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Assessing the influence of geography, land cover and host species on the local abundance of a generalist brood parasite, the brown-headed cowbird

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ABSTRACT

Aim The brown-headed cowbird is an obligate brood parasite known to exploit a large number of host species and use a variety of habitats. 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 influence of geography, land cover and host species on the local abundance of cowbirds.

Location Great Plains region of the USA.

Methods We used data from the North American Breeding Bird Survey and the National Land Cover Database to examine the relationships between cowbird abundance and host species, land cover composition and geographic location of a survey route. 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 modelling of the error term. We then used a model comparison approach to identify the factors that most influence cowbird abundance.

Results Among all models examined, host species richness was the single most strong predictor and the sole statistically significant predictor. Cowbird abundance increased with host species richness but did not change in any significant way with non-host passerine richness or abundance of host species. Models with land cover variables tended to have the poorest fit to the cowbird abundance data.

Main conclusions Our results suggest that cowbirds may be attracted to areas with greater host richness and/or recruit better in such areas, although our data did not allow direct examination of either process. 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.

Keywords

Conservation, geographic range, grassland, habitat, songbird, spatial autocorrelation.

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INTRODUCTION

The local abundance of a broadly distributed species is potentially affected by many other species, particularly if the given species is a generalist in resource use. For example, the brown-headed cowbird (*Molothrus ater*) is a brood 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). Brown-headed cowbirds 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 (availability of hosts) may be an important factor determining cowbird abundance (Lowther & Jonston, 1977; Clark & Robinson, 1979; Hahn & Hatfield, 1995; Barber & Martin, 1997; Purcell & Verner, 1999; Young & Hutto, 1999). The effect of hosts on cowbirds could be manifested in several ways. Cowbirds might be attracted to areas that have higher host densities (e.g. aggregative response), and/or population recruitment of cowbirds (i.e. numerical response) might be greater in such areas. This then would produce a positive relationship between cowbird abundance and host availability. Alternatively, a negative relationship between cowbird abundance and host density might exist if cowbirds are so efficient at parasitism that they actually suppress recruitment of the host species.

Habitat can also be important to the local abundance of a species. Given their continental distribution, it is not surprising that cowbirds occur in a variety of habitats. In general, the preferred habitat of cowbirds seems to be grassland or agricultural land interspersed with scattered trees, shrubs or hedgerows (Lowther, 1993). Cowbirds often use different habitat types for foraging, roosting and breeding (Chace et al., 2005). Breeding habitat depends on the location of host nests although cowbirds tend not to parasitize nests that are in interior areas of forests or in the middle of vast open areas (Lowther, 1993). Overall, cowbirds utilize a variety of land cover types (except expansive forest), and their densities can vary between habitats that are similar, indicating that habitat type is not a sole predictor of cowbird occurrence or density (Rothstein & Robinson, 2000). In addition, individual cowbirds may travel up to 15 km a day between roosting and feeding sites (Curson et al., 2000) and can permanently disperse even greater distances over longer time spans (Anderson et al., 2012). Cowbirds are short-distance migrants, typically not migrating more than a few hundred kilometres. On a broader geographic scale, the local abundances of resident cowbirds can vary greatly; summer-time population densities in the northern Great Plains are several times greater than elsewhere. 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.

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 centre of the cowbirds' historical range and still contain the highest densities of cowbirds across their current range (Chace et al., 2005; Sauer et al., 2011). We limited our analysis to the central USA so as to increase our chances of distinguishing between the various factors that could affect cowbird abundance. A continent-wide comparison could potentially have made this task more difficult if regions (central, western, eastern USA) differ in some unmeasured but important variable(s).

Species abundance data

Species abundance data were extracted from the North American Breeding Bird Survey (BBS) (Sauer et al., 2011) over a span of 17 years centred on 2001. These temporal data were used to quantify annual coupling of cowbird abundance with host species abundance (see section titled 'Predictor variables'). The BBS currently surveys approximately 3700 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 ongoing 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 published reviews (Friedmann & Kiff, 1985; Ortega, 1998); all the host species were passerines (order Passeriformes). Eighty 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
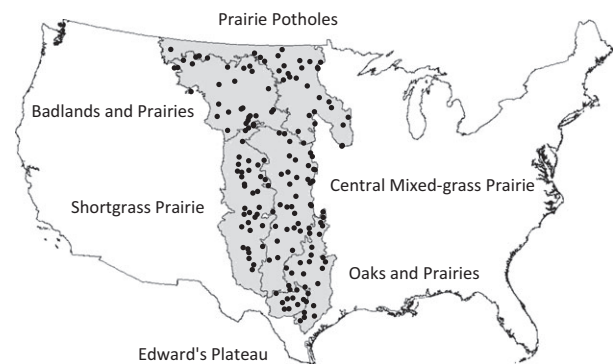
Figure 1 Map shows the region covered in this study, which includes the six Bird Conservation Regions composing the Great Plains. Black dots represent the locations of the 168 Breeding Bird Survey routes used in the study.

species. Potential host species are defined in this study as any species with at least sixty recorded (documented) instances of parasitism (see Appendix S1 in Supporting Information). The group of non-host passerines consisted of 97 species (list provided at the end of 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 prerequisite for deriving two of our predictor variables, see below) (Fig. 1). 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 analysed, hence, the 17-year window centred on 2001. We collapsed the 16 NLCD land cover types into four broad categories: (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. Based on previously reported habitat associations (Lowther, 1993), these four categories represent the major land cover types that could be used by cowbirds to varying degrees. 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). Slightly shorter or greater distances could have been used to define the landscapes without adversely affecting the model results. The data for cowbird and host species abundances do not literally depend on counting every bird out to a distance of 400 m, and percentage cover estimates for the land cover categories are likely to be somewhat scale invariant for most routes (Veech et al., 2012).

Predictor variables

The main goal of the study was to compare the relative influence 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 centre 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 percentage cover in the roughly 0.8×40.2 km landscape surrounding a BBS route. To examine the composite influence 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). These

latter two variables derived from the route-level coupling of host species abundance with cowbird abundance over time, considered separately for each host species. HPOS and HNEG provided a more thorough measure of the relationship between cowbird and host abundances than would a metric that combined all host individuals (regardless of species) and that ignored concordant changes through time (see Model 2-1-4).

HPOS and HNEG were obtained as follows: A multiple regression model with cowbird abundance as the response variable was developed for each combination of route and host species in which there was sufficient data ($N \geq 15$ years). We used SPSS 20 software. The regression models quantified how tightly cowbird and host abundances were coupled over time. 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 between 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 association between a host species and cowbird abundances in a given year. 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 $Y = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + \varepsilon$, 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 association between hosts and cowbird abundances. We assumed a priori that cowbird abundance could potentially have a positive or negative correlation with host abundance, hence our use of both HPOS and HNEG. Another reason for separating positive and negative coefficients is that an average for all correlation coefficients (positive and negative) could be near zero when there are large positive and negative coefficients (values of B_1) 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 modelling.

Model development and comparison

Using spatial autoregressive techniques (see below), we initially developed and tested six regression models to compare geography, land cover and host species as they might influence local cowbird abundance throughout our study region (Table 1). In total, our study included nine predictor variables. We took a conservative approach (to avoid type I error and redundancy) 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 influence of geography, land cover and host species. We tested each of these factors in a full model (Model 1) and separately (Models 4, 5, and 6). Because latitude and longitude can often have substantial effects on biogeographic models and patterns (these variables are proxies for many environmental gradients), we also tested host species and land cover combined separately with geography (Models 2 and 3). Based on the results from Model 2 (i.e. the best fit of the models developed *a priori*), we ran five additional models to see whether there was a minimum adequate model (Diniz-Filho *et al.*, 2008) and better alternative to Model 2.

For all of the models, route-level abundance of cowbirds was the response variable. It was calculated as the mean over all years of the 17-year period, 1993–2009. To be clear, the previously described multiple regression models used to derive the HPOS and HNEG variables were based on yearly cowbird abundance data, not means over all years. All of our variables (response and predictor) contained some amount of spatial autocorrelation. Therefore, to control for this autocorrelation, we used simultaneous autoregressive modelling

of the error term (SAR_{err}). SAR_{err} is a form of spatial statistical modelling 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 geographic 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 modelling 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} modelling. 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.

Our main goal was to assess the relative influence of geography, land cover and host species on the local abundance of

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 (see Table 2 for results).

Model	Description	Predictor variables*
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
2-1-1-sqrt	Host richness only (sqrt. transformed)	sqrt(HRICH)
2-1-2	Non-host richness only	NHRICH
2-1-3	All passerine richness only	APRICH
2-1-4	Mean annual host abundance only	HABD
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

*Abbreviations for the predictor variables are as follows: LAT, latitudinal position of the centre 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; NHRICH, non-host passerine richness; APRICH, all passerine richness; HABD, mean annual host abundance (summed over all hosts); 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 SAR_{err} models examining the effects of geographic location, host species, non-host species and land cover on the local abundance of cowbirds.

Model	K	AICc*	ΔAICc	w_i
(2-1-1-sqrt) Host richness only (sqrt. trans)	3	475.1	0	0.7091
(2-1) Geographic location and host richness	5	477.6	2.5	0.2032
(2) Geographic location and all host variables	7	479.4	4.3	0.0826
(5) Host variables only	5	486.4	11.3	0.0025
(2-1-1) Host richness only	3	486.5	11.4	0.0024
(1) Full	11	490.9	15.8	0.0003
(2-1-3) All passerine richness only	3	505.7	30.6	< 0.0001
(4) Geographic location only	4	525.3	50.2	< 0.0001
(3) Geographic location and land cover	8	536.0	60.9	< 0.0001
(2-1-4) Mean annual host abundance only	3	572.4	97.3	< 0.0001
(2-1-2) Non-host richness only	3	573.3	98.2	< 0.0001
(6) Land cover only	6	593.9	118.8	< 0.0001

*SAM 4.0 software calculates three AICc values for SAR_{err} models. Table presents the AICc values that are based upon only the predictor variable portion ($X\beta$) of the SAR_{err} regression equation: $Y = X\beta + \lambda W\mu + e$. K refers to the number of estimated parameters (predictor variables and y-intercept) in the model; w_i are the Akaike weights.

cowbirds. To do this, we evaluated the fit of the models by comparing their AICc and w_i values. Lower values for AICc and higher values for model weight (w_i) indicate better fit; this is the information-theoretic approach to comparing models as advocated by Burnham & Anderson (2002) and Diniz-Filho *et al.* (2008). For each model and across models, we also compared the standardized partial regression coefficients (β values) for the various predictors to determine whether 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. Among all routes, there was substantial variation in percentage cover of the four land cover types. Percentages for developed land ranged from 0 to 33.9 (mean 7.2, SD 4.3), forest/shrub ranged from 0 to 98.7 (mean 18.2, SD 24.8), grassland/pasture/hay ranged from 0 to 93.8 (mean 43.2, SD 25.4) and cropland ranged from 0 to 92.3 (mean 27.5, SD 28.2). Only a few routes were devoid of developed land (2 routes), forest/shrub

(5 routes) or grassland/pasture/hay (2 routes); however, 22 routes did not have any cropland.

The model with square-root-transformed host species richness as the only predictor variable had the lowest AICc value and an Akaike model weight ($w_i = 0.709$) that was substantially greater than the other models (Table 2). The standardized partial regression coefficient for host richness was statistically significant ($\beta = 0.54$, $P < 0.001$, 95%CI = 0.10–0.98). The next closest model ($\Delta AICc = 2.5$, $w_i = 0.203$) included host richness along with geographic location (latitudinal and longitudinal coordinates of the survey route) as predictor variables. The standardized partial regression coefficient for host richness was significant ($\beta = 0.47$, $P < 0.001$, 95%CI = 0.41–0.53), but non-significant for latitude ($\beta = 0.07$, $P = 0.79$, 95%CI = -0.05 to 0.19) or longitude ($\beta = -0.13$, $P = 0.45$, 95%CI = -0.27 to 0.01). Host species richness (and its square-root transformation) was the only predictor variable that had a significant β coefficient ($P < 0.05$) in any of the models and was significant in all models in which it was included. Local cowbird abundance clearly increased with an increase in host species richness on BBS routes (Fig. 2a). The relationship appeared to be curvilinear, which probably explains why the model with square root-transformed host richness had the best fit.

We included Models 2-1-2 and 2-1-3 (Table 1) to examine whether richness of non-host passerine species and all passerine species were better predictors of cowbird abundance. They were not; each of these models had an AICc value and w_i substantially higher and lower respectively than the model with either square root-transformed or -untransformed host species richness (Table 2). The lack of a relationship between cowbird abundance and non-host passerine richness is also revealed by a scatterplot of these variables (Fig. 2b). We included Model 2-1-4 to examine whether mean annual host abundance (summed over all hosts) was a better predictor than host richness. It was not; AICc value and w_i of Model 2-1-4 were substantially lower than those for the models containing host richness as the only predictor variable (Table 2).

DISCUSSION

Our results clearly indicate that local cowbird abundance is influenced more by host species richness than the other factors that were tested. This likely arises from the evolution of cowbirds as generalist brood parasites. Cowbirds co-evolved with a large number of passerine host species in the Great Plains. However, it is unlikely that any two host species are exactly equal in their capacity to support cowbirds. Some hosts are rejecter species capable of removing cowbird eggs from nest or overlaying nesting material onto cowbird eggs, and the rate of this rejection behaviour may vary between species (Rothstein, 1975; Strausberger & Ashley, 1997; Robinson *et al.*, 1999; Peer *et al.*, 2000). Also, rejection may be more a trait of individual birds rather than entire species, and the rate of rejection can vary geographically for a given host species (Briskie *et al.*, 1992; Burhans *et al.*, 2001).
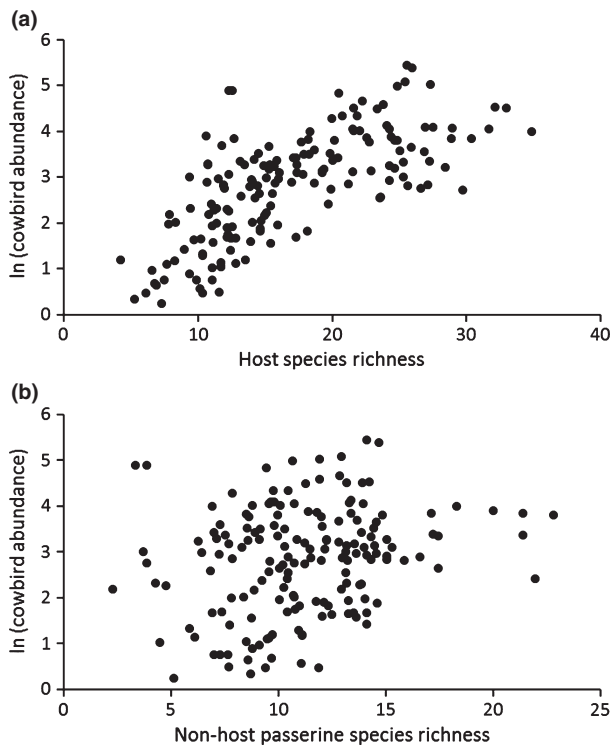
Figure 2 The effect of (a) host species richness and (b) non-host passerine species richness on local cowbird abundance on the routes of the Breeding Bird Survey. Species richness values are means over the period 1993–2009. In both panels, cowbird abundance is shown as the ln-transformed mean value over the period 1993–2009.

Individuals of some rejecter species (e.g. Baltimore Oriole, Brown Thrasher, Grey Catbird) might even imprint on accepting the first eggs laid in their first nest effectively making the pair acceptors of cowbird eggs when this event happens (Strausberger & Rothstein, 2009). Therefore, although host species richness had the greatest influence on cowbird abundance for our collective group of 168 sites, at any one site in any one year, recruitment (successful fledging) of cowbirds likely depends on specific conditions such as total density and rejection (or acceptance) behaviour of particular host species. Cowbirds are known to recruit from the nests of different hosts at substantially different rates (Curson et al., 2010). In addition, the other fundamental agents of population regulation (e.g. weather, food supply and predation) might have varying influences on cowbird populations across space and time.

In our study, the positive relationship between local cowbird abundance and host species richness could also be due to the attraction of cowbirds to areas with a high diversity of hosts. That is, cowbirds may have evolved a behavioural response to settle in areas of high host species richness when returning from migration or when dispersing as juveniles from their natal site. In addition, juvenile cowbirds might be retained (through philopatry) in areas of high host richness. In either scenario, cowbirds would cue in on the variety of host species rather than the absolute abundance or density of host individuals. Barber & Martin (1997) suggested that cowbirds might cue in on host species (e.g. Northern Cardinals) that are visually and acoustically conspicuous. In a separate study, the nests of loud and active female red-winged blackbirds were parasitized more often than the nests of quieter conspecifics (Clotfelter, 1998). Moreover, the attractor species might not even be the ones that suffer greatest parasitism rates (Barber & Martin, 1997). In the context of the present study, greater host species richness might correspond to greater likelihood that many attractor species are also present in the local passerine assemblage.

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 find and use the area for reproduction, given their propensity for dispersing. For example, because cowbirds are good dispersers (Anderson et al., 2005, 2012), trapping and removal programs must be implemented each year to have a continuous effect on suppressing cowbird abundance in locations where the species is considered detrimental to other passerines (e.g. Kelly & DeCapita, 1982; Eckrich et al., 1999; Griffith & Griffith, 2000; Rothstein & Cook, 2000).

The positive association between local abundance of cowbirds and host species richness also makes sense given that the brown-headed cowbird is a generalist parasite. Because they are broadly adapted to exploit many different host species, cowbirds likely do not respond to the selective pressures exerted by just a single or few host species. Cowbirds may not be capable of evolving species-specific responses (such as egg shell mimicry that might minimize rejection) given that they parasitize and must be adapted to a wide range of host species. This situation may be particularly true for localities with high host richness. If cowbirds are either attracted to or recruit best in such areas regardless of host density (abundance), then cowbird females would need to remain broadly adapted to use any available host given that the density of any one host may not be very high. Furthermore, local cowbird abundance was not in any way related to the species richness of non-host passerines, nor related to overall abundance of host species [see Jensen & Cully (2005) for a similar result at a regional scale]. This result further supports the inference that the association of cowbirds with areas of high host diversity is truly a response to the host species and not just the presence of any small perching birds. It is also worth noting that, on average, host species comprise 60% of the passerine species pool on the BBS routes that we examined. Some previous studies [reviewed in Chace et al. (2005)] have documented a relationship between cowbird occurrence (presence/absence) and host species richness as well as overall passerine richness, but these studies typically covered a much smaller region than the present study.

Although our study revealed that the land cover variables were relatively unimportant to cowbird abundance, habitat might still have a role in influencing cowbird populations. Many of the host species, particularly grassland birds in the

Great Plains (Veech, 2006), attain higher densities in landscapes with greater percentage cover of grassland, rangeland, pasture and hayfields than in landscapes dominated by forest and/or developed (urban) land. Thus, habitat could have an indirect effect on cowbirds through a direct effect on host availability. Moreover, our analysis of habitat was based on landscape composition (broad categories of land cover) and did not consider spatial configuration or temporal change. Significant habitat relationships might emerge from a more refined analysis that characterizes landscape configuration (fragmentation), quantifies landscape features [e.g. distance to food sources, Jewell *et al.* (2007)] and includes information on temporal change in land cover. The negative relationship between contiguous forest cover and cowbird abundance (or occurrence) is well established (Robinson *et al.*, 1995; Donovan *et al.*, 1997; Thompson *et al.*, 2000); our study did not have much scope for testing this relationship given that the Great Plains is generally devoid of forest.

Lastly, geographic position of a BBS route appeared to have little influence on cowbird abundance. This result indicates that over the scale of the entire study region, local cowbird populations might not be influenced by a regionwide environmental gradient (e.g. climatic factors) although local weather events could certainly affect particular populations. Host species could also be affected by weather, which in turn might then affect recruitment of cowbirds.

Because brown-headed cowbirds are so widely distributed in North America, local populations likely are affected by different factors and processes. Determinants of cowbird abundance could even vary between different regions (e.g. BCRs). Moreover, cowbirds are generalists in that they can use a wide range of host species and a wide variety of habitat types. This makes it difficult to generalize about population regulation in cowbirds, particularly with regard to identifying one or a few primary determinants of abundance. Nonetheless, our study pinpointed host species richness as a relatively strong influence on local cowbird abundance; the exact mechanism for its action remains to be elucidated.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Host species of brown-headed cowbirds.

BIOSKETCHES

Katherine Cummings participates in environmental education and public outreach regarding endangered and threatened species. Her primary research interest is the behavioural ecology of birds.

Joseph Veech conducts research on a wide range of ecological topics over multiple spatial scales. He specializes in using large databases on species distribution, land cover and weather to address specific questions concerning the ecological determinants of abundance, range size and population trend.

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