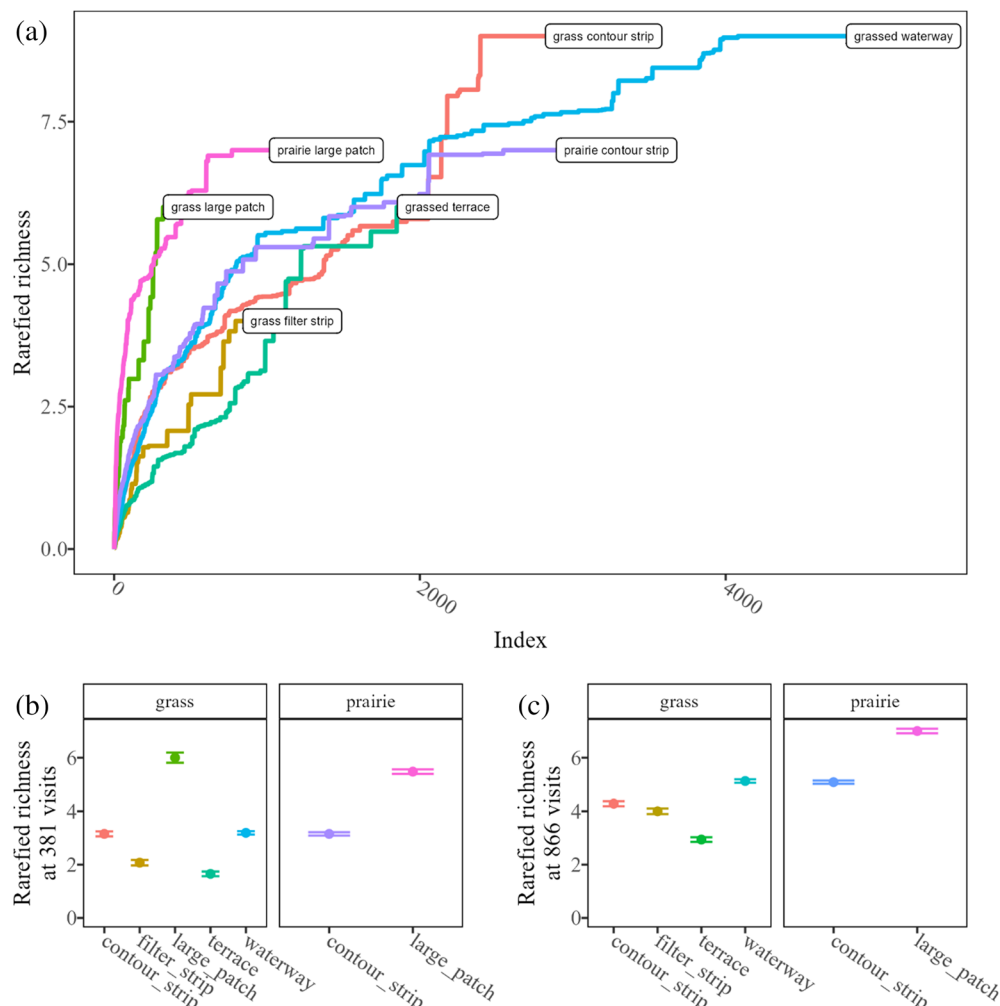
3 | RESULTS

We flipped 695 cover boards at 15 sites a total of 16,441 times from 2015 to 2020. In years sites were used (not all sites were used each year), sites were visited 1–30 days per year (mean = 11.4, SD = 7.1; Appendix S4) and individual boards were checked 1–21 (mean = 6.4, SD = 4.5) times per year. We encountered 10 species of snakes and one species of lizard, but encounter rates were very low (Appendix S4), with non-zero species-by-county board-flip encounter rates ranging from 0.0002 to 0.12. Project-wide encounter rates were highest for common garter

snakes (0.012) and western foxsnakes (0.0069) and lowest for bullsnakes, smooth green snakes, and western ribbon snakes with a single capture each (0.0001). Seven of the 10 species of snakes and the only lizard species we encountered (Appendix S4) were Iowa species of greatest conservation need (Iowa Department of Natural Resources, 2015). Species of greatest conservation need thus comprised 54.2% of encounters.

Uncorrected richness varied from one to seven species per county, and species richness per 100 board-flips varied from a low of 0.15 after 4713 board-flips to a high of 1.78 after 338 board-flips. We used a richness rarefaction curve to correct for unequal sampling effort (Figure 1a) and found that large patches of prairie and grass had the highest species richness (5.5–6) after 381 visits; prairie contour strips, grass contour strips, grass filter strips, and grassed waterways had intermediate (2.1–3.2) species richness; and grassed terraces had the lowest species richness (1.7; Figure 1b); the same relationships held at more than double the number of board visits (Figure 1c). Species accumulation leveled off (Figure 1a) for grassed waterways, grass contour strips, prairie contour strips,

FIGURE 1 Rarefaction curve of reptile species richness by cover board and conservation practice where each sample is one cover board visit. All conservation practices were rarefied to their maximum number of board-turns (a) and equal-effort estimates of richness with 95% confidence intervals for the conservation practice with the lowest (b) and second lowest (c) number of board-turns. “Grass” practices were dominated by low diversity, nonnative, cool-season plant species, while “prairie” practices were composed of higher diversity, native plant species.



and prairie large patches, but did not clearly do so for grassed terraces, grass filter strips, or large grass patches, suggesting we may have found more species in the latter practices with greater sampling effort.

3.1 | Single-season occupancy

We used the same single-season occupancy global model (Equation S1, Appendix S3) for snakes as a group and common garter snakes. The mean predicted occupancy rates from the global model were 0.46 for snakes as a group (prediction interval [PI] 95% = 0.33–0.59) and 0.18 for common garter snakes (PI_{95%} = 0.08–0.34). Mean detection rates predicted from the global model were 0.12 for snakes as a group (PI_{95%} = 0.09–0.16) and 0.08 for common garter snakes (PI_{95%} = 0.05–0.14). When we attempted to fit all subset models for both snakes as a group and for common garter snakes, many combinations of variables failed to estimate due to low detection rates (Durso et al., 2011; Steen, 2010). Because of this, we limited our exploration of detection-corrected occupancy to the global model and simplified our approach for making individual covariate predictions to naïve presence using a GLMM to allow variable importance to factor into effect sizes. We present implications of this decision in the discussion.

3.1.1 | Occupancy for snakes as a group

We encountered at least one snake in 241 of 851 patch survey-years and at every site. The detection-corrected global model for snakes as a group fit the data well ($p_{tb>t0} = 0.56$) and predictions made from the global model using the input data produced mean occupancy estimates by patch for all snake species combined of 0.45 (range = 0.23–0.90, SD = 0.12). The global model contained two significant covariates: patch nearest neighbor (OR = 1.61, CI_{90%} = 1.13–2.31) and amount of developed land cover nearby (OR = 0.75, CI_{90%} = 0.60–0.93; Figure 2). The only significant predictor of detection probability was number of board-flips per week (OR = 1.21, CI_{90%} = 1.14–1.30; Figure 2).

3.1.2 | Occupancy for common garter snake

We encountered common garter snakes in 76 of 851 patch survey-years and at 13 of 15 sites. The detection-corrected occupancy global model for common garter snakes fit the data well ($p_{tb>t0} = .47$) and predictions made from the global model using the input data produced mean occupancy estimates by patch for common garter snakes of 0.18 (range = 0.03–0.79, SD = 0.13). Important covariates on occupancy in the global model included

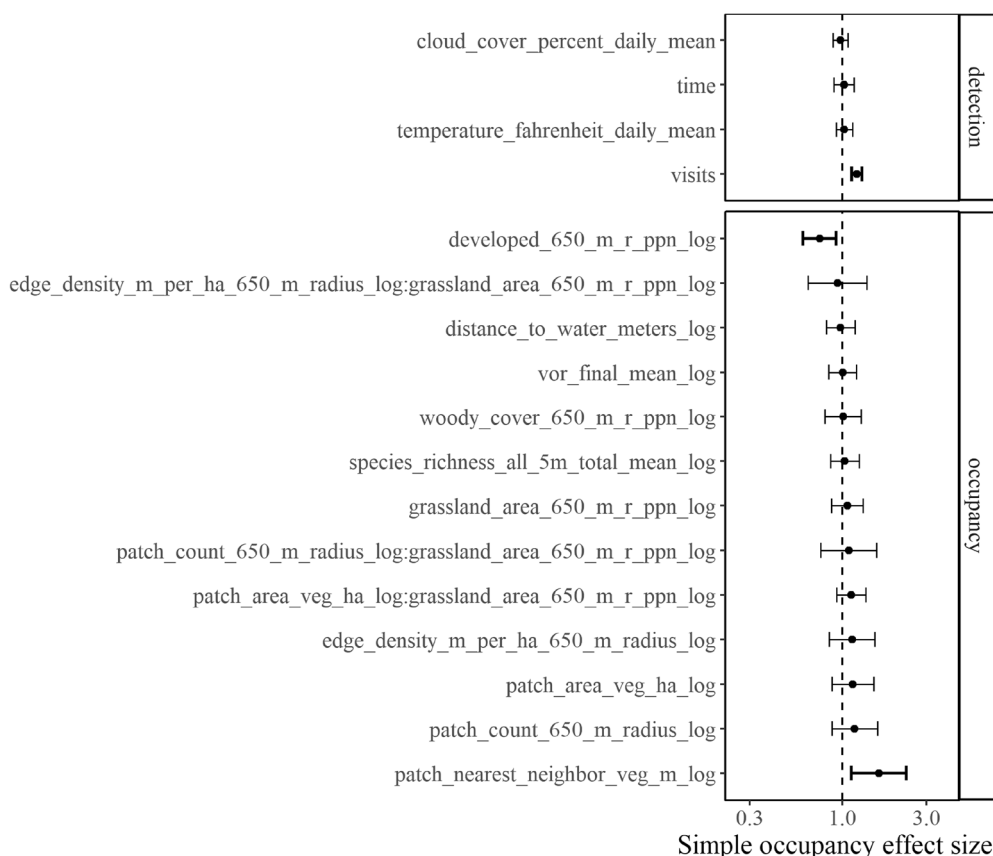


FIGURE 2 Snake suborder single-season detection and occupancy effect sizes expressed as odds ratios with 90% confidence intervals (CI). Bolded CI do not cross one and were significant at $\alpha = 0.1$.

developed land cover within 650 m (OR = 0.68, $CI_{90\%}$ = 0.50–0.92), distance to nearest water body (OR = 1.38, $CI_{90\%}$ = 1.01–1.89), patch nearest neighbor (OR = 1.52, $CI_{90\%}$ = 1.03–2.24), and patch count within 650 m interacting with grass land cover amount (OR = 1.72, $CI_{90\%}$ = 1.13–2.60; Figure 3). The only important predictor of detection probability was number of board-flips per week (OR = 1.30, $CI_{90\%}$ = 1.12–1.50; Figure 3).

3.2 | Presence

3.2.1 | Snakes as a group

We encountered at least one species of snake in 336 of 2845 board-years and at every site. The naïve presence global model explained 10.6% (marginal) and 18.6% (conditional) of the variance in the data. Random effect SDs were 0.79 (site_abbreviation) and 0.23 (coverboardID) with individual intercepts for the site ranging from –1.3 (SMI) to 1.2 (WOR) (Appendix S5). After fitting all possible subset models of the global model, we trimmed the model list to the 454 models containing the top 95% of the AICc model weight.

There were several significant covariates in the naïve presence global model (Figure 4). Interactions between

grassland habitat amount and edge density (OR = 0.68, $CI_{90\%}$ = 0.50–0.92; Figure 5a,b) and patch area (OR = 1.30, $CI_{90\%}$ = 1.08–1.56; Figure 5c); developed land cover within 650 m (OR = 0.70, $CI_{90\%}$ = 0.58–0.86; Figure 5d); vegetation visual obstruction (OR = 0.88, $CI_{90\%}$ = 0.78–1.00; Figure 5e); vegetation diversity (OR = 1.28, $CI_{90\%}$ = 1.12–1.46; Figure 5f); and survey effort (OR = 1.83, $CI_{90\%}$ = 1.62–2.06; Figure 5g) were all significant at α = .1, although the predicted change in probability of presence for snakes as a group was minimal for several covariates (Figure 5).

Large patch prairies were more likely to have snakes present (0.29, $CI_{90\%}$ = 0.19–0.42; Figure 5h) than other conservation practices. Other conservation practices were all approximately equally as likely (0.07–0.13, $CI_{90\%}$ _total = 0.04–0.19) to have snakes present under an average board in a given year (Figure 5h).

3.2.2 | Common garter snake

We encountered at least one common garter snake in 116 of 2845 board-years and in every study site county except Linn and Audubon (Table S4, Appendix S4). The naïve presence global model explained 6.8% (marginal) and 10.4% (conditional) of the variance in the data.

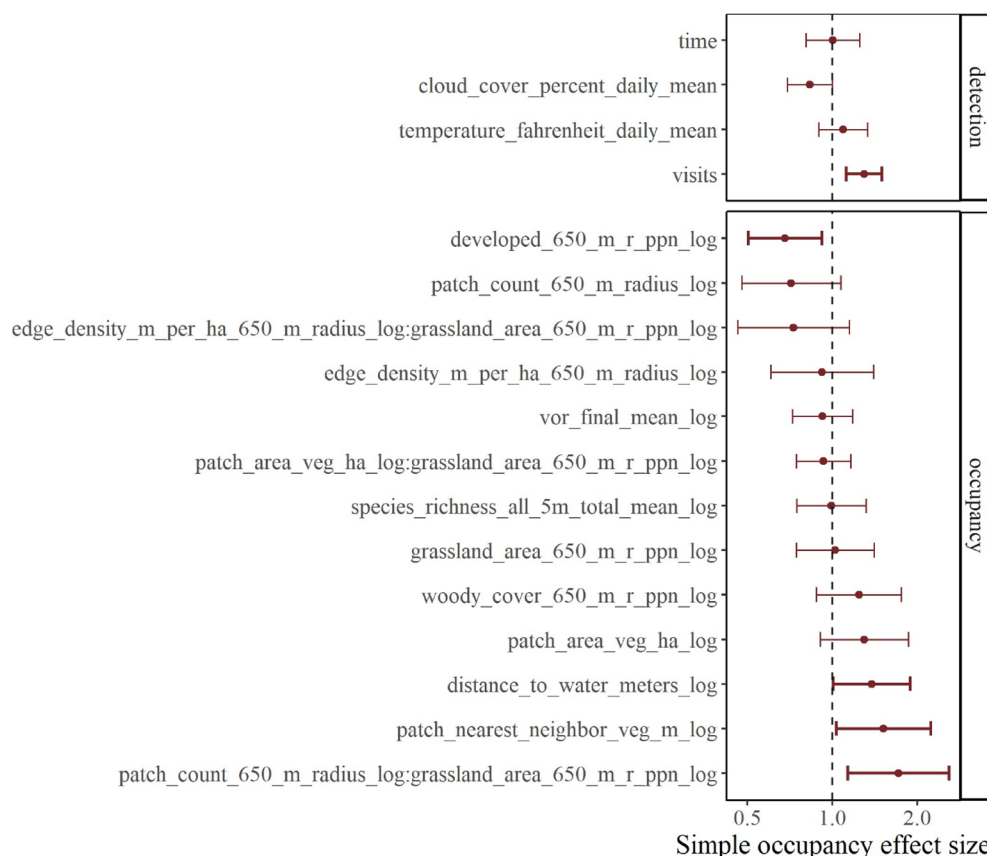


FIGURE 3 Common garter snake (*Thamnophis sirtalis*) single-season detection and occupancy effect sizes expressed as odds ratios with 90% confidence intervals (CI). Bolded CI do not cross one and were significant at α = .1.

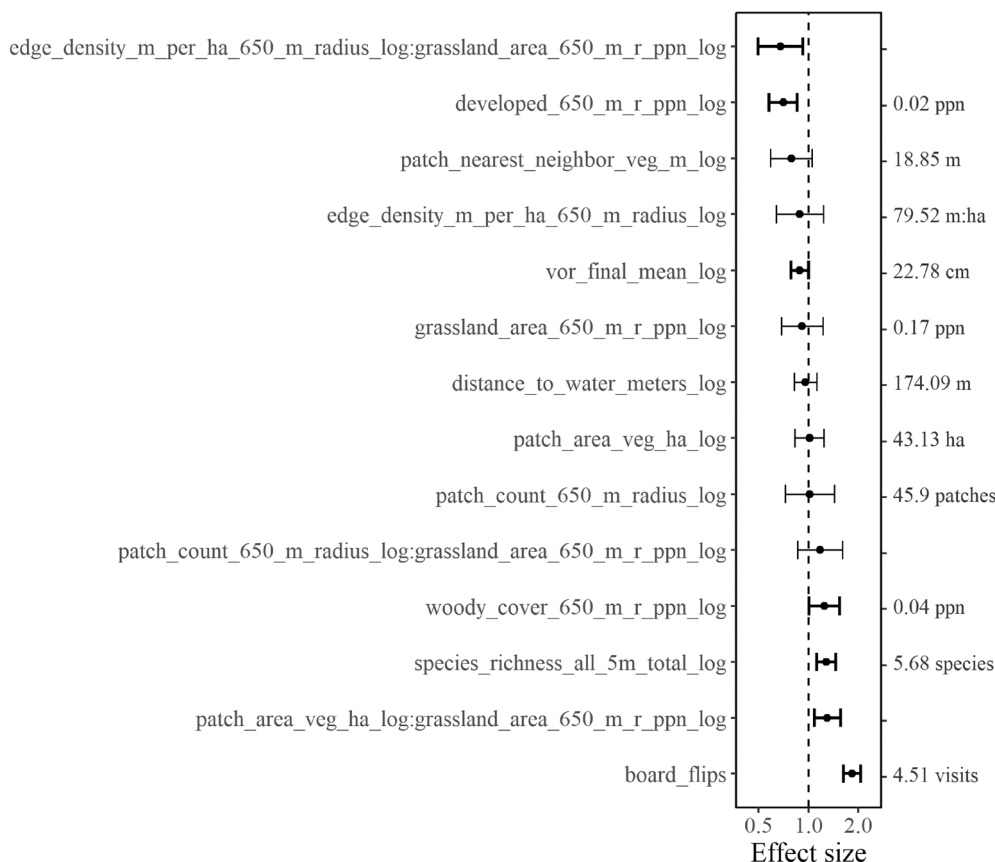


FIGURE 4 Snake suborder presence effect sizes expressed as odds ratios with 90% confidence intervals (CI). Bolded CI do not cross one and were significant at $\alpha = .1$. A one standard deviation (SD) change (right axis) in the predictor variable multiplied the odds of apparent occupancy by the effect size. SDs not listed for interaction terms.

Random effect SDs were 0.77 (site_abbreviation) and 0.0001 (coverboardID) with individual intercepts for the site ranging from -1.0 (SMI) to 1.1 (TER) (Appendix S5). After fitting all possible subset models of the global model, we trimmed the model list to the 1240 models comprising the top 95% of the AICc model weight.

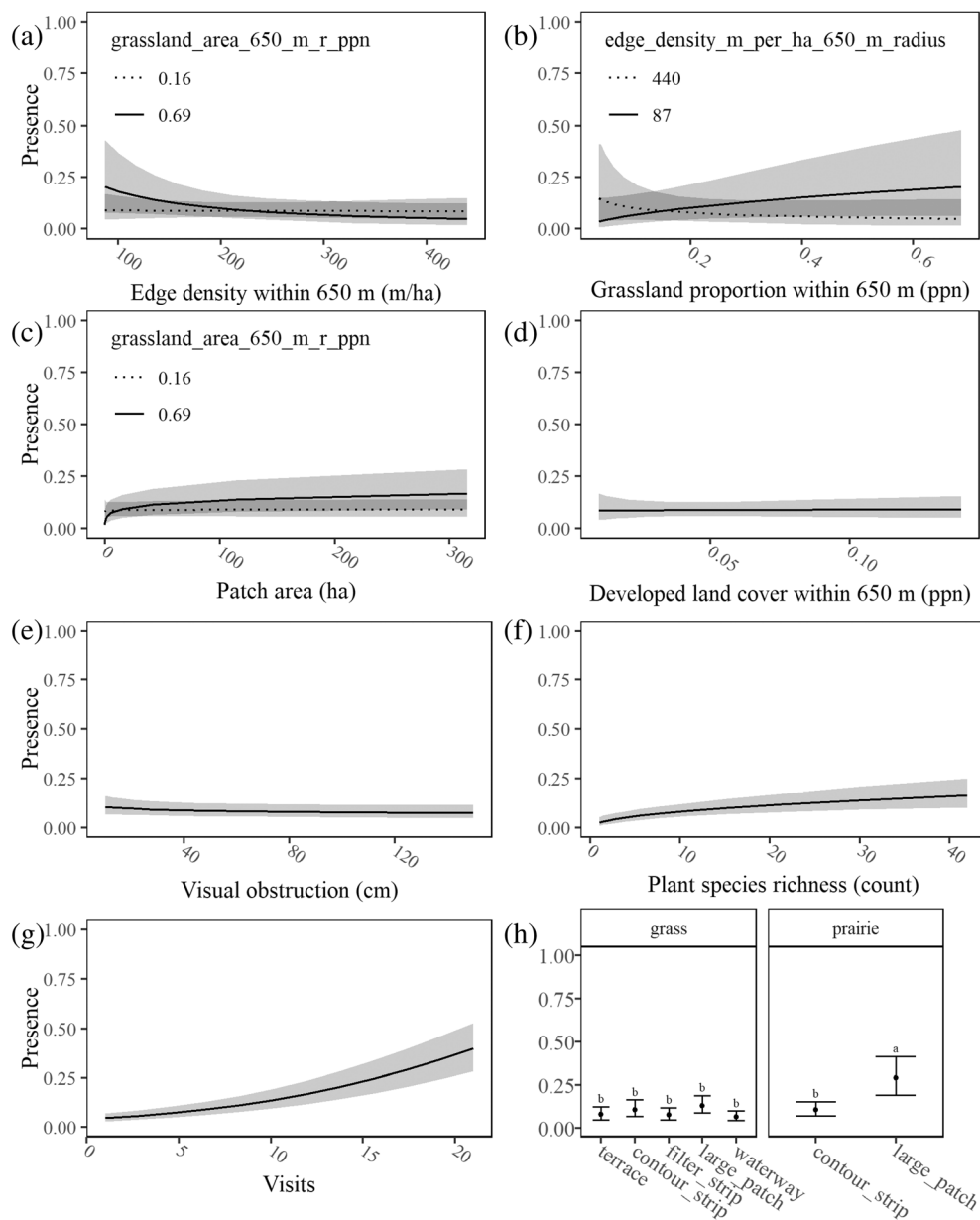
There were several significant terms in the naïve presence global model (Figure 6). Edge density interacting with grassland amount (OR = 0.60, $CI_{90\%} = 0.38–0.94$; Figure 7a,b), as well as main effects for edge density (OR = 0.60, $CI_{90\%} = 0.37–0.97$), vegetation visual obstruction (OR = 0.83, $CI_{90\%} = 0.68–1.00$; Figure 7e) vegetation diversity (OR = 1.28, $CI_{90\%} = 1.03–1.60$; Figure 7f), and survey effort (OR = 1.79, $CI_{90\%} = 1.48–2.15$; Figure 7g) were all significant at $\alpha = .1$, although the predicted change in probability of common garter snake presence was minimal for several covariates (Figure 7).

Large patch prairies were more likely to have common garter snakes present (0.10, $CI_{90\%} = 0.05–0.21$) than prairie contour strips (0.03, $CI_{90\%} = 0.02–0.06$), grassed waterways (0.02, $CI_{90\%} = 0.01–0.03$), contour strips (0.02, $CI_{90\%} = 0.01–0.03$), or terraces (0.01, $CI_{90\%} = 0.006–0.029$), but had similar probabilities of presence as large patch grasslands (0.06, $CI_{90\%} = 0.03–0.10$) and grass filter strips (0.04, $CI_{90\%} = 0.02–0.08$; Figure 7h).

4 | DISCUSSION

We found low occurrence and diversity of snakes and lizards in perennial conservation practices in extensively cropped landscapes in Iowa, United States. Many of the species we encountered were historically locally abundant over a large geographic range in several habitats (Iowa Department of Natural Resources, 2015; Rabinowitz, 1981). Their relative absence from our study sites is indicative of the degree of habitat alteration, and their inability to adapt to the novel, highly fragmented landscapes with a low amount of habitat. Larger prairie reconstructions seemed to be the core snake habitat at sites we surveyed, with significantly higher presence (Figures 5h and 7h) and richness (Figure 1c) than smaller, more fragmented conservation practices. Our conservation practice sampling was imbalanced, however, with only two large prairie sites and inference to other study systems is limited due to non-random site selection. Due to a dearth of research on reptiles in agricultural landscapes, there are few studies to compare to our results. We found fewer snakes in grassed waterways (Figures 5h and 7h) than Knoot and Best (2011), who estimated a 77% occupancy rate for snakes as a group and 58% occupancy for common garter snakes in one southeastern

FIGURE 5 Snake suborder board survey-year presence predicted by (a) edge density within 650 m, (b) grassland habitat amount within 650 m, (c) patch area, (d) developed land cover within 650 m, (e) visual obstruction as a correlate of vegetation density, (f) plant species richness, (g) number of visits, and (h) by conservation practice. Ninety percent prediction intervals are indicated by the shaded area (a–g) and whiskers (h). Groups that do not share letters were significantly different at $\alpha = .1$ (h). “Grass” practices were dominated by low diversity, nonnative, cool-season plant species, while “prairie” practices were composed of higher diversity, native plant species (h).



Iowa county. Glass and Eichholz (2022) estimated detection-corrected occupancy rates of 0.12–0.86 for eight snake species in nearby southern Illinois, United States. Their study landscape was substantially different from ours, however, being conducted on a single 1824 ha state wildlife management area with up to 75% trees within 400 m.

One explanation for why snake presence was low in conservation practices could be that patches without hibernacula underwent annual extinctions and had low recolonization rates. Harvey and Weatherhead (2006) found that for eastern Massasaugas in Ontario, Canada, microhabitats such as refugia and hibernacula were better at describing habitat selection than landscape-scale habitat variables. Within-patch woody cover was the best

predictor of snake presence in a study in southern Illinois (Glass & Eichholz, 2022).

The effect of missing microhabitats could be compounded by a hypothesized reluctance among snakes and lizards to cross barren crop ground in the spring, resulting in low recolonization rates (Appendix S2). Our results provided only mixed support for this hypothesis. Our isolation metric—patch nearest neighbor—was a significant positive predictor of detection-corrected occupancy for both snakes as a group and common garter snakes (Figures 2 and 3), but with a non-significant negative effect on naïve presence for snakes as a group and only a weak negative effect with broadly overlapping CI for common garter snake naïve presence (Figures 4 and 6). On balance, the evidence was stronger for a positive

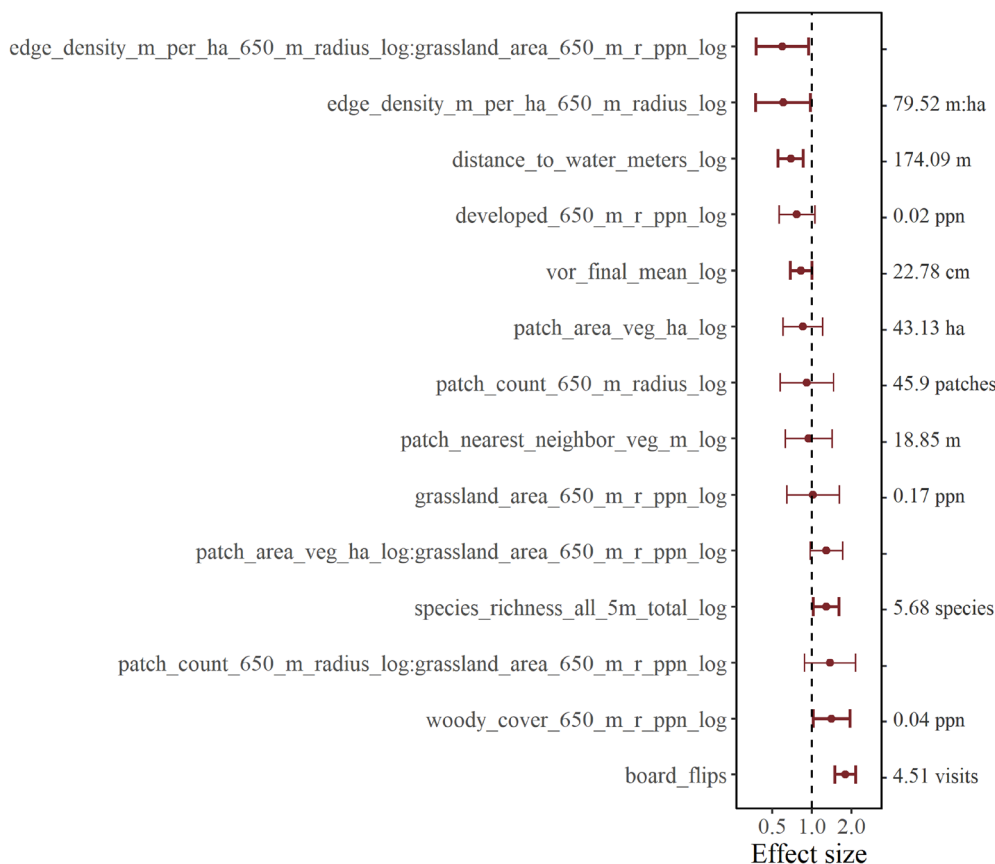


FIGURE 6 Common garter snake (*Thamnophis sirtalis*) presence effect sizes expressed as odds ratios with 90% confidence intervals (CI). Bolded CI do not cross one and were significant at $\alpha = .1$. A one standard deviation (SD) change (right axis) in the predictor variable multiplied the odds of apparent occupancy by the effect size. SDs not listed for interaction terms.

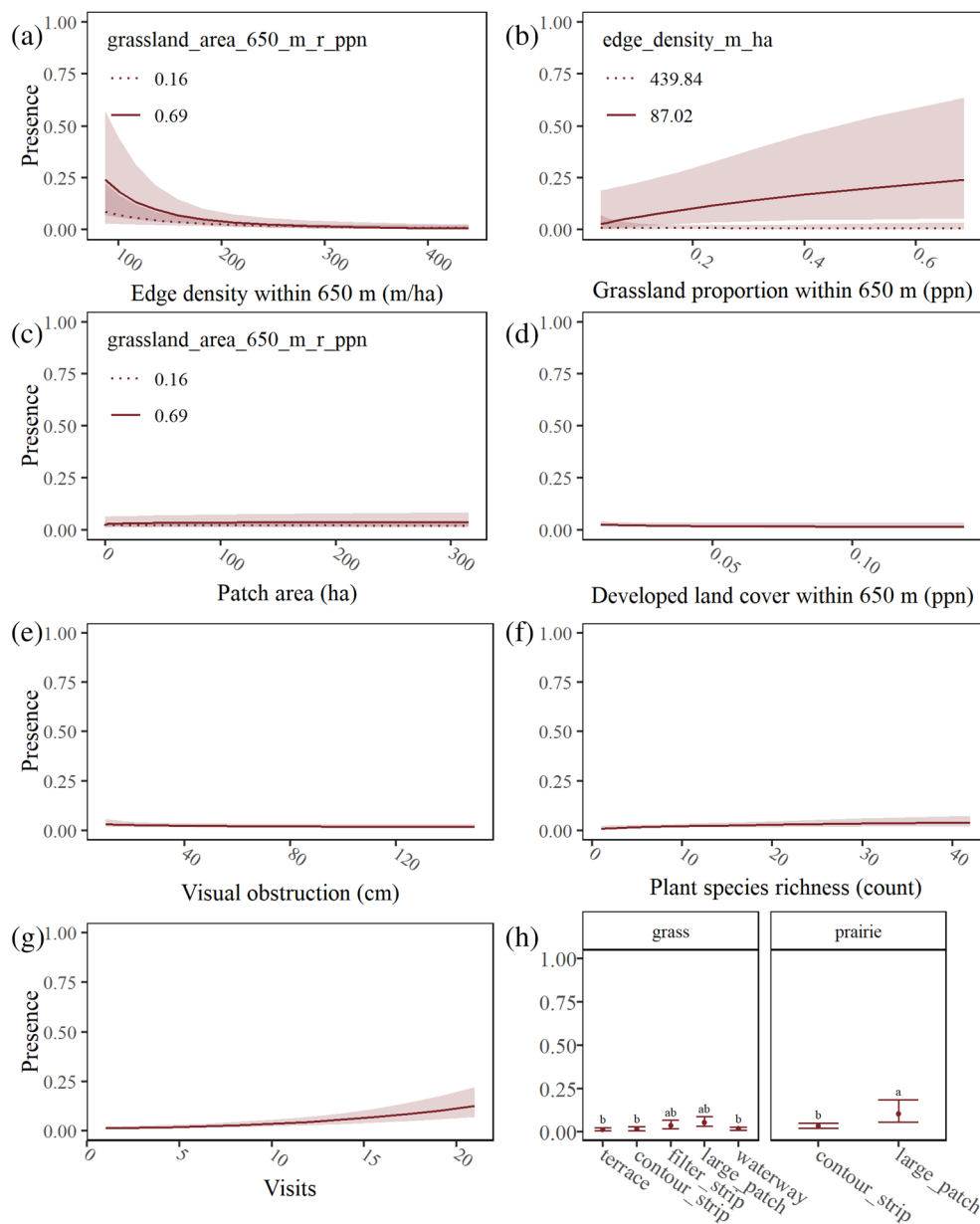
effect of patch isolation on occupancy. Our single-season detection-corrected occupancy analysis for this variable may not have captured some important nuance, however: for snakes as a group, only 2 of the 19 patch survey-years (six patches at four sites) with a patch nearest neighbor distance more than one SD above the mean had captures in consecutive years. This suggests that snakes that colonized the most isolated patches were recaptured repeatedly over the season but did not overwinter or return the next year. We were unable to test this hypothesis using a multi-year robust design occupancy framework due to low detection rates.

Unwillingness to cross a hostile matrix has been proposed as a driver of snake occupancy. For example, Pernetta et al. (2011) found evidence of genetic isolation of the smooth snake (*C. austriaca*) in southern England, indicating a persistent inability to cross modest (<6 km) distances of non-habitat. A prior patch occupancy study, however, Pernetta (2009) indicated that patch size and habitat amount were more important than isolation. Prugh et al. (2008), in an exhaustive meta-analysis, furthermore found that patch size and isolation were both generally poor predictors of species' presence, although they did find that when isolation was predictive, the type of land cover in the intervening matrix had a strong effect on the sensitivity of species to patch isolation.

Regarding the Habitat Amount Hypothesis (Fahrig, 2013), our data suggest that configuration matters. We did not find a strong effect of grassland habitat amount on snake occupancy (Figures 2 and 3) or presence (Figures 4 and 6), but we did consistently see a strong interaction effect between grassland habitat amount and edge density (Figures 5a,b and 7a,b). We expect that having large amounts of habitat or low-edge-density landscapes were not enough separately; snakes in our study landscapes needed both high habitat amounts and low-edge densities to be present at higher rates. This could be another indication that snakes avoided barren crop ground. We also found weak positive effects of woody land cover amount (Figures 4 and 6) and similarly weak negative effects of developed land cover proportion on overall snake presence (Figures 5d and 7d), although not significantly so for common garter snakes. These trends were also present in our detection-corrected occupancy analysis (Figures 2 and 3) and generally agreed with Glass and Eichholz (2022), who found snake relative abundance increased with the amount of woody and grass cover within 400 m.

We encountered snakes more frequently in high grass land cover landscapes that had larger patches of prairie or grass cover, but patch size did not have an ecologically meaningful effect in low grass land cover landscapes

FIGURE 7 Common garter snake (*Thamnophis sirtalis*) board survey-year presence predicted by (a) edge density within 650 m, (b) grassland habitat amount within 650 m, (c) patch size, (d) developed land cover within 650 m, (e) visual obstruction as a correlate of vegetation density, (f) plant species richness, (g) number of visits, and by (h) conservation practice. Ninety percent prediction intervals are indicated by the shaded area (a–g) and whiskers (h). Groups that do not share letters were significantly different at $\alpha = .1$ (h). “Grass” practices were dominated by low diversity, nonnative, cool-season plant species, while “prairie” practices were composed of higher diversity, native plant species (h).



(Figure 5c). There was no ecologically meaningful effect of patch size on common garter snake presence (Figure 7c). Patch size also had a weakly positive, but not statistically significant, effect for snakes as a group and common garter snakes in our detection-corrected occupancy models (Figures 2 and 3). Our finding of patch size as a modest predictor of snake occupancy agreed with similar studies on snakes (Kjoss & Litvaitis, 2001; Pernetta, 2009), but not a larger meta-analysis that included many vertebrate (including 50 species of lizard, but not snake) and invertebrate taxa (Prugh et al., 2008).

Vegetation richness was a significant positive predictor of snake presence, with a modest effect size for snakes as a group (Figure 5f) and a weak effect for common garter snakes (Figure 7f). Vegetation richness was not a

significant variable in our global model for detection-corrected occupancy (Figures 2 and 3). We could only locate one other test of directly measured plant species richness on the presence or abundance of snakes or lizards, although other studies have hinted at such an effect. Mizsei et al. (2020) found that vegetation Shannon diversity negatively predicted the presence of meadow vipers (*V. ursinii*) in Europe, but was not predictive for three species of lizards. Glass and Eichholz (2022) found that snake relative abundance decreased with forb percent cover, which could be positively correlated with vegetation diversity in our study landscapes.

Despite considerable survey effort, our ability to fit subset models of our occupancy global model was hampered by low detection rates (Durso et al., 2011;

Steen, 2010), limiting our ability to examine collinear habitat variables in isolation from one another. To avoid further simplifying the global model and lose our ability to tease apart collinear effects, we chose to examine individual variables in a simple presence framework. While this limited our ability to partition variation due to detection probability, the occupancy global model fit the data well with only survey effort and weather as detection-related covariates. Weather was unbiased toward any of our predictor variables, and we included survey effort as a variable in our presence model to account for unequal sampling effort.

In addition to low detection rates, the rarity of individual species also caused us to analyze all snakes as a single taxonomic group rather than as individual species, with the exception of common garter snakes, the most common species we encountered. This decision was validated by an improved model fit for snakes as a group compared with our largest single-species group, indicating that lumping species together gained more in sample size than it sacrificed in noise due to differences among species (Smith et al., 2019). We expect the results of our analysis on presence of snakes as a taxonomic group to be useful to conservation planners specifically because it is broad (Norton, 1998). The results provided by such a combined study highlight the commonalities among species that are more similar to one another in physiology, dispersal, and life-history requirements than to other taxonomic groups that are more common conservation foci (Smith et al., 2019).

Future studies may benefit from higher detection rates, perhaps from locating study sites in landscapes expected to have larger snake and lizard populations, or by integrating multiple survey protocols such as drift fences, pitfall traps, metal artificial cover objects, or visual encounter surveys. Using multiple survey techniques could also increase the likelihood of finding species that rarely use cover boards or other artificial cover objects.

In this study, we provide evidence that snakes and lizards occur in agricultural conservation practices at low rates compared with larger patches of restored prairie. Habitat area, configuration, and vegetation diversity all influenced reptile presence with approximately equal effect sizes. We encountered snakes at higher rates in landscapes with more grass land cover, lower edge densities, larger patch sizes, and higher-diversity vegetation. Conservation planners could consider incorporating important microhabitats such as refugia and hibernacula in agricultural conservation practices to improve habitat value for reptiles. Even if reptiles are not the highest conservation priority in these landscapes, improving the connectivity among nature reserves could be beneficial.

Over half the species we encountered were species of greatest conservation need, demonstrating that at-risk species still use these landscapes and indicating these may be areas for conservation consideration. To preserve the presence of rare and declining terrestrial reptiles, larger core nature reserves may be necessary in low habitat amount, highly fragmented agricultural landscapes.

AUTHOR CONTRIBUTIONS

MDS conceived of the study and methodology, curated the data, performed the investigation, and administered the project. Formal analysis was conducted by MDS with guidance from RWK and LAS. LAS and MDS acquired funding, LAS and RWK provided resources, and LAS supervised the project. MDS wrote the first draft and led the writing with review and editing by LAS and RWK.

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DATA AVAILABILITY STATEMENT

Project raw data, formatted data, and analysis code are available at <https://doi.org/10.25380/iastate.25250839>.

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REFERENCES

- Allender, M. C., Raudabaugh, D. B., Gleason, F. H., & Miller, A. N. (2015). The natural history, ecology, and epidemiology of *Ophiomyces ophioidicola* and its potential impact on free-ranging snake populations. *Fungal Ecology*, 17, 187–196.
- Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K. O., & Bivand, M. R. (2017). Package 'rgeos.'

- The Comprehensive R Archive Network (CRAN). Available from <https://cran.r-project.org/web/packages/rgeos/index.html>; Accessed January 1, 2022.
- Böhm, M., Collen, B., Baillie, J. E. M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S. R., Ram, M., Rhodin, A. G. J., Stuart, S. N., van Dijk, P. P., Young, B. E., Afuang, L. E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., ... Zug, G. (2013). The conservation status of the world's reptiles. *Biological Conservation*, 157, 372–385.
- Brodman, R., Cortwright, S., & Resetar, A. (2002). Historical changes of reptiles and amphibians of northwest Indiana fish and wildlife properties. *American Midland Naturalist*, 147, 135–144.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer.
- Busby, W. H., & Parmelee, J. R. (1996). Historical changes in a herpetofaunal assemblage in the Flint Hills of Kansas. *American Midland Naturalist*, 135, 81–91.
- Cagle, N. L. (2008). Snake species distributions and temperate grasslands: A case study from the American tallgrass prairie. *Biological Conservation*, 141, 744–755.
- Carfagno, G. L. F., & Weatherhead, P. J. (2006). Intraspecific and interspecific variation in use of forest-edge habitat by snakes. *Canadian Journal of Zoology*, 84, 1440–1452.
- Chamberlin, T. C. (1890). The method of multiple working hypotheses. *Science*, 148, 92–96.
- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67.
- Chiarucci, A., Bacaro, G., Rocchini, D., Ricotta, C., Palmer, M. W., & Scheiner, S. M. (2009). Spatially constrained rarefaction: Incorporating the autocorrelated structure of biological communities into sample-based rarefaction. *Community Ecology*, 10, 209–214.
- Clark, R. W., Marchand, M. N., Clifford, B. J., Stechert, R., & Stephens, S. (2011). Decline of an isolated timber rattlesnake (*Crotalus horridus*) population: Interactions between climate change, disease, and loss of genetic diversity. *Biological Conservation*, 144, 886–891.
- DeGregorio, B. A., Putman, B. J., & Kingsbury, B. A. (2011). Which habitat selection method is most applicable to snakes? Case studies of the eastern massasauga (*Sistrurus catenatus*) and eastern fox snake (*Pantherophis gloydi*). *Herpetological Conservation and Biology*, 6, 372–382.
- Driscoll, D. A. (2004). Extinction and outbreaks accompany fragmentation of a reptile community. *Ecological Applications*, 14, 220–240.
- Durso, A. M., Willson, J. D., & Winne, C. T. (2011). Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation*, 144, 1508–1515.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515.
- Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, 40, 1649–1663.
- Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48, 1–23.
- Farm Service Agency. (2021). *NAIP digital ortho photo image*. Aerial Photography Field Office. <https://www.fisheries.noaa.gov/inport/item/49508>
- Fiske, I. J., & Chandler, R. B. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43, 1–23.
- Fletcher, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., Holt, R. D., Gonzalez, A., Pardini, R., Damschen, E. I., Melo, F. P. L., Ries, L., Prevedello, J. A., Tscharrntke, T., Laurance, W. F., Lovejoy, T., & Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological Conservation*, 226, 9–15.
- Gallant, A. L., Sadinski, W., Roth, M. F., & Rewa, C. A. (2011). Changes in historical Iowa land cover as context for assessing the environmental benefits of current and future conservation efforts on agricultural lands. *Journal of Soil and Water Conservation*, 66, 67A–77A.
- Glass, A., & Eichholz, M. W. (2022). Snakes on the plains: The impacts of habitat structure on snake communities in Illinois grasslands. *Wildlife Society Bulletin*, 46(5), e1366.
- Harvey, D. S., & Weatherhead, P. J. (2006). A test of the hierarchical model of habitat selection using eastern massasauga rattlesnakes (*Sistrurus c. catenatus*). *Biological Conservation*, 130, 206–216.
- Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). Landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography*, 42, 1648–1657.
- Hijmans, R. J., van Etten, J., Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Fasoli, B., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J. A., Hiemstra, P., Hingee, K., Ilich, A., Institute for Mathematics Applied Geosciences, Karney, C., ... Wueest, R. (2022). *Package 'raster'*. Comprehensive R Archive Network. Available from <https://cran.r-project.org/web/packages/raster/index.html>; Accessed January 1, 2022.
- Iowa Department of Natural Resources. (2015). *Iowa wildlife action plan: Securing a future for fish and wildlife – A conservation legacy for Iowans*. Iowa Department of Natural Resources.
- Iowa LiDAR Consortium. (2021). *Iowa LiDAR project*. Iowa Department of Natural Resources, Cedar Falls, Iowa. http://www.geotree.uni.edu/static/lidar/iowa_lidar_metadata.html
- Kapfer, J. M., Pekar, C. W., Reineke, D. M., Coggins, J. R., & Hay, R. (2010). Modeling the relationship between habitat preferences and home-range size: A case study on a large mobile colubrid snake from North America. *Journal of Zoology*, 282, 13–20.
- Kjoss, V. A., & Litvaitis, J. A. (2001). Community structure of snakes in a human-dominated landscape. *Biological Conservation*, 98, 285–292.
- Knott, T. G., & Best, L. B. (2011). A multiscale approach to understanding snake use of conservation buffer strips in an

- agricultural landscape. *Herpetological Conservation and Biology*, 6, 191–201.
- Lawrence, A., O'Connor, K., Haroutounian, V., & Swee, A. (2018). Patterns of diversity along a habitat size gradient in a biodiversity hotspot. *Ecosphere*, 9(1), e02183.
- Macartney, J. M., Gregory, P. T., & Larsen, K. W. (1988). A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology*, 22, 61–73.
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255.
- Mizsei, E., Fejes, Z., Malatinszky, Á., Lengyel, S., & Vadász, C. (2020). Reptile responses to vegetation structure in a grassland restored for an endangered snake. *Community Ecology*, 21, 203–212.
- Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, 14, 20170213.
- National Weather Service. (2022). *Automated Surface Observing System (ASOS)*. Retrieved January 1, 2022, from <https://www.weather.gov/asos/>
- Nordberg, E., Ashley, J., Hoekstra, A. A., Kirkpatrick, S., & Cobb, V. A. (2021). Small nature preserves do not adequately support large-ranging snakes: Movement ecology and site fidelity in a fragmented rural landscape. *Global Ecology and Conservation*, 28, e01715.
- Norton, B. G. (1998). Biological resources and endangered species: History, values, and policy. In *Protection of global biodiversity: Converging strategies* (pp. 247–264). Duke University Press.
- Pernetta, A. P. (2009). *Population ecology and conservation genetics of the smooth snake (Coronella austriaca) in a fragmented heath landscape*. University of Southampton.
- Pernetta, A. P., Allen, J. A., Beebee, T. J. C., & Reading, C. J. (2011). Fine-scale population genetic structure and sex-biased dispersal in the smooth snake (*Coronella austriaca*) in southern England. *Heredity*, 107, 231–238.
- Prugh, L. R., Hodges, K. E., Sinclair, A. R. E., & Brashares, J. S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences*, 105, 20770–20775.
- R Foundation for Statistical Computing. (2020). *R: A language and environment for statistical computing*. Vienna, Austria. <https://www.r-project.org/>
- Rabinowitz, D. (1981). Seven forms of rarity. In H. Synge (Ed.), *Biological aspects of rare plant conservation* (pp. 205–217). Wiley.
- Rita, H., & Komonen, A. (2008). Odds ratio: An ecologically sound tool to compare proportions. *Annales Zoologici Fennici*, 45, 66–72.
- Robel, R. J., Briggs, J. N., Dayton, A. D., & Hulbert, L. C. (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management*, 23, 295–297.
- Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87, 1075–1085.
- Samson, F., & Knopf, F. (2006). Prairie conservation in North America. *Bioscience*, 44, 418–421.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113.
- Schulte, L. A., Niemi, J., Helmers, M. J., Liebman, M., Arbuckle, J. G., James, D. E., Kolka, R. K., O'Neal, M. E., Tomer, M. D., Tyndall, J. C., Asbjornsen, H., Drobney, P., Neal, J., van Ryswyk, G., & Witte, C. (2017). Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn-soybean croplands. *Proceedings of the National Academy of Sciences*, 114, 11247–11252.
- Smith, A. B., Godsoe, W., Rodriguez-Sánchez, F., Wang, H.-H., & Warren, D. (2019). Niche estimation above and below the species level. *Trends in Ecology and Evolution*, 34, 260–273.
- Smith, D. (1998). Iowa prairie: Original extent and loss, preservation and recovery attempts. *Journal of the Iowa Academy of Science*, 105, 94–108.
- Steen, D. A. (2010). Snakes in the grass: Secretive natural histories defy both conventional and progressive statistics. *Herpetological Conservation and Biology*, 5, 183–188.
- Steen, D. A., McClure, C. J. W., Brock, J. C., Rudolph, D. C., Pierce, J. B., Lee, J. R., Humphries, W. J., Gregory, B. B., Sutton, W. B., Smith, L. L., Baxley, D. L., Stevenson, D. J., & Guyer, C. (2012). Landscape-level influences of terrestrial snake occupancy within the southeastern United States. *Ecological Applications*, 22, 1084–1097.
- Thouvenai, E., Pavoine, S., Tordoni, E., Rocchini, D., Ricotta, C., Chiarucci, A., & Bacaro, G. (2021). *Rarefy: Rarefaction methods*. Comprehensive R Archive Network. <https://cran.r-project.org/package=Rarefy>
- White, R., Murray, S., & Rohweder, M. (2000). *Pilot analysis of global ecosystems: Grassland ecosystems* (pp. 1–69). World Resources Institute. <http://www.wri.org/wr2000>
- Wright, C. K., & Wimberly, M. C. (2013). Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 4134–4139.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

SUPPORTING INFORMATION

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