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LAZULI BUNTINGS AND BROWN-HEADED COWBIRDS IN MONTANA: A STATE-WIDE LANDSCAPE ANALYSIS OF POTENTIAL SOURCES AND SINKS

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Abstract. Although Lazuli Buntings (*Passerina amoena*) are currently widely distributed in the western United States and southwestern Canada, parasitization by Brown-headed Cowbirds (*Molothrus ater*) is high in many populations. Demographic models suggest that isolated Lazuli Bunting populations with greater than about 20% parasitization are not self-sustaining. To examine the spatial structure of potential source and sink populations, we developed landscape models of Lazuli Bunting and Brown-headed Cowbird distributions for Montana. These models were derived from a comprehensive GIS database that contains information on vegetation types, topographic relief, and hydrography for all 38,081,490 ha in Montana, with a resolution of land cover types of 90 m^2. These models suggest that Lazuli Buntings may be more vulnerable to Brown-headed Cowbirds than is currently appreciated: of the 8,070,163 ha identified as potential Lazuli Bunting breeding habitat, 98.5% fell in areas with a high and medium risk of Brown-headed Cowbird presence; only 1.5% of potential Lazuli Bunting breeding habitat was in areas in which Brown-headed Cowbirds are not predicted to occur. Furthermore, Lazuli Buntings breed in vegetation patches that occur in spatial configurations that make them especially vulnerable to Brown-headed Cowbirds; patches tend to be small (more than 90% of patches are less than 10 ha in size) with high edge to interior ratios, and are generally surrounded by locations that could support livestock.

Key Words: brood parasite, Brown-headed Cowbird, demography, GIS models, landscape ecology, Lazuli Bunting, metapopulation, *Molothrus ater,* parasitization, *Passerina amoena,* source-sink populations.

Many natural areas are becoming degraded and fragmented by human activities, with many organisms living in increasingly remote or isolated patches (Askins 1995). Concern over such threats has lead to monitoring programs for populations of many species, which rely on estimates of the distribution and abundance of the species of interest. Although these data are important, they do not in themselves provide information on the reproductive performance of a population, and they may be misleading about its underlying dynamics (Donovan et al. 1995a, Brawn and Robinson 1996). For example, a species may be a common resident in an area, thus suggesting that the local population is reproducing well enough to be self-sustaining, but persists because of immigration and recolonization by individuals from other source populations. Although some species of neotropical migrant birds still occur in many small woodlots during the spring and summer in mid-western and eastern North America, their reproductive success can be well below that required for replacement. These ecological sinks are being replenished by frequent immigration of individuals from source areas (Robinson et al. 1995a, Villard et al. 1989).

Thus, the number, sizes, spatial relationships of breeding sub-populations, correlation of ecological conditions among patches, reproductive performance and survivorship in patches across a landscape, and the patterns of dispersal of individuals between patches are important in determining the dynamics of a species on a large spatial scale (Harrison and Quinn 1989, Gutzwiller and Anderson 1992, Donovan et al. 1995a, b, Brawn and Robinson 1996). These characteristics are difficult to measure and are generally poorly known for most species, but have been the impetus for such population monitoring programs as Breeding Biology Research and Monitoring Database (BBIRD) and Monitoring Avian Productivity and Survivorship (MAPS). The emerging fields of metapopulation dynamics and landscape ecology seek to provide insights to such critical questions.

Lazuli Buntings (*Passerina amoena*) occur commonly during the breeding season in a variety of vegetation types throughout western United States and southwestern Canada (Greene et al. 1996). In many areas with high shrub cover in western Montana they are the among the most abundant species during the breeding season. Based solely on their distribution and abundance, this species appears to be doing well. Indeed, Partners in Flight's monitoring scheme suggests that Lazuli Buntings are not at risk; an analysis of Breeding Bird Survey data suggests that most populations are stable, or perhaps even increasing (Butcher et al. 1992).

However, the apparent abundance and wide geographic distribution of Lazuli Buntings may mask serious underlying problems. Although Lazuli Buntings had been reported to be rare hosts of Brown-headed Cowbirds (*Molothrus ater*; Friedmann 1929, Friedmann et al. 1977, Friedmann and Kiff 1985), it has recently been discovered that parasitization levels are high in many populations (Greene et al. 1996). The demographic consequences of parasitization appear severe, and parasitization levels above about 20% are likely to reduce population growth rate below that required for replacement (Greene et al. 1996, Greene *this volume*). Thus, some Lazuli Bunting breeding populations may consist of source populations in which reproduction is good, and these sources may resupply sink populations.

We currently have no information on possible location of source and sink areas for Lazuli Buntings. Our objective is to predict the breeding distribution of Lazuli Buntings and Brown-headed Cowbirds for Montana. We estimate the amounts, locations, and spatial configurations of potential Lazuli Bunting breeding habitat that is at various degrees of risk from Brown-headed Cowbirds. This general approach may also serve as a model for other species of birds (Tucker et al. 1997), and may help inform management decisions (Thompson 1993, Doak and Mills 1994, Petit et al. 1995).

METHODS

We modeled the potential breeding habitats for Lazuli Buntings and Brown-headed Cowbirds using a GIS database containing information on types of land cover, elevation, slope, aspect, and hydrography for the entire state of Montana. We briefly describe the construction of this database, followed by descriptions of the specific habitat models for Lazuli Buntings and Brown-headed Cowbirds.

GIS DATABASE

A two stage, digital classification process was used to map vegetation and land cover across Montana. In the first stage, land cover patterns were derived from false-color composite images from Landsat Thematic Mapper (TM) channels 4, 5, and 3 (R, G, and B) using an unsupervised classification algorithm (www.wru.umt.edu/default.shtml). Thirty-three different Landsat TM scenes were used to map existing vegetation and land cover across the state. All scenes were recorded during the growing seasons (mid-June to mid-September) of 1991–1993. The scenes were obtained in terrain-corrected form and projected into an Albers Equal Area Conic projection (NAD27 datum). The final pixel size was 30 m^2. Adjacent pixels of the same spectral class were grouped into contiguous areas equal to or greater than 2 ha for upland cover types (Ma 1995, Ford et al. 1997). In riparian and woody draw areas, pixels were merged to 0.4 ha minimum map units (MMU) in eastern Montana and 0.1 ha in western Montana. These spatial units were imported into ARC/INFO GIS as raster polygons (and were termed "regions").

The second stage involved a supervised classification (based on ground reference data) run within ARC/INFO to label all regions according to existing vegetation and land cover types (Ford et al. 1997). This process was carried out independently for each TM scene, then all 33 scenes were edge-matched to create a seamless raster database containing cover type attributes for each region. The resulting database contained more than 4 million regions labeled to one of 50 different land cover types. To reduce the file size for GIS modeling, the statewide land cover grid was resampled to 90 m^2, which still resulted in a very large database with over 4.232×10^9 pixels covering Montana (38,081,490 ha).

Information on elevation, slope, and aspect were derived from digital elevation data. U. S. Geological Survey (USGS) 7.5' Digital Elevation Models were used when available ($\approx$ 1,500). Some quadrangles, particularly in eastern Montana, were not available in digital form. Data for these quadrangles were estimated with 3-arc-second data from USGS (source scale 1: 250,000), resampled to 30 m^2 cells, and co-registered to the TM scenes. Digital Elevation Models for each TM scene were appended to the state boundary and then resampled to the same 90 m^2 pixel size as the land cover data set. Data on rivers, streams, and lakes, in the form of USGS 1:100,000 scale digital line graphs were acquired for all Montana. These were merged to create a seamless, statewide hydrography database.

All analyses were conducted with ARC/INFO (version 7.11) and Erdas Imagine (version 8.1) on IBM RS/6000 workstations running AIX (version 4.1). In addition, customized software for many processing steps was written in FORTRAN and C, or scripts written in ARC Macro Language. Descriptions of the land cover types used the species habitat models are summarized in the Appendix. Additional information on the database, along with detailed descriptions and photographs of the 50 vegetation cover categories can be found at the University of Montana's Wildlife Spatial Analysis Lab's web site (www.wru.umt.edu/default.shtml).

HABITAT MODELS

We developed habitat models to predict the breeding distribution of Lazuli Buntings and Brown-headed Cowbirds by selecting combinations of variables from the statewide land cover, hydrography, and topography data sets. We selected the distributional rules based on both published sources, as well as our unpublished information on the distribution of Lazuli Buntings in western Montana. All GIS operations were done in raster format using the Grid Module in ARC/INFO. The selection rules described below produced distributional layers that corresponded closely with actual bunting and cowbird distributions in western Montana.

Lazuli Bunting Model

Lazuli Buntings breed in habitats that have thick shrubs, low trees, and/or dense herbaceous vegetation (Greene et al. 1996). These areas include arid brushy canyons, slopes of hills and escarpments, riparian edges, and thicketed swales. On the prairies east of the continental divide, Lazuli Buntings typically breed in riparian areas, vegetated gullies, thickets on hillsides, sagebrush, and along ravines and gullies (Dobkin 1994, Greene et al. 1996). In western Montana, Lazuli Buntings breed from the lowest valleys to at least 3,000 m on mountain slopes, alpine meadows, and in high elevation aspen forests with thick shrub cover. The highest breeding densities occur in recent post-fire areas, but lower breeding densities are typical in post-logged treatments such as group-selection cuts, seed-tree cuts, and clearcuts (Hutto 1995b, Greene et al. 1996). Lazuli Buntings also breed in open forests with low canopy closure.

To model potential Lazuli Bunting breeding habitat, the GIS database was queried to find suitable combinations of land cover, topography, and proximity to water. In the following query descriptions, numbers in parentheses refer to land cover type codes (descriptions and photographs are available at www.wru.umt.edu/default.shtml). All grassland (3110, 3130, 3150, 3170), agriculture (2010, 2020), and urban (1100) land cover types were selected, along with a 90-m wide buffer strip into adjacent shrub or forest lands (3200 through 4400). Similar 90-m wide buffer strips were selected along both sides of all streams if the land cover represented montane parkland and subalpine meadow (3180), grassland (3110, 3130, 3150, 3170), xeric forest (4290), or broadleaf-conifer forest (4300). Grassland cover types (3110, 3130, 3150, and 3170) were included if the associated slope was greater than 20%. Low canopy closure (10–39%) was selected for ponderosa pine (*Pinus ponderosa*) (4206), xeric forest (4290), and broadleaf forest (4140) within 90 m of streams and rivers. All burns (4400) were included.

Brown-headed Cowbird Model

Brown-headed Cowbirds have expanded their range into nearly all of Montana. They are common in a wide variety of areas within commuting distances of livestock, including agriculture areas, grasslands, riparian vegetation, woodlands and woodland edges, brushy thickets, and residential areas (Robinson et al. 1995a, Hutto 1995b). Brown-headed Cowbird females commute between separate breeding and feeding ranges, and typical commuting distances are in the range of 1–7 km, although females can travel longer distances to their foraging areas (Rothstein et al. 1980, 1984, 1986b; Dufty 1982a, Thompson 1994, Robinson et al. 1995a).

We predicted two different Brown-headed Cowbird distributional layers: (1) a High Risk layer included areas within 2700 m of cover types that contain suitable afternoon foraging areas for Brown-headed Cowbirds, and (2) a Low Risk layer that included areas 2700–4500 m from cover types suitable for afternoon foraging by Brown-headed Cowbirds. The High Risk layer included all vegetation along riparian cover types (6110–6400), plus all areas within 2700 m of all urban (1100), agricultural (2010, 2020), and grassland cover types (3110, 3130, 3150, and 3170). The Low Risk layer included areas that were farther than 2700 m but less than 4500 m from any of the cover types used to define the High Risk areas. These risk areas are conservative, because female Brown-headed Cowbirds can commute more than 4500 m from foraging areas to egg-laying areas (Rothstein et al. 1980, 1995a; Dufty 1982a).

Accuracy of Models

To assess the accuracy of the land cover map, the probability of misclassifying cover types was estimated using a bootstrap method, in which the training data were subsampled 50 times, randomly and with replacement; each time the bootstrap sample was used to classify the remaining reference data (details in Steele et al. 1998). Because the land cover classification scheme is complex, and some cover types were quite similar in terms of their constituent plant species, some types of misclassification were considered less serious than others. For example, confusion between sagebrush (3350) and xeric shrub-grasslands (3520) was considered to be acceptable, since sagebrush (*Artemesia* spp.) is a dominant component of each cover type. In contrast, a confusion between very low cover grassland (3130) and Douglas-fir forest (4212) was considered an absolutely wrong mismatch. The average classification accuracy at the acceptable level (i.e., the cover type was classified correctly, or classified as another cover type which shares the same dominant plant species) was 82.8% for the cover types used in the species habitat models (Appendix).

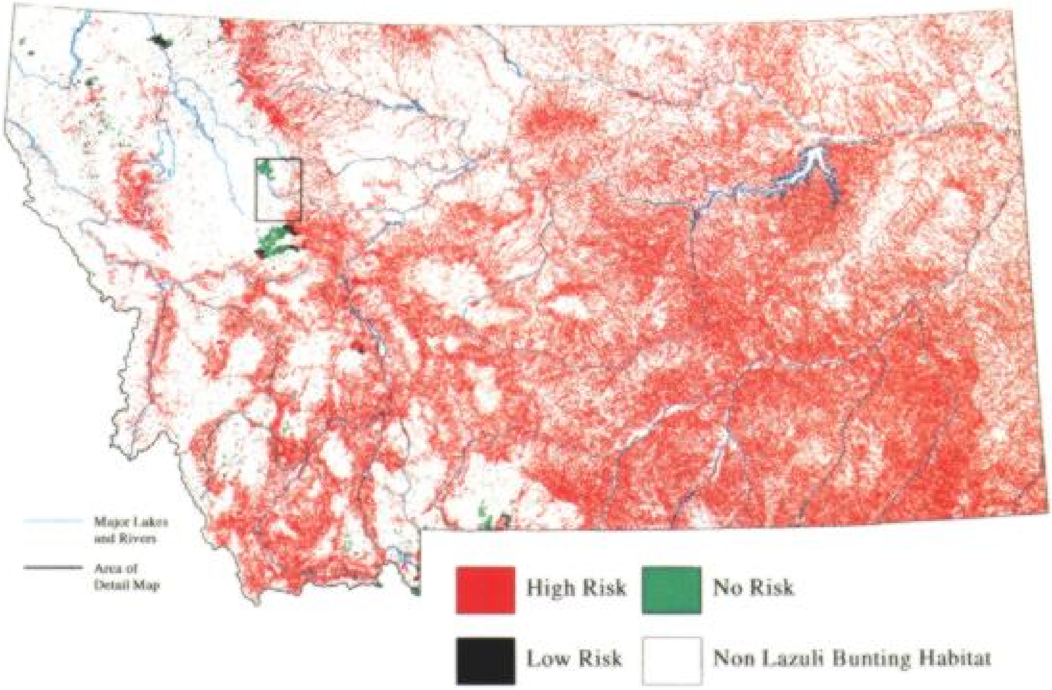

FIGURE 1. GIS habitat model for potential Lazuli Bunting breeding habitat for Montana. Inset box in west-central part of state indicates location of area shown in more detail in Fig. 2.

The accuracy of the bird habitat models was assessed following the recommendations of Edwards et al. (1996). The predicted and observed occurrence of Lazuli Buntings and Brown-headed Cowbirds was compared at 14 validation sites around the state for which checklists were available. For Brown-headed Cowbirds, there was 100% agreement between the predicted and observed occurrence. For Lazuli Buntings, there was 86% agreement; in no case were buntings recorded where we did not predict them to occur (error of omission), but there were two areas where we predicted they would occur but they have not been recorded (errors of commission).

Overlapping Layers

We intersected the predicted High Risk and Low Risk Brown-headed Cowbird layers with the Lazuli Bunting distribution. This predicted three different categories of potential Lazuli Bunting breeding habitat corresponding to three different levels of risk of Brown-headed Cowbird parasitization. We defined (1) High Risk Lazuli Bunting habitat as that within 2700 m of potential afternoon foraging areas for Brown-headed Cowbirds; (2) Low Risk Lazuli Bunting habitat as potential breeding habitat between 2700 and 4500 m away from potential afternoon foraging areas for Brown-headed Cowbirds; and (3) No Risk areas as all potential Lazuli Bunting breeding habitat that was farther than 4500 m away from potential afternoon foraging areas for Brown-headed Cowbirds.

To obtain perimeter measurements for all the No Risk patches of potential Lazuli Bunting breeding habitat, we converted the patch boundaries from 90 m^2 raster format to smooth, vector lines (using ARC/INFO). For each No Risk bunting patch, we also estimated the distance to the nearest High Risk and Low Risk areas, measured from the centroid of each patch.

RESULTS

The model identified 8,070,163 ha as potential breeding habitat for Lazuli Buntings in Montana (Fig. 1). Of this habitat, over 97.2 % (7,846,315 ha) occurred in areas that are potentially at High Risk of Brown-headed Cowbird parasitization; 1.3 % (100,793 ha) occurs in areas of Low Risk; and only 1.5 % (123,055 ha) occurred in areas where Brown-headed Cowbirds are unlikely to occur.

The distribution of potential High Risk, Low Risk, and No Risk habitats for Lazuli Buntings varied across the state. East of the continental divide, all potential Lazuli Bunting breeding habitat was classified as High Risk. This is because Lazuli Bunting breeding habitat was main-

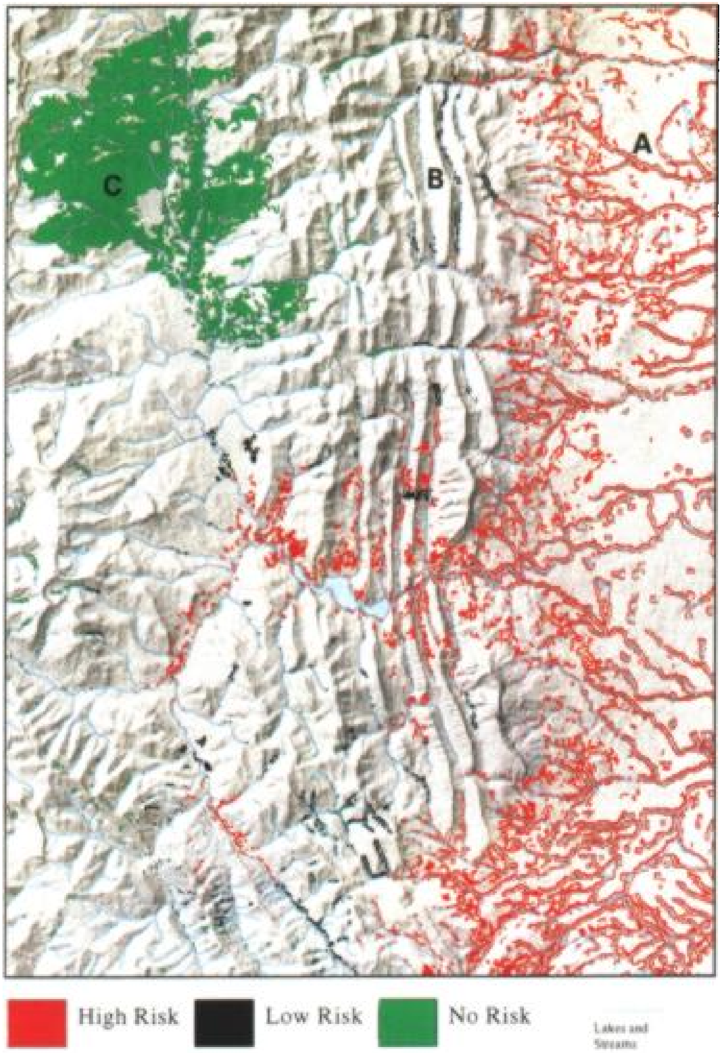

FIGURE 2. Detail of inset area shown in Fig. 1 along the Rocky Mountain front, where prairies (to the east) meet the Rocky Mountains. Potential High Risk, Low Risk, and No Risk Lazuli Bunting breeding habitats are shown in relation to topographic relief.

ly restricted to riparian edges and small patches of vegetation that were close to areas that could be grazed by livestock. West of the continental divide, Brown-headed Cowbirds and Lazuli Buntings both occur in mountain valleys, and their overlap was predicted to be substantial at lower elevations. However, Lazuli Buntings also breed at higher elevations farther away from areas likely to support Brown-headed Cowbirds. Thus, west of the continental divide, patches of No Risk habitat were widely distributed on the slopes above the mountain valleys.

This analysis also suggested that there are three qualitatively and quantitatively different patterns of spatial configuration of Lazuli Bunting breeding habitat in Montana. All three spatial patterns are illustrated in Fig. 2, which is an enlargement of an area along the east front of the Rocky Mountains (shown as a rectangle in Fig. 1). First, east of the Rocky Mountain front, potential Lazuli Bunting breeding habitat occurred primarily in thin, highly-dissected strips along streams, gullies and rivers (A in Fig. 2). Second, west of the Rocky Mountain front, small, isolated patches of Low Risk or No Risk habitat were distributed mainly at mid-elevations above valley bottoms (B in Fig. 2). Third, extremely large patches of No Risk habitat were

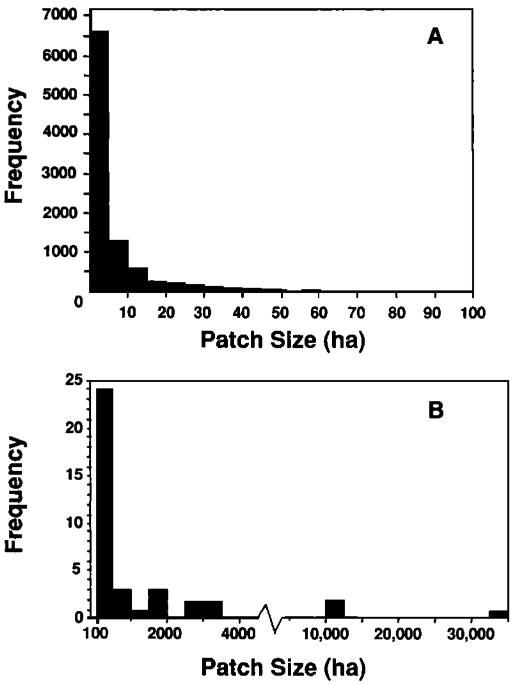

FIGURE 3. A. Distribution of sizes of potential patches of No Risk breeding habitat of Lazuli Bunting. (N = 9,673 patches). Thirty eight patches are larger than 100 ha, but they do not show up at this scale. B. Distribution of patch size of potential breeding habitat larger than 100 ha; all patches larger than 1000 ha occurred in burns. Notice the different scales in panels A and B.

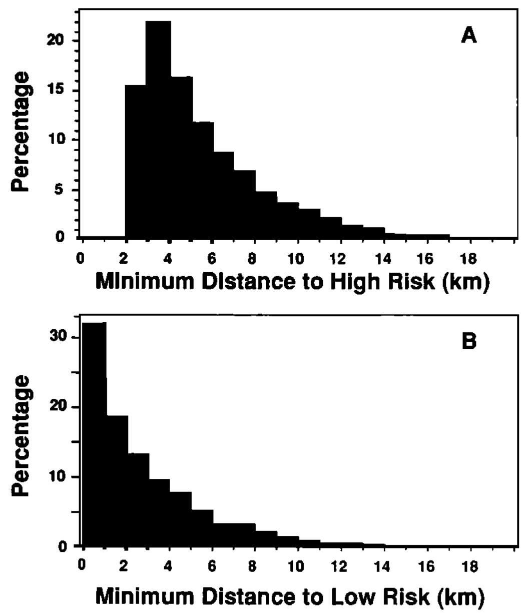

FIGURE 4. Minimum distance from patches of No Risk Lazuli Bunting breeding habitat (N = 9,673 habitat patches) to (A) High Risk habitat, and (B) Low Risk habitat.

limited to burned areas in the western mountains (C in Fig. 2), and near Yellowstone National Park along the borders of Wyoming and Idaho.

In general, Lazuli Bunting breeding habitat occurred in small patches (Fig. 3). Of all habitat patches in No Risk areas, 72% were less than 5 ha, 85% were less than 10 ha, and 95% were less than 20 ha in size (Fig. 3A). Only 38 (0.29%) potential patches of No Risk breeding habitat in Montana were larger than 100 ha (Fig. 3B); 27 of these patches were between 100 and 1,000 ha. All patches larger than 1,000 ha occurred in old burns. The three patches larger than 10,000 ha were in the 1988 Scapegoat Wilderness burn (33,880 ha), visible as the largest green patch in west-central Montana in Fig. 1; part of the 1988 Yellowstone fire complex visible on the Montana-Wyoming border (10,998 ha in Montana); and the 1984 Charlotte Peak burn (10,387 ha), visible in Fig. 1 north of the Scapegoat burn, and shown in close-up at C in Fig. 2.

In addition to their small size, patches of No Risk breeding habitat were located fairly close to habitats that could support Brown-headed Cowbirds (Fig. 4). Out of 9,673 patches of potential No Risk habitat, 38.5% were within 4 km of High Risk areas, and 76.1% were within 7 km of High Risk areas (Fig. 4A); 75.4% of patches were within 4 km of Low Risk areas, while 91.6% were within 7 km of Low Risk areas (Fig. 4B). There was no relationship between the size of No Risk habitat patches and the distance away from potential areas with Brown-headed Cowbirds (Fig. 5). This figure shows the

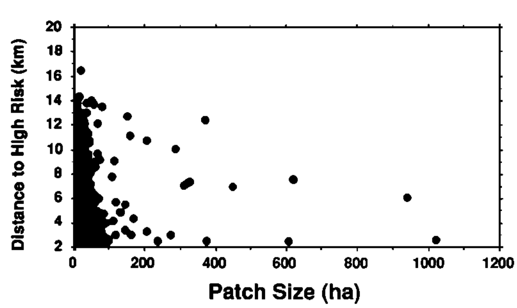

FIGURE 5. Relationship between size of potential breeding habitat in No Risk areas and distance to the nearest High Risk area. This graph shows the relationship for the 1500 largest patches (N = 1500 patches, r^2 = 0.00026, ns). Ten largest patches omitted from this graph for scaling purposes; the relationship does not change when all patches included.

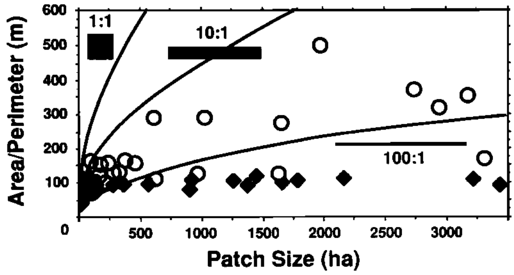

FIGURE 6. Shape indices for patches of potential breeding habitat. Lines show theoretical curves for area/perimeter ratios for patches of different shapes (square patches, rectangular patches ten times longer than wide, and rectangular patches 100 times longer than wide). Circles show area/perimeter ratios for 1,500 randomly selected patches of potential No Risk habitat in western Montana; diamonds show area/perimeter ratios for 500 randomly selected patches of potential High Risk habitat in eastern Montana.

relationship for the largest 1500 patches (the ten largest patches were omitted for scaling purposes; there was no change if all patches are included).

Potential breeding habitat of Lazuli Buntings occurred in long, thin strips or in highly dissected patches, with lots of edge relative to area (Fig. 6). The distribution of area-perimeter ratios for No Risk habitat patches (from west of the Rocky Mountain front) were clustered between the lines showing area-perimeter ratios for rectangles ten and 100 times longer than wide. Potential patches of breeding habitat were even more elongated in the eastern part of Montana, with most patches even more extreme than the 100:1 line (Fig. 6).

DISCUSSION

Our landscape-level GIS model is a first step towards a better understanding of the population dynamics of Lazuli Buntings on a large spatial scale; we present these results as testable hypotheses in need of ground-truthing. Our model identified a large proportion (97%) of potential Lazuli Bunting breeding habitat in Montana at high vulnerability to Brown-headed Cowbirds. This is especially true for eastern Montana. However, the Brown-headed Cowbird distributional model was based solely on land cover types, and did not incorporate any information on the actual spatial distribution of livestock (since such information is not currently available). This model assumes that all areas that could support livestock actually contain cattle. Although this assumption may be correct for some parts of the state, we need more information on the spatial and temporal distribution of livestock, and thus Brown-headed Cowbirds, for many western locations. It is probable that cattle and Brown-headed Cowbirds are much more clumped in time and space than suggested by the red, High Risk areas identified in Fig. 1. If this is the case, there may be many more safe, No Risk or Low Risk habitats east of the Rocky Mountain front than was identified by this model. We are currently conducting ground-truthing studies to identify the spatial and temporal distribution of cows and Brown-headed Cowbirds, especially within areas identified as High Risk for Lazuli Buntings.

Potential Lazuli Bunting breeding habitat occurs in three quantitatively different spatial configurations. First, potential breeding habitat in non-mountainous areas tends to occur in long, linear, strips along streams and in gullies. These patches have low ratios of interior to edge, and are typically embedded in vegetation types that could support livestock, such as rangeland or grassland. Brown-headed Cowbirds are able to search vegetation with these characteristics extremely effectively (Robinson et al. 1995a). In the western part of Montana, most potential Lazuli Bunting breeding habitat that occurred in the valley bottoms was predicted to be at High Risk of parasitization. Many small (usually less than 20 ha) Low Risk and No Risk habitat patches occurred above the valley bottoms; a few extremely large patches of No Risk habitats occurred in old burns.

We defined High Risk and Low Risk Lazuli Bunting habitats as those occurring within 2.7 km, and 2.7–4.5 km, respectively, of potential habitats that could support livestock. This is a conservative choice of buffer distances, since radio-tracking studies indicate that female Brown-headed Cowbirds can commute up to 7 km between their morning breeding areas and afternoon feeding sites (Rothstein et al. 1984, Thompson 1994). However, most female cowbirds commute shorter distances than these maximum values, and parasitization levels typically fall off with increasing distance from afternoon feeding areas.

Lazuli Bunting populations appear to consist of spatially-separated subpopulations, interconnected by dispersal of individuals between patches (i.e., metapopulations). Realistic metapopulation models for Lazuli Buntings will require more information on the sizes, spatial relationships, and demographic characteristics (reproductive performance, survivorship) of bunting sub-populations, and dispersal behavior of buntings between sub-populations.

Dispersal abilities and recolonization behavior are unknown for most species of birds, including Lazuli Buntings. Dispersal distances for many species may be much larger than previously thought, and thus the appropriate spatial scale for metapopulation models may be large. Information on the dispersal of Lazuli Buntings is limited, but anecdotal evidence suggests that this species can disperse large distances and quickly colonize suitable areas. First, Lazuli Buntings breed in early successional vegetation that is created unpredictably in time and space. Forest fires (or other events such as draining reservoirs) create patches of suitable vegetation that are often a long way from other suitable areas; Lazuli Buntings typically colonize these areas rapidly and in large numbers (Greene et al. 1996). Second, banding studies suggest that natal philopatry by juvenile buntings is low, and that adults can disperse among suitable breeding habitats between years (Greene et al. 1996). Third, there does not appear to be any large-scale geographic structure to song dialects. Yearling males learn their song after they return to the breeding grounds (Greene et al. 1996). With local or regional philopatry, we would expect some hint of cultural evolution of song types, giving rise to some sort of geographic song dialects.

These issues of dispersal behavior aid in understanding the dynamics of interconnected populations, and in formulating ecologically realistic metapopulation models (Pulliam 1988, Robinson et al. 1995b, Brawn and Robinson 1996). The original formulation of metapopulation models consisted of habitat patches in which isolated subpopulations of about the same size exchanged migrants with each other (Levin 1974, Gilpin and Hanski 1991). Several variations on this theme have been proposed, and they differ mainly in the relative size of habitat patches and the spatial scale of dispersal relative to the spatial heterogeneity of the environment. The core-satellite model (Hanski 1982, Harrison 1991) refers to a population that is subdivided into a large, central population with smaller peripheral satellite populations. Most of the reproduction occurs in the core area, and it provides dispersers to the outlying satellite populations, but not vice versa. The dynamics and persistence of such a system is determined by events in the core area and does not depend upon the satellite populations. Such may be the case for Lazuli Buntings if it is found that reproductive success is high only in the large burns (source populations) and much lower in other areas (satellite populations).

Patchy population models describe individual patches that are separated from other patches, but the patches are close enough to each other so that dispersal of individuals among patches is extremely frequent. The spatial scale of dispersal is much larger than the spatial scale of habitat heterogeneity (Harrison 1991). In this case, the relevant demographic unit is a larger network of interconnected patches that are isolated demographically from other networks of patches.

IDENTIFICATION OF RESEARCH PRIORITIES

This landscape analysis helps to focus attention on some research and management priorities.

Spatial and temporal distribution of Brown-headed Cowbirds in western landscapes

We currently have much less understanding of Brown-headed Cowbird movements and spatial relationships with livestock in western than in eastern and mid-western landscapes (Robinson et al. 1995a). Rather than isolated islands of undisturbed vegetation embedded in landscapes modified by human activities (e.g., agricultural and urban lands), many western landscapes consist of relatively large tracts of forested areas inset with smaller patches of disturbed areas. We need to document the spatial and temporal distributions of livestock and Brown-headed Cowbirds in these western landscapes.

Management implications

Once we have a better understanding of the relationship between the distribution of livestock and Brown-headed Cowbirds, it may be possible to suggest ways to modify grazing regimes that would result in large improvements in reproductive success for many species of Brown-headed Cowbird hosts (Robinson et al. 1993, 1995a; Thompson 1993, Petit et al. 1995). For example, cattle may be concentrated for short periods during the time when many species initiate nesting. Although areas surrounding the cattle might experience extremely high levels of parasitization, larger areas farther away from the cattle could be converted into source areas experiencing much lower levels of parasitization.

Ecological importance of burns

Ecologists recognize that fires play a critical role in western forest ecosystems. Their ecological effects can be different from other sorts of disturbances, such as different types of forest harvesting practices. The only large, No Risk habitats identified by our model were burned areas. Indeed, the highest breeding densities of Lazuli Buntings have been reported in post-burn areas (Hutto 1995b). These few, large burns may be significant source locations, producing excess buntings that disperse to other areas in which reproductive success is lower. The importance of large, post-burn areas for Lazuli Bunting reproduction needs to be determined.

Dispersal behavior and metapopulation models

Dispersal behavior remains one of the most poorly studied aspect of the ecology of many organisms. This information is crucial for constructing realistic metapopulation models, and for understanding the population dynamics of spatially-fragmented species.

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APPENDIX. DESCRIPTIONS OF MONTANA GAP ANALYSIS LAND COVER TYPES USED IN GIS MODELS

Cover type code	Name	Area (ha)	Number of patches	% of state	Estimated Level 3 accuracy[a]
1100	Urban or developed lands	63,733	1,109	0.17	—
2010	Agricultural lands non-irrigated	3,632,611	96,092	9.54	—
2020	Agricultural lands	1,957,294	94,928	5.14	—
3110	Altered herbaceous	1,104,946	109,396	2.67	89.5
3130	Very low cover grasslands	1,104,361	139,493	2.90	97.8
3150	Low/moderate cover grasslands	10,427,464	432,016	27.38	95.1
3170	Moderate/high cover grasslands	1,236,660	196,470	3.25	88.5
3180	Montane parklands and subalpine meadows	528,201	59,185	1.39	79.6
3200	Mixed mesic shrubs	949,873	172,497	2.49	68.1
3300	Mixed xeric shrubs	1,227,852	184,013	3.22	81.1
3309	Silver sage	73,334	20,022	0.19	61.5
3310	Salt-desert shrub/dry salt flat	131,141	22,824	0.34	96.9
3350	Sagebrush	2,145,574	220,288	5.63	90.9
3510	Mesic shrub–grassland	280,075	64,714	0.74	83.6
3520	Xeric shrub–grassland	524,061	79,041	1.38	90.8
4000	Low density xeric forest	286,187	63,913	0.75	76.2
4140	Mixed broadleaf forest	357,539	72,262	0.94	76.2
4203	Lodgepole pine	1,286,156	98,028	3.38	96.3
4205	Limber pine	120,372	22,148	0.32	63.0
4206	Ponderosa pine	1,066,130	127,272	2.80	92.8
4207	Grand fir	22,017	3,328	0.06	94.5
4210	Western red cedar	36,339	4,551	0.10	88.9
4211	Western hemlock	20,940	1,990	0.05	94.8
4212	Douglas-fir	1,329,994	139,735	3.49	93.1
4214	Rocky Mountain juniper	80,379	17,669	0.21	75.6
4215	Larch	90,437	13,652	0.24	85.2
4216	Utah juniper	14,843	2,686	0.04	50.7
4223	Douglas-fir/lodgepole pine	451,332	50,494	1.19	93.8
4260	Mixed whitebark pine forest	394,340	38,963	1.04	81.3
4270	Mixed subalpine forest	1,582,611	83,658	4.16	96.2
4280	Mixed mexic forest	1,227,309	62,871	3.22	95.7
4290	Mixed xeric forest	542,049	79,625	1.42	89.9
4300	Mixed broadleaf and conifer forest	99,843	23,137	0.26	87.1
4400	Standing burnt forest	139,261	3,431	0.37	59.9
6100	Conifer riparian	85,004	71,033	0.22	83.8
6120	Broadleaf riparian	198,372	91,838	0.52	83.2
6130	Mixed broadleaf conifer riparian	34,932	29,923	0.09	60.9
6200	Graminoid and forb riparian	702,574	281,322	1.84	74.5
6300	Shrub riparian	363,596	200,240	0.95	74.0
6400	Mixed riparian	122,662	88,540	0.32	73.7

[a] Level 3 Acceptability was assigned if the cover type was classified correctly, or if the cover type was misclassified, but the dominant plant species were the same in the two cover types.