

Significance of Riparian Vegetation to Breeding Birds Across an Altitudinal Cline¹

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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

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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 mountainmahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), and gooseberry (*Ribes* 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 Glendevy, 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 Englemann 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 menziesii*) 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*), Englemann 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 (46%) 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 3 most abundant species at each site are listed in table 1.

Between-Habitat Comparisons

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).

Study area	Riparian	Upland
SSMP (1,200 m)	HOWR NOOR (44) AMRO	GRSP WEME (80) MODO
MST (1,909 m)	YEWA LABU (30) HOWR	RSTO VESP (61) GTTO
P (2,293 m)	AMRO BTHU (38) MGWA	YRWA AMRO (38) GTTO
SDS (2,500 m)	YEWA BHCO (42) SASP	BRSP CTTO (72) HOLA
A (2,631 m)	WIWA AMRO (41) YEWA	YRWA WAVI (63) BTHU
SFF (2,747 m)	WIWA LISP (52) AMRO	EVCR YRWA (31) RCKI

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.

Within habitat types, a percentage similarity (Whittaker 1975:118) matrix among sites and for both years combined indicated a mean (+ SE) similarity of 0.265+0.027 among riparian communities as opposed to 0.130+0.032 among upland communities ($t=3.51$; $df=83$; $P<0.01$). Thus, bird communities in riparian sites were twice as similar as those in upland sites; upland sites had greater beta diversity across the cline.

Species richness was higher in riparian than adjacent upland sites (table 2), except in SSF 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 lended 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.

Study area	No. of Species			
	Riparian only	Upland only	Both sites	Area total
SSMP (1,200 m)	38/35	5/4	4/5	47/44
MST (1,909 m)	31/33	8/8	9/8	48/49
P (2,293 m)	15/14	10/16	12/28	37/58
SDS (2,500 m)	22/21	9/4	13/6	44/31
A (2,631 m)	25/15	9/12	6/6	43/37
SFF (2,747 m)	15/15	19/12	6/6	40/33

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.

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

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).

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

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, Balda 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

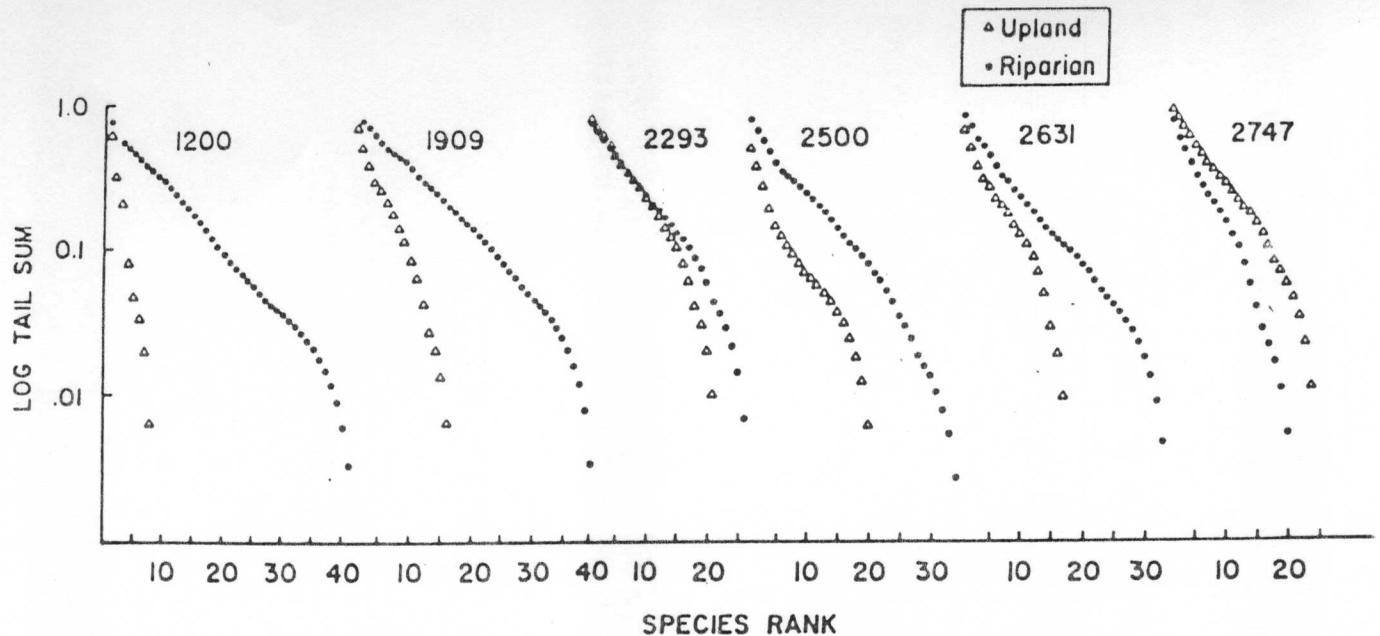


Figure 1.--Dominance-diversity curves for riparian and upland bird communities at 6 elevations in northern Colorado, 1981.

in the canopy for flycatching species). 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.

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APPENDIX

Species of birds observed during 1,440 10-min stationary census at 6 study areas in northern Colorado, 1981-1982.

Great Blue Heron <u>Ardea herodias</u>	Western Flycatcher <u>Empidonax difficilis</u>	Red-eyed Vireo <u>Vireo olivaceus</u>
Black-crowned Night-Heron <u>Nycticorax nycticorax</u>	Ash-throated Flycatcher <u>Myiarchus cinerascens</u>	Orange-crowned Warbler <u>Vermivora celata</u>
Wood Duck <u>Aix sponsa</u>	Great Crested Flycatcher <u>Myiarchus crinitus</u>	Nashville Warbler <u>Vermivora ruficapilla</u>
Green-winged Teal <u>Anas crecca</u>	Western Kingbird <u>Tyrannus verticalis</u>	Virginia's Warbler <u>Vermivora virginiae</u>
Mallard <u>Anas platyrhynchos</u>	Eastern Kingbird <u>Tyrannus tyrannus</u>	Yellow Warbler <u>Dendroica petechia</u>
Northern Pintail <u>Anas acuta</u>	Horned Lark <u>Eremophila alpestris</u>	Magnolia Warbler <u>Dendroica magnolia</u>
Blue-winged Teal <u>Anas diazona</u>	Tree Swallow <u>Tachycineta bicolor</u>	Yellow-rumped Warbler <u>Dendroica coronata</u>
Cinnamon Teal <u>Anas cyanoptera</u>	Violet-green Swallow <u>Tachycineta thalassina</u>	American Redstart <u>Setophaga ruticilla</u>
Northern Shoveler <u>Anas clypeata</u>	Northern Rough-winged Swallow <u>Stelgidopteryx serripennis</u>	Ovenbird <u>Seiurus aurocapillus</u>
Gadwall <u>Anas strepera</u>	Cliff Swallow <u>Hirundo pyrrhonota</u>	Northern Waterthrush <u>Seiurus noveboracensis</u>
Common Merganser <u>Mergus merganser</u>	Barn Swallow <u>Hirundo rustica</u>	MacGillivray's Warbler <u>Oporornis tolmiei</u>
Northern Harrier <u>Circus cyaneus</u>	Gray Jay <u>Perisoreus canadensis</u>	Common Yellowthroat <u>Geothlypis trichas</u>
Sharp-shinned Hawk <u>Accipiter striatus</u>	Stellar's Jay <u>Cyanocitta stelleri</u>	Wilson's Warbler <u>Wilsonia pusilla</u>
Northern Goshawk <u>Accipiter gentilis</u>	Blue Jay <u>Cyanocitta cristata</u>	Yellow-breasted Chat <u>Icterus virens</u>
Swainson's Hawk <u>Buteo swainsoni</u>	Clark's Nutcracker <u>Nucifraga columbiana</u>	Western Tanager <u>Piranga ludoviciana</u>
Red-tailed Hawk <u>Buteo jamaicensis</u>	Black-billed Magpie <u>Pica pica</u>	Rose-breasted Grosbeak <u>Pheucticus ludovicianus</u>
American Kestrel <u>Falco sparverius</u>	American Crow <u>Corvus brachyrhynchos</u>	Black-headed Grosbeak <u>Pheucticus melanocephalus</u>
Ring-necked Pheasant <u>Phasianus colchicus</u>	Common Raven <u>Corvus corax</u>	Lazuli Bunting <u>Passerina amoena</u>
Blue Grouse <u>Dendragapus obscurus</u>	Black-capped Chickadee <u>Parus atricapillus</u>	Indigo Bunting <u>Passerina cyanea</u>
Wild Turkey <u>Meleagris gallopavo</u>	Mountain Chickadee <u>Parus gambell</u>	Green-tailed Towhee <u>Pipilo chlorurus</u>
Killdeer <u>Charadrius vociferus</u>	Red-breasted Nuthatch <u>Sitta canadensis</u>	Rufous-sided Towhee <u>Pipilo erythrophthalmus</u>
Spotted Sandpiper <u>Actitis macularia</u>	White-breasted Nuthatch <u>Sitta carolinensis</u>	Cassin's Sparrow <u>Aimophila cassinii</u>
Long-billed Curlew <u>Numenius americanus</u>	Pygmy Nuthatch <u>Sitta pygmaea</u>	Chipping Sparrow <u>Spizella passerina</u>
Common Snipe <u>Callinago gallinago</u>	Brown Creeper <u>Certhia americana</u>	Clay-colored Sparrow <u>Spizella pallida</u>
Forster's Tern <u>Sterna forsteri</u>	Rock Wren <u>Salpinctes obsoletus</u>	Brewer's Sparrow <u>Spizella breweri</u>
Mourning Dove <u>Zenaidura macroura</u>	House Wren <u>Troglodytes aedon</u>	Veep Sparrow <u>Pooecetes gramineus</u>
Great Horned Owl <u>Bubo virginianus</u>	American Dipper <u>Cinclus mexicanus</u>	Lark Sparrow <u>Chondestes grammacus</u>
Burrowing Owl <u>Athene cunicularia</u>	Ruby-crowned Kinglet <u>Regulus calendula</u>	Savannah Sparrow <u>Passerculus sandwichensis</u>
Common Nighthawk <u>Chordeiles minor</u>	Blue-gray Gnatcatcher <u>Poliophtila caerulea</u>	Grasshopper Sparrow <u>Ammodramus saviannarum</u>
White-throated Swift <u>Aeronautes saxatilis</u>	Mountain Bluebird <u>Sialia currucoides</u>	Song Sparrow <u>Melospiza melodia</u>
Broad-tailed Hummingbird <u>Selasphorus platycircus</u>	Townsend's Solitaire <u>Myadestes townsendi</u>	Lincoln's Sparrow <u>Melospiza lincolni</u>
Belted Kingfisher <u>Ceryle alcyon</u>	Veery <u>Catherus fuscescens</u>	White-crowned Sparrow <u>Zonotrichia leucophrys</u>
Lewis' Woodpecker <u>Melanerpes lewis</u>	Swainson's Thrush <u>Catherus ustulatus</u>	Dark-eyed Junco <u>Junco hyemalis</u>
Red-headed Woodpecker <u>Melanerpes erythrocephalus</u>	Hermit Thrush <u>Catherus guttatus</u>	Red-winged Blackbird <u>Agelaius phoeniceus</u>
Yellow-bellied Sapsucker <u>Sphyrapicus varius</u>	American Robin <u>Turdus migratorius</u>	Western Meadowlark <u>Sturnella neglecta</u>
Williamson's Sapsucker <u>Sphyrapicus thyroideus</u>	Gray Catbird <u>Dumetella carolinensis</u>	Yellow-headed Blackbird <u>Xanthocephalus xanthocephalus</u>
Downy Woodpecker <u>Picoides pubescens</u>	Sage Thrasher <u>Oreoscoptes montanus</u>	Brewer's Blackbird <u>Euphagus cyanocephalus</u>
Hairy Woodpecker <u>Picoides villosus</u>	Brown Thrasher <u>Toxostoma rufum</u>	Common Grackle <u>Quiscalus quiscula</u>
Northern Flicker <u>Colaptes auratus</u>	Cedar Waxwing <u>Bombusilla cedrorum</u>	Brown-headed Cowbird <u>Molothrus ater</u>
Olive-sided Flycatcher <u>Contopus borealis</u>	Loggerhead Shrike <u>Lanius ludovicianus</u>	Orchard Oriole <u>Icterus spurius</u>
Western Wood-Pewee <u>Contopus sordidulus</u>	European Starling <u>Sturnus vulgaris</u>	Northern Oriole <u>Icterus galbula</u>
Willow Flycatcher <u>Empidonax traillii</u>	Bell's Vireo <u>Vireo bellii</u>	Red Crossbill <u>Loxia curvirostris</u>
Hammond's Flycatcher <u>Empidonax hammondi</u>	Solitary Vireo <u>Vireo solitarius</u>	Pine Siskin <u>Carduelis pinus</u>
Dusky Flycatcher <u>Empidonax oberholseri</u>	Warbling Vireo <u>Vireo gilvus</u>	American Goldfinch <u>Carduelis tristis</u>
		Evening Grosbeak <u>Coccothreustes vespertinus</u>

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Keywords: Riparian habitats, endangered habitats, aquatic ecosystems.

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