



# Habitat amount and edge effects, not perch proximity, nest exposure, or vegetation diversity affect cowbird parasitism in agricultural landscapes

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## Abstract

**Context** Prior research documented relationships between brown-headed cowbird (*Molothrus ater*) brood parasitism and edge effects, proximity of perches, and nest exposure. Those relationships have not been evaluated in agroecosystems containing extremes of fragmentation and vegetation diversity.

**Objectives** We compared three existing hypotheses on how cowbirds locate host nests with two new hypotheses regarding habitat amount and vegetation diversity to determine how the configuration and location of agricultural conservation practices affect grassland bird nest parasitism rates and predicted rates for eight common conservation practices.

**Methods** We assessed cowbird parasitism of grassland bird nests on corn and soybean farms in Iowa, USA, and measured perch proximity, nest exposure, edge effects, habitat amount, and vegetation diversity for each nest. We fit a global generalized linear mixed-effects model and compared importance of model parameters using odds ratios. We predicted

parasitism likelihood for every subset model and averaged predictions to explore individual effects.

**Results** The variables that most influenced parasitism rates included main effects for nest initiation day-of-season (OR = 0.71, CI<sub>95</sub> = 0.60–0.84) and the landscape variables of distance to nearest crop edge (0.63, 0.51–0.76) and proportion of grass land cover within 660 m (0.75, 0.57–1.00). We found little support that perch proximity, nest exposure, or native vegetation diversity affected parasitism. We also assessed parasitism likelihood by conservation practice and found no significant differences.

**Conclusions** Our results provide evidence to support the edge effect and habitat amount hypotheses, but not the nest exposure, vegetation diversity, or perch proximity hypotheses.

**Keywords** Brood parasitism · Brown-headed cowbird · *Molothrus ater* · Conservation reserve program · Grassland passerines · Habitat amount hypothesis · Iowa USA · Prairie strips

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## Introduction

Ecologists have long been interested in brood parasitism by brown-headed cowbirds (*Molothrus ater*) (Bendire 1895; Friedmann 1929; Soler 2017) for reasons both theoretical (e.g., Widmann 1897) and practical (e.g., Peer et al. 2020). Brood parasitism is a reproductive strategy where female birds lay their

eggs in the nests of other birds to raise, often the nests of other species. This allows the parasitic females to spend more energy developing eggs and less energy caring for young (Ricklefs 1974). Brown-headed cowbirds are an obligate brood parasite, meaning they do not construct nests and reproduce solely through brood parasitism (Friedmann 1929). Brood parasitism as a breeding strategy is interesting in its own right, but also has important effects on host species, including species of greatest conservation need. Parasitism by brown-headed cowbirds often reduces the success of the host species' nest and young, lowering fecundity and putting negative pressure on the host species' population growth rate (Schmidt and Whelan 1999; Jensen and Cully 2005; Forehead 2019). The ecology of brown-headed cowbird brood parasitism is therefore of broad interest to ecologists, including those managing declining grassland songbird populations.

The reproductive success of brood parasites is contingent upon the density of host nests within a brood parasite's home range as well as their ability to locate host nests at the appropriate time in the egg-laying cycle (Payne 1977; Rothstein 1990; Russo and Hauber 2000). The 'perch proximity' hypothesis asserts that host nests located near tall perches experience a higher likelihood of being parasitized, as perches offer a vantage point for female cowbirds as they observe host targets (Russo and Hauber 2000; Jensen and Cully 2005; Patten et al. 2011). The 'nest exposure' hypothesis predicts that nest concealment factors into brood parasitism likelihood by reducing the chances of a female cowbird incidentally discovering a nest (Barber and Martin 1997; Clotfelter 1998; Burhans and Thompson 1998; Patten et al. 2011). The 'edge effect' hypothesis states that the frequency of parasitized host nests increases near habitat edges, potentially due to increased host nest density and availability of perches near forested edges (Winter et al. 2000; Jensen and Finck 2004; Jensen and Cully 2005; Patten et al. 2006, 2011). In this paper we defined 'habitat' as the vegetative communities needed by grassland birds to breed, including native grasslands, non-native monoculture grasslands, and pasture lands in the form of pastures, conservation practices (Table 1), roadside ditches, and habitat restoration plantings.

Despite the considerable attention given to brood parasitism, there remains a lack of research addressing the extremes of fragmentation present in

agroecosystems. Extensive agricultural production is often located in areas that historically comprised core breeding range of grassland birds, a guild in steep population decline (Rosenberg et al. 2019). North American grassland bird population declines from the time of European colonization to the early 20th century have been attributed primarily to land-use changes (Gaston et al. 2003), including the conversion of historical prairie vegetation to row-crop agriculture in the U.S. Midwest region (Reif 2013; Hill et al. 2014). More recent declines (Rosenberg et al. 2019) have been attributed to agricultural practices such as pesticide use, further habitat loss and alteration, and mowing/harvesting (Reif 2013; Hill et al. 2014; Stanton et al. 2018).

In landscapes dominated by extensive annual row-crop agriculture, such as those of the U.S. Midwest, grassland birds may be forced to use vegetative cover that is historically novel compared to their evolutionary plant communities, and may be particularly attracted to patches that have more of those native species (Conover et al. 2011; Monroe et al. 2016). Within such agricultural landscapes, more-natural vegetation cover is often established for conservation purposes (Table 1); for mitigating soil erosion, but also to address agriculture's typically adverse impacts on water quality and wildlife (McGranahan et al. 2013). The effect of vegetation diversity on brood parasitism has received little study, but we hypothesize that higher diversity habitat may decrease parasitism rates by providing a greater number of suitable nest microhabitats that are situated in more dense cover, thus decreasing nest exposure, particularly in comparison to the limited microhabitats available in grass monocultures such as smooth brome (*Bromus inermis*) and reed canary grass (*Phalaris arundinacea*).

Fragmented landscapes that force birds to breed in a limited number of patches of suitable vegetation could result in population sinks, or ecological traps if birds do not select safer available patches, through exposure to increased parasitism or predation (Schlaepfer et al. 2002; Robertson and Hutto 2006; Hale and Swearer 2016). Landscapes with few, small, or isolated grassland patches have often been found to be low quality habitat (Stephens et al. 2003; Ries and Sisk 2004; Fletcher et al. 2018). However, in a review that challenged prevailing viewpoints, Fahrig (2017) found the majority of reported wildlife responses to fragmentation were positive, although

**Table 1** Conservation practice descriptions based on patch shape, slope position, and vegetation diversity. Cost share program designations were archetypical; actual enrollment in a cost share program was not verified or required for inclusion in study

Conservation practice	Example cost share program	Description
Grass contour strip	CP-15 A	Linear strip (3–100 m wide, typically – 10 m) of low diversity grass planted along a contour within a field. Often planted to non-native cool-season grass species such as smooth brome ( <i>Bromus inermis</i> ).
Grassed terrace	IA-600 grassed backslope terraces, narrow base terraces	Linear earthen berm (2–5 m wide) along a contour within a field, typically planted to cool-season non-native grasses (e.g., smooth brome) when established, but were frequently affected by herbicide drift and filled with annual weeds and woody species.
Grass filter strip	CP-21	Linear strips (3–30 m wide, typically – 10 m) of low diversity grass planted at toe slope position adjacent to a permeant water body. Typically planted to cool-season non-native grasses such as reed canary grass ( <i>Phalaris arundinacea</i> ).
Grassed waterway	CP-8 A	Linear strips of variable width (typically – 10 m) of low diversity grass planted along drainage paths to conduct surface water off fields. Typically planted with non-native cool-season grasses such as smooth brome.
Grass large patch	CP-1, CP-4D	Low diversity grass planted in larger patches (9–315 ha) such as field corners, areas isolated by streams, or entire fields. Plantings contained non-native or native warm or cool season grasses.
Prairie contour strip	CP-43	Linear strips (3–100 m wide, typically – 10 m) of medium-high diversity native grasses and forbs planted along a contour within a field. Common species included big bluestem ( <i>Andropogon gerardi</i> ), little bluestem ( <i>Schizachyrium scoparium</i> ), Canada wild rye ( <i>Elymus canadensis</i> ), gray coneflower ( <i>Ratibida pinnata</i> ), wild bergamot ( <i>Monarda fistulosa</i> ), rattlesnake master ( <i>Eryngium yuccifolium</i> ), ox-eye ( <i>Heliopsis helianthoides</i> ), etc.
Prairie filter strip	CP-43	Linear strips (3–30 m wide, typically – 10 m) of medium-high diversity native grasses and forbs planted along permeant water bodies with plant communities similar to prairie contour strips.
Prairie large patch	CP-33, CP-38, CP-42	Medium-high diversity native grasses and forbs planted in larger patches (9–315 ha) such as field corners, strips wider than 100 m, or whole fields.

that assertion has been challenged (Haddad et al. 2017; Fletcher et al. 2018). In the ‘habitat amount hypothesis’, Fahrig (2003) argued that patch size and isolation were correlated with overall habitat amount and that effects attributed to configuration were really driven by lower habitat amounts through the sample-area effect, i.e., the larger the sampled area, the more species will be found (MacArthur and Wilson 1963, Fahrig 2013). Among other responses (Martin 2018), Villard (2014) argued that while habitat amount is always important, configuration has the potential to mitigate the effects of habitat loss. While recognizing that the relationship between habitat area and biodiversity independent of configuration is not settled, we propose that just as biodiversity may be affected by the total amount of nearby habitat through the sample-area effect, population-level demographic parameters also may be influenced by landscape-level

ecological relationships, where effect sizes and directions are averaged over nearby habitat conditions.

We expect the relative importance of factors affecting brood parasitism to vary with species and the degree of alteration of the landscape (Turner et al. 2001; Tscharrntke et al. 2012). Our goal was thus to compare evidence of established nest parasitism hypotheses and possible effects of vegetation diversity and habitat amount on brood parasitism in agricultural landscapes dominated by extensive row crop production. We hypothesized that parasitism of grassland bird host nests will be positively associated with (1) proximity to suitable perches, (2) nest exposure, and (3) edge effects, and be negatively associated with (4) habitat amount and (5) vegetation diversity. Given significant population declines across most grassland bird species, we also seek to inform grassland bird conservation by identifying how agricultural landscape management, specifically the design

and location of agricultural conservation practices such as prairie strips (Schulte et al. 2017), affects brood parasitism among grassland birds, especially in systems managed by individual private landowners (Shaffer et al. 2022).

## Methods

### Study area

Our study sites were located on private commercial monocultural row-crop farms growing corn (*Zea mays* Gaertn.) and soybeans (*Glycine max* L.) within 100 km of Ames, Iowa, USA, separated by 4–120 km. Exact farm locations are not available to maintain landowner confidentiality. Between 2015 and 2019, we surveyed 11 sites for 2–5 years each. Our sites were opportunistically selected from a list of landowners with prairie contour strips on their property, from which we selected sites based on the presence of prairie contour strip, grass contour strip, or large patch prairie conservation practices (Table 1). Most sites (8–220 ha) contained multiple conservation practices (1–6, median=3), which we defined by plant diversity, configuration, and slope position (Table 1). Plant species within the non-prairie conservation features were dominated by cool-season non-native species such as smooth brome and reed canary grass. Prairie strips and large patch prairies included warm- and cool-season grasses and forbs native to eastern tallgrass prairies, such as big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), wild bergamot (*Monarda fistulosa*), and gray-headed coneflower (*Ratibida pinnata*). Longer-established conservation practices typically contained some woody species such as eastern red cedar (*Juniperus virginiana*), mulberry (*Morus* sp.), and Siberian elm (*Ulmus pumila*); however, shrub height did not typically exceed 1 m due to periodic mowing, except within grassed terraces, which were typically not accessible for mowing. Six of nine farm sites contained high-diversity prairie contour strips ranging from 0 to 12 years in age. Landscapes surrounding farm sites were characterized by small, isolated, low-diversity grassland patches (e.g., ditches, grassed waterways, grass contour or filter strips). The median land cover amounts within 1 km of our sites were 73.2% row crop (28.6–84.8%), 15.2% grassland

(11.1–51.1%), 2.1% woody (0.9–21.3%), 1.5% developed (0.4–4.2%), and 0.8% water (0.2–1.1%) and landscapes had average grassland patch sizes of 0.8–7.0 ha. Because sites with uncorrelated habitat fragmentation and amount were not available, we controlled for differing amounts of habitat area at our study sites by including interaction terms with grassland area to isolate effects of configuration, per recommendations in the ‘habitat amount hypothesis’ (Fahrig 2013).

### Data collection

We searched areas of perennial vegetation for grassland bird nests from mid-May to mid-August 2015–2019. We searched for nests both systematically in pre-determined plots and opportunistically in appropriate habitat. Plot searches consisted of two observers searching a 0.1 ha plot for 3 min by systematically walking through the plot sweeping the vegetation with 1-m sticks while watching for flushes or behavioral cues that might indicate the presence of a nest. Non-systematic nest searches were conducted in any grassy habitat and targeted microhabitats such as dense clumps of forbs, small shrubs, and areas near water bodies (Stephenson 2022). Once nests were located, we recorded their location using global positioning system devices (2015: Garmin eTrex 10, ~2–5 m accuracy, Garmin Ltd., Olathe, KS; 2016–2019: Trimble Geo7X devices, <1 m accuracy, Trimble Inc., Sunnyvale, CA). We candled host and cowbird eggs to determine their developmental stage (Lokemon and Koford 1996) and installed miniature temperature data-logging devices (iButton Thermochron DS1921G, Maxim Integrated, San Jose, California, USA) within the cups of most nests to monitor incubation activity (Hartman and Oring 2006; Stephenson et al. 2021). We visited nests every 3–4 days to determine the nest status and presence of cowbird eggs and young (Clotfelter 1998; Russo and Hauber 2000; Jensen and Cully 2005; Pattem et al. 2011). Additional details of related nest survival, density, and detection modeling can be found in Stephenson (2022).

### Habitat configuration and amount

To minimize trampling of vegetation, we visually estimated the distance from each nest to the nearest

clearly distinguishable habitat edge (between grass and crop or trees) in the field if it was within 5 m, or measured it using a geographic information system if the distance was greater than 5 m. We created land cover maps by manually digitizing land cover polygons using aerial imagery from the National Agriculture Imagery Program (Farm Service Agency 2021) for each year of the study, using geographic information systems software (ArcMap, ESRI, Redlands, CA, version 10.3). We calculated proportions of land cover classifications and converted the native polygon layer to a 3 m pixel raster layer to calculate patch-scale metrics. A 3 m pixel size was chosen to balance capturing very small patches while still allowing very narrow linear features to serve as break points between patches to help avoid landscapes where a single, lace-like patch comprised all the grass within the square-mile road grid. We classified land cover as crop, developed, water, trees, or “grassy”, which included ditches, grass contour or filter strips, grassed terraces, grassed waterways, grass large patch grasslands, prairie contour or filter strips, or prairie large patch grasslands.

#### *Perch proximity*

We defined a suitable cowbird perch as an object taller than the surrounding vegetation (typically > 1.5–2 m tall) that a cowbird would be capable of perching on that would allow a clear view of nearby habitat. We manually digitized locations of cowbird perches (large shrubs, trees, powerlines, and fences) visible in the NAIP, Light Detection And Ranging (Iowa LiDAR Consortium 2021), and online mapping software (Google Maps Street View, Google LLC, Mountain View, CA) imagery, augmented with personal observations from researchers.

#### *Nest exposure*

We measured nest cup concealment, vegetation density, and native plant richness to estimate nest exposure. To normalize vegetation growth relative to nest stage and to reduce disturbance near active nests, we made vegetation-related measurements on or near the predicted fledge date when the nest was no longer active (McConnell et al. 2017). We used a circular visual obstruction disk separated into eight equal alternating black-and-white sections and sized

for different species’ nests (6.3–7.6 cm), to measure how visible the cup of the nest was from 1 m above the nest and 1 m from each of the cardinal directions at nest discovery and again near the predicted fledge date (Davis and Sealy 2000). Because nest concealment may be correlated with vegetation growth through the season, we used the concealment measured near the predicted fledge date when possible, but used the initial discovery measurement when a nest was destroyed and unavailable for measurement after the predicted fledge date. In a few cases, the nest was not accessible for the visual obstruction disk and an un-aided ocular estimation of the percent nest concealment was used instead. We measured vegetation density near the nest using the Robel method, with measurements taken approximately 5 m from the nest in each of the cardinal directions and viewed from approximately 1 m off the ground (Robel et al. 1970). We identified all plants found within 1 m<sup>2</sup> quadrats at the nest and 5 m away in each of 0°, 120°, and 240° azimuthal directions. We identified to species where possible, otherwise to genus, and classified them as either native or introduced according to the USDA Plants Database (National Plant Data Team et al. 2019). We recorded mowing activity at the quadrat locations to partition the variation that mowing introduced in plant identification and density measurements but found it did not have a strong effect on these metrics and subsequently removed it from consideration to reduce the number of models.

#### Statistical analysis

We modeled predictors of cowbird parasitism using a generalized linear mixed-effects model (GLMM) framework in statistical analysis software (R version 4.1.1, R Core Team 2017) using the package ‘glmmTMB’ version 1.7.22 (Brooks et al. 2017) and package ‘MuMIn’ version 1.44 (Barton 2022). We used a binary response variable (parasitized/not parasitized) and included site and host species as random effects to account for local differences in cowbird abundance (Herkert et al. 2003) and for differences in host nest characteristics and anti-parasitic behaviors (Clotfelter 1998). We also included nest initiation day-of-season as an ‘expert opinion’ fixed effect to mitigate temporal autocorrelation (Thompson and Gottfried 1981). We initially included an indicator for miniature data logger use to allow for an effect from the device’s



presence on cowbird nest preference and other related behaviors; however, the indicator variable was later removed to reduce the number of models after preliminary analyses did not show evidence of an effect on cowbird nest selection. We analyzed nests that were active at the time of discovery for species that both were known acceptors of cowbird eggs (Lowther 2020) and that nest in grasslands with no shrubs (Billerman et al. 2020).

Prior to conducting model selection, we performed a series of tests to ensure our data met model assumptions (Zuur et al. 2010). First, we inspected the response variable and all predictor variables for outliers to limit overdispersion. We corrected datapoints found to be verifiable errors and left other datapoints as recorded (Hilbe 2007). We considered potential interactions between predictor variables by examining a panel of scatterplots with linear regression lines and variables that showed noticeable differences in slopes between groups were considered for an interaction term (Zuur et al. 2010). Variables with a small percentage of missing records were replaced with mean values by site, year, and/or land cover classification.

We then assembled a provisional global model to test statistical assumptions regarding model fit. We assessed overdispersion and zero-inflation using functions provided by the package ‘DHARMA’ version 0.4.5 (Hartig 2020). We examined predictor variable multicollinearity by calculating the Variance Inflation

Factor (VIF) for each variable in the model (Lüdecke et al. 2020) and sequentially dropping the variable with the highest VIF until all VIFs were under a pre-defined threshold ( $VIF < 7$ ) (Montgomery and Peck 1992). To meet the assumption of normally distributed residuals, we examined plots of the normalized/Pearson residuals versus fitted values as well as residuals versus each explanatory variable using the package ‘DHARMA’ (Hartig 2020) and transformed and removed variables or interactions from the provisional global model to achieve an approximately normal residual distribution. We centered and standardized all variables to increase the chances of model convergence (Hartig 2020) and to allow comparison among odds ratios (Rita and Komonen 2008). We checked the provisional global model for temporal and spatial autocorrelation with the package ‘DHARMA’ (Hartig 2020) using Moran’s I test (Moran 1948) and the Durbin-Watson test (Durbin and Watson 1950) to confirm that autocorrelation in the residuals was not significant at  $\alpha = 0.05$ . After making the above adjustments to improve distribution or correlation issues, the provisional global model was accepted as the final global model.

Explanatory variables were grouped by hypothesis: perch proximity, nest exposure, vegetation diversity, edge effect, habitat amount, or expert opinion (Table 2). We selected a 660-m radius around each host nest for landscape measurements

**Table 2** Variables included in the final global model estimating parasitism as a binary response in a generalized linear mixed model, categorized by hypothesis. Random effects for

host species and study site were also included. Nests belonging to grassland birds were monitored from 2015–2019 in central Iowa

Hypothesis	Variable	Description
Perch proximity	distance_to_trees_meters_log	Distance to nearest tree cover (m)
Perch proximity	distance_to_fence_meters_log	Distance to nearest fence (m)
Perch proximity	distance_to_powerlines_meters_log	Distance to nearest powerline (m)
Nest exposure	conceal_log	% Concealment measured 1 m above nest rim at time of nest completion
Nest exposure	vor_final_mean_log	Visual obstruction reading taken 5 m away at time of nest completion (cm)
Vegetation diversity	species_richness_native_quadrats_mean_log	Native vegetation species richness within 5 m of nest
Edge effect	distance_to_crop_meters_log	Distance to nearest crop body (m)
Habitat amount	grassland_660_m_r_ppn_log	Proportion of grassland cover within 660 m radius of nest
Habitat amount	patch_area_veg_ha_log	Area of nest patch (ha)
Habitat amount	mean_nearest_neighbor_m_660_m_radius_log	Mean distance to nearest neighboring patch within 660 m radius of nest
Expert opinion	nest_initiation_day_of_season	Days since start of field season (Apr 1)

to encompass a distance five times an average Midwest cowbird's home range radius (Shaffer et al. 2003) to capture effects occurring at the local population level (one circular cowbird territory surrounded with two ranks of adjacent territories). We defined grassland as cover that contained perennial grasses and forbs excluding mowed lawns and patches of shrubs distinguishable on aerial imagery.

To compare variable importance, we fit the final global model and exponentiated the beta parameters to give odds ratios (Rita and Komonen 2008) so that a one standard deviation change in the predictor variable indicated an [odds]-fold change in the likelihood of parasitism. We assessed model fit as  $R^2_{\text{GLMM}}$  using the delta method (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017) implemented through function 'r.squaredGLMM' in package 'MuMIn'. Then, to demonstrate the importance of individual variables, we predicted parasitism likelihood for each of the subset models across the range of observed values for each variable of interest. We used an all-subsets model averaging approach to produce precise, unbiased predictions of parasitism rates based on *a priori* single-variable hypotheses while avoiding inflated Type I error rates associated with stepwise model building approaches (Doherty et al. 2010; Lukacs et al. 2010; Cade 2015). We predicted parasitism likelihood by conservation practice and compared prediction intervals to determine if there were significant difference between practices. Figures were produced with package 'ggplot2' (Wickham 2016).

## Results

We monitored 1,602 nests of 30 bird species over a 5-year period between 2015 and 2019. Of these, 1,192 nests belonged to grass-nesting passerine species known to accept cowbird eggs (Billerman et al. 2020). A total of 398 (33.4%) monitored nests were parasitized and eight species met our criteria for analysis and had at least one parasitism event (Table 3). The largest Pearson correlation coefficients between habitat configuration and amount variables were between 'patch\_area\_veg\_ha' and 'distance\_to\_crop\_meters' ( $r=0.50$ ) and 'grassland\_660\_m\_r\_ppn' ( $r=0.48$ ).

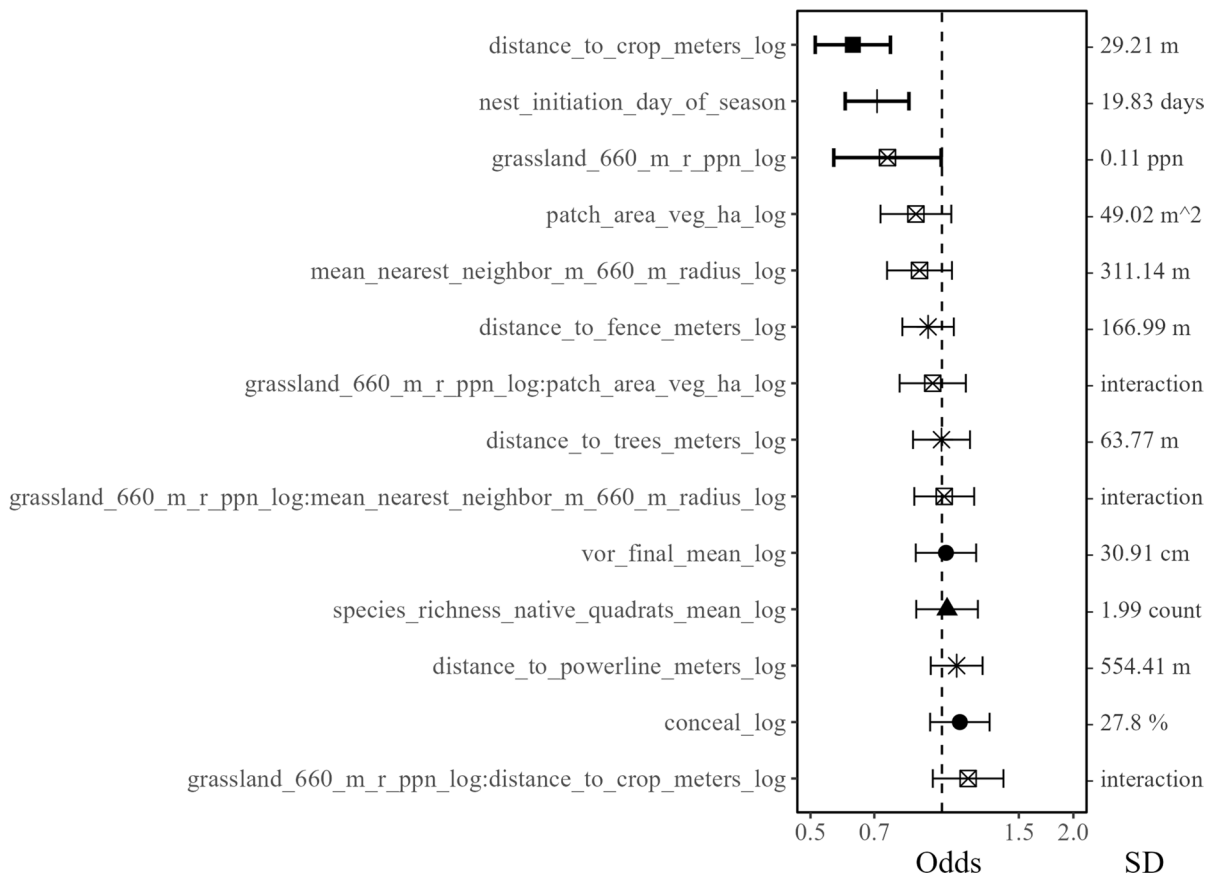
The fixed effects within the global model explained 8.1% of the observation-level variance ( $R^2_{\text{GLMM\_marginal}}$ ), while 26.3% of the variance was explained by the fixed and random effects together ( $R^2_{\text{GLMM\_conditional}}$ ). Of the 4,480 subset models of the global model, 937 models accounted for 95% of the AICc model weight (Table 4). Nest initiation day-of-season (Figs. 1 and 2a), distance to nearest crop edge (Figs. 1 and 2b), and grass land cover amount (Figs. 1 and 2c) had the largest effects on the odds of parasitism in the global model (Fig. 1). Distance to crop was included in 100% of the models in the 95% model weight set, grassland area appeared in 94.1% of models, and nest initiation day-of-season was included in 100% of models (Table 4). When other variables were held at mean values (Table 5), nests whose eggs were laid on May 2 had a 3.8-times higher likelihood of being parasitized than those laid on Aug. 14 (Fig. 2a). Holding other variables at their means, an increase

**Table 3** Grassland bird nests by species and observed parasitism rates 2015–2019 in central Iowa

Common name	Scientific name	Sample size	Parasitized	Rate parasitized (%)
American goldfinch	<i>Spinus tristis</i>	15	1	6.7
Grasshopper sparrow	<i>Ammodrammus savannarum</i>	6	2	33.3
Lark sparrow	<i>Chondestes grammacus</i>	1	1	100.0
Vesper sparrow	<i>Pooecetes grammacus</i>	41	19	22.0
Song sparrow	<i>Melospiza melodia</i>	14	6	42.9
Red-winged blackbird	<i>Agelaius phoeniceus</i>	772	202	26.2
Common yellowthroat	<i>Geothlypis trichas</i>	47	14	29.8
Dickcissel	<i>Spiza Americana</i>	297	164	55.2
Overall		1192	398	33.4

**Table 4** All-subset model variables by hypothesis and representation in the 95% of the AICc model weight list (N=937 of 4480 total models). All models also contained random effects for host species and study site

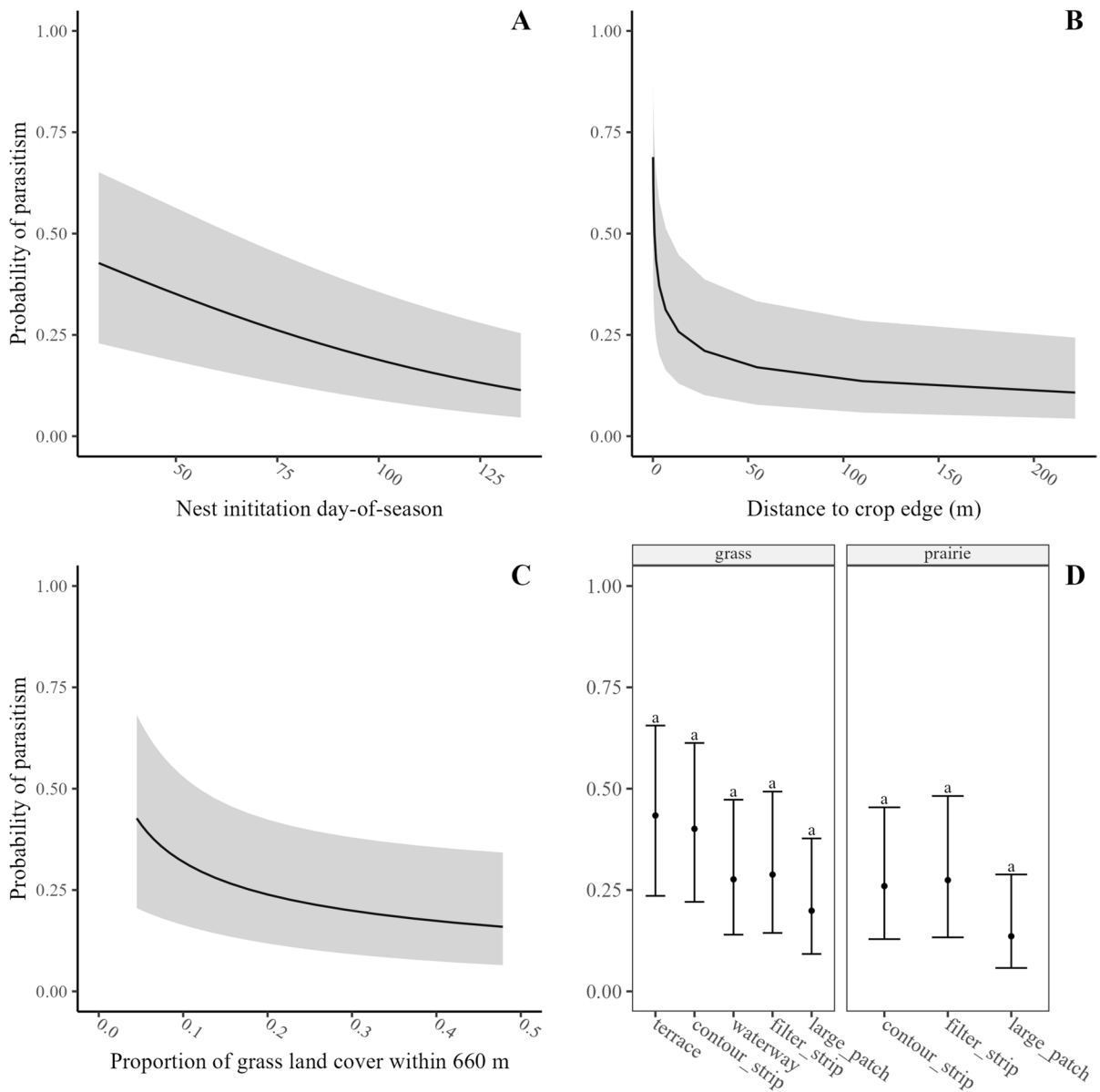
Hypothesis	Variable	95% Cum. wt. count	95% Cum. wt. ppn.
Perch proximity	distance_to_trees_meters_log	370	0.395
Perch proximity	distance_to_fence_meters_log	411	0.439
Perch proximity	distance_to_powerlines_meters_log	430	0.459
Nest exposure	conceal_log	441	0.471
Nest exposure	vor_final_mean_log	386	0.412
Vegetation diversity	species_richness_native_quadrats_mean_log	377	0.402
Edge effect	distance_to_crop_meters_log	937	1.00
Habitat amount	grassland_660_m_r_ppn_log	882	0.941
Habitat amount	patch_area_veg_ha_log	604	0.645
Habitat amount	mean_nearest_neighbor_m_660_m_radius_log	579	0.618
Expert opinion	nest_initiation_day_of_season	937	1.00



**Fig. 1** Odds ratios (OR) of a parasitism event for each parameter in the global model with 95% confidence intervals. Bold confidence intervals are statistically significant. Variables whose point estimates are represented with an asterisk (\*) were related to perch proximity, circles (●) were related to nest exposure, triangles (▲) were related to vegetation diversity, closed squares (■) were related to edge effects, open squares (□) were related to habitat amount, and the tick mark symbol

(|) was an expert opinion variable. Standard deviations (SD) are listed on the right axis. Interaction terms do not have their own SD. For every SD change in the predictor variable, the odds of parasitism changed [odds]-fold. An OR of one indicates no effect on the odds of a parasitism event, OR > 1.0 indicates higher odds of a parasitism event, and OR < 1.0 indicates reduced odds of a parasitism event





**Fig. 2** Predicted likelihood of parasitism by **A** nest initiation day-of-season, **B** distance to crop edge, **C** grass land cover within 660 m, and **D** conservation practice

Predictions were made across the range of observed values for the variable of interest, or at mean observed values for conservation practices **D**. Conservation practices that share a letter were not significantly different at  $\alpha=0.05$

in the distance to the nearest crop edge from 0 to 222 m resulted in a 6.4-times lower likelihood of parasitism (Fig. 2b) with a 1.9-times decrease in the first 3.2 m from crop edge. An increase in the percentage of grass land cover within 660 m of the host nest from 4.5 to 47.9% resulted in a 2.7-times lower

likelihood of parasitism (Fig. 2c). We found no significant differences in parasitism rates among conservation practices at  $\alpha=0.05$ ; however, the smallest conservation practices trended toward higher parasitism likelihoods with largely overlapping prediction intervals (Fig. 2d).

## Discussion

We hypothesized that parasitism of grassland bird host nests by brown-headed cowbirds would be positively associated with (1) proximity to suitable perches, (2) nest exposure, and (3) edge effects, and negatively associated with (4) habitat amount and (5) vegetation diversity. We evaluated these hypotheses based on nest data from eight grassland bird species (Table 3) in the highly anthropogenic landscape of Iowa, USA, which contains extremes of landscape fragmentation and vegetation diversity.

In comparing the nest parasitism rates to other studies, we found that red-winged blackbird nests in our study were parasitized (PR=26.2%) at rates within the range reported by other studies in Iowa (PR=11–22%, 39%, 46%) (Camp and Best 1994; Hultquist and Best 2001; Henningsen and Best 2005) as well as those reported in Kansas (PR=21.9%) (Rivers et al. 2010). We observed parasitism rates for dickcissels (PR=55.2%) that were on the high end of the range reported by other studies in Iowa agricultural landscape (PR=19%, 21%, 33%, 53.3%, 68%) (Frawley and Best 1991; Patterson and Best 1996; Fletcher et al. 2006; Maresh Nelson et al. 2018; Shaffer et al. 2022), and within the range of those reported in Kansas (PR=43–47%, 69.6%) (Rahmig et al. 2009; Rivers et al. 2010). Published estimates of brood parasitism for Common yellowthroat nests were less common, but the parasitism rate we observed (PR=29.8%) was higher than those reported in Iowa switchgrass fields (17%) (Murray and Best 2014) but lower than those for nests found in Michigan and Minnesota (PR=38%, 45%) (Stewart 1953; Hofslund 1957). The parasitism rate we observed for Vesper sparrows (PR=22%) was higher than reported by studies in Iowa in similar landscapes (PR=0%, 11%) (Rodenhous and Best 1983; Frawley and Best 1991). The other four species (Table 3) together comprised 3% of the sample ( $n=36$ ).

### Habitat amount hypothesis

We found that habitat amount was an important term in the global model (Fig. 1), but that patch size and isolation were not, and were included in only a modest number of the top-weighted all-subsets models (Table 4). This provides evidence supporting an extension of the ‘habitat amount hypothesis’

to demographic parameters such as nest parasitism. Fahrig (2013) argues in the ‘habitat amount hypothesis’ that landscape habitat amount and not patch size or isolation could be responsible for patterns observed in biodiversity due to the sample-area effect. Analogous to the sample-area effect, the relationship we detected between landscape habitat amount and incidence of cowbird parasitism may represent the average of many landscape-linked ecological relationships involving cowbirds, their hosts, and the interactions between the two. However, while the generality implied by the ‘habitat amount hypothesis’ is what makes it of broad interest, when modeling a demographic parameter dominated by the ecology of a single species, researchers may be more interested in the individual landscape-linked ecological relationships that the ‘habitat area’ variable represents in our study. One of these landscape-linked ecological relationships, edge proximity, has received substantial research attention (Winter et al. 2000; Jensen and Finck 2004; Jensen and Cully 2005; Patten et al. 2006, 2011).

### Edge effect hypothesis

We found that the proximity to a crop edge was one of the strongest predictors of brown-headed cowbird nest parasitism, congruent with previous research on female cowbird behavior (Maresh Nelson et al. 2018; Thompson and Dijak 2021). Previous studies have associated landscape fragmentation in grassland systems with higher densities of host species and therefore increased density of cowbirds and incidence of parasitism (Tewksbury et al. 1999; Davis and Sealy 2000; Koford et al. 2000). Because female cowbirds spend their afternoons feeding in grassland, hayfields, and cropland (Thompson and Dijak 2021) and fly directly to a potential host nest to lay an egg as soon as it is light enough to fly (Neudorf and Sealy 1994), it is possible that they may discover nests near grassland edges while feeding that they then parasitize the following morning (Davis and Sealy 2000).

We did not find distance to tree edge to be an influential variable. In a review, Cavitt and Martin (2002) found the relationship between brood parasitism and forest fragmentation was only detectable in the Eastern US and was absent west of the Rocky Mountains, which they attributed to heterogeneous landscapes in the West. Similarly, it is possible that cowbirds display

different host targeting behaviors in ecoregions dominated by agricultural grasslands with very few trees. Alternatively, Pietz et al. (2009) found a *negative* relationship between brood parasitism and percentage of landscape in tree land cover within 2 km for four grassland bird species on Sheyenne National Grassland, North Dakota. This supports the idea that cowbirds may preferentially target nests in forest patches (Robinson et al. 1999), reducing parasitism pressure on grassland nesting birds in those landscapes. Our study landscapes had small proportions of tree land cover ( $\bar{x} = 1.7\%$ ,  $SD=0.025$ ) and our finding of no effect of distance to trees could also be due to a threshold or non-linear effect that was rare on our landscapes. In a tallgrass prairie system in Kansas, Jensen and Finck (2004) found a negative effect of distance to wooded edge on brood parasitism but no effect from distance to crop edge. We were unable to locate any other studies comparing the two edge types.

#### Nest exposure hypothesis

Our results did not support nest concealment or vegetation density as being influential in predicting the likelihood of parasitism. While there have been numerous studies on nest concealment and exposure in relation to parasitism, there has been little support when compared directly to other hypotheses (Patten et al. 2011). Female cowbirds appear to strongly rely on host activity (i.e., nest building, flushing, aggression) to locate active nests (Thompson and Gottfried 1981; Patten et al. 2011). However, cowbird egg-laying in inactive nests was documented in this study and in previous studies (Norman and Robertson 1975), indicating that female cowbirds do not rely solely on host activity for locating nests. Differences in methodology may explain differences in our findings from previous studies (Barber and Martin 1997; Clotfelter 1998; Burhans and Thompson 1998). For instance, while this study and others (Davis and Sealy 2000; Russo and Hauber 2000) measured only overhead nest concealment, other brood parasitism studies accounted for the visibility of the entire nest structure from several directions (Burhans and Thompson 1998; Patten et al. 2011). If cowbirds do rely partially on nest exposure, it is unclear which part of the nest structure is most relevant to this locating strategy. We also accounted for the vegetation density in the area immediately surrounding the nest as a measure of concealment; however,

vegetation density was weakly correlated with overhead nest cup concealment ( $r=0.13$ ). To remove age-of-discovery bias from our nest concealment score, we measured concealment scores at the predicted fledge date. However, due to differential plant growth rates, this concealment score was only moderately correlated with concealment measured at the time of discovery ( $r^2=0.53$ ), which may have limited its usefulness for representing nest concealment early in the nesting attempt when parasitism occurred.

#### Vegetation diversity hypothesis

We hypothesized that increased plant species richness should provide more, higher-quality nesting microhabitats, requiring cowbird females to search more locations and be more likely to overlook better concealed nests. In a concurrent study (Stephenson 2022), we found that vegetation species richness predicted higher densities of host nests, which suggested more suitable nesting micro-habits were present, but also confounded the prediction of higher incidence of parasitism through the presence of more host nests for (presumably) the same number of cowbirds, potentially lowering overall parasitism rates by flooding female cowbirds with target nests. We were thus surprised that native vegetation richness was not an important variable in our models (Fig. 1; Table 3). However, we also found that native vegetation richness was not correlated with nest concealment ( $r = -0.03$ ) or with vegetation density ( $r=0.09$ ), providing evidence against our hypothesized mechanism of host nests being better concealed in higher-diversity conservation practices. Overall, our results suggest that the richness of native plant species surrounding a host nest does not influence the likelihood of it being parasitized.

#### Perch proximity hypothesis

Our data did not support the perch proximity hypothesis for this study system, contrary to our expectations based on previous research (Clotfelter 1998; Russo and Hauber 2000; Jensen and Cully 2005; Patten et al. 2011). Perch abundance, rather than distance to closest perch, may have been a more important factor in parasitism likelihood. While we did not measure perch abundance, it is possible there may have been fewer elevated ( $>2$  m) perches available compared to other study systems, due to shrub management and fewer

trees on the landscape. Fewer elevated perches paired with high densities of red-winged blackbirds may have led to strong competition for tall perches (Clotfelter 1998). Red-winged blackbirds rely on aggression as an anti-parasitism behavior (Clotfelter 1998; Yasukawa et al. 2016), and we frequently observed male blackbirds successfully defending the sparse elevated perches available at our study sites, forcing cowbirds to switch nest-finding strategies and removing perch proximity as an important factor. Alternatively, our strategy of relying on remote-sensing approaches to quantify perches excluded tall, stiff-stemmed forb species (e.g., compass plant [*Silphium laciniatum*]), which may provide adequate perches for female cowbirds. We rarely witnessed this behavior, however, and most commonly encountered cowbirds on the ground in row crop fields.

### Conservation practices

We found that the likelihood of parasitism trended higher in the narrower conservation practices (contour strips, filter strips, terraces, waterways), but the differences were not significant (Fig. 2d). This may have been because distance to crop and grass land cover proportion were the most important predictors of parasitism, but conservation practice width and nearby habitat amount varied within and overlapped among conservation practices.

### Conclusions

We provide evidence supporting an extension of the ‘habitat amount hypothesis’ to demographic parameters such as cowbird parasitism and supporting the ‘edge effect’ hypothesis, but did not find support for the ‘perch proximity’, ‘nest exposure’, or ‘vegetation diversity’ hypotheses. Because our global model only accounted for 26.3% of the variance present in the data, we may not have captured all the ecological interactions affecting cowbird parasitism. Including a term for host nest density within the patch (Strausberger 2001) and directly estimating local cowbird abundance (Patten et al. 2011) may have improved our models. As our study was exploratory and thus inference is limited, we suggest that replicated studies be conducted in other landscapes of interest to further test the relationships we present for agricultural landscapes with extremes of fragmentation and vegetation diversity.

In this study we tested multiple existing and novel hypotheses of the ecological mechanisms influencing cowbird parasitism of grassland bird nests in an under-studied agricultural landscape. We established a strong relationship between time of year, distance to crop edges, and the nearby grassland habitat amount with the likelihood of a host nest being parasitized. We did not find a difference in parasitism likelihood between categorical classifications of conservation practices, although nests in smaller conservation practices tended to have higher predicted rates of parasitism. We did not find support for perch proximity, nest exposure, or vegetation diversity as important factors within our agricultural study system. Instead, our study supports the edge effect hypothesis and an extension of the habitat amount hypothesis to nest parasitism in agricultural landscapes.

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**Author contributions** KY conceived the idea for the study using methods and data provided by MS. MS and KY collected the data, MS lead the statistical analysis with advice from Jarad Niemi, MS and KY contributed substantially to the analysis and writing, and MS led the final editing and submission process. LAS and RK oversaw the research and edited the manuscript. LAS secured funding for the research program.

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**Data availability** The data and code to replicate the analyses presented in this study are available at <https://doi.org/10.25380/iastate.24545899.v1>.

### Declarations

**Competing interests** The authors declare no competing interests.

### Appendix

See Tables 5, 6.

**Table 5** Summary statistics of variables concerning the nest exposure, perch, and fragmentation hypotheses measured at each grassland bird nest monitored from 2015–2019 in central Iowa, USA. Mean, standard deviation (S.D.), and median are

presented in non-transformed units for ease of interpretation. Patches that had no neighbors within 660 m were assigned a mean\_nearest\_neighbor\_m\_660\_m\_radius value of 660

Hypothesis	Variable	Mean	S.D.	Median	Unit
Perch proximity	Distance_to_trees_meters_log	62.0	63.8	41.2	m
Perch proximity	Distance_to_fence_meters_log	185.7	167.0	142.2	m
Perch proximity	Distance_to_powerlines_meters_log	544.5	554.4	388.5	m
Nest exposure	Conceal_log	58.2	27.8	61	%
Nest exposure	vor_final_mean_log	78.1	30.9	77.5	cm
Vegetation diversity	species_richness_native_quadrats_mean_log	3.0	2.0	2.4	count
Edge effect	distance_to_crop_meters_log	22.8	29.2	13.6	m
Habitat amount	grassland_660_m_r_ppn_log	0.18	0.11	0.13	ppn
Habitat amount	patch_area_veg_ha_log	51.7	49.0	44.1	ha
Habitat amount	mean_nearest_neighbor_m_660_m_radius_log	395.2	311.1	660	m
Expert opinion	nest_initiation_day_of_season	72.6	19.8	72	day

**Table 6** Pearson correlation coefficients for habitat amount and fragmentation metrics for 1192 nests of 8 species of grass-nesting birds monitored from 2015–2019 in Iowa, USA

	Grassland_660_m_r_ppn	Patch_area_veg_ha	Mean_nearest_neighbor_m_660_m_radius	Distance_to_crop_meters	Distance_to_trees_meters
Grassland_660_m_r_ppn	1.00				
Patch_area_veg_ha	0.48	1.00			
Mean_nearest_neighbor_m_660_m_radius	-0.20	-0.38	1.00		
Distance_to_crop_meters	0.22	0.50	-0.05	1.00	
Distance_to_trees_meters	0.00	-0.05	0.10	-0.01	1.00

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