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HABITAT AND LANDSCAPE FACTORS AFFECTING COWBIRD DISTRIBUTION IN THE NORTHERN ROCKIES

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Abstract. We studied the habitat and landscape factors influencing the distribution of Brown-headed Cowbirds (*Molothrus ater*), using data from a region-wide monitoring program conducted in the northern Rockies. Bird, habitat, and landscape data were collected at 7,153 points along 761 transects that were distributed throughout western Montana and northern Idaho. Brown-headed Cowbirds were largely absent from dense, old-growth, and high-elevation forests. They were most abundant in open conifer forest (ponderosa pine [*Pinus ponderosa*] and partially logged sites) as well as grassland, agricultural, and riparian cover types. We found that open lands such as grasslands and agricultural areas were more likely to be used than were clearcuts. In addition, cowbird presence was negatively related to canopy cover when we included data from all cover types, but was not significantly related to this variable within coniferous forest cover types. It appears that the presence of clearcuts does not draw cowbirds into forested regions. The density of potential host species was one of the most important local-scale correlates of cowbird presence. Nonetheless, multivariate models were dominated by landscape variables, and distance to agricultural lands was the strongest predictor of cowbird presence. Cowbirds were so strongly associated with the proximity of agricultural areas that many areas of the forested mountains are probably still safe from parasitism pressure. Our data suggest that cattle grazing and other agricultural practices appear to be directly involved with the expansion of cowbirds in this region (and other parts of the West). Cowbirds may be a textbook example of the importance of landscape context in the distribution of a bird species.

Key Words: habitat, human-induced changes, landscape, *Molothrus ater*, northern Rockies.

The Brown-headed Cowbird (*Molothrus ater*) was historically rare or nonexistent in many parts of the West (Rothstein 1994). The sudden presence of this brood parasite may, therefore, have a serious impact on hosts that are not adapted to its presence. Because the recent spread of cowbirds throughout the West has probably been associated with human land-use activity, we need to better understand exactly which activities or land conditions favor the presence and/or spread of cowbirds. Moreover, because landscape conditions may contribute, in part, to the suitability of a site to cowbirds, there is need for a regional study that incorporates both landscape and local-scale factors into a study of cowbird distribution.

Several years ago, the Northern Region of the U.S. Forest Service (USFS) initiated a Landbird Monitoring Program designed to provide a regional picture of bird-habitat relationships across the region's National Forests and to estimate the overall population trends of a variety of diurnal landbird species. The program involves periodic surveys of birds and habitat conditions surrounding more than 7,000 points that are distributed throughout the region. As far as we know, this is the largest program of its kind in North America, and it provides a unique opportunity to couple information on both local-scale and landscape conditions surrounding points of occurrence for many landbird species, including cowbirds. In this paper, we report on the variables that appear to be most important in predicting the presence of cowbirds within this northern Rocky Mountain region.

METHODS

All 13 National Forests in the USFS Northern Region and the Potlatch Timber Company (a large private landowner in central Idaho) participated in the collection of data on cowbird presence and abundance for our study. The study region covered all of western Montana and northern Idaho (including 19 million acres of non-wilderness Forest Service lands). This entire region is dominated by conifer forest, with deciduous trees largely restricted to riparian areas. Forest composition includes a mixture of conifer species throughout the region, with the most common tree species, in decreasing order of importance, being Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*) and ponderosa pine (*Pinus ponderosa*). There is a major climate gradient, with the moister, denser cedar/hemlock (*Thuja plicata/Tsuga heterophyla*) and grand fir (*Abies grandis*) forests restricted to the northwestern portion of the region, and drier, sparser forests (mostly Douglas-fir and lodgepole pine) predominating east of the continental divide. Spruce/fir (*Picea engelmannii/Abies lasiocarpa*) forests occur at higher elevations as well as in some riparian situations. Valley bottoms are usually dominated by agriculture (pasture and cropland) and other human disturbance, with grasslands in the foothills, and sagebrush (*Artemisia*

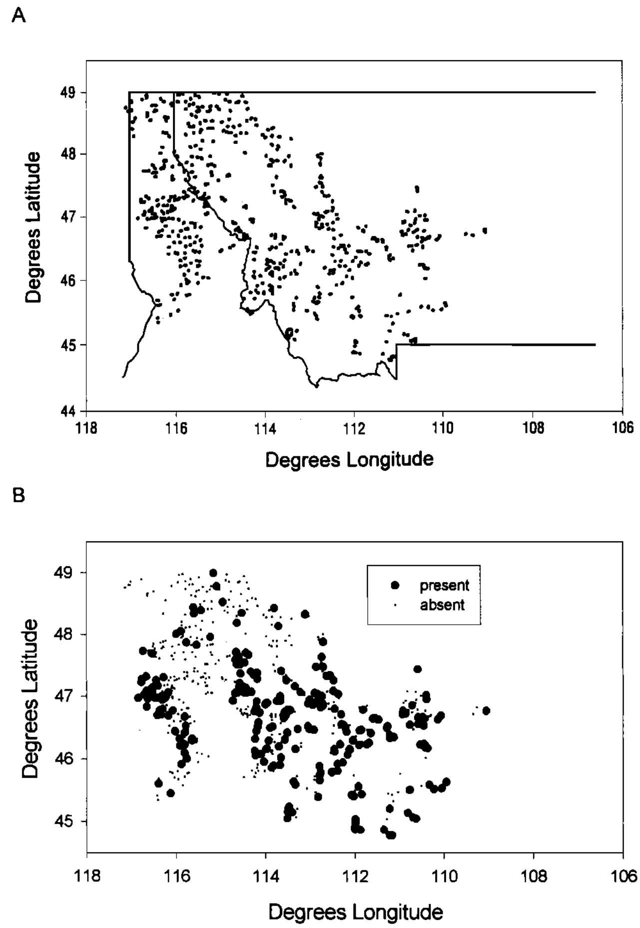

FIGURE 1. A) Distribution of sampled transects across northern Idaho and western Montana; B) The geographic distribution of Brown-headed Cowbirds across all transects. Each large dot indicates that the species was present on at least one point on that transect, and each small dot represents an entire transect sampled without detecting cowbirds.

spp.) being more extensive in the southeastern section.

We collected bird, habitat, and landscape data at a total of 7,153 points along 761 transects (Fig. 1A). Most of these transects (545), each containing 10 points, were permanently marked as part of a long-term monitoring program. The distribution of these 545 transects was geographically stratified by US Geological Survey 7.5-minute topographic quad maps. Transect start points were located by positioning a random point within each quad quarter-section and then finding the nearest point on an unpaved secondary or tertiary road, or on a trail. The remaining nine points constituting a transect were positioned at 300-m intervals in a single direction along the road or trail. Potential transects were retained only if there was reasonable access. Used transects were selected from these potential transects as randomly as possible under logistic constraints. There were usually two observers on each National Forest, covering one transect each per day. In addition to these permanently marked points, in 1993 and 1994 we conducted one-time visits to 1,825 additional sampling points (along 216 transects of varying length) that were stratified by cover type to provide greater coverage of some of the rarer vegetation types.

Field Methods

The bird counts followed recommendations discussed by Ralph et al. (1995) and methods described by Hutto et al. (1986). A 10-min point count was conducted at each of the 10 sampling points along a transect. Points were visited once

TABLE 1. DISTRIBUTION OF THE 3,406 NON-EDGE SAMPLE POINTS (IN THE NORTHERN ROCKIES) AMONG 18 MAJOR COVER TYPES, WITH THE PERCENT OCCURRENCES OF BROWN-HEADED COWBIRDS (AS DISPLAYED IN FIG. 2)

Cover type	Number of points	Percent of points	Cowbird occurrence (%)	Median distance to agriculture (km)
Cedar/hemlock	63	1.8	0.0	28.5
Spruce/fir	133	3.9	0.8	16.3
Lodgepole pine	215	6.3	1.9	16.7
Mixed-conifer	1,121	32.9	8.3	11.6
Douglas-fir	289	8.5	6.2	13.3
Ponderosa pine	77	2.3	18.2	3.7
Group selection	112	3.3	12.5	7.1
Shelterwood	75	2.2	21.3	7.7
Seed-tree cut	116	3.4	10.3	9.6
Clearcut	341	10.0	5.0	14.2
Post-fire	58	1.7	8.6	13.5
Sagebrush	88	2.6	13.6	8.2
Grassland	167	4.9	12.6	3.4
Agricultural	56	1.6	19.6	0.0
Marsh, wetland	71	2.1	14.1	10.3
Riparian shrub	294	8.6	18.0	12.3
Cottonwood/aspen	84	2.5	22.6	10.6
Residential	46	1.4	30.4	2.8

each breeding season between mid-May and mid-July. All birds seen or heard within the count period were recorded, noting species, number of individuals, and distance to the bird(s). Field observers began counts at least 15 min after sunrise, and completed transects before 11:30. Counts were not conducted on days with continuous rain or high winds. The order of visits to transects was set by elevation and seasonal access.

We recorded the vegetation cover type in a 100-m radius circle surrounding each point. Cover type was defined according to a scheme based on a combination of the dominant plant species in the tallest vegetation layer and the vertical and horizontal vegetation structure. A series of successional stages for each conifer forest type was included. Our classification of such disturbed forest types was based on the dominant tree species composition and stand structure, without regard to the process that actually caused the structure. We recorded over 200 cover types in the field, but we merged them into 18 general types so that all groups had at least 50 points (Table 1). There were six relatively undisturbed conifer forest types, four relatively disturbed conifer forest types representing different logging regimes, three nonforested cover types, and three riparian vegetation types. The undisturbed conifer types were defined by tree species composition, with >80% of the canopy composed of the named tree species.

To further characterize the surrounding vegetation for use in regression models, we made estimates of the following variables within a 30-m-radius circle centered on each count point: (1) average height of the tree canopy layer; (2) percent cover of canopy trees (larger than saplings); (3) percent cover of sapling trees (between 5 and 10 cm dbh); (4) percent cover of seedling trees (<5 cm dbh); (5) percent cover of tall shrubs (multi-stemmed woody plants >1 m tall); (6) percent cover of low shrubs (<1 m tall); (7) percent cover of grasses and forbs; and (8) tree species composition, as estimated by the proportionate makeup of each tree species in the overstory canopy.

We used two different sets of species to model host density as a variable that might influence the probability of cowbird presence (Robinson and Wilcove 1994), because it is difficult to decide which species cowbirds may consider as potential hosts in any particular region. Cowbirds have been known to parasitize most open-cup nesting passerines of appropriate size (Friedmann 1963). Therefore, for one species set, we simply chose all open-cup nesting passerine species up to the size of the Brown Thrasher (*Toxostoma rufum*), which is the largest species known to successfully host cowbirds (Friedmann et al. 1977). There were 69 species that fit this criterion, although only 26 of these made up 90 % of the individuals, and seven species made up almost 50% (Dark-eyed Junco [*Junco hyemalis*], Yellow-rumped Warbler [*Dendroica coronata*], Chipping Sparrow [*Spizella passerina*], Swainson's Thrush [*Catharus ustulatus*], American Robin [*Turdus migratorius*], Townsend's Warbler [*Dendroica townsendi*], and Ruby-crowned Kinglet [*Regulus calendula*]). However, it is possible that cowbirds may discriminate among available hosts, or some nests may simply be better hidden. Some species are consistently avoided, and parasitism rates of a single species may vary greatly in different regions (Hoover and Brittingham 1993, Robinson et al. 1995a, Hahn and Hatfield 1995). In the Sierra Nevada of California, tree-nesting species such as Cassin's Vireo (*Vireo cassinii*) and Yellow-rumped Warbler are often parasitized (Rothstein et al. 1980, Verner and Ritter 1983, Airola 1986), even though few records had been recorded for these species previously (Friedmann and Kiff 1985). Cowbird parasitism in western conifer forests has not been sufficiently studied. In an attempt to model a more restricted set of potential hosts that may be more biologically meaningful, we created a second set of likely hosts by excluding species known to reject eggs (Friedman and Kiff 1985), and excluding all species with fewer than 10 records of parasitism in the compilations of Friedman et al. (1977, 1985), unless they were found to be primary hosts (>15 % parasitism) in an ongoing local study (Tewksbury et al. *this volume*). This resulted in 45 species of likely hosts. It is not known if these were actually the most widely used hosts throughout this region, however.

TABLE 2. Distribution of the 7,153 Sample Points Among the Major GIS Cover Types, With the Average % Coverage of Each Type Across All 1-km Radius Landscape Circles in the Northern Rockies

Cover type	Number of points	Percent of points	Mean coverage (%)
Mesic conifer	3,633	50.8	55.5
Xeric conifer	510	7.1	7.9
Subalpine conifer	639	8.9	9.9
Mixed conifer/broadleaf	69	1.0	0.9
Broadleaf forest	68	1.0	0.7
Forested riparian	324	4.5	2.3
Non-forested riparian	132	1.8	0.9
Grassland/shrubland	1,530	21.4	17.8
Agricultural land	37	0.5	0.6
Barren land	138	1.9	1.8
Urban/developed	50	0.7	0.8

Landscape Variables

The precise location of both permanent and non-permanent points were marked in the field on the aerial photo associated with each transect, and the aerial photo was subsequently used to position points onto a Geographic Information System (GIS) data layer. The GIS database we used was developed at the University of Montana Wildlife Spatial Analysis Lab, using Landsat TM imagery and ground-truthing in a two-stage classification process (Redmond et al. 1996). Agriculture and riparian areas were added manually to the database from aerial photos, which is a more accurate method than remote sensing.

Within a 1-km radius circle surrounding each point, we calculated several landscape variables from the GIS database. We created variables based on an additional merging of the cover type classification into 15 cover types that correspond as well as possible with our field cover types. These included a conifer series, a riparian series, and an open land series (Table 2). For each of these cover types we calculated the proportion of the 1-km radius circle that was covered by that type, and the distance from the point to the nearest occurrence of each type.

Analytical Methods

To determine habitat associations, we used only bird detections that were estimated to be within 100 m of the observer (very few cowbirds were detected beyond this range), and excluded birds flying over the site. If more than one vegetation cover type occurred within 100 m, the point was designated as being an edge point and was excluded from the local-scale habitat analyses, which cut the sample size nearly in half (3,406). This reduced the chance that birds were detected within a cover type that differed from that associated with a particular census point. We also performed landscape analyses using all points, however.

For a more detailed look at factors affecting the distribution of cowbirds among points, we used logistic regression to predict cowbird presence vs. absence, looking at the continuous habitat variables collected at the point, and combining these with the landscape context of the point taken from the GIS database.

With each point count as a sample unit, almost 98 % of cowbird counts were zero or one (only one cowbird was detected at 77 % of occupied points), so logistic regression is especially appropriate. However, multiple samples of a given cover type within a single transect may not have been statistically independent estimates of bird composition within that cover type. Nevertheless, we used individual points as sample units for all local-scale habitat analyses because (1) transects were inappropriate sample units at this scale, since they crossed multiple cover types, and (2) an average of only four points from each transect were non-edge points that could be used in the analyses.

The landscape variables, however, were based on 1-km radius circles, and points only 300 m apart were clearly pseudoreplicate sample units. Therefore, we redid the landscape analyses using the transect as the sample unit. These analyses did not include local habitat variables because these could not be meaningfully averaged across a transect. The results of these additional landscape analyses were used to corroborate the point-scale analyses.

As a first step in selecting variables for the habitat-relationship model, we fit separate univariate logistic regression equations for each variable (Hosmer and Lemeshow 1989:83). Variables considered for entry into a multivariate model were those for which the univariate test indicated potential significance ($P < 0.15$). Local-scale variables were combined with the landscape variables in a single parsimonious model to explain the distribution of Brown-headed Cowbirds. We used both forward and backward stepwise procedures for building multivariate models. The selection of variables for use in these models was based not only on the statistical significance of each measured variable, but also on our biological knowledge of the species.

We followed the above model-building methods for three different subsets of the data. The first set contained all 7,153 points (including edge points) in all cover types. These models involved comparisons across very different cover types and could only show general patterns of habitat use, as well as landscape effects. It would be valuable to have more detailed information on habitat and landscape effects within a smaller subset of cover types. Specifically, we wanted to predict where cowbirds would occur when they penetrated a typical western coniferous forest landscape (e.g., does opening the forest in various ways affect cowbird distribution, allowing them to penetrate where they otherwise might not?). Therefore, we also conducted analyses using just the subset of 2,250 non-edge points from conifer cover types, ranging from clearcuts to undisturbed forest. This data set still included a wide range of forest types and landscapes, with a multitude of potential reasons for cowbird absences. We used multivariate tests to tease these potential reasons apart. However, in a final attempt to separate local-scale influences from landscape conditions, we analyzed a third subset of the data that included the 517 conifer points within occupied transects only. We assumed that all occupied transects were in at least marginally appropriate landscapes. The discrimination of individual points of use and nonuse by cowbirds within occupied transects (which were less than 3 km in length) would, therefore, likely be due to local factors.

RESULTS

The 3,406 non-edge points were distributed unevenly among the 18 cover types categories (Table 1), with mixed-conifer stands represented by 33 % of the points, and nine cover types having fewer than 100 points.

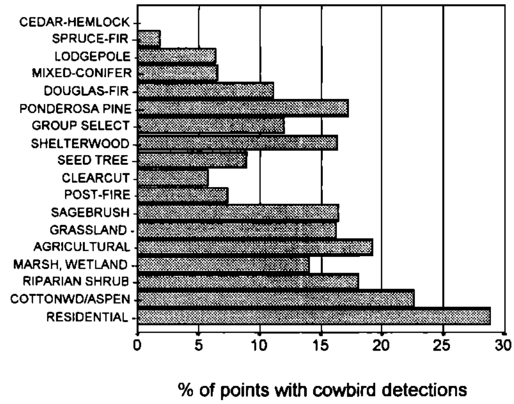

FIGURE 2. The distribution of Brown-headed Cowbirds among 18 major cover types in the northern Rockies. Cowbirds were detected (within 100 m) on 334 of the 3,406 points represented here. Sample sizes for each cover type are given in Table 1. Points with an edge within 100 m were excluded from all non-riparian cover types. The three riparian types (marsh, riparian shrub, and cottonwood bottomland), however, included all points because most of those patches were small or narrow and there was almost always another cover type within 100 m.

There were 91 landbird species (54 of which were potential cowbird hosts) that we detected on at least 30 points. We detected Brown-headed Cowbirds on 653 points, or about 9% of the total, but on over one third of the transects (238 of the 638 transects with at least 8 points). Occupied transects were distributed throughout the region, although relatively fewer transects were occupied by cowbirds in the moister forests of northwestern Montana and northern Idaho (Fig. 1B). Cowbirds were relatively common in south-central Montana, with its drier, sparser forests and wider agricultural valleys, and on our extra points in western Montana, which included more agricultural areas, towns, and riparian bottomlands than the permanently marked points.

Cowbirds were uncommon in denser forest cover types and high-elevation forests (Fig. 2), and the only relatively undisturbed forest type in which they were especially common was that dominated by ponderosa pine. All of the relatively undisturbed forest categories (the first six categories in Fig. 2) included a variety of stand ages and even many thinned stands. To further explore these data, we pooled them, and then divided them into different categories based on stand age and disturbance status. We found cowbirds at 1.3 % of 154 points in old growth, 5.1 % of 630 points in mature forest, 5.6 % of 198

TABLE 3. SIGNIFICANCE LEVELS (P-VALUES) OF UNIVARIATE LOGISTIC REGRESSIONS FOR EACH LOCAL-SCALE AND LANDSCAPE VARIABLE, AND FOR ALL THREE SUBSETS OF THE DATA DISCUSSED IN THE TEXT (ONLY CONIFER POINTS INCLUDED WITHIN OCCUPIED TRANSECTS)

Variable	Sign[a]	All points		Conifer points		Occupied transects
		Statistic[b]	P	Statistic[b]	P	P
Canopy height	+			1	0.35	0.08
Canopy cover	−	64	< 0.01	4	0.06	0.60
Sapling cover	−	22	< 0.01	0	0.88	0.54
Seedling cover	−	12	< 0.01	1	0.44	0.80
Tall shrub cover	−	3	0.07	0	0.99	0.50
Low shrub cover	−	3	0.10	0	0.96	0.86
Ground cover	+	101	< 0.01	36	< 0.01	0.31
Proportion ponderosa pine	+			78	< 0.01	0.02
Proportion Douglas-fir	+			6	0.01	0.45
Proportion western larch				0	0.73	0.41
Proportion lodgepole pine	−			30	< 0.01	0.58
Proportion mesic species	−			5	0.02	0.64
Abundance of all hosts	+	131	< 0.01	83	< 0.01	< 0.01
Richness of all hosts	+	148	< 0.01	108	< 0.01	0.05
Abundance of likely hosts	+	164	< 0.01	110	< 0.01	< 0.01
Richness of likely hosts	+	176	< 0.01	123	< 0.01	0.02
Elevation	−	20	< 0.01	24	< 0.01	0.92
Distance (developed)	−	209	< 0.01	102	< 0.01	0.92
Distance (agriculture)	−	298	< 0.01	112	< 0.01	0.41
Distance (grass/shrubland)	−	52	< 0.01	11	< 0.01	0.58
Distance (riparian)	−	23	< 0.01	14	< 0.01	0.12
Coverage (agriculture)	+	24	< 0.01	0	0.66	0.18
Coverage (grass/shrubland)	+	98	< 0.01	29	< 0.01	0.30
Coverage (subalpine forest)	−	136	< 0.01	88	< 0.01	0.07
Coverage (mesic forest)	−	94	< 0.01	8	< 0.01	0.04
Coverage (xeric forest)	+	68	< 0.01	68	< 0.01	0.02
Coverage (riparian)	+	36	< 0.01	1	0.42	0.62

[a] The sign of the relationship was the same for all data sets.
[b] The chi-square statistic for the likelihood ratio test indicates relative statistical importance.

points in young forest, and 10.0 % of 769 points in selectively cut stands. Cowbirds were also common in more extensively logged forests, but were observed more often in partially logged stands than in clearcuts (Fig. 2). As expected, cowbirds were most commonly detected in open areas, including grassland and agriculture, and riparian vegetation.

Both landscape and local-scale habitat variables were significantly related to cowbird occurrence using logistic regression models that involved all 7,153 points (Table 3). Most landscape variables were significant in the univariate tests, but distance to agricultural lands was the strongest predictor of cowbird presence (Table 3). In fact, about 73 % of points with cowbirds were within 10 km of agricultural areas, and almost 90 % were within 20 km (Fig. 3). Cowbirds were also found closer to developed areas, as well as in landscapes with more open areas and xeric forests, but less subalpine and mesic forests. All of these relationships were strong enough ($P < 0.001$) to remain significant when the data were averaged over each transect, and the 638 transects were then used as sample units.

Most local-scale vegetation variables were also important in the univariate logistic regressions, although some were not examined because they were not relevant to all cover types (height and species composition of canopy were not defined if there was no canopy). Cowbirds were negatively associated with canopy cover, as expected, since they were common in grasslands and agricultural areas, where canopy cover was zero. Ground cover was the strongest predictor of cowbird occurrence among habitat variables. Ground cover tended to be high in areas where cowbirds were common, such as grasslands, ponderosa pine forests, and partially logged forests. All of the measures of host abundance and species richness were strong predictors of cowbird presence (Table 3). The restricted subset of likely hosts appeared to fit the data best. Although species richness was a slightly better predictor than abundance, we thought that abundance was more biologically meaningful.

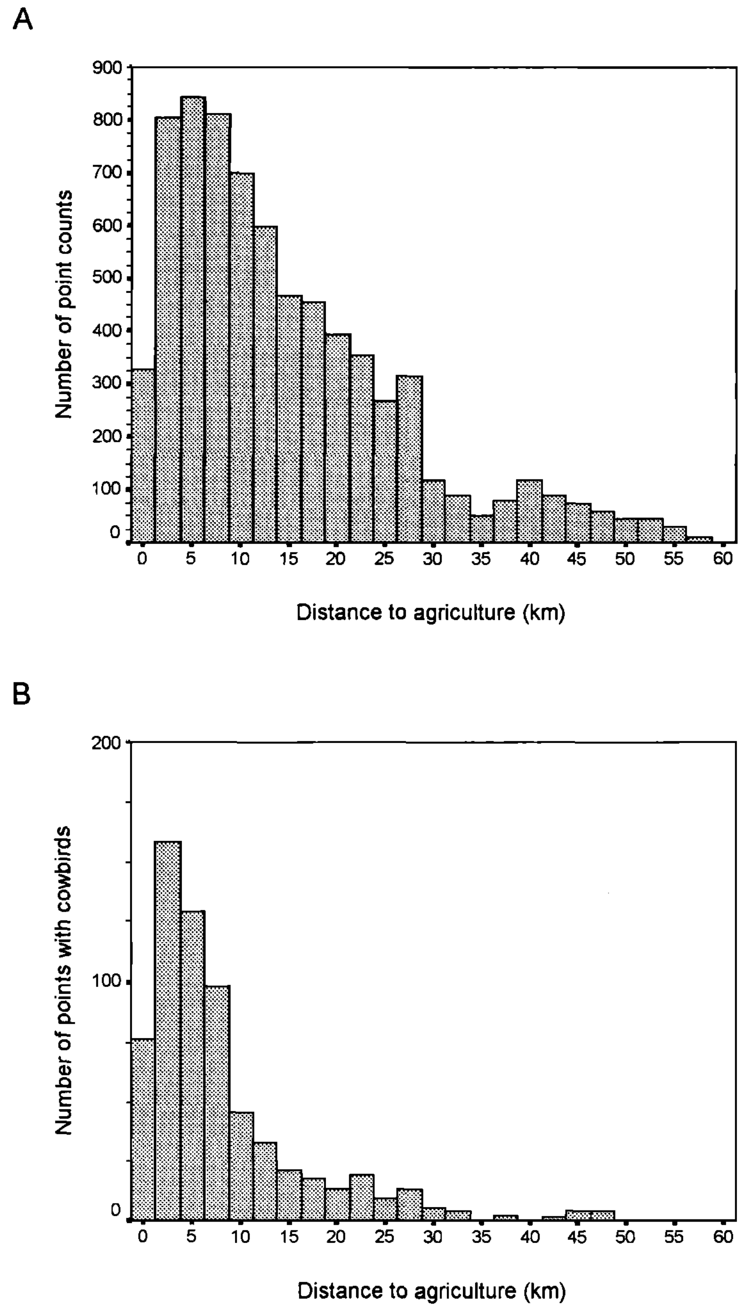

FIGURE 3. Frequency distribution for the distance to the nearest agricultural lands from A) all 7,153 points used in the analyses (median = 11.6 km); B) the 653 points where cowbirds occurred (median = 5.3 km) in northern Idaho and western Montana.

Therefore, we chose the abundance of likely hosts as the variable to test in the multivariate analyses.

When these variables were put together in a multivariate model (Table 4), it was still apparent that cowbirds were closer to agriculture and urban areas, on average. They were not in landscapes with subalpine forests, and they were more common in landscapes with less mesic conifer and more xeric conifer stands, which in-

TABLE 4. SIGNIFICANCE LEVELS (P-VALUES) OF VARIABLES INCLUDED IN MULTIPLE LOGISTIC REGRESSION MODELS FOR ALL THREE SUBSETS OF THE DATA DISCUSSED IN THE TEXT

Variable	Sign[a]	All points	Conifer points	Occupied transects
Canopy height	+	< 0.01		0.02
Canopy cover	−	< 0.01		
Tall shrub cover	−	0.02		
Ground cover	+	0.02		
Proportion ponderosa pine	+		0.05	
Abundance of likely hosts	+	< 0.01	< 0.01	< 0.01
Distance (developed)	−	< 0.01	< 0.01	
Distance (agriculture)	−	< 0.01	< 0.01	
Distance (riparian)	−	< 0.01		
Coverage (subalpine forest)	−	< 0.01	< 0.01	
Coverage (mesic forest)	−	< 0.01		
Coverage (xeric forest)	+	0.04	0.02	0.02
Coverage (riparian)	+	< 0.01		

[a] The sign of the relationship was the same for all data sets.

cluded ponderosa pine, juniper (*Juniperus scopularum*), and limber pine (*Pinus flexilis*). An association with riparian areas was indicated by the inclusion of both the coverage of and distance to these lands. There were also local-scale variables in this multivariate model. Canopy cover and the abundance of likely hosts were the most important. The same model was produced by both forward and backward stepwise variable selection.

To examine the habitat distribution of cowbirds within the conifer cover types only, we conducted additional analyses using the restricted data set of 2,250 non-edge points from conifer habitats. Cowbirds were detected on 172 of these points. Most of the landscape variables were still significant in univariate tests, whereas most of the local vegetation variables were not (Table 3). Although cowbirds tended to occur in sites with less canopy cover ($P = 0.06$), this relationship was much less apparent when other variables were included in a multivariate model ($P = 0.24$). The multivariate model was dominated by landscape variables (Table 4), although the abundance of likely hosts was the strongest predictor ($P < 0.001$). Again, cowbirds were found closer to agricultural areas and were not found in subalpine landscapes. They were more likely to be present in stands with more ponderosa pine in the tree canopy ($P = 0.05$), which was the only vegetation variable that was even close to significant. The same model was produced by both forward and backward stepwise variable selection. Although the relationships were not significant in the multivariate analyses, cowbirds tended to be in stands closer to riparian areas ($P = 0.09$), and in landscapes surrounded by more agricultural areas ($P = 0.07$).

The data set representing only occupied transects contained 517 points, including the same 172 points with cowbirds as above. As expected, landscape variables were of greatly reduced importance when unoccupied transects were removed from the analyses. There was no trend toward a relationship with canopy cover within occupied transects ($P = 0.60$). Very few variables were significantly related to cowbird presence in this data set (Table 3), and only three were retained in the multivariate model (Table 4). The best predictor was the abundance of potential hosts. There was also a positive association with canopy height. The coverage of xeric forest was the third variable retained in the forward stepwise procedure, and we report it here because it fit the data slightly better than the coverage of mesic forest, which was selected by the backward elimination procedure. These two variables were strongly correlated ($r = -0.70$). It was not clear whether the local or landscape variable involving xeric pine was the most important, since they were also highly correlated ($r = 0.49$) and had similar significance levels, both separately ($P = 0.02$) and together ($P = 0.18$).

In the above analyses, we used a merged cover type category for non-forested lands other than agriculture and riparian (it included all types of grasslands and upland shrublands). This variable was strongly related to cowbird presence, as expected, with cowbirds occurring closer to these lands, on average. However, it would be interesting to know if different kinds of open lands affect cowbird occurrence differently. To explore this, we separated these lands into components relating to low-elevation grasslands, high-elevation grasslands, upland mesic shrublands, and xeric shrublands. Unfortunately, clearcuts were not well differentiated in the GIS database, since the satellite imagery responded to the reflectance of the ground cover, rather than anything relevant to logging per se. However, clear differences emerged between these categories in their relation to cowbird distribution. Cowbirds were seen more often near low-elevation grasslands. This relationship was nearly as strong as that with the distance to agriculture (although these two variables were correlated, with r = 0.30, they both would enter a regression model together). Cowbirds were less likely to occur nearer high-elevation grasslands, however. Cowbird presence was not correlated with distance to upland shrublands, which was the category that should have included shrubby clearcuts. These relationships held whether we looked at all points or only those in conifer cover types.

Elevation at the sample points ranged from 465 m to 2,620 m. The highest elevation we detected cowbirds was 2,318 m (there were 133 points higher than this without cowbirds). Cowbirds were more abundant at lower elevations (Table 3). However, elevation was correlated with all of the other variables influencing cowbird occurrence in the multivariate models. Therefore, the relationship with elevation was not retained in these models.

Cowbirds were more likely to occur at points where more potential hosts were also observed. The distribution of these potential hosts among cover types (Fig. 4) was generally similar to that of the Brown-headed Cowbird (Fig. 2). Host density was also an important predictor in regression models (Tables 3 and 4). There was not much difference in the predictive abilities of host species richness and the number of potential host individuals. These relationships held within all points and within conifer cover types, and were still highly significant after distance to agriculture and the other variables were included in a multivariate model. We also found that host density was significantly related to cowbird presence on points within occupied transects only. In fact, the abundance of the subset of likely hosts was a better predictor than any other variable in this data set (P = 0.003).

DISCUSSION

The Brown-headed Cowbird can be found in a broad range of cover types in the northern Rockies (Fig. 2), as has been found elsewhere. Rothstein (1994) found that this species was reported on about 60 % of all Breeding Bird Censuses throughout North America during a 5-year period, more than any other species. In a more extensive literature review of studies (including Breeding Bird Censuses) in the northern Rocky Mountain region, Hutto (1995a) found the cowbird to be among the most diverse species in its use of major cover types. In our study, cowbirds occurred in all major cover types except cedar-hemlock forest. It was not one of the most commonly detected bird species, however, occurring on only 9 % of all points. Nineteen species were seen on more points, and four were detected on over 30 % of the points.

Brown-headed Cowbirds did not use all cover types equally. They were largely absent from dense, old-growth, and high-elevation forests. They were most abundant in open conifer forest (ponderosa pine and partially logged sites) as well as grassland, agricultural, and riparian cover types. A preference for open forests would be biologically understandable, since these habitats would provide numerous perches combined with high visibility for the observation of host species (Norman and Robertson 1975, Gates and Gysel 1978). However, it should be noted that these habitats were also more likely to be closer to agricultural lands (Table 1), so the apparent pattern of habitat use may have been partly a landscape-driven phenomenon.

When detected in conifer forest, cowbirds were much more likely to be near open lands (grassland and agriculture), and when in open lands they were slightly more likely to be near riparian areas (but not conifer forest). Cowbirds are widely known to prefer edges between shrubs or forest and open lands, where breeding and foraging opportunities can be found together (Rothstein et al. 1980, Robinson et al. 1995a). Johnson and Temple (1990) found that rates of cowbird parasitism were higher near forested edges of prairies than in more continuous tallgrass prairie. To use breeding habitat farther from foraging habitat, cowbirds have been known to travel several kilometers (Rothstein et al. 1984).

The arrangement of cover types in the northern Rockies is similar to that of the Sierra Nevada, with extensive open lands and human activity at lower elevations only intermittently penetrating into the conifer forests on the mountain slopes. It is likely that cowbirds exhibit the same type of commuting pattern between breeding and foraging habitats (Rothstein et al. 1980, Verner and Ritter 1983), especially since this behavior is widespread, albeit less strongly expressed, even in regions with better interspersion of cover types (Dufty 1982a, Thompson 1994). Potential feeding sources away from the major agricultural areas were also similar (e.g., pack stations, and small, dispersed meadows with grazing cattle). Many of these microhabitats would not have registered in our GIS database. Our finding that cowbird presence was strongly associated with the proximity of agricultural areas suggests that whatever non-agricultural foraging sites there may be, they have not yet re-

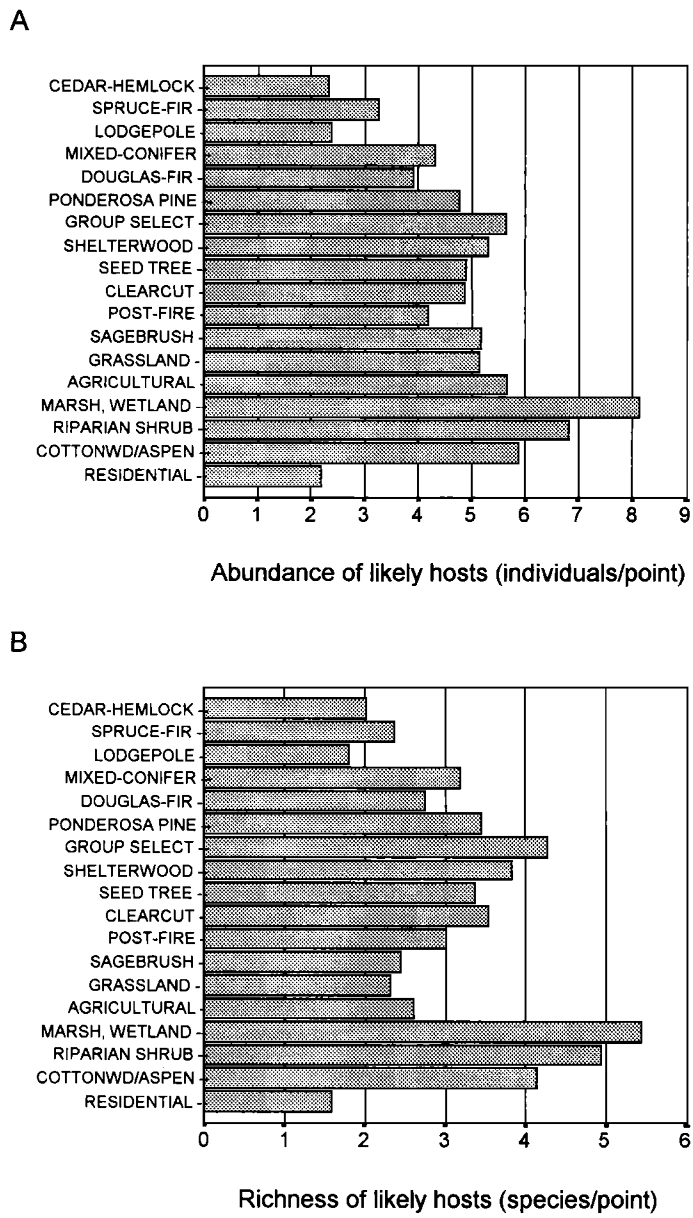

FIGURE 4. Abundance of potential host species across the same major cover types as in Fig. 2: A) total individuals detected per point of likely hosts; B) number of species of likely hosts detected per point in each cover type. Likely hosts were defined as open-cup nesting passerine species of appropriate size, that were not rejectors and had more than 10 published records of parasitism, or were considered primary hosts in a local study (see text).

sulted in widespread penetration of the forested mountains by cowbirds.

We found that open lands such as grasslands and agricultural areas were more commonly used than clearcuts. In addition, canopy cover was not strongly associated with cowbird occurrence within coniferous forest areas. On the landscape scale, the proximity of upland shrub sites, such as clearcuts, was not significantly related to cowbird occurrence. Clearcuts would not be expected to provide good foraging habitat for cowbirds (unless they were grassy and were grazed by cattle, which is sometimes the case), but they may provide good opportunities for nest searching (Robinson et al. 1995a). We found as many potential hosts in clearcuts as in forest cover types (Fig. 4), but perhaps clearcuts did not provide sufficient perches for displaying or observing potential hosts. Hahn and Hatfield (1995) found higher parasitism rates in deciduous forest than in old fields with abundant host populations. Thompson et al. (1992) found that cowbird numbers were similar between extensive forest sites with and without clearcuts. In a review of studies on the effects of logging on bird abundance in the Rocky Mountains, Hejl et al. (1995) found that only three of 19 studies even had cowbirds, and there was no indication that they were more likely to occur in clearcuts than uncut forest. Thus, it appears that the presence of clearcuts does not draw cowbirds into forested regions.

For a species that undergoes such widespread movement patterns, it is not unexpected that we detected cowbirds in a variety of situations. It would, therefore, be useful to know more precisely what our detections represent. Most detections were probably of males. Females are often quiet in breeding habitats (Norman and Robertson 1975, Rothstein et al. 1984), and field observers were less likely to recognize female calls as cowbirds. Like Rothstein et al. (1984), we usually observed cowbirds in forests either socializing and singing from tree perches, or flying overhead emitting characteristic whistle calls (although the latter observations were not included in habitat relationships). Most cowbirds were likely to have been in breeding habitats during the morning hours when we were observing (Rothstein et al. 1984). Although it is the less conspicuous females that parasitize the host species, males also commute to breeding grounds (Rothstein et al. 1984), and often accompany females throughout their breeding ranges (Dufty 1982a). Mate guarding may result in our observations being a reasonable indicator of where female cowbirds searched for host nests, especially since males are often vocal while accompanying females (Darley 1983, Rothstein et al. 1984). It is not known if males accompany females in our region, but it has been shown in several populations of wild (Darley 1983, Dufty 1982a, Rothstein et al. 1984) and captive (Rothstein et al. 1986b) cowbirds.

In terms of major cover types, there appears to be little refuge from cowbirds in the northern Rocky Mountains. Nonetheless, bird species that occupy conifer forests tend to be especially widespread across conifer forest types, and may find refuge from cowbird parasitism in many denser forested areas where cowbirds are uncommon. Remoteness may also provide a refuge for many populations. It is not known whether populations may be negatively affected by cowbirds in forests near agricultural edges. Many of these bird species that occupy conifer forests have few published records of parasitism (Friedman and Kiff 1985), perhaps because they are less-studied western species with hard-to-find nests. The assumption that cowbirds may also have difficulty finding these nests may be incorrect, since the few studies in western forests have found many of them to be parasitized (Verner and Ritter 1983, Airola 1986, Tewksbury et al. *this volume*).

Not all species may be able to find refuge from parasitism, however. Many species are restricted to riparian bottomlands, which are heavily used by cowbirds (Fig. 2) and are often near agricultural areas. These species may be at serious risk from cowbird parasitism. Any other species largely restricted to lowland riparian or open forest habitats may be at risk, as shown for the Lazuli Bunting (*Passerina amoena*; Greene *this volume*). Another possibility may be the Olive-sided Flycatcher (*Contopus cooperi*), which is relatively restricted to open forests such as frequented by the cowbird, and is declining in the West. More needs to be known about this species. In addition, threats to local populations of any species may still be a concern even if the entire species is not at risk.

MANAGEMENT IMPLICATIONS

Our data suggest that cattle grazing and other agricultural practices appear to be directly involved with the expansion of cowbirds in this region. Based on this association, it would certainly be wise to restrict agriculture to areas already dominated by this land use. Because there was such a clear relationship with distance to agricultural areas, it may be supposed that clearcutting, pack stations, and other human activities removed from areas of intense agriculture have not been the primary reasons behind the widespread cowbird invasion in this region. However, we cannot say that such disturbance will continue to be benign. Further penetration of human disturbance to remote areas may still draw more cowbirds into the backcountry.

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