ASSESSING THE IMPRINT OF GEOGRAPHY, HOST SPECIES, LAND COVER, AND SPACE ON THE LOCAL ABUNDANCE OF A GENERALIST NEST PARASITE, THE BROWN-HEADED COWBIRD

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ASSESSING THE IMPRINT OF GEOGRAPHY, HOST SPECIES, LAND COVER, AND SPACE ON THE LOCAL ABUNDANCE OF A GENERALIST NEST PARASITE, THE BROWN-HEADED COWBIRD

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ABSTRACT

ASSESSING THE IMPRINT OF GEOGRAPHY, HOST SPECIES, LAND COVER, AND SPACE ON THE LOCAL ABUNDANCE OF A GENERALIST NEST PARASITE, THE BROWN-HEADED COWBIRD

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The Brown-headed Cowbird is an obligate nest parasite suspected of causing local population declines in several threatened and endangered passerine species. Much attention has been directed towards uncovering the fundamental factors that affect cowbird abundance; however, no study has evaluated these factors in the context of a biogeographic-scale analysis that takes into account spatial autocorrelation. Our primary objective was to compare the relative effects of geography, land cover, host species, and space on the local abundance of cowbirds.

We used data from the North American Breeding Bird Survey, the National Land Cover Database, and the latitudinal/longitudinal coordinates of the bird survey routes to examine the effects that host species, land cover composition, and geographical location have on cowbird abundance. Multiple regression models were developed for various combinations of these factors. To control for spatial autocorrelation, we used SAM 4.0 (Spatial Analysis in Macroecology) software to implement simultaneous autoregressive modeling of the error term. We then used a model comparison approach to identify the factors that most affect cowbird abundance.

Among all models examined, host species richness was the single strongest predictor and the sole statistically significant predictor. Cowbird abundance increased with host species richness. Furthermore, accounting for the effects of spatial autocorrelation resulted in AIC_c values that were approximately half the magnitude of models that did not account for space.

Our results raise questions regarding the efficacy of cowbird removal programs. If cowbirds have evolved an adaptation to aggregate in areas with high host richness, then cowbird removal programs may not be effective over the long term. In a greater context, our study demonstrates the utility of a spatially-based and geographically-extensive analysis in finding range-wide factors that affect the local abundance of a species.

CHAPTER I.

ASSESSING THE IMPRINT OF GEOGRAPHY, HOST SPECIES, LAND COVER, AND SPACE ON THE LOCAL ABUNDANCE OF A GENERALIST NEST PARASITE, THE BROWN-HEADED COWBIRD

INTRODUCTION

One fundamental goal of ecology is to explain the population abundances of species, whether referring to detailed field-based and experimental studies at a few localities or broader scale analyses of abundance as measured at hundreds of localities throughout a species' range. The latter type of study is within the domain of macroecology, particularly given that such studies often involve analysis of many different fundamental factors that could potentially affect local abundance in a common way among all localities. These types of studies are particularly relevant (and needed) for species that have some type of conservation relevance. The studies inform us of the core processes and factors that affect population size regardless of where the population may be located and the specific environmental conditions present at the location at any one particular time. Management and conservation of the species must then operate within the constraints represented by these fundamental factors.

For example, the Brown-headed Cowbird (*Molothrus ater*) is a nest parasite with a very broad geographic distribution throughout most of North America. Cowbirds lay their eggs in the nests of small to medium-sized passerine birds in edge, open, and forest habitats (Strausberger & Ashley, 1997). Such parasitism can have immediate and drastic effects on the fitness of the host parents (Lorenzana & Sealy, 1999) and perhaps cause local population declines in some species (Mayfield, 1965; Gaines, 1974; Rothstein *et al.*, 1980; Brittingham & Temple, 1983; Robinson, 1992). As such, there have been efforts to control cowbirds in some areas where they are thought to negatively affect local song birds. The most drastic of these efforts involves removal and eradication (Hayden *et al.*, 2000). Knowledge of the core factors affecting cowbird abundance could give some *a priori* indication as to whether such efforts could succeed (or fail) and possibly suggest alternative ways of managing cowbirds.

Brown-headed Cowbirds do not have specific host preferences; they have been recorded laying their eggs in the nests of over 220 other bird species (Friedmann & Kiff, 1985). Because cowbirds are obligate and generalist brood parasites, the composition of avian communities may be an important factor determining cowbird abundance (Lowther & Johnston, 1977; Clark & Robinson, 1979; Hahn & Hatfield, 1995; Barber & Martin, 1997; Purcell & Verner, 1999; Young & Hutto, 1999). Cowbirds utilize distinct habitats for feeding, “nesting”, and roosting and may travel up to 13 km a day between them (Curson *et al.*, 2000). They typically use open, prairie, or grassland areas for foraging. They most often parasitize nests that are concentrated along forest edges, a habitat also commonly used for roosting (Robinson *et al.*, 1995). Overall**,** cowbirds utilize a variety of land cover types and their densities can vary among habitats that are similar indicating that habitat type is not a sole predictor of cowbird occurrence or density (Rothstein, 2000). On a broader geographic scale, cowbird breeding density during summer is highest in the northern Great Plains. Thus, even the geographic location of a population could be a predictor of abundance. To sort out and compare these various factors (host species, land cover composition, geography) we conducted a study of cowbird abundance at 168 localities spread throughout the Great Plains region of the USA.

In addition to the conservation relevance, an additional feature of our study was an analysis of the effect of space on local abundance of a widespread species. Ecologists are increasingly recognizing what can be called "pure spatial effects" or the fact that localities in close proximity are more likely to be similar (in various ways) to one another than are localities that are further apart (Legendre, 1993). There are established statistical techniques (which we employ) to estimate and thereby control for spatial autocorrelation, but there is also real biological relevance to such spatial effects (Legendre, 1993; Lichstein *et al.*, 2002; Peres-Neto and Legendre, 2010; Hawkins, 2012). The spatial effects represent the fact that various unmeasured and unidentified processes are at work causing similar environmental conditions and ecological responses in populations that are near to one another (Hawkins, 2012).

METHODS

Study Area

Land cover and species abundance data (Brown-headed Cowbirds and host species) were obtained for six Bird Conservation Regions (BCRs). BCRs are delineated such that the area within a BCR has a relatively consistent pattern of land cover types, land use, topography, and bird community composition (North American Bird Conservation Initiative, 2000; Sauer *et al.*, 2003). The study incorporated data from the following BCRs: Prairie Potholes, Badlands and Prairies, Shortgrass Prairie, Central Mixed Grass Prairie, Oaks and Prairies, and the Edwards Plateau (Fig. 1). These regions likely represent the center of the cowbirds' historical range and still contain the highest densities of cowbirds across their current range (Sauer *et al.*, 2011). Together these regions compose the vast grassland expanse of the Great Plains. Although they differ somewhat in the degree to which woody vegetation can develop, none have expansive forested areas. The Edwards Plateau is now dominated by mesquite, juniper, and oak due to grazing and urbanization, however prior to European settlement it was a grassland savannah (North American Bird Conservation Initiative, 2000).

Species Abundance Data

Species abundance data were extracted from the North American Breeding Bird Survey (BBS) over a span of 17 years centered on 2001. The BBS currently surveys approximately 3,700 routes in the United States and Canada and contains data on > 400 species. The survey is conducted each year in May and June, and has been on-going since 1966. On each 39.4 km long route (rural roads and highways), a highly skilled observer stops for three minutes every 0.8 km. At each stop, all birds detected (visually and acoustically) by the observer are recorded (Robbins *et al.*, 1986; Sauer *et al.*, 2011). We compiled route-level abundance data for cowbirds and cowbird host species. The host species were identified by a thorough literature search and by consulting a few key references (Friedmann, 1929; Friedmann, 1963; Friedmann, 1966; Friedmann *et al.*, 1977; Friedmann & Kiff, 1985), all the host species were passerines (order Passeriformes). Eighty-eight potential cowbird host species are found in the collective group of six BCRs used in this study. No one BCR or single BBS route contains all these species. Potential host species are defined in this study as any species with at least sixty recorded (documented) instances of parasitism (Appendix S1).

Land Cover Data

There are 722 survey routes within the six BCRs, 168 of the 722 routes have been surveyed for fifteen or more years between 1993 and 2009 (a pre-requisite for deriving two of our predictor variables, see below). In order to assess whether local cowbird abundance is affected by landscape composition along a BBS route, land cover data from the 2001 release of the National Land Cover Database (NLCD) were analyzed; hence the 17-year window centered on 2001. For the continental USA, the NLCD has 16 land cover types, however we combined some of these 16 into four land cover categories. Combining similar land cover types decreases the classification error that is inherent in remotely-sensed and image-categorized data. In addition, combining data is justified when similar land cover types (e.g., grassland, pasture, and hayfields) likely have the same effect on the variable of interest (e.g., cowbird abundance). Another beneficial feature of combining land cover data is that it reduces the number of predictor variables that must be tested in subsequent models. The following categories were used: (1) developed land – includes open space, low intensity, medium intensity, and high intensity urbanization, (2) forest/shrub – includes deciduous forest, evergreen forest, mixed forest, and shrub cover all of which have canopy cover > 20%, (3) grassland/pasture/hay – includes grassy vegetation with < 20% woody canopy cover, and (4) cropland – includes cultivated crops. We did not use any of the NLCD cover types that represent aquatic cover, permanent ice, or the "barren land" categories as these are very minor landscape components in our study region. For each of the 168 routes we obtained the land cover data following the GIS processing procedure described in Veech *et al.* (2012). Land cover data for a 400 m spatial extent (i.e., landscape consists of a 400 m buffer along both sides of a route for its entire length) were used given that the BBS is assumed to survey birds only to a maximum distance of 400 m (Robbins *et al.*, 1986).

Predictor variables

The main goal of the study was to compare the relative effects of geography, land cover, and host species on the local abundance of Brown-headed Cowbirds. For geography, we had two predictor variables, latitude and longitude of the center point of a BBS route. For land cover, we had four variables (as described in previous section): developed land, forest/shrub, grassland/pasture/hay, and cropland. Each of these was expressed as the percent cover in the roughly 0.8 × 40.2 km landscape surrounding a BBS route. To examine the composite effect of host species, we derived three variables for each route: (1) host species richness – determined as the mean richness of host species over the 17-year period, (2) host positive abundance coefficient (HPOS), and (3) host negative abundance coefficient (HNEG).

The latter two variables measured the route-level effect of host species abundance on cowbird abundance. These variables were derived as follows: A multiple regression model was developed for each combination of route and host species in which there was sufficient data (N = 15 years). In addition to host abundance, the regression models also included year and observer effect. The "year" effect accounts for any spurious temporal autocorrelation in the response variable, cowbird abundance. "Observer effect" is the mean cowbird abundance recorded by the BBS observer per year for that observer (even if the years are not consecutive). Ideally, a BBS route is surveyed by the same observer every year; however, some routes in our data set were surveyed by multiple observers over the 17-year period and thus we needed to account for a possible observer effect (Sauer *et al.*, 1994). Our observer variable statistically controls for potential differences among observers in counting cowbirds. Because we include (estimate) the year effect and the observer effect in our multiple regression models, the partial regression coefficient for the host abundance variable is a reliable measure of the effect of a host species on cowbird abundance in a given year. In effect, the coefficient represents the additional number of cowbird individuals "attracted to" the route for each additional host individual present on the route. The multiple regression model can be expressed as $Y = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + \epsilon$, where Y= cowbird abundance, X_1 = host abundance, X_2 = year, and X_3 = observer effect. Partial regression coefficients (B_1) for each host species on a route were divided into two groups: positive and negative coefficients. We then calculated the mean (across host species) for each group to represent HPOS and HNEG. For each route, HPOS and HNEG represent the mean positive and negative "effects" that hosts have on cowbird abundance. We assumed *a priori* that host abundance could potentially have a positive or negative correlation with cowbird abundance, hence our use of two variables instead of just one. In the latter case, an average for all correlation coefficients (positive and negative) could be near zero when there are large positive and negative coefficients that essentially cancel one another. We did not interpret the statistical significance of any of the correlation coefficients; however, we point out that non-significant coefficients would be near zero and hence would lead to low values of HPOS or HNEG thus appropriately representing very little combined host effect on cowbird abundance on the given route. Our use of multiple regression in this step was intended only to derive HPOS and HNEG as predictor variables to use in subsequent modeling.

Model development and comparison

We initially developed and tested six regression models to compare the effects of space, geography, land cover, and host species on local cowbird abundance throughout our study region (Table 1). In total, our study included nine predictor variables. We took a conservative approach in not testing every possible combination of these variables; rather we constructed and tested a limited set of models that allowed us to compare the broad effects of space, geography, land cover, and host species. Based on the results from Model 2, we ran two additional models that were reduced versions of Model 2 (Table 1). Local abundance of cowbirds was determined as the mean abundance per year on a route over the 17-year period, 1993 - 2009. All of our variables (response and predictor) contained some amount of spatial autocorrelation. Therefore, to control for this autocorrelation, we used simultaneous autoregressive modeling of the error term

(SAR_{err}). SAR_{err} is a form of spatial statistical modeling that explicitly models spatial autocorrelation in the error term of the multiple regression equation (Rangel *et al.*, 2006; Dormann *et al.*, 2007; Kissling & Carl, 2008). The following regression equation is fit to the data, $Y = X\beta + \lambda W\mu + e$ where Y is the response variable (e.g. mean cowbird abundance on a route), X is a matrix of the predictor variables, β is a vector of the partial regression coefficients, λ is the spatial autoregression coefficient, W is a matrix of weights based on the Euclidean distances between all pairs of observations (route locations), μ is the error term that models spatial dependence (autocorrelation), and *e* is the typical error term (non-spatial) common to all regression equations (Dormann *et al.*, 2007). Further, $\lambda W\mu$ is actually represented by the error variance-covariance matrix defined as $C = \sigma^2[(I - \rho W)^T]^{-1}[I - \rho W]^{-1}$ where σ^2 is the variance of the residuals, I is an identity matrix of size n = number of observations (or routes), and ρ (or λ) is the autoregressive parameter as presented by Rangel et al. (2006). SAR_{err} models control for spatial autocorrelation where it matters most, in fitting the regression equation to data (and estimating the spatially dependent error term); other spatial modeling approaches (e.g., lagged models) estimate the spatial autocorrelation in the predictor or response variables themselves.

We used the SAM 4.0 (Spatial Analysis in Macroecology) (Rangel *et al.*, 2010) software to implement the SAR_{err} modeling. More specifically, in the software program, we selected “Modeling” >> “Spatial Autoregression” >> “Autoregressive Models (SAR/CAR)” >> “Simultaneous Autoregression”. Prior to running our models, we ln-transformed mean cowbird abundances given that they ranged from 0.3 to 226.6 per route and were right-skewed (mean abundance < 50 on 83% of routes). Although not a strict statistical requirement of SAR_{err} models, normality of the response variable helps in fitting the model.

In all of our models we wanted to isolate the spatial autocorrelation as much as possible so that we could estimate the pure spatial effect and so that the remaining variation in the data (not explained by space) could be ascribed to the other predictor variables. The matrix W consists of all the pairwise weights, w_{ij}. These can be set so that nearby (or far off) pairs can be given more or less weight, $w_{ij} = d_{ij}^{\alpha}$, where d_{ij} is the geographic distance between observations (routes) *i* and *j* (Rangel *et al.*, 2006). Alpha can be adjusted to an "optimal value" (typically between 1 and 2) so that the maximum amount of spatial autocorrelation is modeled (or removed from the data) and most importantly so that the estimated β values for the remaining variables have as little unwanted spatial dependence as possible. We used an iterative "trial-and-error" process in SAM 4.0 to find the optimal alpha value for each model. We began by setting alpha equal to 1.0 and then increased (or decreased) it in 0.1 and 0.01 increments until we found the model with the lowest AICc. Selected alpha values did not differ by much among the models, ranging from 1.74 to 1.77.

Our main goal was to assess the relative influence of space, geography, land cover, and host species on the local abundance of cowbirds. To do this we evaluated the fit of the models by comparing their AICc and r^2 values. For each model and across models, we also compared the partial regression coefficients (β values) for the various predictors in order to determine if any variables could be singled out as much more important than the others.

RESULTS

Among the 168 BBS routes, there was substantial variation in the mean annual abundance of cowbirds during the period 1993 – 2009. The lowest mean was 0.27 birds and the highest was 227.6 birds; the mean of the means over all routes was 29.6 birds per year. Mean annual species richness of hosts during the same time period ranged from 4.3 to 34.9 with a mean over all routes of 17.0 species. The BBS routes were spread throughout the Great Plains region (Fig. 1). Among all routes, there was substantial variation in percent cover of the four land cover types. Percentages for developed land ranged from 0 to 33.9 (mean 7.2), forest/shrub ranged from 0 to 98.7 (mean 18.2), grassland/pasture/hay ranged from 0 to 93.8 (mean 43.2), and cropland ranged from 0 to 92.3 (mean 27.5). Only a few routes were devoid of either developed land (2 routes), forest/shrub (5 routes), or grassland/pasture/hay (2 routes); however, 22 routes did not have any cropland.

The full model that included all nine predictor variables representing the factors of geographic location, host species, and land cover had the lowest AICc value and one that was substantially lower than the next closest competing model (ΔAICc = -20.2, Table 2). Host species richness was the only predictor variable in the full model that had a significant regression coefficient ($\beta = 0.097$, $t = 3.18$, $P = 0.002$). Furthermore, this predictor variable was statistically significant ($P < 0.05$) in all of the models that included it and no other predictor variable was significant in any of the models. Local cowbird abundance increased with an increase in host species richness on BBS routes (Fig. 2A).

At a richness of about 20 host species, cowbird abundance appeared to level off (with substantial variation) without increasing further. This suggested that a quadratic term (host species richness^2) might fit the data well. Therefore, we conducted an additional SAR_{err} model with square-root transformed host species richness (linear form of x^2) as the sole predictor variable. The AICc of this model (277.4) was less than that of the equivalent model with the linear effect of host species richness (AICc = 282.4, Model 2-1-1 of Table 2).

The single strongest predictor of local cowbird abundance was host species richness, although the other factors (geographic location and land cover) also contributed toward explaining cowbird abundance as evidenced by the relatively low AICc value of the full model. Indeed, Model 5 included only the three host variables and it had one of the highest AICc values (Table 2). Overall, space (i.e., estimation of the spatial autoregression coefficient λ) had a very large contribution to the fit of all models as indicated by the "w/o Space" AICc values being about twice the magnitude of the "w/Space" AICc values (Table 2). The λ values ranged from 0.927 to 0.931. Note also that the r^2 values for the "w/o Space" models were about half of those for the "w/Space" models (Table 2).

DISCUSSION

Our results clearly indicate that local cowbird abundance is most affected by host species richness. This likely arises from the evolution of cowbirds as generalist nest parasites. Cowbirds co-evolved with a large number of host species in the Great Plains. Many of these species developed defense mechanisms (e.g. re-nesting, cowbird egg removal, burying cowbird eggs within the nest, and mobbing behavior) which alleviated the pressures of parasitism. Although rejecter species may be present, areas with high host richness most likely contain a large number of acceptor host species as well. Given that local cowbird abundance is positively related to host species richness, there must not be a high percentage of rejecter species in most local assemblages or if there is then the rejection rate is not so great as to prevent the positive relationship that we uncovered (also see Robinson et al. 1999). It is also worth noting that no rejecter species is completely successful at avoiding cowbird parasitism all of the time (Rothstein, 1975; Strausberger & Ashley, 1997; Robinson et al., 1999).

Because the Brown-headed Cowbird is a generalist nest parasite it may not easily respond to the negative feedback seen in nest parasites that have specific host preferences (Rothstein, S.I. and Robinson, S. K., 1998; May & Robinson, 1985; Takasu *et al.*, 1993). That is, cowbirds may not be capable of evolving species-specific responses (such as egg shell mimicry) given that they parasitize (and must be adapted to) a wide range of host species and given that no single host species exerts a strong selective pressure. This situation may be particularly true for communities with high host richness. Interestingly, we found no evidence of a cowbird response to hosts in ecological time. The variables (HPOS and HNEG) that measured the standardized effect of host abundance on cowbird abundance over a 17-year period had negligible influence in the three models that they were included in. HPOS and HNEG had the lowest partial regression coefficients (between -0.031 and 0.021) of all the predictor variables. By comparison, the partial regression coefficient for HRICH (mean host species richness on a BBS route) was between 0.441 and 0.526 in the six models that included it.

It also appears that local cowbird abundance reaches an upper limit when there are 20 or more host species available along a BBS route (Fig. 2A). In those areas, cowbird abundances are likely limited by factors other than host availability. Furthermore, local cowbird abundance was not in any way related to the species richness of non-host passerines (defined as the mean richness of passerine birds exclusive of the species in the group of 88 known hosts) (Fig. 2B). These results further support the inference that cowbird abundance is in part an evolutionary response to the diversity of host species and not just the presence of any small perching bird species. The threshold of 20 host species could represent an adaptive limit beyond which any additional host species in the environment do not necessarily accrue greater fitness for individuals in the cowbird population and hence do not increase local abundance. It is also worth noting that host richness tends to be about twice that of non-host richness (Fig 2A compared to 2B), again in accordance with the Brown-headed Cowbird being a generalist nest parasite.

The full model included all the predictor variables and had the lowest AICc value of all the models. Therefore, in addition to host species richness, it may seem as though the other predictor variables (geography and land cover) also have some effect on local cowbird abundance. However, in the full model, the standardized partial regression coefficients for these other variables were non-significant: $\beta_{LAT} = 0.053$, $P = 0.86$; $\beta_{LONG} = -0.143$, $P = 0.49$; $\beta_{HPOS} = 0.021$, $P = 0.81$; $\beta_{HNEG} = -0.020$, $P = 0.81$; $\beta_{DEV} = -0.03$, $P = 0.79$; $\beta_{FS} = 0.211$, $P = 0.57$; $\beta_{GPH} = 0.294$, $P = 0.44$; and $\beta_{CROP} = 0.335$, $P = 0.43$. When compared to the highly significant effect of host species richness ($\beta_{HRICH} = 0.468$, $P = 0.002$) the other variables have a much weaker and possibly negligible effect on cowbird abundance.

The fit of all of our models was substantially improved by incorporating the effect of space (Table 2). Our analytical approach (use of SAR_{err} modeling) was slightly different from variation partitioning; however, what we refer to as “spatial effects” likely represents the combined fractions “spatial legacy” and “spatial nuisance” described by Peres-Neto and Legendre (2010). That is, for our models, the difference between r^2 values for models with and without space is an approximation of the additional variation in cowbird abundance explained by adding a term (to the regression equation: $Y = X\beta + \lambda W\mu + e$) to estimate the spatial autocorrelation in the residuals. The additional term, $\lambda W\mu$, doubled the “explanatory power” of some models and increased it by a factor of 1.6 for the full model. In the context of biology and our study, the spatial effect is likely due to a variety of factors including dispersal (population connectivity) of cowbirds and hosts, conspecific attraction, spatially-linked weather patterns and landscape disturbance regimes, in addition to the black box of unexamined and unknown environmental variables affecting cowbirds and their hosts.

Our results raise questions regarding the effectiveness of cowbird removal programs. Due to the high recolonization rate of cowbirds, trapping (i.e., removal) must be implemented each year in order to have a continuous effect on cowbird abundance at any given location (e.g., Kelly and DeCapita, 1982; Eckrich et al., 1999; Griffith & Griffith, 2000; Rothstein & Cook, 2000). Our results suggest that cowbirds may have evolved a behavioral response to settle in areas of high host species richness. At the very least, there is a positive association between cowbird abundance and the richness of host species that has likely developed over millennia and would be hard to break by any management strategy. If a given area with many host species truly does represent a resource-rich environment that cowbirds are highly adapted to, then cowbirds will eventually return after being temporarily eradicated. Cowbird removal programs may never be an effective long-term management option, particularly on large landscape to regional scales. In our view, the most viable long-term solution for preserving populations of threatened and endangered songbirds is to redirect attention and resources from cowbird removal to acquisition and preservation of habitat for the songbirds.

CONCLUSIONS

One of the applied goals of conservation biogeography is to develop broad-scale strategic plans for species with conservation relevance. Obtaining an understanding of the core processes that affect species abundance, not only at a landscape scale, but also throughout a large portion of a species' range is necessary for creating management strategies that can be implemented across a broad geographic range. In the present study, we used a model comparison approach to compare some of these core factors. Our study also demonstrates the importance of including space in addition to other core factors that affect a species' abundance. Space represents a set of real biological factors, even if not measured and explicitly included in an analysis. Excluding these factors altogether can result in erroneous conclusions regarding the determinants of species abundances. Such false conclusions can result in management strategies that incorrectly allocate resources, fail to address the primary causes of declines in threatened and endangered species and, in the case of cowbirds, may result in the unnecessary destruction of a native species.

APPENDIX

Appendix S1. Host species of Brown-headed Cowbirds as identified by an exhaustive literature search. Species in this list have at least 60 documented instances (nests) of parasitism. These species were included in calculation of HPOS, HNEG and host species richness.

Family	Common Name	Scientific Name
Alaudidae	Horned Lark	*Eremophila alpestris*
Bombycillidae	Cedar Waxwing	*Bombycilla cedrorum*
Calcaridae	Chestnut-collared Longspur	*Calcarius ornatus*
Cardinalidae	Blue Grosbeak	*Passerina caerulea*
Cardinalidae	Dickcissel	*Spiza americana*
Cardinalidae	Indigo Bunting	*Passerina cyanea*
Cardinalidae	Northern Cardinal	*Cardinalis cardinalis*
Cardinalidae	Painted Bunting	*Passerina ciris*
Cardinalidae	Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Cardinalidae	Scarlet Tanager	*Piranga olivacea*
Cardinalidae	Summer Tanager	*Piranga rubra*
Cardinalidae	Western Tanager	*Piranga ludoviciana*
Emberizidae	Song Sparrow	*Melospiza melodia*
Emberizidae	Spotted Towhee	*Pipilo maculatus*

Emberizidae	Baird's Sparrow	*Ammodramus bairdii*
Emberizidae	Chipping Sparrow	*Spizella passerina*
Emberizidae	Clay-colored Sparrow	*Spizella pallida*
Emberizidae	Dark-eyed Junco	*Junco hyemalis*
Emberizidae	Eastern Towhee	*Pipilo erythrophthalmus*
Emberizidae	Field Sparrow	*Spizella pusilla*
Emberizidae	Henslow's Sparrow	*Ammodramus henslowii*
Emberizidae	Lark Bunting	*Calamospiza melanocorys*
Emberizidae	Lark Sparrow	*Chondestes grammacus*
Emberizidae	Lazuli Bunting	*Calamospiza melanocorys*
Emberizidae	Savannah Sparrow	*Passerculus sandwichensis*
Emberizidae	Swamp Sparrow	*Melospiza georgiana*
Emberizidae	Vesper Sparrow	*Pooecetes gramineus*
Emberizidae	White-crowned Sparrow	*Zonotrichia leucophrys*
Emberizidae	White-throated Sparrow	*Zonotrichia albicollis*
Emberizidae	Black-throated Sparrow	*Amphispiza bilineata*
Emberizidae	Grasshopper Sparrow	*Ammodramus savannarum*
Fringillidae	American Goldfinch	*Spinus tristis*
Fringillidae	House Finch	*Haemorhous mexicanus*
Fringillidae	Pine Siskin	*Spinus pinus*
Fringillidae	Purple Finch	*Haemorhous purpureus*
Icteridae	Bobolink	*Dolichonyx oryzivorus*
Icteridae	Brewer's Blackbird	*Euphagus cyanocephalus*

Icteridae	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*
Icteridae	Baltimore Oriole	*Icterus galbula*
Icteridae	Common Grackle	*Quiscalus quiscula*
Icteridae	Eastern Meadowlark	*Sturnella magna*
Icteridae	Great-tailed Grackle	*Quiscalus mexicanus*
Icteridae	Hooded Oriole	*Icterus cucullatus*
Icteridae	Orchard Oriole	*Icterus spurius*
Icteridae	Red-winged Blackbird	*Agelaius phoeniceus*
Icteridae	Western Meadowlark	*Sturnella neglecta*
Mimidae	Brown Thrasher	*Toxostoma rufum*
Mimidae	Gray Catbird	*Dumetella carolinensis*
Parulidae	American Redstart	*Setophaga ruticilla*
Parulidae	Black-and-white Warbler	*Mniotilta varia*
Parulidae	Chestnut-sided Warbler	*Setophaga pensylvanica*
Parulidae	Common Yellowthroat	*Geothlypis trichas*
Parulidae	Kentucky Warbler	*Geothlypis formosa*
Parulidae	Louisiana Waterthrush	*Parkesia motacilla*
Parulidae	MacGillivray's Warbler	*Geothlypis tolmiei*
Parulidae	Magnolia Warbler	*Setophaga magnolia*
Parulidae	Nashville Warbler	*Oreothlypis ruficapilla*
Parulidae	Northern Waterthrush	*Parkesia noveboracensis*
Parulidae	Ovenbird	*Seiurus aurocapilla*
Parulidae	Prothonotary Warbler	*Protonotaria citrea*

Parulidae	Swainson's Warbler	*Limnothlypis swainsonii*
Parulidae	Yellow Warbler	*Setophaga petechia*
Parulidae	Yellow-breasted Chat	*Icteria virens*
Parulidae	Yellow-rumped Warbler	*Setophaga coronata*
Polioptilidae	Blue-gray Gnatcatcher	*Polioptila caerulea*
Sittidae	White-breasted Nuthatch	*Sitta carolinensis*
Troglodytidae	Rock Wren	*Salpinctes obsoletus*
Turdidae	Eastern Bluebird	*Sialia sialis*
Turdidae	Swainson's Thrush	*Catharus ustulatus*
Turdidae	Veery	*Catharus fuscescens*
Turdidae	Wood Thrush	*Hylocichla mustelina*
Turdidae	American Robin	*Turdus migratorius*
Tyrannidae	Acadian Flycatcher	*Empidonax virescens*
Tyrannidae	Dusky Flycatcher	*Empidonax oberholseri*
Tyrannidae	Eastern Kingbird	*Tyrannus tyrannus*
Tyrannidae	Eastern Phoebe	*Sayornis phoebe*
Tyrannidae	Eastern Wood-Pewee	*Contopus virens*
Tyrannidae	Least Flycatcher	*Empidonax minimus*
Tyrannidae	Vermilion Flycatcher	*Pyrocephalus rubinus*
Tyrannidae	Western Wood-Pewee	*Contopus sordidulus*
Vireonidae	Bell's Vireo	*Vireo bellii*
Vireonidae	Blue-headed Vireo	*Vireo solitarius*
Vireonidae	Plumbeous Vireo	*Vireo plumbeus*

Vireonidae	Red-eyed Vireo	*Vireo olivaceus*
Vireonidae	Warbling Vireo	*Vireo gilvus*
Vireonidae	White-eyed Vireo	*Vireo griseus*
Vireonidae	Yellow-throated Vireo	*Vireo flavifrons*

Table 1. Regression models used to examine the effects of geography, host species, and land cover on local cowbird abundance (BBS routes) within the Great Plains study region. The effect of space was included in each model by the use of simultaneous autoregressive modeling (see Table 2 for results).

Model	Description	Predictor variables[1]
1	Full model	LAT, LONG, HRICH, HPOS, HNEG, DEV, FS, GPH, CROP
2	Geographic location and host variables	LAT, LONG, HRICH, HPOS, HNEG
2-1	Geographic location and host richness	LAT, LONG, HRICH
2-1-1	Host richness only	HRICH
3	Geographic location and land cover variables	LAT, LONG, DEV, FS, GPH, CROP
4	Geographic location only	LAT, LONG
5	Host variables only	HRICH, HPOS, HNEG
6	Land cover variables only	DEV, FS, GPH, CROP

[1]Abbreviations for the predictor variables are as follows: LAT – latitudinal position of the center-point of the BBS route, LONG – longitudinal position, HRICH – host species richness, HPOS – mean positive route-level effect of host abundance on cowbird abundance , HNEG – mean negative route-level effect, DEV – percentage of developed land within the BBS route-landscape, FS – percentage of forest/shrub land, GPH – percentage of grassland/pasture/hayfield, and CROP – percentage of cropland (see text for further details).

Table 2. Comparison of the regression models examining the effects of space, geographic location, host species, and land cover on the local abundance of cowbirds. Models are arranged in order of increasing values of AICc with space. Columns representing "w/o Space" refer to ordinary least-squares regression models that do not take into account spatial autocorrelation. Columns labeled "w/Space" are regression models in which a term quantifying the effect of spatial autocorrelation is included in the regression equation (SAR_{err} models). K refers to number of predictor variables in the model.

Model	K	w/o Space		w/ Space		
		r^2	AICc	r^2	AICc	ΔAICc
(1) Full model	9	0.54	475.9	0.88	250.9	0
(3) Geographic location and land cover	6	0.38	521.0	0.86	271.1	-20.2
(2-1) Geographic location and host richness	3	0.52	470.5	0.85	272.8	-21.9
(4) Geographic location only	2	0.36	515.4	0.85	278.2	-27.3
(2) Geographic location and host variables	5	0.54	469.3	0.85	278.8	-27.9
(2-1-1) Host richness only	1	0.49	477.0	0.84	282.4	-31.5
(5) Host variables only	3	0.52	472.2	0.84	288.4	-37.5
(6) Land cover variables only	4	0.11	576.6	0.83	294.4	-43.5

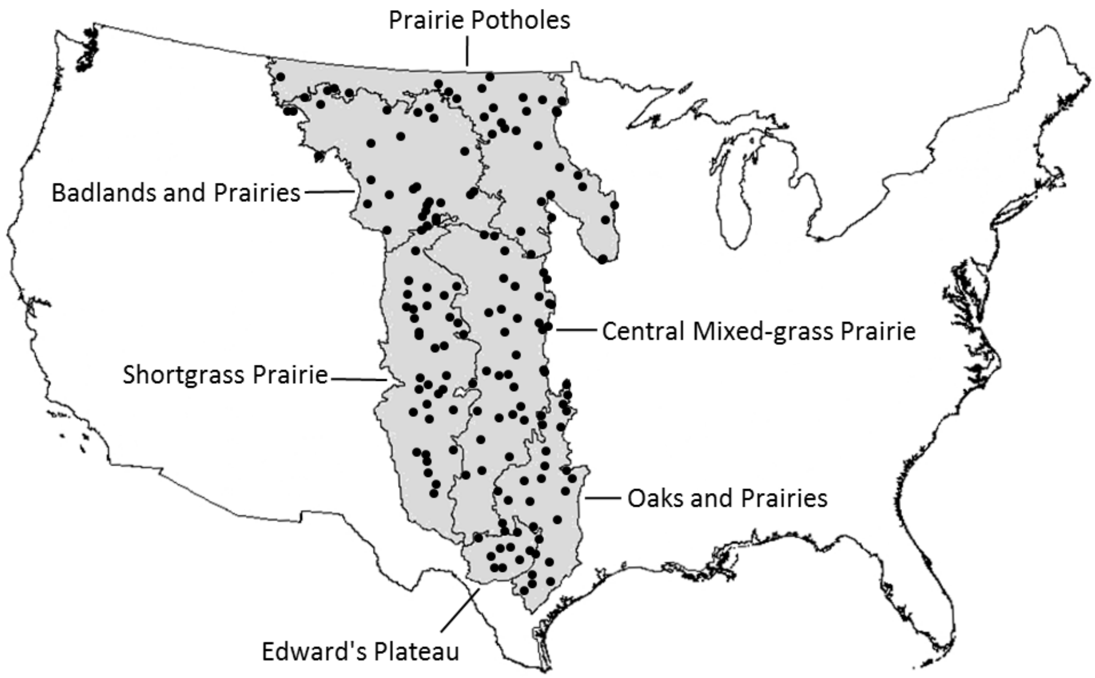

Figure 1. Map shows the region covered in this study, which includes the six Bird Conservation Regions composing the Great Plains. Black dots represent the locations of the 168 Breeding Bird Survey routes used in the study.

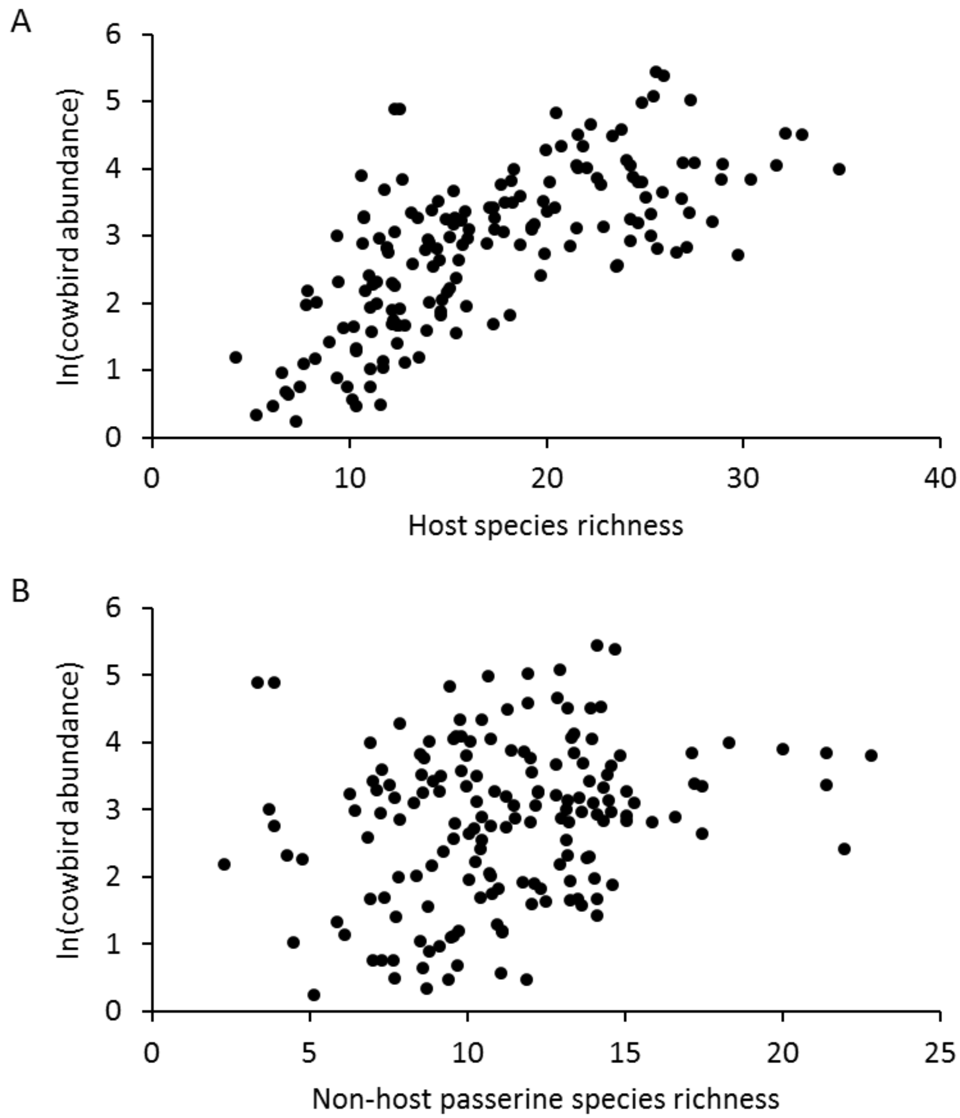

Figure 2. The effect of (A) host species richness and (B) non-host passerine species richness on local cowbird abundance on routes of the Breeding Bird Survey. Species richness values are means over the period 1993 – 2009. In both panels, cowbird abundance is show as the ln-transformed mean value over the period 1993 – 2009.

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