COWBIRDS IN A WESTERN VALLEY: EFFECTS OF LANDSCAPE STRUCTURE, VEGETATION, AND HOST DENSITY

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Abstract. Brown-headed Cowbird (*Molothrus ater*) abundance varies dramatically over both large and small spatial scales, causing extreme heterogeneity in parasitism pressure. Understanding the factors responsible for the occurrence and relative abundance of cowbirds is thus essential for properly predicting the regional impact of cowbirds on different host species. We studied the occurrence and relative abundance of Brown-headed Cowbirds across three vegetation types in the foothills and valley floor of the Bitterroot Valley in western Montana. Using multiple logistic regression and univariate analyses, we examined the potential impacts of landscape structure, habitat type, distance to agricultural areas, and the density of the cowbird host community on the occurrence and relative abundance of cowbirds. We never encountered cowbirds more than 4 km from agricultural areas, and the distance to large agricultural areas was the strongest predictor of cowbird occurrence and relative abundance. Topographic location of survey points was also important in predicting cowbird occurrence, as cowbirds were almost never encountered within steep-sided canyons. Outside of canyons, both host density and vegetation type appear to influence cowbird abundance, with more cowbirds in deciduous riparian areas and areas of higher host density. Cowbird occurrence and abundance may be mediated by multiple features of the landscape and host community, but in the Bitterroot Valley, cowbird abundance appears greatest in deciduous riparian communities within 2 km of agricultural areas. Intensive research into the demographic impact of cowbirds and the effectiveness of different management options should be directed at species that are confined to these areas for breeding.

Key Words: Brown-headed Cowbirds, fragmentation, host density, landscape ecology, *Molothrus ater*, parasitism pressure.

Numerous studies have demonstrated the detrimental impacts of Brown-headed Cowbirds (*Molothrus ater*) on a wide variety of hosts (Nolan 1978, Sedgwick and Knopf 1988, Marvil and Cruz 1989, Trail and Baptista 1993, Greene *this volume,* Whitfield and Sogge *this volume*) and the potential for cowbirds to precipitate the decline and extirpation of some species (Mayfield 1960, 1977; Gaines 1974, Goldwasser et al. 1980, Harris et al. 1987, Franzreb 1989b). Given the large impact cowbirds can have on host populations, and the continental range of cowbirds, understanding the landscape features correlated with the distribution of cowbirds is important in identifying habitats and species that are potentially at risk from parasitism (Verner and Ritter 1983; Donovan et al. 1997, in press; Thompson et al. in press).

Due to their parasitic nature and lack of parental care, cowbirds can decouple breeding and feeding behaviors and choose breeding habitats that have the highest density of nests available for parasitism regardless of food availability (Rothstein et al. 1984, Robinson et al. 1995a, Thompson 1994). Cowbirds are constrained to some extent, however, by the distance between breeding and feeding areas (Verner and Ritter 1983, Rothstein et al. 1984, Thompson 1994), and thus the distribution of cowbirds may be strongly dependent on the distribution of breeding and feeding areas on the landscape. Cow-

birds have been reported to move as far as 7 to 12 km from breeding areas to feeding locations (Rothstein et al. 1980, 1984, 1987; Thompson 1994; Goguen and Mathews *this volume*), but whereas a few cowbirds may move long distances, the majority of cowbirds appear to move less than 1.5 km between these areas (Thompson 1994), and the proximity and abundance of feeding habitat are the most often cited variables explaining the presence and abundance of cowbirds on the landscape (Rothstein et al. 1980, 1984; Robinson 1992, Rothstein 1994, Thompson 1994, Robinson et al 1995b; Donovan et al. 1995a, 1997, in press; Hejl and Young *this volume,* Young and Hutto *this volume*). However, the presence and abundance of cowbirds may also be influenced by a variety of other variables affecting the quality and quantity of breeding habitat. Vegetation (Rothstein et al. 1984, Rosenburg et al. 1991, Robinson et al. *this volume*), topography (Curson and Mathews *this volume*), and host abundance (Barber and Martin 1997, Tewksbury et al. 1998, Robinson et al. *this volume*) may all affect cowbird distribution and abundance. While these variables have been examined separately, few studies have included all these variables to predict the occurrence or relative abundance of cowbirds (but see Young and Hutto *this volume*).

We develop a model for predicting cowbird occurrence in the Bitterroot Valley of western

Montana using relative abundance point-count sampling and logistic regression. We examine how cowbirds are distributed in relation to agriculture, vegetation, topography, and the density of hosts in this western landscape, compare these relations with eastern and midwestern landscapes, and discuss the implications for the management of western forests.

METHODS

STUDY AREA AND STUDY SITES

The study was conducted in the Bitterroot Valley of western Montana. Primary point count locations were originally established in 1994 in conjunction with 16 nest-monitoring sites (Martin et al. 1996) in deciduous riparian communities. These sites were set in local landscapes that ranged from highly fragmented by agriculture to predominantly forested and unfragmented (Fig. 1). Within each nest monitoring site, we established 2–7 point counts for a total of 73 point locations. We stratified these points within each site so that all points were greater than 200m from all other points on the site. All points were located in habitats dominated by deciduous trees and shrubs typical of either the black cottonwood (*Populus trichocarpa*)/red-osier dogwood (*Cornus stolonifera*) community type, the quaking aspen (*Populus tremuloides*)/red-osier dogwood community type, or the mountain alder (*Alnus incana*) community type (Hansen et al. 1995).

To understand the features affecting cowbird abundance at a landscape scale in multiple vegetation types, we established an additional 117 point locations in 14 transects extending from the forest-farmland interface into the Selway-Bitterroot Wilderness Area (Fig. 1). This area is predominantly Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forest with numerous streams flowing east from the wilderness area to join the Bitterroot River in the valley floor. Stream-side vegetation ranges from coniferous riparian areas dominated by Engelmann spruce (*Picea engelmannii*) and grand fir (*Abies grandis*), to deciduous riparian areas dominated by aspen, alder and willow (*Salix spp.*) We established points in three vegetation types: conifer forest (referred to as xeric conifer), conifer riparian, and deciduous riparian. All points were a minimum of 500 m from neighboring points, and we chose locations within vegetation types at least 50 m from the edge of the vegetation type whenever possible (many deciduous riparian areas sampled were too narrow to meet this criterion). We positioned points in an attempt to census all three vegetation types over the full range of distances from agriculture.

Deciduous riparian vegetation, however, was concentrated near the valley floor where virtually all of the agriculture is located, and our original points (all in deciduous riparian) were on average closer to agriculture than the points established in transects. This prevented us from establishing a completely balanced design (Fig 1). Census locations varied from 40 to 7,700 m from agriculture, with a mean distance of 2,080 m from agricultural development. The Bitterroot Mountains are dissected by steep-sided canyons, and thus some transect points were located within canyons, while others were on much more open terrain. Because of the large differences in topography between these locations, we noted topographic location (canyon or open topography) and included this in our analysis of cowbird distribution. We identified agricultural land use throughout the Bitterroot Valley using existing Landsat satellite data (Redmond and Prather 1996) and determined the distance of all point-count locations to agricultural areas defined by this data set. This agricultural delineation has a minimum mapping unit of 2 ha and thus depicts only large agricultural areas. While cowbirds may also respond to smaller agricultural units and the presence of farm buildings and bird feeders (Tewksbury et al. 1998), if reliable associations between cowbird abundance and distance to agricultural areas can be found at this resolution of landscape structure, it will allow managers to use existing information to predict and manage cowbird populations.

ASSESSING COWBIRD AND HOST ABUNDANCE

For this paper, we use point-count data from 1996 only, as this is the only year in which all points were sampled. Point count locations were censused three times during the season, each count was 10 minutes long, and all birds seen or heard were recorded. We standardized detection effort by using only birds seen or heard within 50 m of the observer (Hutto et al. 1986, Ralph et al. 1995). We recorded vocalizations of males and females separately where possible. Two experienced observers (T.S.R. and F.J.W.) conducted all surveys, switching off transects so that all locations were surveyed by both observers. We recorded noise level at each point (mostly from streams), determined the level at which noise caused a decline in detections, and excluded results from all high noise censuses. All censuses analyzed were conducted at least one-half hr after sunrise and before 11:00.

To examine the effect of relative host density on cowbird abundance, we calculated the average abundance of all hosts at each survey location based on all censuses. A species was considered a host if it was parasitized greater than

FIGURE 1. Study site locations and general agricultural land use in the Bitterroot Valley. Large dark gray points are nest searching plots where parasitism rates were monitored, smaller points are census locations in the three habitat types: deciduous riparian areas (triangles), coniferous riparian areas (squares) and xeric conifer forest (circles). Agricultural land (light gray) is from Landsat image data.

15% of the time on our nest-monitoring sites (See Tewksbury et al. 1998 for parasitism rates and nest monitoring methods) or known to be regularly parasitized by cowbirds elsewhere (Table 1). We included this latter category because we have not determined parasitism rates across species in xeric conifer or mesic conifer forests, but we wanted to include all potential hosts in our calculation of host density across all three habitat types. The complete list of hosts (Table 1) includes two species that were not often parasitized on our deciduous riparian nest-monitoring sites, the Chipping Sparrow (see Table 1 for scientific names of bird species) and Dark-eyed

TABLE 1. RELATIVE ABUNDANCE (DETECTIONS ≤ 50 M PER 10 MIN CENSUS PERIOD) OF BROWN-HEADED COWBIRDS AND ALL SPECIES INCLUDED AS COWBIRD HOSTS IN THREE HABITATS AND TWO TOPOGRAPHIC LOCATIONS, BITTER-ROOT VALLEY, MT, 1996

| | | Coniferous Riparian | | Xeric Conifer | | Deciduous Riparian | |
	Topography: # of census locations:	Open 9	Canyon 18	Open 33	Canyon 19	Open 98	Canyon 13
Brown-headed Cowbird	*Molothrus ater*	0.037	0	0.283	0.035	0.862	0.026
Willow Flycatcher	*Empidonax traillii*	0	0	0	0	0.061	0
Least Flycatcher	*Empidonax minimus*	0	0	0	0	0.003	0
Hammond's Flycatcher	*Empidonax hammondii*	0.148	0.056	0.293	0.105	0.122	0.231
Dusky Flycatcher	*Empidonax wrightii*	0.074	0	0.061	0.017	0.264	0.115
Veery	*Catharus fuscescens*	0	0	0	0	0.124	0
Swainson's Thrush	*Catharus ustulatus*	0.259	0.398	0.167	0.158	0.151	0.385
Hermit Thrush	*Catharus guttatus*	0	0	0	0.017	0	0
Cassin's Vireo	*Vireo cassinii*	0	0	0.212	0.035	0.092	0.09
Red-eyed Vireo	*Vireo olivaceus*	0	0	0	0	0.032	0
Warbling Vireo	*Vireo gilvus*	0.185	0.139	0.05	0.053	0.541	0.410
Orange-crowned Warbler	*Vermivora celata*	0	0	0.03	0	0.121	0.064
Nashville Warbler	*Vermivora ruficapilla*	0	0	0	0.017	0.012	0
Yellow Warbler	*Dendroica petechia*	0	0	0.010	0	0.599	0.026
Yellow-rumped Warbler	*Dendroica coronata*	0.037	0.102	0.263	0.184	0.08	0.051
Townsend's Warbler	*Dendroica townsendi*	0.741	0.62	0.227	0.263	0.056	0.731
American Redstart	*Setophaga ruticilla*	0	0	0	0	0.179	0
Northern Waterthrush	*Seiurus noveboracensis*	0	0	0	0	0.107	0
MacGillivray's Warbler	*Oporornis tolmiei*	0.333	0.083	0.071	0.07	0.360	0.538
Common Yellowthroat	*Geothlypis trichas*	0	0	0	0	0.059	0
Chipping Sparrow	*Spizella passerina*	0.037	0	0.328	0.228	0.095	0.026
Song Sparrow	*Melospiza melodia*	0	0	0	0	0.124	0
Dark-eyed Junco	*Junco hyemalis*	0.148	0.028	0.359	0.105	0.082	0.064
Lazuli Bunting	*Passerina amoena*	0	0	0	0	0.005	0

Junco, but neither of these species are very abundant in deciduous riparian areas, and both of these species known to be parasitized elsewhere (Buech 1982, Wolf 1987, Graham 1988, Scott and Lemon 1996). These species were included because they may be parasitized more often in coniferous areas where their abundance relative to other hosts is greater. Though we were unable to find data addressing parasitism rates in the Townsend's Warbler, we included this species in our list of hosts because we have seen adults feeding cowbird fledglings, and virtually all other open-cup nesting *Dendroica* species are common cowbird hosts.

DATA ANALYSIS

We examined the importance of landscapes, vegetation and host communities on cowbird occurrence using multiple logistic regression. On the subset of locations where cowbirds were detected, we examined the importance of these same factors on the relative abundance of cowbirds. This approach has statistical advantages because it avoids the difficulties of properly characterizing relative abundance when a large percentage of sampling points have zero detections, and may be more biologically meaningful if the factors that influence the presence of a

species are different than those that influence density.

We included distance to agriculture, vegetation type, host abundance, and topographic location to predict cowbird occurrence through logistic regression. Our a priori hypothesis considered all of these variables important predictors of cowbird occurrence, and we made no predictions regarding interactions; therefore our primary model includes all variables entered without interactions. We also used a forward stepwise model selection procedure to compare with our a priori model. For forward stepwise selection, we used the likelihood ratio method in SPSS v7.5 (SPSS 1996), which calculates P-values using the likelihood-ratio Chi-square test. Variables are entered into the model based on their improvement to the likelihood of obtaining the observed results. The variable that most significantly improves the probability of obtaining the observed results is added to the model first, and all variables are reevaluated after each step. The entry criteria was $P = 0.05$.

Stepwise procedures have been criticized as unreliable at properly ranking the importance of variables or finding the most parsimonious model (James and McCulloch 1990). Moreover, the predictive power of any logistic model cannot

be assessed without validation using data independent of those used to build the model (Hosmer and Lemeshow 1989). To address these problems and compare the predictive ability of our models, we used a jackknife procedure to predict the occurrence of cowbirds at locations excluded from data used to create the models. We surveyed 190 locations for the occurrence of cowbirds. Our jackknife procedure was to run 190 logistic regressions for each model (our primary model, the model chosen by forward stepwise selection, and a full model including all two-way interactions for comparison). In each regression, we left a single location out of the data used to create the model and asked the model created with 189 locations to predict the occurrence of cowbirds on the location left out. The case left out was changed each run, so that in 190 runs we made independent predictions for each location under the model being jackknifed. We then compared the predictive ability of our model with that of the forward stepwise model and the full model by comparing the percent of points correctly classified with and without cowbirds using McNemar's test, which tests for differences in response (0 or 1) of individuals or locations tested twice (Sokal and Rohlf 1995). If our a priori model classifies independent cases as well as the forward stepwise and full models, we consider it the best working model to use in predicting cowbirds, as it is simpler than the full model, and avoids the uncertainties of stepwise procedures (James and McCulloch 1990). If the other models are significantly better at classifying cases, we have shown that our a priori model is not sufficient to predict cowbird occurrence accurately, and alternative models will need to be developed.

In all logistic regressions, cowbird occurrence at a location was coded as 1 if any cowbirds were detected within 50m of the observer during any of the censuses at the location, and 0 if no cowbirds were detected. As we excluded surveys where noise at a location prevented accurate detection, some locations include data for less than three visits. To correct for this unequal effort, we weighted logistic regression by the number of visits to each location. We also analyzed the occurrence of female cowbirds separately, but as this metric was correlated with the occurrence of all cowbirds (Spearman's rank correlation coefficient = 0.412, P < 0.001), and as results from logistic regression were similar, we only present the results from all cowbirds. We used distance to agriculture, topography, vegetation type, host density, and all two-way interactions as potential predictive variables. We checked for correlations between the two continuous variables, distance to agriculture and

host density, and found no significant correlations in any combination of habitat type and topographic location (bivariate correlations, all P's > 0.7, except within xeric conifer forests, where P = 0.112 in open topography, and P = 0.186 in canyon habitats).

To examine the factors affecting cowbird occurrence further, we also present the proportion of locations in which cowbirds were detected by distance from agriculture (1 km categories), host density (< 1 host per point, 1–2 hosts, 2–3 hosts, etc.), and vegetation type. These data were analyzed using Kruskal-Wallis H-tests for two sample tests and Mann-Whitney U for multiway tests.

Analysis of relative abundance of cowbirds was confined to points where cowbirds were detected and thus is not confounded with the logistic analysis of occurrence. Relative abundance is defined as the number of cowbirds detected per 10-min survey period averaged over all surveys at a given location. To examine the influence of distance from agriculture on cowbird abundance, we used nonlinear regression though the Curvefit function in Sigmaplot version 4 (SPSS 1997). We also analyzed the effect of host density, vegetation type, and topographic location on cowbird abundance using Kruskal-Wallis and Mann-Whitney U-tests. Test statistics reported are for Kruskal-Wallis tests unless otherwise noted.

RESULTS

The distance from the census location to the nearest agricultural area was the strongest, most consistent predictor of cowbird occurrence in all logistic models (Table 2). In open topography cowbirds were detected at more than 80% of all points located within 1 km of agricultural areas, but declined rapidly, with less than 40% occurrence in points 2–3 km from agriculture and no cowbirds detected in any points farther than 4 km from agriculture (Fig. 2A). On points where cowbirds were present, relative abundance also declined with increasing distance to agriculture (Fig. 2B). This relationship was fit best by an exponential curve (R^2 = 0.166; df = 1, 94; P < 0.001).

The topographic location was also a strong predictor of cowbird occurrence; cowbirds were detected in a total of 68% of the 140 open topography locations, and only two of the 50 canyon locations (4%). Some of this difference in occurrence is a function of the location of canyon points, which are rarely close to agriculture due to the topography of the Bitterroot Mountains. Additionally, canyon points had lower host density in all habitat types (Fig. 3). However, topographic location was significant in our

TABLE 2. LOGISTIC REGRESSION MODELS: RESULTS OF THE PRIMARY MODEL, WHICH INCLUDED ALL MAIN EFFECTS BUT NO INTERACTIONS, THE MODEL GENERATED THROUGH FORWARD STEPWISE SELECTION, AND THE FULL MODEL WITH INTERACTIONS

	B[b]	SE	Exp (B)[b]	r[c]	P
Primary model: $\chi^2 = 125$, P < 0.001[a]					
Distance to agriculture (m)	−0.0008	0.0002	0.999	−0.2448	<0.001
Topographic location[d]	2.0865	0.7946	8.057	0.1365	0.009
Vegetation type[e]				0.0374	0.113
Deciduous riparian[e]	2.2094	1.1038	9.110	0.0874	0.045
Xeric conifer[e]	1.6760	1.1068	5.344	0.0334	0.130
Host density	0.2911	0.1766	1.338	0.0522	0.099
Constant	−2.7848	1.3549			0.040
Forward step-wise model: $\chi^2 = 119$, P < 0.001[a]					
Distance to agriculture (m)	−0.0008	0.0002	0.999	−0.2414	<0.001
Vegetation type[e] × Topographic location[d]				0.2381	<0.001
Deciduous riparian × Topographic location[d]	2.9549	0.6860	19.201	0.2510	<0.001
Xeric conifer forest × Topographic location[d]	2.0705	0.7198	7.929	0.1545	0.004
Constant	−0.5784	0.7229			0.423
Full model: $\chi^2 = 127$, P < 0.001[a]					
Distance to agriculture	−0.0016	0.0018	0.998	0.0000	0.375
Topographic location[d]	5.9436	18.4935	381.292	0.0000	0.748
Vegetation type[e]				0.0000	0.925
Deciduous riparian[e]	7.3160	18.5851	1504.178	0.0000	0.694
Xeric conifer[e]	7.2171	18.4377	1362.466	0.0000	0.696
Host density	−0.2946	1.8471	0.745	0.0000	0.873
Vegetation type[e] × Host density				0.0000	0.554
Deciduous riparian[e] × Host density	0.0020	1.4145	1.002	0.0000	0.999
Xeric conifer[e] × Host density	−0.4829	1.4488	0.617	0.0000	0.739
Topographic location[d] × Host density	0.6527	1.0136	1.921	0.0000	0.520
Distance to agriculture × Host density	5.57 E-05	0.0002	1.000	0.0000	0.928
Vegetation type[e] × Topographic location[d]				0.0000	0.824
Deciduous riparian[e] × Topographic location[d]	−6.4737	18.8693	0.002	0.0000	0.729
Xeric conifer[e] × Topographic location[d]	−5.1432	18.5290	0.006	0.0000	0.781
Distance to agriculture × Vegetation type[e]				0.0000	0.732
Distance to agriculture × Deciduous riparian[e]	0.0005	0.0016	1.001	0.0000	0.739
Distance to agriculture × Xeric conifer[e]	0.0001	0.0017	1.000	0.0000	0.933
Distance to agriculture × Topographic location[d]	0.0003	0.0008	1.000	0.0000	0.717

[a] Model χ^2 measures the difference between the likelihood of obtaining the observed results under the final model and the null model without any variables included.

[b] B is the regression coefficient for each effect, representing the change in the log odds of cowbird detection with a one unit change in the independent variable. Exp (B) represents the change in actual odds of cowbird occurrence with a one unit change in the independent variable. Odds are defined as the ratio of the probability that an event will occur to the probability that it will not (SPSS 1996).

[c] Correlation between the independent variable and the probability of cowbird occurrence.

[d] Canyon topography is the reference category. Coefficient (B) and Exp (B) for topographic location refers to the increase in the probability of encountering a cowbird in open topography over canyons

[e] Coniferous riparian is the reference category. All coefficients for deciduous riparian and xeric conifer represent the change in probability of encountering a cowbird in these vegetation types when compared to coniferous riparian areas.

primary logistic model without interaction terms, and had a larger influence on cowbird occurrence than host density (Table 2), suggesting a strong independent affect of topographic location on cowbird occurrence. Cowbirds occurred at only two canyon locations, precluding a comparison of mean cowbird abundance between open topography and canyons for points where cowbirds were present.

The affects of vegetation type and host density were difficult to separate. Deciduous riparian areas had the highest host density (Fig. 3; open topography N = 140, df = 2, χ^2 = 21, P

< 0.001; canyons N = 50, df = 2, χ^2 = 19, P < 0.001), and whereas cowbird occurrence was not related to vegetation type in canyons (Fig. 4A; N = 50, df = 2, χ^2 = 1.1, P = 0.57), in open topography deciduous areas had higher cowbird occurrence as well (Fig. 4A; N = 140, df = 2, χ^2 = 29.8, P < 0.001). When we considered only locations where cowbirds were detected, the relative abundance of cowbirds was also much higher in deciduous riparian areas than either of the other two vegetation types (Fig. 4B; Mann-Whitney U = 358, N = 95, P = 0.005), but the ratio of cowbirds to hosts did
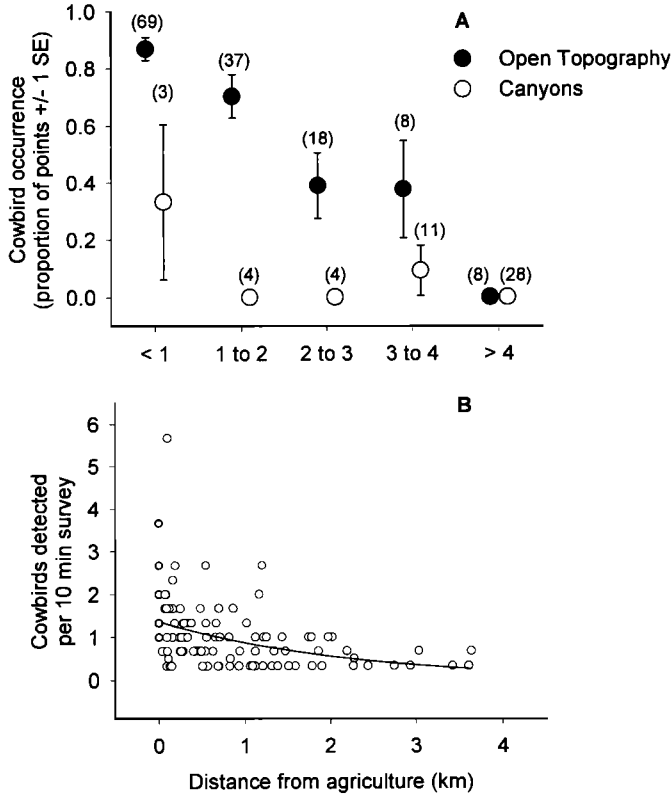
FIGURE 2. A. Proportion of all census points where cowbirds were detected (mean cowbird occurrence ± 1 SE) in open topography and canyon points as a function of distance from agricultural development. Samples sizes (in parentheses), are the number of point locations surveyed. B. The mean number of cowbirds detected per 10 min survey for points where cowbirds were detected. As cowbirds were only encountered at two canyon points, data presented are for open topography. The regression line follows an exponential fit.
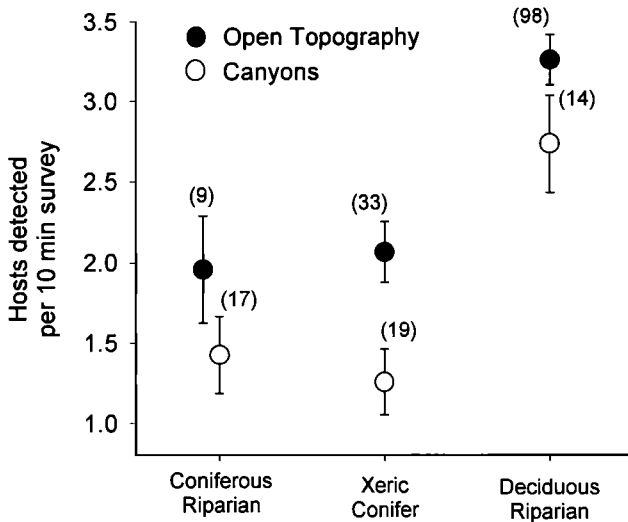
FIGURE 3. Density of all hosts (mean ± 1 SE) by habitat type and topographic location.
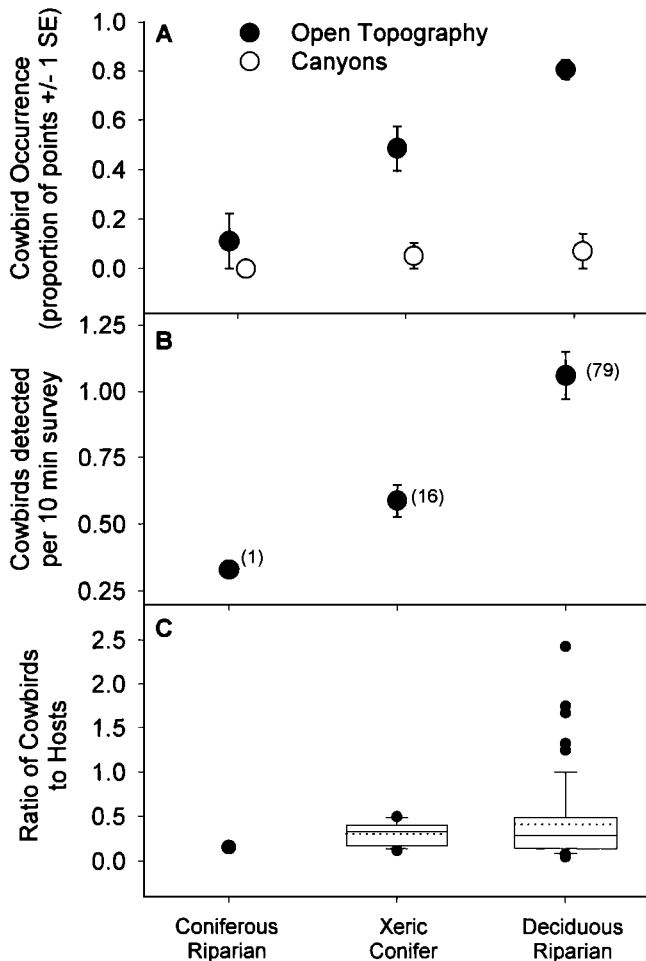
FIGURE 4. A. Cowbird occurrence (mean $\pm$ 1 SE) in the three vegetation types (sample sizes are the same as Fig. 3) in both open topography and canyon locations. B. Mean number ($\pm$ 1 SE) of cowbirds detected per 10 min census for all survey locations where cowbirds were detected. C. Ratio of cowbirds to hosts in the three vegetation types using only points where cowbirds were detected. Shown are the median (solid line), mean (dotted line), 25th and 75th percentiles (boxes), 10th and 95th percentiles (whiskers), and individual points beyond the 10th and 90th percentiles. Cowbirds were detected in only one mesic conifer point (ratio shown as dot in C). Sample sizes for B and C are the same, and are shown in parentheses in B.

not differ between deciduous riparian areas and xeric conifer forest (Fig. 4C; N = 95, P = 0.873).

In logistic regression, host density had a slightly stronger affect on cowbird occurrence than vegetation type, but neither variable appears as important as distance from agriculture and topographic location (Table 2). Stepwise selection failed to enter both variables, further suggesting that they explain much of the same variance in cowbird occurrence (Table 2). The interaction between host density and topographic location included in the stepwise model is due to the very low frequency of cowbird occurrence

in canyons, regardless of host density, coupled with the strong effect of host density on cowbird occurrence in open topography (Fig. 5A; N = 140, df = 5, χ^2 = 14.1, P = 0.015). However, the relative abundance of cowbirds at open topography locations was not strongly affected by host density (Fig. 5B; N = 96, df = 5, χ^2 = 4.6, P = 0.475).

Our a priori logistic regression model correctly predicted the occurrence of brown-headed cowbirds in 84.8% of all cases, better than the full model and slightly better than the model chosen by forward stepwise section (Table 3). All models correctly classified locations with
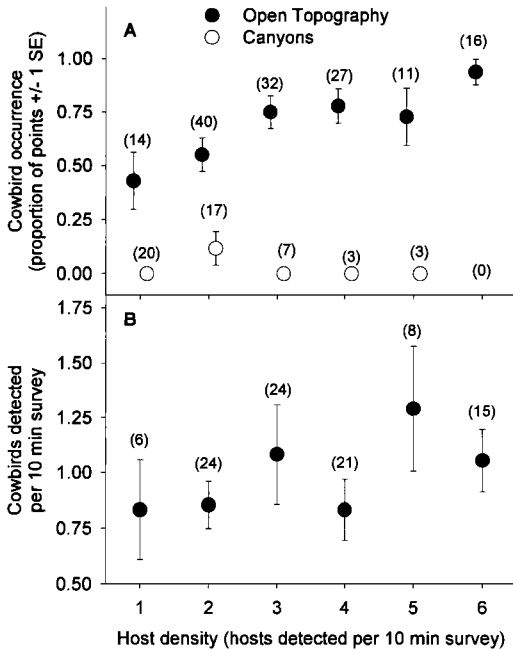
FIGURE 5. A. The relationship between cowbird occurrence (mean ± 1 SE) and the relative density of suitable hosts in open topography and canyons. B. Relative abundance of cowbirds (where present) as a function of relative host density in open topography. See Table 2 for list of all species included in host density calculations.

cowbirds more often than locations where cowbirds were absent.

DISCUSSION

The distribution of cowbirds across potential breeding sites in the Bitterroot Valley appears to be limited by aspects of breeding-site quality and the distance between breeding and feeding areas. Despite our coarse-grain delineation of agricultural areas in the Bitterroot Valley, the distance to the nearest large agricultural area (>2 ha) was the strongest predictor of cowbird occurrence across the landscape. In the Bitterroot Valley, most agricultural areas are used for pasture and row crops, and the strong relationship with agriculture suggests that cowbird distribution in the Bitterroot Valley is limited by the presence and distribution of largely supplemental food sources supplied by human activities. Rothstein et al. (1980), Verner and Ritter (1983), and Wright (*this volume*) reached a similar conclusion in the Sierra Nevada Mountains, where cowbird numbers declined substantially with increasing distance from pack-stations. Young and Hutto (*this volume*) found a similar relationship between cowbird abundance and ag-

TABLE 3. JACKKNIFE RESULTS—EACH MODEL WAS JACKKNIFED 190 TIMES WITH ONE LOCATION LEFT OUT FOR INDEPENDENT CLASSIFICATION

| Model | Percent of locations classified correctly | | | |
	Without cow-birds	With cow-birds	Overall	P[a]
Primary model	78.9%	90.1%	84.8%	
Forward stepwise model	79.3%	89.8%	84.7%	0.137
Full model	75%	89.8%	82.6%	0.063

[a] Two-tailed McNemar test for difference in predictive power between primary model and other models.

riculture throughout the interior Northwest, and Donovan et al.(in press) and Thompson et al. (in press) found the same relationship in the Midwest.

We found no cowbirds beyond 4 km from agricultural development, and while studies in the Sierra Nevada and the Midwest document cowbirds moving farther than 7 km from feeding areas to breeding areas (Rothstein et al. 1984, Thompson 1994) and greater than 10 km in Texas (Goguen and Mathews *this volume*), the majority of cowbirds studied through radio tracking move less than 2 km (Verner and Ritter 1983, Thompson 1994, Goguen and Mathews *this volume*; Tewksbury and Johnson, unpubl. data). Additionally, where there is an abundance of high-quality breeding habitat close to agricultural areas, such as in the Bitterroot Valley, cowbirds may travel shorter distances from breeding sites to feeding areas. In most of the Bitterroot Valley, the distance from any given feeding area to the nearest riparian area is less than 2 km because of the abundant riparian habitat along the river, and the ratio of breeding habitat to feeding habitat appears high throughout the valley floor. In contrast, Midwestern landscapes are dominated by agriculture and the ratio of breeding habitat to feeding habitat is low; thus, cowbirds may be forced to travel further from breeding to feeding areas (Thompson 1994). In general, cowbirds may travel longer distances in areas where breeding habitat is limited and closer breeding habitats are saturated by cowbirds.

A less intuitive feature influencing cowbird distribution was the landscape topography; cowbirds consistently avoided steep-sided canyons. We currently do not have enough information to characterize the overall influence of topography on cowbird occurrence, or to determine whether cowbirds avoid canyons because of dispersal patterns from feeding areas or because of decisions made when selecting laying territories. Host density was consistently lower in canyons

than in open topography (Fig. 3), but this cannot explain the almost complete absence of cowbirds in canyons, as deciduous communities in canyons had higher host density than xeric conifer areas in open topography (Fig. 3), and cowbirds were detected at greater than 40% of these xeric conifer locations. However, canyon points were also on average further from agricultural areas. These effects together make it difficult to judge the generality of topographic effects on the occurrence of cowbirds without further study and testing of the current logistic model on an independent data set.

Outside of canyons, cowbird occurrence in the Bitterroot Valley appears to be influenced not only by distance to agriculture, but also the density of potential hosts (Fig. 5). Host density differed predictably among vegetation types (Fig. 3), making it possible for cowbirds to choose areas of high host density reliably simply by choosing deciduous riparian areas (Fig. 4). Close examination of our results, however, suggests that host density and the ease of finding nests are both primary factors driving cowbird occurrence and relative abundance, and that vegetation type may only be important to the extent that it influences these other factors. Host density was higher in deciduous riparian areas than in xeric conifer, but the ratio of cowbirds to hosts was not different between these habitats, suggesting that cowbird abundance is tracking host density among these habitats. In contrast, host density in coniferous riparian areas was equal to host density in xeric conifer forest, but cowbirds were much less common in coniferous riparian areas (Fig. 4). We suggest that both deciduous riparian and xeric conifer forests are relatively easy habitats for cowbirds to find nests in, but the tall, densely packed trees characteristic of coniferous riparian areas make it difficult for cowbirds to follow hosts to their nests. Additionally, while the diverse host communities characteristic of deciduous riparian and xeric conifer provide suitable nests for cowbirds in all vegetation layers, more than 35% of all hosts detected in coniferous riparian areas were Townsend's Warblers (Table 1), which nest high in conifers (a mean height of 6.7m was reported by Matsuoka et al. [1997]). Cowbirds appear to parasitize lower nests much more frequently than higher nests (Briskie et al. 1990; J. Tewksbury, unpubl. data); thus, Townsend's Warblers may not represent accessible hosts for cowbirds.

Ultimately, if we hold constant the cost of getting to a particular breeding location (e.g., the distance between feeding and breeding areas), the occurrence and abundance of cowbirds should be determined primarily by the density and quality of hosts (Verner and Ritter 1983,

Rothstein et al. 1984, Robinson and Wilcove 1994, Barber and Martin 1996, Tewksbury et al. 1998), modified by any structural differences between habitats that influence the ease with which cowbirds can find host nests (Robinson et al. *this volume*). Our ability to examine the relationship between cowbird abundance and the quality and quantity of available hosts is limited by our understanding of cowbird-host interactions in different vegetation types. Within a vegetation type, cowbirds parasitize some hosts more often than others, and thus may place greater importance on certain hosts (Barber and Martin 1996, Tewksbury et al. 1998). Among vegetation types, the host preference of cowbirds may also change due to differences in the relative abundances of hosts of different quality. Indeed, we may expect cowbirds to switch hosts much like the prey switching of predators (Lawton et al. 1974). A better understanding of host availability and preference in western coniferous forest habitats will allow much greater resolution in predicting the abundance and impact of cowbirds based on attributes of the host community.

MANAGEMENT CONSIDERATIONS

Our results clearly indicate that deciduous riparian areas near agricultural lands have higher cowbird abundance than other habitat types (Fig. 4). These areas also support more species of breeding birds than any other habitat type in the western United States (Johnson et al. 1977, Knopf 1985, Knopf et al. 1988, Dobkin and Wilcox 1986, Saab and Groves 1992, Bock et al. 1993, Knopf and Samson 1994). In many western states, Ohmart (1994) has estimated that as much as 95% of this habitat has been altered or destroyed by human activities. Given the importance and status of deciduous riparian habitats in the West, coupled with the threat of cowbird parasitism in these areas, we feel that research and management efforts should focus on these areas. We found at least 22 species of cowbird hosts in deciduous riparian habitats, and 10 of these species were not found in other habitat types (Table 1). These species fall into two broad management categories with regards to parasitism: species that are heavily parasitized throughout their primary habitats in the region, and species that are parasitized in some areas but escape parasitism in others. The Common Yellowthroat, Red-eyed Vireo, Willow Flycatcher, Yellow Warbler, and Veery all appear to breed only in the large deciduous areas. In the Bitterroot Valley, these areas occur almost exclusively near the Bitterroot River and near agriculture. Detailed studies of the demographic impacts of parasitism should focus on these species, as parasitism pressure on these species may be high

throughout their breeding habitat and has the potential to cause regional population declines. In contrast, species such as MacGillivray's Warbler and Warbling Vireo, though heavily parasitized in areas near agriculture, also breed in smaller riparian areas far from agriculture. Though breeding success in these areas has not been sufficiently studied, smaller deciduous riparian areas far from agriculture likely provide escape from cowbird parasitism. For these species, the creation and maintenance of healthy deciduous communities buffered from cowbird feeding areas may be the best way to insure stable populations. Currently, however, deciduous riparian habitat has diminished substantially on the Bitterroot National Forest due to effective fire suppression over the past 50–60 years (McCune 1983). Management action that reintroduces natural disturbance to these forests and promotes deciduous communities within the forest matrix may protect many host species from population declines due to parasitism.

Although we have identified correlates of cowbird abundance in the Bitterroot Valley, before we can safely extrapolate findings based on cowbird occurrence and relative abundance to parasitism rates, we need to examine the strength of the relationship between point-count data and parasitism (Thompson et al. in press). If the abundance or occurrence of cowbirds on a landscape can be used to index parasitism rates accurately, point-counts can be used as an important tool in directing management, but if these relationships are weak, or vary significantly by habitat, census data can only be used as a qualitative guide in directing more detailed research.

Effective management of cowbirds will require a detailed understanding of the relationships between landscapes and cowbird numbers, and between cowbird numbers and parasitism rates. The specifics of these relationships are unlikely to be constant throughout the range of the cowbird, as differences in host populations, habitat types, topographic features and landscape patterns may all change the density and movements of cowbirds and the impact of cowbirds on host populations. Yet cowbirds may react to these changes in predictable ways throughout their range, and our understanding of the nature of these relationships in one location should help guide research and management in others.