Significance of Riparian Vegetation to Breeding Birds Across an Altitudinal Cline

Fritz L. Knopf

Abstract.--The relative significance of riparian zones to breeding birds was documented at 6 elevations between 1,200 and 2,750 m in the Platte River drainage of the Colorado Front Range. Bird communities were inventoried during 1,440 10-min surveys at points in riparian and upland vegetation on the 6 study areas during May and June 1981-1982. Totals of 124 and 111 species were observed on the 6 study areas during the 2 years; 82% of all species were observed in riparian sites. Species richness was higher in riparian sites than in uplands. Riparian bird communities were simplistically structured at high elevations and most complex at lower elevations; upland communities were more complex at higher elevations. Higher diversity analyses indicated that riparian sites at the lowest and highest elevations are most significant to a regional avifauna. Management actions to enhance avian communities in western states should place primary emphasis on riparian zones at low elevations, secondary emphasis on those at the highest elevations, and de-emphasize efforts at intermediate elevations.

INTRODUCTION

Riparian communities are the relatively mesic vegetative associations occurring along streams, rivers, and moist sites of the western United States. These systems generally: include well-defined vegetative zones within much drier surrounding areas, constitute a minor proportion of the overall area, produce more biomass, and are a critical source of diversity within the ecosystem (Thomas et al. 1979). This latter, seemingly inherent, characteristic of increased biotic diversity has fostered the tendency to define significance of riparian tracts to wildlife in terms of species diversity measures.

The significance of riparian sites to breeding birds has been defined primarily at the alpha diversity level (see Whittaker [1975] for a review of levels of diversity). In a recent analysis, Samson and Knopf (1982) concluded that alpha diversity provides a localized assessment of the significance of a vegetative association to an avifauna, and that between-habitat (beta) and regional (gamma) diversity evaluations are more meaningful. Riparian communities, especially, cannot be addressed as functional entities but must be evaluated and managed relative to patterns within entire watersheds (Odum 1979). To date, studies of the significance of riparian vegetation have been conducted primarily at lower elevation sites where cottonwood (Populus spp.) and willow (Salix spp.) compose most of the woody vegetative structure available to birds (Carothers et al. 1974). Because avian species richness generally declines with increasing elevation (Terborgh 1971, Diamond 1973), riparian zones at higher elevations—where the diversity of upland vegetative structure is greater—may be less unique or important. This study describes the significance of riparian tracts to breeding birds within the Platte River watershed in the east-central Rocky Mountain region.

STUDY AREAS

The study was conducted at 6 areas within the Platte River drainage of northern Colorado. Areas represented the major life zones (excluding alpine) of vegetation along the Front Range. One riparian and 1 upland site were
selected within each area. Riparian sites contained a permanent stream. Cattle had not grazed on sites for at least 3 years prior to the study. The sites and vegetative communities (after Harrington 1954) included:

1. Sand sagebrush mixed-prairie type (SSMP): South Platte River, 2 km S Crook, Logan County (elevation 1,200 m). Sand sagebrush (Artemisia filifolia) is the only woody species occurring on sandhills in the mixed prairie type. The riparian site averages about 1 km wide and is dominated by plains cottonwood (P. sargentii), western snowberry (Symphoricarpos occidentalis), coyote willow (S. exigua), peach-leaf willow (S. amygdaloides), and common poison-ivy (Toxicodendron radicans).

2. Mountain shrub transition type (MST): Lone Pine Creek, 11 km W Livermore, Larimer County (elevation 1,909 m). True mountain mahogany (Cercocarpus montanus), antelope bitterbrush (Purshia tridentata), and gooseberry (Rhus spp.) dominate the upslope, which also includes scattered Rocky Mountain junipers (Juniperus scopulorum). The riparian site ranges up to 10 m wide and is dominated by plains cottonwood, scattered bush willows, and common chokecherry (Prunus virginiana).

3. Pine type (P): Meadow Creek, 16 km NW, and Sheep Creek, 29 km NW, Livermore; and Stub Creek, 4 km ESE Glendevey, Larimer County (mean elevation 2,293 m). Ponderosa pine (Pinus ponderosa) forests cover uplands at Meadow and Sheep creeks; open stands contain scattered big sagebrush (A. tridentata). The upland at Stub Creek is lodgepole pine (P. contorta) forest. Riparian sites range from 2-15 m wide and are dominated by plains cottonwood and alder (Alnus spp.) at Meadow Creek, shrub willow at Stub Creek, and mixed plains cottonwood, narrowleaf cottonwood (P. angustifolia) and willow with occasional aspen (P. tremuloides) and Engelmann spruce (Picea engelmannii) at Sheep Creek.

4. Semi-desert shrub type (SDS): Illinois River, 10 km S Walden, Jackson County (elevation 2,500 m). Upland vegetation is big sagebrush. The riparian site ranges up to 100 m wide and is exclusively shrub willows (see Cannon and Knopf 1984).

5. Aspen type (A): Laramie River, 6.5 km N Chambers Lake, Larimer County (elevation 2,631 m). Upland communities are dominated by aspen with occasional Douglas-fir (Pseudotsuga menziessii) and lodgepole pine. The riparian community ranges from 20-40 m wide and is composed of shrub willows.

6. Spruce-fir forest type (SFF): South Fork of the Cache la Poudre River, Colorado State University Pingree Park Campus, Larimer County (elevation 2,747 m). Upland vegetation includes lodgepole pine, limber pine (P. flexilis), Engelmann spruce, Douglas-fir, and subalpine fir (Abies lasiocarpa) with scattered, stunted aspen occasionally occurring as undergrowth. The riparian site is a glacial moraine, ranges up to 100 m wide, and is exclusively bush willow.

METHODS

Avian communities in riparian and upland vegetation were surveyed at each area using point-transect techniques (Reynolds et al. 1980) during May and June 1981-1982. Sixty survey stations were located in each vegetative type (120/area). Stations were at paced 100-m intervals. Within riparian sites, stations were located along, and at random distances perpendicular to, the streambank. Some stations were located on the streambank in extremely narrow riparian sites, or at greater intervals to avoid visual overlap between stations. Stations within uplands were located along a single transect oriented perpendicular to the riparian zone. The upland transect began at least 100 m from the riparian zone and at least 50 m into the upland vegetation.

Avian surveys were conducted from a half hour before sunrise until 1000 hours, except during periods of inclement weather. Riparian and upland surveys were conducted simultaneously during a 4-day period during late May (lowest elevation) and early-to-mid-June (higher elevations) at each study area. An observer waited at a station for 1 min prior to commencing bird observations, then recorded all individuals seen within a 10-min period. Thus, a motionless observer surveyed each site for 10 hours within a 4-day period. Birds not seen (but heard) were ignored to avoid potential biases due to variability in vocalization rates among species and in observer ability to identify songs and calls.

RESULTS

Totals of 124 and 111 species were observed at the 6 study areas in 1981 and 1982, respectively. In 1981, 57 species (44%) were observed only in riparian sites, 22 (18%) only in upland sites, and 45 (36%) in both. Thus, 82% of the species observed were in riparian vegetation, and 54% in uplands. The data for 1982 were similar with 42 (38%), 20 (18%), and 49 (44%) species observed in only riparian, only upland, or both sites, respectively. Again, 82% of all species were observed in riparian vegetation; a higher proportion (62%) occurred in uplands than in 1981. The 5 most abundant species at each site are listed in table 1.
Table 1.—Three most common bird species (in order of abundance) seen in riparian or upland vegetation at 6 study areas in northern Colorado, 1981. Percentages of sightings that were of these species is in parentheses. Dominance patterns were similar in 1982. Species codes follow Klimkiewicz and Robbins (1978).

<table>
<thead>
<tr>
<th>Study area</th>
<th>Riparian</th>
<th>Upland</th>
</tr>
</thead>
<tbody>
<tr>
<td>SSMP (1,200 m)</td>
<td>HOWR (44)</td>
<td>WENE (80)</td>
</tr>
<tr>
<td>MST (1,909 m)</td>
<td>YEW (30)</td>
<td>VESP (61)</td>
</tr>
<tr>
<td>P (2,293 m)</td>
<td>AMRO (38)</td>
<td>GTTO</td>
</tr>
<tr>
<td>SDS (2,500 m)</td>
<td>YEWA</td>
<td>BHCO (42)</td>
</tr>
<tr>
<td>A (2,631 m)</td>
<td>WIWA</td>
<td>YRWA (63)</td>
</tr>
<tr>
<td>SFF (2,747 m)</td>
<td>WIWA</td>
<td>EVGR</td>
</tr>
</tbody>
</table>

Within-Habitat Comparisons

The greatest number of species unique to a site tended to be in the lowest riparian site (table 2). In 1981, species richness in riparian habitats declined with increasing altitude, with 42 species at the SSMP site vs. 21 at the subalpine site. In 1982, however, richness was comparable (40, 41, 42, respectively) in the 3 lower riparian sites. The only species richness pattern observed in upland sites was that comparatively few species were present at the lowest elevation (SSMP). Species richness of communities in both the riparian and upland vegetation changed most dramatically between years at intermediate elevations (P and SDS sites), probably indicating altitudinal shifts relative to seasonal weather patterns at those elevations.

Between-Habitat Comparisons

Species richness was higher in riparian than adjacent upland sites (table 2), except in SFF uplands in 1981 and P uplands in 1982. More species were common to riparian and upland sites at intermediate elevations. The number of species unique to riparian sites were generally lowest at coniferous (P and SFF) sites. Also, species richness within uplands tended to be highest at coniferous sites.

I plotted dominance-diversity curves (Patil and Taillie 1979) of the bird communities across the elevational cline for 1981. These curves can be interpreted similarly to the species-importance curves of Whittaker (1975). Curves for upland sites were simplistic (being of straight line or geometric form) at lower elevations and showed a tendency toward increasing numbers of species of intermediate or low abundance as elevation increased (fig. 1). Alternatively, curves for riparian sites indicated many species of intermediate and rare abundance at lower elevations. Separation of riparian and upland curves lend further evidence to the greater importance of riparian zones at lower (<1,909 m) sites. Importance of riparian zones decreased above 1,909 m. The highest area (SSF) had a more diverse avifauna on the upland site than on the riparian site.

Table 2.—Avian species richness within riparian and upland vegetation at 6 study areas in northern Colorado, 1981/1982.

<table>
<thead>
<tr>
<th>Study area</th>
<th>Riparian</th>
<th>Upland</th>
<th>Both</th>
<th>Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>SSMP (1,200 m)</td>
<td>38/35</td>
<td>5/4</td>
<td>4/5</td>
<td>47/44</td>
</tr>
<tr>
<td>MST (1,909 m)</td>
<td>31/33</td>
<td>8/8</td>
<td>9/8</td>
<td>48/49</td>
</tr>
<tr>
<td>P (2,293 m)</td>
<td>15/14</td>
<td>10/16</td>
<td>12/28</td>
<td>37/58</td>
</tr>
<tr>
<td>SDS (2,500 m)</td>
<td>22/21</td>
<td>9/4</td>
<td>13/6</td>
<td>44/31</td>
</tr>
<tr>
<td>A (2,631 m)</td>
<td>25/15</td>
<td>9/12</td>
<td>6/6</td>
<td>43/37</td>
</tr>
<tr>
<td>SFF (2,747 m)</td>
<td>15/15</td>
<td>19/12</td>
<td>6/6</td>
<td>40/33</td>
</tr>
</tbody>
</table>

Locally, riparian sites provided habitats for a more diverse avifauna than adjacent uplands (table 3). Only at the highest elevation in 1981 was alpha diversity greater in an upland site. Diversity values were highly comparable between years within riparian and upland sites at lower elevations, suggesting greater stability at those elevations. Calculations of species turnover supported greater stability in the low riparian habitats, but not for uplands. Species turnover between years was greatest in both vegetation types at intermediate elevations.
Table 3.—Shannon-Wiener Function (H') calculations (Pielou 1975:8) and species turnover (op. cit., 99; in parentheses) for avian communities of riparian and upland sites in northern Colorado, 1981-1982.

<table>
<thead>
<tr>
<th>Study area</th>
<th>Riparian</th>
<th>Upland</th>
</tr>
</thead>
<tbody>
<tr>
<td>SSMP (1,200 m)</td>
<td>4.24/4.29 (0.27)</td>
<td>2.26/2.25 (0.34)</td>
</tr>
<tr>
<td>MST (1,909 m)</td>
<td>4.57/4.62 (0.27)</td>
<td>3.20/3.19 (0.29)</td>
</tr>
<tr>
<td>P (2,293 m)</td>
<td>4.05/4.61 (0.38)</td>
<td>3.99/4.59 (0.39)</td>
</tr>
<tr>
<td>SDS (2,500 m)</td>
<td>4.18/3.54 (0.40)</td>
<td>2.69/2.24 (0.44)</td>
</tr>
<tr>
<td>A (2,631 m)</td>
<td>4.20/4.02 (0.41)</td>
<td>3.23/3.95 (0.23)</td>
</tr>
<tr>
<td>SFF (2,747 m)</td>
<td>3.57/3.10 (0.34)</td>
<td>4.21/2.85 (0.35)</td>
</tr>
</tbody>
</table>

Community coefficients (table 4) indicated that (relative to numbers of species present) riparian and upland avian communities were most unique (i.e., low values) at the lowest elevation and most similar (higher values) at intermediate elevations. Similarity indices (that include species abundance information) reflected this pattern, although the avian communities at the highest elevation were as dissimilar as those at the lowest elevation. Riparian and upland communities were most similar at sites of P uplands.

Table 4.—Beta diversity comparisons of riparian and upland avian communities at 6 study areas in northern Colorado (1981/1982).

<table>
<thead>
<tr>
<th>Study area</th>
<th>Community coefficient</th>
<th>Similarity index</th>
</tr>
</thead>
<tbody>
<tr>
<td>SSMP (1,200 m)</td>
<td>0.157/0.204</td>
<td>0.082/0.146</td>
</tr>
<tr>
<td>MST (1,909 m)</td>
<td>0.316/0.281</td>
<td>0.217/0.165</td>
</tr>
<tr>
<td>P (2,293 m)</td>
<td>0.490/0.651</td>
<td>0.403/0.530</td>
</tr>
<tr>
<td>SDS (2,500 m)</td>
<td>0.429/0.324</td>
<td>0.100/0.410</td>
</tr>
<tr>
<td>A (2,631 m)</td>
<td>0.346/0.630</td>
<td>0.203/0.392</td>
</tr>
<tr>
<td>SFF (2,747 m)</td>
<td>0.261/0.308</td>
<td>0.164/0.060</td>
</tr>
</tbody>
</table>

DISCUSSION

Studies of avifaunal associations of riparian zones in the West have established the importance of these vegetative associations to wildlife (Hubbard 1971, Johnson et al. 1977, Stevens et al. 1977). The major emphasis of my study was to describe the pattern of importance within riparian zones across an altitudinal gradient, especially as that pattern relates to prioritization of agency management programs.

To date, floodplain zones at lower elevations have received the most emphasis in western riparian management. Concerted efforts have been initiated to re-establish cottonwood stands in California (Anderson et al. 1984) and Colorado. This study confirms the greater uniqueness of those low-elevation sites both locally and within a continuous drainage. Uniqueness appears independent of the width of the riparian zone when identified by similar species richness and alpha diversities at the extremely narrow zone of the 1,909-m site vs. the broad floodplain at 1,200 m.

Studies of avian communities across elevational gradients in eastern North America (Able and Noon 1976, Sabo 1980) have indicated that communities become simpler and uneven at higher elevations, with decreases in rare species and increasing dominance by a few species. These trends usually are attributed to more severe environmental conditions at higher elevations. My surveys at 6 study areas in Colorado failed to support these patterns in either riparian or upland communities. Where patterns were observed, they generally were inconsistent between years. Although I cannot conclude that climatic associates of elevation influenced avian community structure, annual variation in weather certainly resulted in comparable turnover rates in riparian and upland sites at most elevations.

The uniqueness of a riparian zone at a location was influenced by upland vegetation. Riparian zones tended to support a more diverse avifauna than upland habitats except in areas of coniferous forests. The 2 habitat types shared more species in uplands of P, A, and SDS than in SFF or lowland shrub-grasslands (SSMP and MST).

Studies of avian communities, including those in riparian zones (e.g., Bull and Skovlin 1982), often attribute greater species richness or diversity to greater structural diversity of the vegetative community and, thus, to the availability of more niches. The generality of the relationship has been dismissed (Willson 1974, Ballard 1975), but persists in the literature. Bird species richness in aspen forest was lower than the adjacent riparian shrub-willow community that had avifaunal diversity comparable to a pine forest. Avian community diversity was not related to vegetational structure in northern Colorado.

Beedy (1981) surveyed birds in closed-canopy and open-forest coniferous communities and found greater diversity in the open forests, presumably due to greater structural complexity (i.e., developed shrub community and open spaces.
horizontal patchiness (Roth 1976) likely accounted for the highest avian diversity being observed in the eastern Colorado SSMP site. That community is an old-growth cottonwood (Sedgwick and Knopf, in prep.) savannah with an extensive woody understory. Such open-canopy, low sites are the major sources of avian diversity regionally.

CONCLUSIONS

Based upon these findings, I conclude that:

1. More species of birds occur in riparian vegetation than in adjacent uplands along the Colorado Front Range.

2. Locally, the most diverse avifauna occurs in riparian zones at lower elevations (<2,000 m). Riparian communities also tend to be more stable between years, with lower species turnover.

3. Regionally, the most diverse avifauna occurs in upland vegetation, and upland bird communities strongly influence bird species composition in riparian zones across an elevational cline.

4. Faunal interchange across an elevational gradient is greater among riparian sites than among upland sites.

5. Due to the faunal mixing patterns, bird communities in riparian zones tend to be most unique within a region at the ends of an elevational continuum: in floodplains at low elevations and spruce-fir uplands at high elevations.

ACKNOWLEDGMENTS

This research benefited from the ideas of R. W. Cannon and C. P. Stone. R. Desilet assisted in locating field sites. Field or analytical assistance was provided by R. W. Cannon, J. F. Ellis, T. E. Olson, E. A. Remington, E. L. Smith, and J. P. Ward. E. C. Patten and W. J. Wilson of Arapaho National Wildlife Refuge and M. Gardner of the South Platte Wildlife Management Area permitted us to work at those sites. The Forest Service and Colorado State University granted permission to work within their holdings. This research is a product of Cooperative Agreement No. 2463-4 between the Colorado Division of Wildlife and Denver Wildlife Research Center, U.S. Fish and Wildlife Service. I thank W. D. Graul, J. R. Grieb, C. Jones, R. Moss, and R. K. Towry for administrative assistance. J. L. Oldemeyer and J. A. Sedgwick commented on the manuscript.

LITERATURE CITED


Species of birds observed during 1,440 10-min stationary census at 6 study areas in northern Colorado, 1981-1982.
The regulation of reproductive schedules is an important determinant of avian breeding success. In heterogeneous environments, the optimal breeding period may fluctuate temporally across habitats, often on a spatial scale much shorter than the average dispersal range of individuals. The synchronisation of reproductive events with the most favourable period at a given site therefore involves the integration of a suite of fine-scale environmental signals which contain information about future breeding conditions. Female blue tits therefore appear to use the environmental variable (vegetation phenology) that is most closely linked to the future production of insect prey in order to accurately time laying over the entire spatio-temporal breeding landscape. PMID: 20035434. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105–111 in R.R. Johnson, C.D. Ziebel, D.R. Patten, P.F. Ffolliot, and R.H. Hamre, technical coordinators, Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service, General Technical Report RM-120. 2002. [NOTES. Native vegetation was almost entirely lost from riparian zones when stream flow was regulated by storage reservoir and canalizations in the middle of the 20th century (Schnitzler 1994; González and García 2007). Such regulation was followed by a major change from native vegetation (riparian forest) to crops or planted forests such as poplar plantations. Current national and regional forest policies aim to increase the area occupied by plantation forests, since establishing plantations on degraded land or agricultural land may have multiple benefits, such as wood and biomass production and biod... Breeding birds were sampled by the point-count method with one visit in spring 2006 (Bibby et al.)