Predicting Species Occurrences

Issues of Accuracy and Scale

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CHAPTER

17

Contrasting Determinants of Abundance in Ancestral and Colonized Ranges of an Invasive Brood Parasite

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A generalist parasitic species functions on a different ecological scale than any of its individual hosts. Characterizing the niche of a generalist parasite requires sifting through the complex set of environmental variables underlying the distributions of its multiple hosts, then using an analytical technique that can distinguish between the relative influence of the environmental factors and the presence of the hosts themselves. The brown-headed cowbird (*Molothrus ater*) (henceforth "cowbird") is an obligate parasite that never builds its own nest, and it is an extreme host-generalist that parasitizes over two hundred species of North American passerines (Ortega 1998). The cowbird switches among multiple host species in different geographic areas of its range, and it parasitizes hosts with broad geographic ranges as well as hosts with ranges limited regionally or by habitat. The cowbird has a broad geographical range that covers most of the continental United States (see Fig. 17.1 in color section), an extent that few North American songbirds can match (Price et al. 1995). However, the range also has two distinct areas: an ancestral range and a more recently colonized area. The ancestral range lies in the plains and prairies of the central Great Plains, where cowbirds associated with migratory buffalo. The invaded range is distributed both east and west of the central United States and stretches to the Atlantic and Pacific coasts (Rothstein 1994). The cowbird's range expansion occurred in association with European colonization of North America, so its occupation of the eastern United States is approximately 350 years old and its occupation of the western United States may be as recent as 150 years. The cowbird coexists successfully with domestic livestock and agriculture and also exploits suburban lawns and bird feeders (Ortega 1998).

We hypothesized first that the distribution of the parasitic cowbird would be less influenced by climate and weather factors than are the distributions of other songbirds, and, second, that different niche attributes would characterize the cowbird's ancestral and colonized ranges.

Methods

Our analysis was based on mapping abundance and environmental variables to a spatial grid, followed by statistical analysis to relate cowbird abundance at each location to the environmental conditions and host densities there. Our spatial grid was the hexagonal grid developed for the U.S. Environmental Protection Agency (EPA) for use in the Environmental Monitoring and Assessment Program (EMAP) (White et al. 1992). Each hexagon was approximately 640 square kilometers in area and approximately 12,600 hexagons cover the conterminous United States. A hexagonal grid, unlike a square grid, has a constant center-to-

center distance between adjacent grid cells (here 27 kilometers).

For predictor variables we used the land cover class and environmental data compiled by O'Connor et al. (1996). Loveland et al. (1991) used Advanced Very High Resolution Radiometry (AVHRR) meteorological satellite images to derive a prototype land cover classification for the conterminous United States at 1.1-square-kilometer sensor resolution. O'Connor et al. (1996) added an urban class from the Digital Chart of the World (Danko 1992), summarized the representation of each of the 160 cover classes for each of the 12,600 EMAP hexagons, and computed landscape metrics such as patch size distributions, shape complexity, contagion and dominance, fractal dimension, types and frequencies of habitat edges, road abundance, and total length of riparian systems for each hexagon (Hunsaker et al. 1994; O'Connor et al. 1996). Several climate variables—annual precipitation, mean January and mean July temperatures, and annual temperature variation (seasonality)—in the form of long-term climate averages from the Historical Climatology Network (Quinlan et al. 1987; HCN 1996) were also incorporated. The data were modeled with 1-kilometer resolution (except that precipitation was modeled to 10 kilometers and then resampled to 1 kilometer) and were then summarized within each hexagon as average, minimum, and maximum values. Other variables included in the environmental data set were ownership (federal or nonfederal), road density (separately for major and minor roads), and stream density. All were expressed as within-hexagon averages and corresponding extrema (O'Connor et al. 1996).

The bird data analyzed came from the national Breeding Bird Survey (BBS) (Sauer et al. 1997). The BBS comprises bird surveys of a stratified random sample of 25-mile (40-kilometer) lengths of secondary roadside; for each of fifty stops spaced at half-mile (0.8-kilometer) intervals, an observer records all birds registered in a three-minute count. Criteria concerning timing, weather conditions, and so on must be met for the route to be judged of acceptable quality for inclusion in the survey. In the present analysis, some 1,223 routes within the conterminous United States with at least seven high-quality surveys between 1981 and 1990 were used (following O'Connor et al. 1996). For each species of interest (below), the proportion of surveys in which the species was recorded at the site was computed, to provide a measure of *incidence*; this measure is typically correlated with absolute density and is a relatively robust measure of abundance. To obtain an overall index of cowbird host abundance the incidence values for the different species in two lists of host species were summed. One list was of the fifty most frequently parasitized host species and the other was of geographically widespread hosts (see Appendix). In addition, the numbers of these hosts present at each location were determined and used as a predictor variable in analyses below.

Statistical Analysis and Modeling

We used classification and regression tree (CART) modeling (Sonquist et al. 1973; Breiman et al. 1984) to identify the nonlinear relationships between our response variables and the land-use, pattern metric, and climate covariates. Traditional linear regression and correlation techniques assume that independent variables entering the regression model have common effects across the entire sample, an assumption unlikely to be the case here. Moreover, these techniques require explicit specification of terms for interactions. We used the S-Plus (MathSoft. 1995, Seattle, Wash.) implementation of CART (Clark and Pregibon 1992; Venables and Ripley 1994) to partition our response variables recursively with respect to a set of selected covariates. At each node, the independent variable that best discriminated the response variable was used in the tree as the splitting variable for that node. Discrimination was maximized by trying all possible splitting thresholds for all possible prediction variables and choosing the variable and threshold to maximize the differences in the response variable (maximum between-group diversity) before splitting the dataset into two subsets. The process was then repeated independently and recursively on each increasingly homogenous subgroup until a stopping criterion was satisfied. This tree was then pruned back using tenfold cross-validation (Clark and Pregibon 1992). This strategy reduced the propensity of CART models to over-fit the data. Since cross-validation is currently

the subject of debate among statisticians (e.g., Miller 1994b) we used the criteria developed by Sifneos and her colleagues (J. Sifneos, D. White, and N. S. Urquhart personal communication) on the basis of extensive experiments in optimizing cross-validation recovery of known data structures. We also perturbed the response variable by 5 percent, and re-ran the model to check for overall consistency in tree structure. We controlled for collinearity problems by randomly perturbing each independent variable in the pruned model by up to 5 percent and re-running the analysis to check for inclusion or omission of the variable in the tree. Variables stable in the face of such perturbation could not be markedly collinear with any other variable in the data set. The models presented here passed all these checks.

Geographical Delineation of Regions

We operationally defined the ancestral zone by overlaying the areas of highest cowbird abundance in the present-day distribution (Fig. 17.1) on a map of Omernik ecoregions (Omernik 1987) and defining the range as those ecoregions with cowbirds. The delineated area ranged from North Dakota south to Texas and east to Indiana, Kentucky, and western Tennessee and Mississippi.

Results

Our findings provide insight into the relative importance of physical and biotic variables in predicting the occurrence of cowbirds.

Environmental Factors Determining Cowbird Distribution

Breeding Distribution. Our first analysis examined the relative importance of different predictors of brown-headed cowbird incidence at a national scale. The model explained a significant percentage (50.9 percent) of the variance in cowbird abundance and identified five major predictors: crops, Conservation Reserve Program (CRP) lands, geography (region), weather, and climate (Table 17.1). The single best predictor of cowbird incidence was crops occurrence, which explained 15.7 percent of the variance in cowbird incidence. Specifically, soybeans, maize, sunflowers, and sorghum (in that order) each accounted for 3.8 to 2.1 percent of variability in cowbird presence; other crops were combined in a fifth category. The second-best predictor (11.3 percent) was location of CRP lands, which are formerly farmed areas that have been allowed to go fallow for ten years. The other three major predictors identified were geography/region (9.6 percent), weather (9.0 percent), and climate (5.3 percent). The geography/region variable comprised longitude (7.6 percent) and latitude (2.0 percent) components.

TABLE 17.1.

Major biophysical predictive factors influencing brown-headed cowbird (*Molothrus ater*) distribution.

Factors	Summer distribution (%)	Winter distribution (%)
Climate	5.3	21.7
Weather	9.0	4.8
Geography/region	9.6	5.9
Conservation reserve program	11.3	—
Crops	15.7	4.0
Total R^2	50.9	36.4

Winter Distribution. We compared the major predictors of cowbird incidence on wintering grounds to those on breeding grounds (Table 17.1). Four of the five variables proved to be major predictors for both distributions, although in winter the relative importance shifted away from crops and toward climate. The CRP dropped out in this winter analysis.

Influence of Host Abundance on Cowbird Distribution

When we repeated our analysis of the cowbird's summer distribution with the host variables included, the list of major predictors shifted dramatically from crops to host abundance (Table 17.2, column A). Crops and CRP lands no longer emerged as major predictors, although these factors had accounted for 27 percent of the variance in the previous analysis of cowbird's distribution. Host Abundance Index rose to the top of the list of major predictors (18.9 percent) and accounted for more of the variance in cowbird incidence than had any single variable in the previous

TABLE 17.2.

Major biophysical and avian predictive factors determining distribution of the brown-headed cowbird (*Molothrus ater*).

Predictive factors	A Cowbird range with hosts (national) (%)	B Ancestral cowbird range (regional) (%)	C Colonized cowbird range (regional) (%)	D Grassland passerines' range[a] (%)
Crops	7.1[b]	—	—	33
Climate and weather	16.2	12.8	6.1	18.9
Geography	—	9.5	4.6	7.7
Host abundance	18.9	5.5	26.6	NA
Overall species richness	4.9	—	8.3	NA
Total R^2	47.1	27.8	45.6	59.6

[a]O'Connor et al. (1999:51): obligate grassland passerines of North America: horned lark (*Eremophila alpestris*), vesper sparrow (*Pooecetes gramineus*), lark bunting (*Calamospiza melanocorys*), savannah sparrow (*Passerculus sandwichensis*), grasshopper sparrow (*Ammodramus savannarum*), Baird's sparrow (*Ammodramus bairdii*), Henslow's sparrow (*Ammodramus henslowii*), McCown's longspur (*Calcarius mccownii*), dickcissel (*Spiza americana*), bobolink (*Dolichonyx oryzivorus*), eastern meadowlark (*Sturnella magna*), western meadowlark (*Sturnella neglecta*).
[b]All involved patch size of cropland, pure or mixed.

analysis. A related biological factor, overall species richness, also emerged (4.9 percent).

We present the details of this analysis as they appear in the CART tree in order to explain the sequence and interrelations of the principal factors (Fig. 17.2). The overriding prominence of host abundance in predicting cowbird presence was reflected in its index being the splitting factor at the first tier of the CART analysis. As reflected in the right branch of the tree, when host abundance was high (i.e., a Host Abundance Index value for the route greater than 5.4), cowbirds were recorded in 93 percent of the surveys there. Host abundance was more important than overall avian abundance or diversity, though total species richness did appear as a splitting factor in the second tier of the left branch (segregating the locations in end node A from those in nodes B through E).

The predictive values second and third in importance in this analysis were climate (16.2 percent) and patch variables (7.1 percent). Among the climate variables, seasonality—differences between mean January and mean July temperature—was the major contributor. Areas of high seasonality are those that experience a strong seasonal flush of productivity and that attract a rich assemblage of breeding species that take advantage of the abundant food resources (Ashmole 1963). Figure 17.2 shows that on routes associated with the higher seasonality index (in nodes C, D, and E on the left branch of the tree) 77 percent of the surveys recorded cowbirds versus a 35 percent incidence for less-seasonal areas (node B). On the right branch, in colder areas associated with lower maximum January temperatures (nodes F, G, H, and I) 94 percent of the surveys recorded cowbirds against only 5 percent of the surveys in the warmer areas of node J. Thus, the northern United States has many more cowbirds than the southern United States but in association with different predictors in different regions.

The specific land cover classes for which patch variables were predictors were dominated respectively by crop/grassland mixtures (node C versus nodes D and E), small forests of maple-birch-beech in corn-soybean areas (nodes F and G), and row crops (nodes H and I). In the case of the row crops variable, it was the size of the patches of row crops relative to the national average for patches of this type that had predictive power: hexagons in which blocks of row crops were relatively small—less than about 5 percent of the national average—were more likely to hold cowbirds than were hexagons with larger expanses of row crops. Patch variables can point to habitat fragmentation effects, and their emergence here indicates their strong predictive value in determining cowbird abundance. All three patch-size variables identified are involved in area sensitivity, with cowbirds more abundant in hexagons with small rather than large patch sizes (note the higher value in the left-hand nodes in each

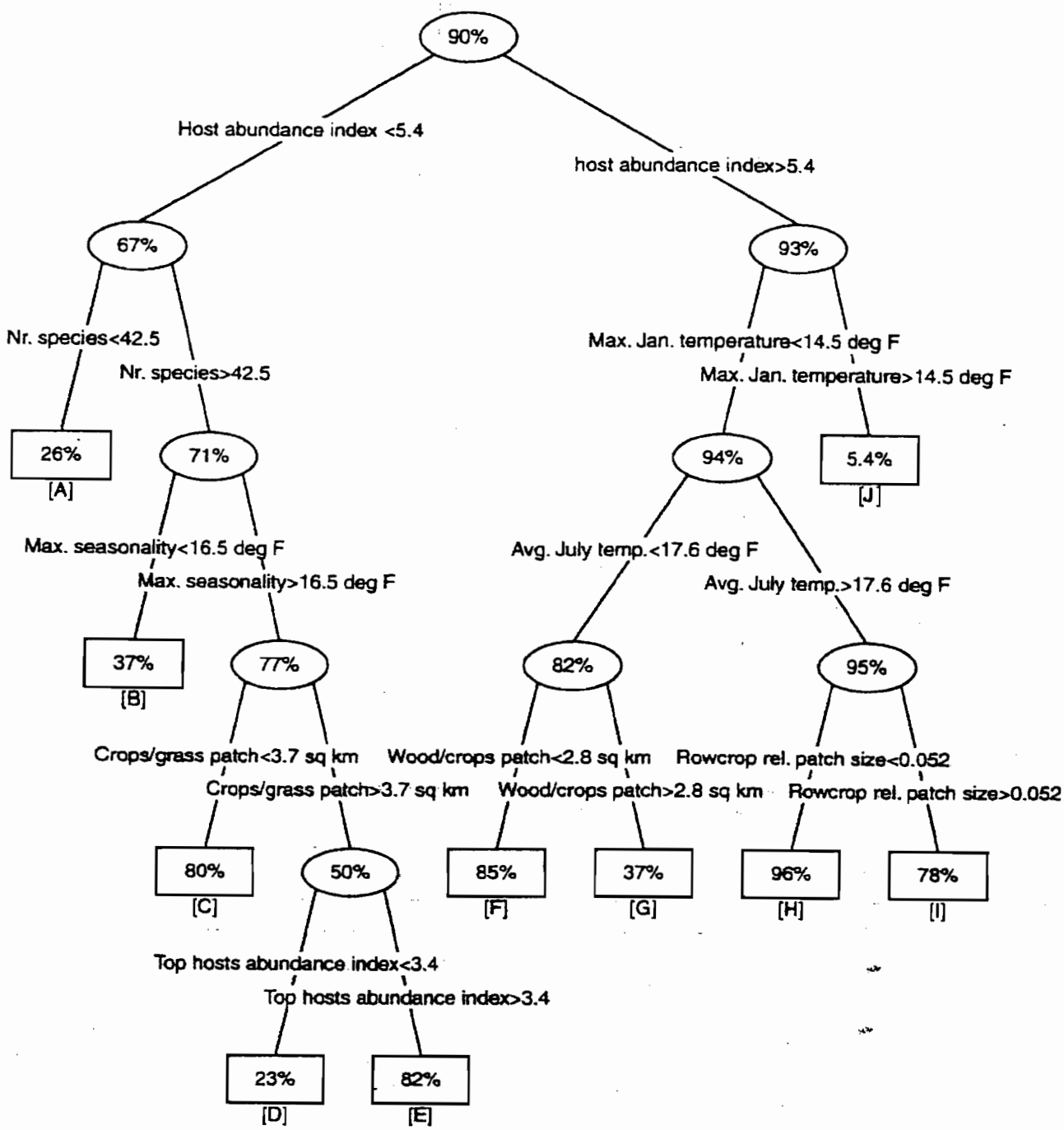

Figure 17.2. Classification and regression tree (CART) model for brown-headed cowbird abundance across the conterminous United States. Numbers inside the oval (intermediate nodes) or rectangles (end nodes) are the percentage of Breeding Bird Survey (BBS) routes, rounded to whole numbers, on which the brown-headed cowbird (*Molothrus ater*) was detected. The splitting variable and its threshold value are shown at each node. The end nodes are labeled from A through J and represent a set of hexagons with the characteristics of the unique set of splitting variables preceding it.

TABLE 17.3.

Predictive model for the probability of occurrence of brown-headed cowbirds (*Molothrus ater*).[a]

Alternative		Host abundance index	Total species richness index	Seasonality index		Probability that cowbirds are present (% routes)
1.	If	> 5.4 spp / route,	[any value}	[any value]	then	93
2.	If	≤ 5.4 spp / route, and				
a.			> 42 spp, and	> 16.5 deg. F,	then	76.7
b.			> 42 spp, **but**	< 16.5 deg. F,	then	36.9
3.	If	≤ 5.4 spp / route, **but**	< 42 spp,	[any value]	then	26.2

[a]Other predictors (e.g., climate, land use, and habitat patchiness) modify these rules locally.

of the sibling nodes involving patch variables: C versus the DE parent, F versus G, and H versus I).

Predictive Model for the Probability of Occurrence of Cowbirds

The information depicted in Figure 17.2 can be recast as a series of explicit predictive rules (Table 17.3). This hierarchy of rules specifies (1) if Host Abundance Index in a hexagon or on a route is greater than 5.4 species/route, then the probability of cowbirds being present is 93.5 percent; (2) if the Host Abundance Index is less than or equal to 5.4 species/route, then two additional factors must be assessed to make a prediction, yielding (a) if the number of species present (total of hosts and nonhosts) is greater than forty-two species and the seasonality index is greater than 16.5 degrees Fahrenheit, then the probability of cowbirds being present is still high (76.7 percent); otherwise (b) in hexagons where Host Abundance Index is less than or equal to 5.4 species and the total number of avian species present is greater than 42, but the seasonality index is less than 16.5 degrees Fahrenheit, the probability of cowbirds being present is only 36.9 percent; and finally (3) if the Host Abundance Index is less than or equal to 5.4 species and the total number of avian species present is less than 42 species, then the probability of cowbirds being present—regardless of seasonality index—drops to 26.2 percent.

Role of Host Species' Habitat Preferences

Shared habitat correlates between host and parasite might explain why host abundance figured so prominently for cowbirds in Table 17.2. Our perturbation tests (see "Methods") precluded simple confounding of variables but more complex commonality in habitat requirements would not necessarily be excluded. We therefore analyzed host abundance data with respect to land cover and climate variables and compared the spectrum of predictors against that for cowbirds. Precipitation was the strongest predictive factor (44.2 percent): host abundance was low where precipitation was low; intermediate in wetter areas where total species richness was low and also in areas where species richness was high but seasonality was weak; and highest where seasonality was high. The second and third major predictive variables were species richness (14.2 percent) followed by seasonality (8.8 percent). Since the variables that predict host abundance are quite different from those identified for the brown-headed cowbird (Table 17.1), it is unlikely that the cowbird-host abundance association above was due to shared habitat requirements.

Regional Analysis: Ancestral Versus Colonized Range

Host abundance was a major predictor in both ancestral and colonized regions, although its influence relative to biophysical factors was markedly different in the two regions (Table 17.2, columns B and C). In the ancestral range, biophysical factors (topography and elevation) carried over four times as much influence (24 percent) on cowbird incidence as did biological ones (5.5 percent). In this model, the principal host abundance factor was presence of host species with ge-

ographically broad distributions, and the level was similar to that found for overall species richness (4.9 percent) on the previous national-scale analysis (Table 17.2). The major host abundance indicator that had appeared on the national scale analysis, or in other words the extent of the presence of the fifty most frequently parasitized hosts (18.9 percent), did not emerge as a major predictor within the ancestral range.

In contrast, within the colonized range the relative importance of biological versus biophysical factors was reversed, and host abundance indices carried five times as much influence on cowbird incidence as did biophysical factors (Table 17.2, column C). Specifically, host abundance indices accounted for 34.9 percent of the variability in cowbird incidence, the highest value for a predictor in any of our models of cowbird incidence. Within the general category of host abundance, the specific factor of abundance was an index of the fifty most frequently parasitized cowbird hosts (26.6 percent).

Among the biophysical factors that emerged as predictors in both the ancestral and the colonized range, climate appeared in the cowbird's ancestral range at a level (12.8 percent) similar to that in the national analysis (16.2 percent) (Table 17.2) and with the same components, specifically high average July temperature (8.6 percent) and the degree of seasonality (4.2 percent). Topography, as the importance of lack of elevation, accounted for 9.5 percent of the variation in the model but the crops and patch variable predictors of the continental analyses were not important. The total variance accounted for in this CART model for the ancestral cowbird range was 27.8 percent, a level approximately half that in previous models at the national scale. In the region of colonized range, the physical factors that emerged were topography (4.6 percent) and climate (6.1 percent) (Table 17.2). The total variability accounted for by the CART model for the colonized range was 45.6 percent, again similar to the levels explained by CART in both the national-scale analyses (Table 17.2).

Discussion

The brown-headed cowbird is recognized as a textbook example of a species that must be studied at different scales to answer different questions (Robinson 1999; Morrison and Hahn, in press). Before 1990, most studies of the species were local-scale field studies conducted at sites in the cowbird's ancestral range, and they typically looked at parasite behavioral strategies such as nest-searching or mating system and at the rates and effects of parasitism on different host species (see Ortega 1998). Attempts to extract general principles from local studies often yielded contradictory patterns that reflected the large number of host species and habitats exploited by the brood parasite.

Since 1990, much work has been done at larger areas (extent and resolution) and at sites in the colonized range of the brown-headed cowbird (see Morrison et al. 1999; Smith et al. 2000). The design and location of these studies reflect recent interest in investigating which ecological factors are driving the cowbird's expansion into new habitats and new hosts, particularly in the forest interior. Facilitated by advances in radiotelemetry and GIS (geographic information system) techniques, many of these studies were conducted across landscapes, with a few at the regional scale (Robinson et al. 1995a; Morrison et al. 1999; Smith et al. 2000).

From these studies, generalizations emerged that apply within landscapes but questions remained as to how these patterns might change at larger scales and what other patterns might appear at larger areas. Robinson (1999) summarized the core conclusions from landscape and regional studies: cowbird abundance and parasitism rates are much lower in forested landscapes where foraging opportunities are limited; cowbird abundance decreases with distance from rich feeding areas; and cowbird abundance is correlated with host abundance in landscapes with unlimited foraging habitat. The only national-scale analyses of cowbird abundance are three studies of population trends based on BBS data, which concluded that cowbird numbers are stable nationally, with slight regional increases or decreases in some regions that are not linked to declines or increases in host populations (Maurer 1993; Peterjohn et al. 2000; Wiedenfeld 2000).

Our study provides the first national perspective on the principal factors that underlie the abundance of the parasitic cowbird. Our findings unambiguously identified host abundance as the fundamental predictor of the

cowbird's distribution at the national scale. Although avian species distributions are typically constrained by spatially extensive variables such as climate, habitat, spatial patchiness, and microhabitat attributes, we had hypothesized that the distribution of a brood parasite depends as strongly on host distribution patterns as on biophysical factors. Our findings suggest that the distribution of hosts does indeed take precedence over habitat attributes in shaping the cowbird's distribution at a national scale, within an envelope of constraint set by biophysical factors. The importance of hosts can be missed, because an analysis of the predictive values of biophysical factors alone (Table 17.1) yields the result that crops and CRP lands are dominant predictors, a result that fits the profile of the brown-headed cowbird as a bird of the central prairies that associates with agriculture.

Many studies have weighed the relative importance of host availability versus food ability. Our results suggest that while host availability is predominant for the national distribution of cowbirds, food availability (associated with the three patch variables that include foraging habitats) is a major factor in particular habitats. Three different patch types were detected in widely separate nodes in our CART model for cowbird abundance reflecting the importance of this landscape pattern. Robinson (1999) concluded that host abundance was the most influential environmental variable, with the caveat that this was true only when food is sufficient. Several studies have found food availability a more fundamental determinant of cowbird incidence, particularly in habitats such as those where forested areas are extensive (Morrison et al. 1999). The influence of food availability on the winter distribution of cowbirds is a separate question, also much debated, and our analysis showed a sharp repositioning of the major predictors from summer to winter distribution, dropping crops to 4.0 percent and increasing climate nearly fourfold to 21.7 percent (Table 17.1). These results suggest that either food availability is a significant constraint on cowbird populations (Robinson 1999) or energetic constraints limit the cowbird's ability to exploit cold areas (Root 1988c).

Our CART analysis of summer distribution also distinguished the influential size of patch variables and found that cowbirds are more abundant in hexagons with small rather than large patch size. This result confirms the observations of many local studies that larger forest stand size limits cowbird incidence (Morrison et al. 1999). Since the reverse pattern of area sensitivity characterizes Neotropical migrants (i.e. they are more abundant in hexagons with large patch sizes), this result indicates that separate niches still exist between cowbirds and forest-interior nesting birds.

Our analysis identified climate and weather as the second most important predictors. Local- and landscape-scale studies have rarely addressed climate and weather, which illustrates how an overlooked variable can emerge when an analysis shifts from a local to a continental scale. The areas of high seasonality in the north-central region of the United States experience a strong seasonal flush of productivity that attracts a rich assemblage of breeding species that take advantage of the abundant food resources (O'Connor et al. 1996). These are the areas of greatest cowbird abundance. Seasonality is very highly correlated with the portion of Neotropical migratory songbirds in an area, a pattern first hypothesized by Ashmole (1963) and since supported by Wilson (1974), Herrera (1978), and Ricklefs (1980). Thus, cowbirds can exploit both the flush of productivity and the abundance of breeding hosts.

The importance of host abundance to cowbird distribution is further put into perspective by the regional analysis. Distinguishing the cowbird's ancestral range from its colonized range revealed a strong geographical bias in the influence exerted by host species. In the colonized range, host abundance indices carried five times as much influence as biophysical factors. This result may reflect the fact that there is greater variance in incidence of cowbirds in the colonized range and that cowbirds colonize new areas only where conditions are good. In the East, although cowbird hosts are more abundant, much of their breeding habitat is in large forests, where they are inaccessible. In the West, host species are concentrated in riparian areas, which draws cowbirds to those sites. We plan more detailed analyses of the colonized range in which we look at the eastern and western ranges separately, since both the habitat types and host abundance levels are distinctly different (O'Connor et al. 1996).

Host abundance is not the dominant predictor of cowbird incidence in its ancestral range, although it does emerge as a lesser predictor. Here topography and elevation carried over four times as much influence as biological factors (24 versus 5.5 percent). These results may reflect conditions that are relatively uniformly good for cowbirds and consequently the variance in cowbird incidence is lower. In future analyses, we plan to subdivide the area we designated as ancestral into the core area where cowbird abundance is greater than thirty birds per route (i.e., the Dakotas, eastern Nebraska and Kansas, western Missouri, and Iowa) and the surrounding zones where cowbird abundance is eleven to thirty birds per route (see Fig. 17.1).

The analyses in this study accurately distinguished the cowbird's ecological niche as a parasite. The CART results identified a different set of predictors for cowbirds and for their most frequently parasitized hosts, illustrating that the cowbird distribution is not simply the result of shared habitat preferences. Moreover, the CART analysis distinguished a different set of predictors for the parasitic cowbird and the guild of obligate grassland passerines that are its ancestral hosts (O'Connor et al 1999). An important reservation about the findings here is that the CART models we used, despite their sophistication, return only estimates of correlation. Therefore, our conclusions are subject to the normal caveats of correlation analysis, in particular that correlation does not ensure causation. Our emphasis on host availability and patch size arrives at the same conclusions as those of earlier investigators, and since ours are based on analyses with very different biases than those in site-specific studies, this lends strength to all the studies. We distinguished the strong influence of climate and weather, largely overlooked in landscape-scales studies, and we described differences between the cowbird's ancestral and colonized range in the role of host abundance. The broad spatial extent of our analyses provides a robust overview of the correlates of the distribution of the principal North American brood parasite that has not previously been available.

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Appendix

The fifty most frequently parasitized host species as identified by Friedmann (1963) by a review of published studies. No comparable reassessment of frequency of parasitism has been done, but these fifty hosts still appear representative (Rothstein, pers. comm.; DCH pers. obs). Friedmann designated a first (primary) group of seventeen hosts ("1," more than one hundred records of parasitism), a second group of seventeen hosts ("2," more than fifty records of parasitism), and a third group of sixteen hosts ("3," twenty-five to fifty records of parasitism). Twelve host species that Friedmann designated common hosts of great geographic availability are indicated with a "g." Three host species indicated by an asterisk (*) are obligate grassland species included in Table 17.2.

Acadian flycatcher (*Empidonax virescens*): 3
American goldfinch (*Carduelis tristis*): 2, g
American redstart (*Setophaga ruticilla*): 1
Bell's vireo (*Vireo bellii*): 1
Black-and-white warbler (*Mniotilta varia*): 3

Blue grosbeak (*Guiraca caerulea*): 3
Blue-gray gnatcatcher (*Polioptila caerulea*): 3
Blue-winged warbler (*Vermivora pinus*): 3
Brown thrasher (*Toxostoma rufum*): 3
Chestnut-sided warbler (*Dendroica pensylvanica*): 2
Chipping sparrow (*Spizella passerina*): 1, g
Clay-colored sparrow (*Spizella pallida*): 2
Common yellowthroat (*Geothlypis trichas*): 1, g
Dickcissel (*Spiza americana*): 2, *
Eastern bluebird (*Sialia sialis*): 3
Eastern phoebe (*Sayornis phoebe*): 1
Eastern towhee (*Pipilo erythrophthalmus*): 1, g
Eastern wood-pewee (*Contopus virens*): 2
Field sparrow (*Spizella pusilla*): 1
Gray catbird (*Dumetella carolinensis*): 3
Hermit thrush (*Catharus guttatus*): 3
Indigo bunting (*Passerina cyanea*): 1
Kentucky warbler (*Oporornis formosus*): 1
Kirtland's warbler (*Dendroica kirtlandii*): 2
Lark sparrow (*Chondestes grammacus*): 3, g
Louisiana waterthrush (*Seiurus motacilla*): 2
Yellow-rumped warbler (*Dendroica coronata*): 2
Northern cardinal (*Cardinalis cardinalis*): 2
Ovenbird (*Seiurus aurocapillus*): 1
Painted bunting (*Passerina ciris*): 2
Prairie warbler (*Dendroica discolor*): 3
Prothonotary warbler (*Protonotaria citrea*): 2
Red-eyed vireo (*Vireo olivaceus*): 1, g
Red-winged blackbird (*Agelaius phoeniceus*): 1, g
Rose-breasted grosbeak (*Pheucticus ludovicianus*): 3
Savannah sparrow (*Passerculus sandwichensis*): 3, *
Scarlet tanager (*Piranga olivacea*): 2
Song sparrow (*Melospiza melodia*): 1, g
Swamp sparrow (*Melospiza georgiana*): 2
Willow flycatcher (*Empidonax traillii*): 1
Veery (*Catharus fuscescens*): 2
Vesper sparrow (*Pooecetes gramineus*): 2, *
Warbling vireo (*Vireo gilvus*): 2, g
White-eyed vireo (*Vireo griseus*): 3
White-throated sparrow (*Zonotrichia albicollis*): 3
Wood thrush (*Hylocichla mustelina*): 2
Worm-eating warbler (*Helmitheros vermivorus*): 3
Yellow warbler (*Dendroica petechia*): 1, g
Yellow-breasted chat (*Icteria virens*): 1, g
Yellow-throated vireo (*Vireo flavifrons*): 1, g

D. Caldwell Hahn and Raymond J. O'Connor. 2002. **Contrasting determinants of abundance in ancestral and colonized ranges of an invasive brood parasite**. Pages 219-228 *in* J. Michael Scott, Patricia J. Heglund, Michael L. Morrison, Jonathan B. Haufler, and William A. Wall, editors. Predicting species occurrences issues of accuracy and scale. Island Press, Washington, DC. xvii, 868 pp.

Avian species distributions are typically regarded as constrained by spatially extensive variables such as climate, habitat, spatial patchiness, and microhabitat attributes. We hypothesized that the distribution of a brood parasite depends as strongly on host distribution patterns as on biophysical factors and examined this hypothesis with respect to the national distribution of the Brown-headed Cowbird (*Molothrus ater*). We applied a classification and regression (CART) analysis to data from the Breeding Bird Survey (BBS) and the Christmas Bird Count (CBC) and derived hierarchically organized statistical models of the influence of climate and weather, cropping and land use, and host abundance and distribution on the distribution of the Brown-headed Cowbird within the conterminous United States. The model accounted for 47.2% of the variation in cowbird incidence, and host abundance was the top predictor with an R2 of 18.9%. The other predictors identified by the model (crops 15.7%, weather and climate 14.3%, and region 9.6%) fit the ecological profile of this cowbird. We showed that host abundance was independent of these environmental predictors of cowbird distribution. At the regional scale host abundance played a very strong role in determining cowbird abundance in the cowbird's colonized range east and west of their ancestral range in the Great Plains (26.6%). Crops were not a major predictor for cowbirds in their ancestral range, although they are the most important predictive factor (33%) for the grassland passerines that are the cowbird's ancestral hosts. Consequently our findings suggest that the distribution of hosts does indeed take precedence over habitat attributes in shaping the cowbird's distribution at a national scale, within an envelope of constraint set by biophysical factors.