Research Article

Breeding Birds in Riparian and Upland Dry Forests of the Cascade Range

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ABSTRACT We quantified breeding bird abundance, diversity, and indicator species in riparian and upland dry forests along 6 third- to fourth-order streams on the east slope of the Cascade Range, Washington, USA. Upland dry forest on southerly aspects was dominated by open ponderosa pine (*Pinus ponderosa*) and dry Douglas-fir (*Pseudotsuga menziesii*) plant associations. Upland mesic forest on northerly aspects was dominated by closed-canopy Douglas-fir or dry grand fir (*Abies grandis*) plant associations. Riparian overstory vegetation was dominated by black cottonwood (*Populus trichocarpa*) plant associations with a prominent hardwood tree and shrub component. We quantified bird assemblages, diversity, and abundance from parallel point transects on riparian and adjacent dry and mesic upslope forests. We detected 80 bird species from >12,000 point-transect observations during 1998–1999. Eighteen species accounted for 75% of all detections. Species richness and evenness were similar in all 3 forest types, with approximately 35 species and high evenness (0.85) in each forest type. Bird species assemblages differed among dry, mesic, and riparian forest types, with the greatest differences between riparian and both dry and mesic upland forests. Riparian forest had the greatest number (9) of strong characteristic, or indictor, species among the 3 forest types. Upland mesic forest was characterized by 7 indicator species. Upland dry forest had 4 indicator species. Our results indicate that current standards and guidelines for riparian buffers zones would allow for avian refuge and corridor functions along these streams. Forest managers could use our indicator species to predict and monitor shifts in upland forest species composition from thinning and prescribed burning practices that are used to reduce fuels in uplands and to reduce continuity of fire effects between riparian and upland zones. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2632–2643; 2007)

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Riparian communities are well-known as rich avian habitats created by the combination of a relatively mesic streamside environment and a complex of aquatic and upland disturbance regimes (Thomas et al. 1979, Kelsey and West 1998, Kauffman et al. 2001). The contribution of riparian areas to biodiversity can vary, however, both regionally and locally, depending on the climate, physiographic conditions, and disturbance regimes that determine ecosystem productivity, species pools, and upland and riparian vegetation (Finch 1991, Knopf and Samson 1994, Pollock 1998). The importance of riparian areas as avian habitat in arid regions of western North America, where the contrast between grassland and shrub-dominated uplands and riparian vegetation is high, has been well-established (Austin 1970, Szaro and Jakle 1985, Hunter et al. 1987, Strong and Bock 1990, Szaro 1991). Riparian habitats in western forests are generally considered to be critically important for forest birds (Saab and Rich 1997, Kauffman et al. 2001), but the relative importance of forested riparian areas along low- and mid-order streams is unclear.

In coniferous forest, the uniqueness and diversity of terrestrial birds in riparian habitats can vary latitudinally in watersheds. In riparian areas of coastal forests in the Pacific Northwest, avian alpha (within-patch) and beta (among-patch) diversity generally increases from negligible along low-order stream reaches, where contrasts between riparian and upland vegetation are low, to high along high-order stream reaches with relatively wide and complex channels that support diverse herbaceous and woody plant communities (McGarigal and McComb 1992, Lock and Naiman 1998, Wiebe and Martin 1998). Conflicting reports, however, variously describe riparian avian assemblages along low-order streams as unique (Bub et al. 2004) or similar to uplands (Whitaker and Montevecchi 1997) and avian assemblages along high-order streams as similar to those in adjacent uplands (Shirley 2005). In some western interior forests, avian diversity may be high in low-order headwaters areas that are dominated by low-gradient channels supporting herbaceous and shrub wetlands and high along high-order low-elevation channels with complex riparian vegetation; whereas, constrained mid-elevation stream reaches with relatively less contrast between riparian and upland vegetation support low avian diversity (Finch 1989, Knopf and Samson 1994).

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Understanding the multi-scale relationships between riparian ecosystems and avian diversity is critical for conservation (Knopf and Samson 1994). Conservation prescriptions usually involve the creation of uniform-distance riparian buffer zones to conserve the patterns of riparian vegetation and the interacting disturbance processes in channels and uplands (Forest Ecosystem Management Assessment Team [FEMAT] 1993, Hickey and Doran 2004, MacDonald et al. 2004). From a wildlife perspective, buffer zones are intended to preserve unique riparian habitats and wildlife, serve as movement corridors for upland species, or be refugia for upland species isolated by upland disturbance (FEMAT 1993, Washington Department of Fish and Wildlife 1996). Yet, few data exist to list those terrestrial vertebrate species that are dependent on riparian areas as primary habitat or use those areas as movement corridors, determine how those habitat relationships might vary by stream order within watersheds, or determine how well riparian systems function as refugia in disturbed landscapes (McGarigal and McComb 1992, Knopf and Samson 1994, Lock and Naiman 1998).

Moreover, the contribution of riparian areas to landscape-scale biodiversity and their biotic interactions with upland forest, particularly in middle stream reaches, varies regionally and understanding that variation is particularly important for management of interior dry forests of western North America (Finch 1989, Knopf and Samson 1994). In contrast to wet coastal forests in the Pacific Northwest, the composition and structure of interior dry forests, such as those along the east slope of the Cascade Range, varies strongly along environmental gradients determined largely by aspect and elevation (Franklin and Dyrness 1973). At middle and low elevations, southerly aspects historically supported dry forests dominated by ponderosa pine (*Pinus ponderosa*), whereas northerly aspects supported dry forests of mixed ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*). Fire disturbance regimes historically varied from low-intensity, high-frequency fires in low-elevation dry forest to high-intensity, low-frequency fire regimes at high elevations, with local variation along moisture gradients (Agee 1991, 1993).

After nearly a century of fire exclusion in these interior dry forests and consequent shifts from low- to high-intensity fire regimes (Hann et al. 1997, Agee 2003), management has become focused on restoration of stable fire regimes by thinning and prescribed burning to change composition from relatively dense mixed-conifer forest to open stands dominated by ponderosa pine (Graham et al. 2004). Changing current upland disturbance regimes and management will have consequences for maintaining the integrity of adjacent riparian systems, in which fire regimes can have high continuity with upland fire regimes (Camp et al. 1997, Everett et al. 2003). Managers need information on species assemblages and their habitat associations in riparian and adjacent upland habitats to evaluate the potential impacts of dry forest management (Schmoldt et al. 1999). Knowledge of characteristic, or indicator, species (sensu Dufrene and Legendre 1997) will help focus efforts to assess and monitor impacts of vegetation management for fuel reduction and dry forest restoration (Altman 2000).

We studied breeding birds to quantify species' abundances, diversity, and indicator species in riparian and upland dry forests along third- and fourth-order streams on the east slope of the Cascade Range. We hypothesized that riparian bird assemblages would be richer, more diverse, and unique in composition relative to adjacent uplands because of high habitat diversity. We also hypothesized that bird assemblages in mesic upland forest would be richer and more diverse than dry forests because of the greater density and vertical diversity of the forest canopy.

STUDY AREA

We studied birds along 6 stream reaches and their adjacent forested uplands on the east slope of the Cascade Range in north-central Washington, USA (Fig. 1). Stream reaches were third- and fourth-order streams with narrow, but distinct, riparian zones. Smaller streams were unlikely to have marked riparian zones and disturbance regimes different than the adjacent upland areas, and higher order streams had well-defined riparian areas with unambiguous qualities distinct from uplands (Agee 1988). Channel types were Rosgen (1994) B-type channels (T. Robison, Okanogan and Wenatchee National Forests, personal communication) with moderate gradients of 5%, moderate entrenchment with low sinuosity, and steep (45%) adjacent slopes. Valley bottom width was mostly narrow (≤50 m). Elevations ranged from 475 m to 925 m.

To study beta diversity, we chose streams with contrasting open-canopy dry ponderosa pine forest on an adjacent slope (i.e., south-facing aspects) and closed-canopy mixed-conifer forests (north-facing aspects) on the other side. Upland dry forest on southerly aspects was dominated by open (<50% canopy cover) ponderosa pine and dry Douglas-fir plant associations (Lillybridge et al. 1995; Table 1). Upland mesic forest on northerly aspects was dominated by closed-canopy Douglas-fir or dry grand fir plant associations. Riparian overstory vegetation was dominated by black cottonwood (*Populus trichocarpa*) plant associations (Kovalchik and Clausnitzer 2004) with a prominent hardwood tree and shrub component of maple (*Acer* spp.), alder (*Alnus* spp.), aspen (*Populus tremuloides*), willow (*Salix* spp.), and other species (Table 1).

We chose stream reaches based on the following criteria: third- or fourth-order streams, little human impact, stream orientation generally east- or west-flowing, well-developed riparian vegetation, 1,000 m long to accommodate a bird point-transect, and access from roads or trails. We chose east- or west-flowing streams to get the necessary contrasts between north- and south-facing upland slopes. Streams meeting those criteria were difficult to find, mostly because stream bottoms have been heavily affected by roads and associated human disturbance, so we did not select sampled stream reaches randomly from a candidate pool. The 6 selected stream reaches were along Devil's Gulch (West

Fork of Mission Creek), Derby Canyon, Mission Creek, Sand Creek, Spromberg Canyon, and Stafford Creek (Fig. 1).

METHODS

Field Methods

Birds.—At each of the 6 stream reaches, we established point transects in 3 habitats: the riparian corridor and the adjacent mesic and dry upland slopes. Each upland transect was parallel and >200 m from the riparian transect. Along each transect, we located 6 stations where we counted birds within variable circular-plots (Reynolds et al. 1980). We randomly located the first station within 100 m of the starting point, then placed subsequent stations 175 m apart along the transect following regional protocols for bird monitoring (Huff et al. 2000).

We counted birds at each station 5 times during the spring breeding seasons (mid-May through the first week of Jul) of 1998 and 1999. Crew members were experienced birders and we gave them training in local bird identification and distance estimation. We rotated observers daily between transect type (i.e., dry, mesic, and riparian) among stream reaches. Surveys began within one-half hour of sunrise. Upon arriving at a station, the observer waited 1 minute for birds to settle, then recorded birds for 10 minutes. We recorded all individual birds detected by song, call note, or sight. We estimated the distance to the bird to the nearest meter using preflagged distance markers as guides. When ≥2 birds of the same species were together, we recorded a single entry and the number of individuals. Observers minimized double-counting of birds by plotting the location of each detection on their data sheet. We recorded birds flying above the canopy (i.e., flyovers) separately. Observations of birds from riparian areas that were obviously in upland forest were recorded as outside the riparian area and later excluded from analysis. Distinguishing between Hammond's (*Empidonax hammondii*) and dusky flycatchers (*E. oberholseri*) is difficult and not always possible (Sedgwick 1993); data for those species were recorded in the field as Hammond's-dusky flycatcher when distinguishing between the species was not possible. Because of that uncertainty in identification, we present only total relative abundance for those 2 species. We were unable to differentiate Pacific-slope flycatchers (*E. difficilis*) and Cordilleran flycatchers (*E. occidentalis*) with certainty in this area of range overlap and taxonomic confusion (Smith et al. 1997), so we used the old common name of western flycatcher to designate these species.

Vegetation.—We sampled vegetation around each point-transect station using the basic Level 2 protocol of the Regional Vegetation Protocol for Bird Count Monitoring Stations in Washington and Oregon, USA (Huff et al. 1999). Briefly, the protocol samples vegetation near each point-transect station with a series of plots and transects. We measured the density of very large trees (>80 cm dbh) in a circular 1-ha plot around the point-transect station. In 3 nested plots randomly located 16 m from the bird point-transect station, we measured small (<8 cm dbh) live and dead tree density in a 0.004-ha plot, understory vegetation cover and medium (8–33 cm dbh) tree density in a 0.017-ha plot, and large (34–80 cm dbh) tree density in a 0.076-ha plot. We measured percentage cover of ground cover categories on a 30-m line-intercept transect that spanned the nested plots. We estimated canopy cover as the mean of 5 moosehorn densiometer readings in the nested plot area. We estimated volume and condition of down woody debris by a tally of pieces >20 cm basal diameter along a 50-m transect along the azimuth of the nested plots and along another 50-m transect at a right angle. We estimated the density of large (>33 cm dbh) standing dead trees for the entire 6-station point transect on 3 parallel 18-m × 45-m belt transects between each of the 6 point-transect stations. We used vegetation data to describe habitats (Table 1) and help explain patterns of species occurrence; we did not model species–habitat relationships.

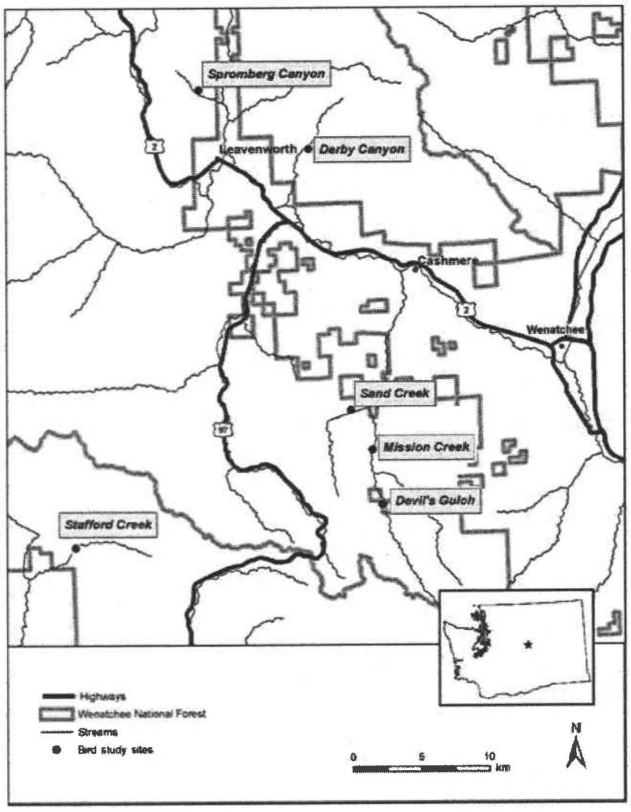

Figure 1. Locations of 6 stream reaches on the Okanogan and Wenatchee National Forests in north-central Washington, USA, where we studied riparian and upland bird habitat relationships during 1998 and 1999.

Data Analysis

Species abundances and diversity.—We estimated bird species richness and evenness and the relative abundance or density of species in riparian, mesic, and dry forest types for each sample stream reach ($n = 6$). We calculated an index of relative abundance as the mean number of detections per point per 10 visits per year within 35 m of the point-transect station as a common basis for quantifying bird diversity and to compare differences in abundance of all species among

Table 1. Mean vegetation attributes of dry and mesic upland forested and riparian sites in 6 low-elevation stream reaches of the eastern Washington Cascade Range, USA, during 1998 and 1999.

	Upland forest					
	Dry		Mesic		Riparian forest	
Characteristic	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Tree species richness ($\bar{x}$ no./plot)	1.8	0.36	1.8	0.17	3.1	0.43
Shannon–Weiner tree diversity basal area	1.5	0.29	1.6	0.18	2.3	0.45
Snag >33 cm dbh density (no./ha)	12	12.7	100	94.0	62	84.1
Conifers						
Canopy cover (%)	28	6.6	52	6.1	39	20.9
Canopy cover patchiness CV	108	27.9	65	15.3	79	27.3
Tree density (no./ha)	252	103.2	806	509.8	176	175.2
Basal area (m^2/ha)	17	5.3	32	10.0	14	9.1
$\bar{x}$ tree dbh (cm)	50	12.6	42	8.5	62	8.1
Hardwoods						
Tree density (no./ha)	0.0		63	131.5	360	320.2
Basal area (m^2/ha)	0.0		0.5	0.85	7.7	6.68
Dominant tree species basal area (m^2/ha)						
Ponderosa pine	9.4	3.45	6.2	3.28	1.7	1.16
Douglas-fir	7.3	5.43	23.5	7.31	8.3	9.05
Grand fir	0.3	0.67	1.9	4.58	3.7	5.50
Black cottonwood	0.0		0.0		4.0	4.12
Big-leaf maple (*Acer macrophyllum*)	0.0		0.4	0.68	1.2	2.61
Alder (*Alnus* spp.)	0.0		0.0		0.9	1.23
Aspen	0.0		0.0		0.6	1.38
Hawthorn (*Crataegus* spp.)	0.0		0.0		0.3	0.35
Willow (*Salix* spp.)	0.0		0.0		0.3	0.66
Bitter cherry (*Prunus emarginata*)	0.0		0.1	0.27	0.2	0.21
Understory cover (%)						
Down wood	3	0.9	9	5.5	8	5.1
Bare soil	12	5.6	3	2.3	3	3.4
Shrubs	20	8.6	23	9.6	29	16.2
Herbs	13	7.6	9	4.8	14	5.1
Grass	26	5.5	25	10.1	12	7.9
Understory species richness (no. species)	7.6	1.30	9.0	1.60	12.1	2.90

forest types. We selected a 35-m threshold for detections by screening data for the 10 most common species in all 3 forest types to determine the distance that would include 75% (third quartile) of the detections as an approximation of the shoulder of the detection curve where detections decline markedly (Carey et al. 1991). Limited detection distances in the narrow riparian corridor dictated selection of 35 m as the common cutoff for detection distance. We used relative abundances to estimate species evenness as one minus the Berger–Parker (BP) dominance index $d = N_{max}/N$, where N = total number of individuals, N_{max} = number of individuals in the most abundant species, and d ranges from 0 to 1 (1 = completely dominated by one species; Magurran 1988). Richness was simply the number of species encountered at a point-transect station.

We estimated true abundance and density with Program DISTANCE (Thomas et al. 2004) for 22 species with sufficient numbers of detections to estimate density functions. Transects were the sample unit in the analysis. Species' data for each transect were the pooled observations for stations along the transect for both years. We estimated species' detection functions and densities separately by forest type (dry, mesic, and riparian), or strata in DISTANCE terminology (Buckland et al. 2001), because data were too few to estimate detection functions for each transect (Thomas et al. 2004). Survey effort for each species on each transect was 60 visits (6 stations/transect × 5 visits/yr × 2 yr).

We used a 3-step process to estimate density for each species separately in the 3 forest types. First, we evaluated the fit to data of 4 recommended (Buckland et al. 2001) detection models: the half-normal key with cosine expansion, the half-normal key with Hermite polynomial expansion, the uniform key with cosine expansion, and the hazard-rate key with simple polynomial expansion. We selected the best model using Akaike's Information Criterion model-selection criteria (Burnham and Anderson 2002). Next, we examined different distance truncations and interval groupings with the selected model to account for heaping, error in distance estimation, and to ensure the best goodness-of-fit to data. Most datasets were lumped into 6–9 intervals, but datasets with small numbers of observation were lumped into as few as 4 or 5 intervals to yield acceptable detection function graphs. Finally, we evaluated covariate variants of the best model using observer, year, and habitat as covariates to detect observer, temporal, and spatial

Table 2. Mean relative abundance (birds/point/10 visits/yr) of terrestrial birds in dry and mesic upland forest and riparian forest in 6 low-elevation stream reaches of the eastern Washington Cascade Range, USA, during 1998 and 1999.

Species	Upland forest		Riparian forest	Total	*P*-value[a]
	Dry	Mesic			
Ruffed grouse (*Bonasa umbellus*)	0.03	0.06	0.14	0.22	0.636
Dusky grouse (*Dendragapus obscurus*)		0.06		0.06	0.132
Sharp-shinned hawk (*Accipiter striatus*)		0.11		0.11	0.402
Red-tailed hawk (*Buteo jamaicensis*)	0.03			0.03	0.402
American kestrel (*Falco sparverius*)	0.03			0.03	0.402
Mourning dove (*Zenaida macroura*)	0.03			0.03	0.402
Great horned owl (*Bubo virginianus*)	0.06			0.06	0.402
Northern pygmy-owl (*Glaucidium gnoma*)	0.03	0.06		0.08	0.402
White-throated swift (*Aeronautes saxatalis*)	0.08	0.03		0.11	0.538
Anna's hummingbird (*Calypte anna*)			0.03	0.03	0.402
Calliope hummingbird (*Stellula calliope*)	0.92	0.22	1.00	2.14	0.120
Rufous hummingbird (*Selasphorus rufus*)	0.19	0.11	0.03	0.33	0.237
Red-naped sapsucker (*Sphyrapicus nuchalis*)	0.03		0.09	0.12	0.168
Downy woodpecker (*Picoides pubescens*)	0.03		0.03	0.06	0.647
Hairy woodpecker (*P. villosus*)	0.25	0.43	0.25	0.93	0.556
White-headed woodpecker (*P. albolarvatus*)	0.22	0.03	0.06	0.31	0.420
Northern flicker (*Colaptes auratus*)	0.28	0.20		0.48	0.167
Pileated woodpecker (*Dryocopus pileatus*)		0.06	0.06	0.11	0.555
Western wood-pewee (*Contopus sordidulus*)	0.50[b]	0.11	0.72	1.33	0.336
Willow flycatcher (*Empidonax traillii*)		0.03	0.67	0.69	0.420
Hammond's flycatcher[c] (*E. hammondii*)				3.32	0.003
Dusky flycatcher[c] (*E. oberholseri*)				1.42	0.085
Hammond's (dusky) flycatchers[c]				5.76	0.010
Western flycatcher (*E. difficilis and E. occidentalis*)	0.39A[dc]	0.53A	1.69B	2.61	0.053
Cassin's vireo (*Vireo cassinii*)	0.81[e]	0.97	0.65	2.43	0.635
Warbling vireo (*V. gilvus*)	0.83A[e]	0.75A	5.51B	7.10	0.005
Red-eyed vireo (*V. olivaceus*)	0.03	0.06	0.03	0.11	0.808
Gray jay (*Perisoreus canadensis*)	0.08	0.21		0.29	0.537
Stellar's jay (*Cyanocitta stelleri*)	0.28	0.19	0.11	0.58	0.337
Clark's nutcracker (*Nucifraga columbiana*)		0.06		0.06	0.402
Common raven (*Corvus corax*)	0.03	0.06	0.09	0.17	0.552
Violet-green swallow (*Tachycineta thalassina*)	0.67	0.33		1.00	0.590
Black-capped chickadee (*Poecile atricapillus*)	0.19A	0.14A	1.08B	1.41	0.002
Mountain chickadee (*P. gambeli*)	2.28A[e]	1.09B	0.03B	3.39	0.006
Chestnut-backed chickadee (*P. rufescens*)	0.33A	1.57B	0.92AB	2.82	0.067
Red-breasted nuthatch (*Sitta canadensis*)	1.81A[e]	3.59B	0.58A	5.97	0.003
White-breasted nuthatch (*S. carolinensis*)	0.11	0.06		0.17	0.237
Pygmy nuthatch (*S. pygmaea*)		0.08		0.08	0.402
Brown creeper (*Certhia americana*)	0.42A	2.06B	0.33A	2.81	0.006
House wren (*Troglodytes aedon*)		0.06		0.06	0.132
Winter wren (*T. troglodytes*)	0.06	0.25	0.22	0.53	0.146
Golden-crowned kinglet (*Regulus satrapa*)	0.92A[b]	2.64B	1.12A	4.68	0.015
Ruby-crowned kinglet (*R. calendula*)	0.03	0.03		0.06	0.647
Townsend's solitaire (*Myadestes townsendi*)	0.89A	0.25B	0.09B	1.23	0.023
Veery (*Catharus fuscescens*)	0.11A[e]	0.22A	3.87B	4.21	<0.001
Swainson's thrush (*C. ustulatus*)	0.08A[e]	0.44A	3.28B	3.80	0.001
Hermit thrush (*C. guttatus*)	0.11A[e]	0.79B	0.14A	1.04	0.002
American robin (*Turdus migratorius*)	1.78A[e]	0.83B	1.90A	4.51	0.015
Varied thrush (*Ixoreus naevius*)		0.06	0.06	0.11	0.402
Cedar waxwing (*Bombycilla cedrorum*)			0.49	0.49	0.008
Orange-crowned warbler (*Vermivora celata*)		0.06	0.14	0.20	0.148
Nashville warbler (*V. ruficapilla*)	3.58[e]	4.22	5.20	13.01	0.458
Yellow warbler (*Dendroica petechia*)		0.03	2.33	2.36	0.129
Yellow-rumped warbler (*D. coronata*)	3.36A[b]	2.65AB	1.23B	7.23	0.065
Black-throated gray warbler (*D. nigrescens*)		0.42	0.25	0.67	0.422
Townsend's warbler (*D. townsendi*)	2.78A[e]	8.57B	3.59A	14.94	<0.001
MacGillivray's warbler (*Oporornis tolmiei*)	1.58A[e]	2.83A	6.40B	10.82	0.001
Wilson's warbler (*Wilsonia pusilla*)	0.03	0.14	0.28	0.44	0.304
Western tanager (*Piranga ludoviciana*)	4.28A[e]	3.98A	1.69B	9.96	0.005
Spotted towhee (*Pipilo maculatus*)	5.94A[e]	1.71B	2.52B	10.17	0.003
Chipping sparrow (*Spizella passerina*)	4.17A[e]	1.78B	0.81B	6.75	0.009
Song sparrow (*Melospiza melodia*)			2.81	2.81	0.004
Dark-eyed junco (*Junco hyemalis*)	6.42A[b]	8.47A	3.46B	18.35	0.008
Black-headed grosbeak (*Pheucticus melanocephalus*)	0.78[b]	0.67	0.92	2.36	0.871
Lazuli bunting (*Passerina amoena*)	0.03			0.03	0.402
Brown-headed cowbird (*Molothrus ater*)	1.28[b]	0.73	1.04	3.05	0.258

Table 2. Continued.

Species	Upland forest		Riparian forest	Total	*P*-value[a]
	Dry	Mesic			
Purple finch (*Carpodacus purpureus*)	1.81A[c]	1.19AB	0.73B	3.73	0.082
Cassin's finch (*C. cassinii*)	1.44A	1.64A	0.28B	3.37	0.025
Red crossbill (*Loxia curvirostra*)	0.47	0.50	0.11	1.08	0.334
Pine siskin (*Carduelis pinus*)	1.86	1.42	0.64	3.92	0.310
Evening grosbeak (*Coccothraustes vespertinus*)	0.03		0.11	0.14	0.506
Total	54.76	59.84	59.84	184.87	

[a] *P*-value for forest type effects from randomized block analysis of variance.
[b] Different pattern of density among cover types as estimated by Program DISTANCE.
[c] Detections by forest type not given due to field identification issues.
[d] Different letters in rows indicate significant ($P \leq 0.10$) differences by Tukey's honestly significant difference test. Absent letters indicate no significant differences.
[e] Similar pattern of density among cover types as estimated by Program DISTANCE.

bias. We developed separate detection functions for species in each of the 3 forest types because the optimal truncation or grouping of observations often differed. Ultimately, we used the hazard-rate key with polynomial expansion to model detection functions in 79% of the cases, and we used the half-normal key with cosine expansion to model the remaining 21% of the cases (Appendix).

Statistical analysis.—We used one-way blocked analysis of variance to test for differences among the 3 habitat types in bird species richness, evenness, relative abundance, and density. Stream reach was the blocking factor ($n = 6$) providing replication in the study design. Forest type was the treatment ($k = 3$). We used Tukey's honestly significant difference test for multiple comparisons to assess differences in dependent variables among cover types. We used SPSS (v.10.1) statistical software (SPSS Inc., Chicago, IL) for all univariate data analysis.

We examined compositional similarity in bird assemblages among forest types and identified bird indicator species for forest types with 2 nonparametric multivariate analyses of community structure, as implemented in PCORD software (McCune and Mefford 1999). We used blocked Multi-Response Permutation Procedures (MRPP) to test the hypothesis of no difference in species composition among forest types based on species frequency and relative abundance (Zimmerman et al. 1985, Biondini et al. 1988). An A statistic measured the grouping effect size, or the distinctiveness of groups on a scale of 0–1. Values of $A > 0.3$ are fairly high. Monte Carlo permutations calculated probabilities for differences between types. We compared those probabilities to a Bonferroni-adjusted $P < 0.10$ for multiple comparisons among forest types.

We used Indicator Species Analysis (ISA) to identify indicator species (i.e., characteristic species found mostly in a single type and present in the majority of the sites belonging to that type [Dufrene and Legendre 1997]). Our use of indicator species should not be confused with ecological indicator species that represent bird guilds or communities (sensu Landres et al. 1988) or with focal species (Lambeck 1997) for monitoring specific limiting habitat factors in those vegetation types. The ISA combined information on both species' relative abundance and constancy to estimate indicator values for each species in each group. The maximum indicator value of a species among cover types was tested for statistical significance against the random expectation calculated by Monte Carlo permutation. We used $P < 0.10$ as the significance level for strong indicator species and $P < 0.25$ for weak indicator species. The modifiers "strong" and "weak" refer to the strength of statistical inference, indicated by the *P*-value, as an index of the ecological association.

We accepted a probability of Type I error $P = 0.10$ for hypothesis testing. Although less conservative than $P = 0.05$, particularly with the relatively small sample size in our study ($n = 6$ stream reaches), we considered $P = 0.10$ to be an acceptable chance of error for ecological field studies, well within the bounds of statistical convention, and conservative in committing Type II errors (Zar 1999). A significant difference is implied where a difference among means is reported, but we reported exact *P*-values in the text to allow readers to assess the probability of error relative to their own standard of significance (Zar 1999).

RESULTS

We detected 80 bird species from >12,000 recorded point-transect observations during 1998–1999. We analyzed data for 72 species (Table 2) and 6,615 observations after truncating data to 35 m for analysis. Eighteen species accounted for 75% of all detections: dark-eyed junco (*Junco hyemalis*), Townsend's warbler (*Dendroica townsendi*), Nashville warbler (*Vermivora ruficapilla*), MacGillivray's warbler (*Oporornis tolmiei*), spotted towhee (*Pipilo maculatus*), western tanager (*Piranga ludoviciana*), yellow-rumped warbler (*D. coronata*), warbling vireo (*Vireo gilvus*), chipping sparrow (*Spizella passerina*), red-breasted nuthatch (*Sitta canadensis*), Hammond's-dusky flycatchers, golden-crowned kinglet (*Regulus satrapa*), American robin (*Turdus migratorius*), veery (*Catharus fuscescens*), pine siskin (*Carduelis pinus*), Swainson's thrush (*Catharus ustulatus*), Cassin's (*Carpodacus cassinii*) and purple finches (*C. purpureus*), and mountain chickadee (*Poecile gambeli*). Relative abundance (detection index) was a relatively good index of density ($r = 0.81$, $P <$

Table 3. Density (no./ha) of breeding birds in dry and mesic upland forest and riparian forest in 6 low-elevation stream reaches of the eastern Washington Cascade Range, USA, during 1998 and 1999. We listed only birds with sufficient captures for density estimation with Program DISTANCE.

Species	Upland forest		Riparian forest	Total	*P*-value[a]
	Dry	Mesic			
Western wood-pewee	0.15A[b]	0.03AB	0.21B	0.38	0.055
Western flycatcher	0.10A	0.28A	1.30B	1.68	0.025
Cassin's vireo	0.20	0.47	0.29	0.96	0.191
Warbling vireo	0.31A	0.20A	2.42B	2.93	0.003
Mountain chickadee	1.03A	0.35B	0.00B	1.38	0.001
Red-breasted nuthatch	0.72A	1.28B	0.46A	2.45	0.002
Golden-crowned kinglet	0.88AB	1.63B	0.68A	3.19	0.061
Veery	0.03A	0.07A	2.72B	2.81	<0.001
Swainson's thrush	0.02A	0.11A	1.50B	1.63	0.001
Hermit thrush	0.03A	0.21B	0.04A	0.28	0.002
American robin	0.68A	0.23B	0.83A	1.73	0.001
Nashville warbler	1.19	1.63	2.27	5.09	0.129
Yellow-rumped warbler	1.27	1.30	2.05	4.62	0.495
Townsend's warbler	0.82A	2.73B	0.91A	4.47	<0.001
Macgillivray's warbler	0.46A	0.91A	6.55B	7.91	<0.001
Western tanager	1.55A	1.64A	0.38B	3.57	<0.001
Spotted towhee	2.88A	0.55B	1.20B	4.63	0.001
Chipping sparrow	1.51A	0.70B	0.40B	2.61	0.007
Dark-eyed junco	7.32A	10.13B	3.58C	21.02	<0.001
Black-headed grosbeak	0.22AB	0.20A	0.50B	0.92	0.065
Brown-headed cowbird	0.33A	0.14B	0.36A	0.83	0.027
Purple finch	0.48A	0.42AB	0.18B	1.07	0.038

[a] *P*-values are given for the primary randomized block analysis of variance.

[b] Different letters in rows indicate significant ($P \leq 0.10$) differences by Tukey's honestly significant difference test. Absence of letters indicates no difference among forest types.

0.001, $n = 72$) among the 22 species in 3 forest types for which we estimated density. We estimated density to be about 75% of relative abundance values (density = −0.44 + [0.85 × relative abundance]). Moreover, patterns of density (Table 3) and relative abundance among forest types were consistent for 16 of 22 species (73%) for which we estimated density.

Bird species richness was approximately 35 species in the upland and riparian forest types (Table 4). Overall, species evenness was high, averaging 0.85 relative to the maximum value of one. Evenness in mesic upland forest was marginally 4% lower than in dry upland or riparian forest types, but that small statistical difference likely has little ecological importance.

Despite similar richness and evenness, the composition of species assemblages did differ among dry, mesic, and riparian forest types (MRPP $A = 0.255$, $P < 0.001$). The greatest differences in bird assemblages were between riparian and dry ($A = 0.291$, $P < 0.01$) and riparian and mesic ($A = 0.335$, $P = 0.008$) upland forests. Bird assemblages found in dry and mesic upland forests differed ($A = 0.216$, $P = 0.012$) but were more similar compared to riparian areas (Table 2).

Each forest type had a number of indicator, or characteristic, species in their bird assemblages as shown by indicator species analysis of relative abundance (Table 5) and supporting patterns of density among cover types (Table 3). With the exclusion of the problematic Hammond's-dusky flycatcher complex, riparian forest had the greatest number (11) of indictor species among the 3 forest types: 9 strong and 2 weak indicator species. The western wood-pewee (*Contopus sordidulus*) and black-headed grosbeak (*Pheucticus melanochephalus*) likely are 2 more species characteristic of riparian forest, based on the more reliable density data (Table 3).

Upland mesic forest was characterized by 7 strong and one weak indicator species (Table 5). Although Cassin's finch was a weak indicator of mesic upland forest, it was equally abundant in both dry and mesic upland forests (Table 2).

Upland dry forest had 4 strong indicator species whose status was supported by density data. Based on patterns of density (Table 3) or detections among forest types (Table 2), 3 weak indicator species seemed at best to be general indicators of upland forests. Densities of American robins and brown-headed cowbirds (*Molothrus ater*) showed the curious result of being equally abundant in dry and riparian forests (Table 3), which most likely was related to relatively more open canopies in those types compared to mesic forest.

DISCUSSION

Riparian areas of our mid-elevation third- and fourth-order streams were not more species-rich or diverse than upland forest as hypothesized, but they did support a unique assemblage of breeding birds that contributed to high beta diversity between riparian and upland forests. That uniqueness of species composition in riparian areas is well-established (e.g., Thomas et al. 1979, Kauffman et al. 2001), but differences in breeding bird richness in riparian versus upland vegetation have been variously reported as present or absent for different ecosystems. A unifying theory

Table 4. Mean diversity indices of terrestrial bird communities in dry and mesic upland forest and riparian forest in 6 low-elevation stream reaches of the eastern Washington Cascade Range, USA, during 1998 and 1999. Estimates are based on detection indices of relative abundance.

Diversity index	Upland forest		Riparian forest
	Dry	Mesic	
Species richness	34.3A[a]	35.5A	35.0A
Species evenness	0.85A	0.82B	0.88A

[a] Different letters in rows indicate significant ($P \leq 0.10$) differences by Tukey's honestly significant difference test.

for riparian bird diversity perhaps comes from work in the Mojave desert where Fleishman et al. (2003) found bird species richness increased with foliage volume (i.e., complexity of vegetation physiognomy) of riparian and desert shrub vegetation but that differences in breeding bird composition increased with diverging floristics. Consistent with that theory, breeding bird richness in deserts and grasslands appears to be higher in structurally complex riparian areas compared to adjacent low-volume and low-stature vegetation (Austin 1970, Szaro and Jakle 1985, Strong and Bock 1990, Knopf and Samson 1994). In forested riparian and upland areas, where contrasts between vegetation physiognomy are small or variable, the difference in richness between habitats likewise is small or variable (Finch 1989, Knopf and Samson 1994, Whitaker and Montevecchi 1997, Bub et al. 2004, Shirley 2005) and depends on location (e.g., stream order), topography, and disturbance regimes that affect the magnitude of contrast between riparian and upland vegetation structure.

Fleishman et al.'s (2003) hypothesis for birds is mostly supported by Sabo et al.'s (2005) meta-analysis of worldwide riparian biodiversity for a variety of taxa (invertebrates to primates). As discussed above for riparian birds, Sabo et al. (2005) found that riparian vegetation supported unique species assemblages that differed from adjacent vegetation and differed more strongly in dry than in wet climates. Riparian areas on average, however, were not richer in species than adjacent habitats, but the reported variation in animal richness was high, which provides scope for exception with birds. Greater contrasts (turnover) in bird species richness between dry (e.g., desert) versus mesic (e.g., forests) riparian and upland habitats, as discussed above, are consistent with Sabo et al.'s conclusions. High turnover between habitats would contribute to reported higher richness in desert riparian versus upland habitats but not in wetter forested ecosystems.

We confirmed the close association of the cedar waxwing (*Bombycilla cedrorum*), veery, warbling vireo, western flycatcher, and yellow warbler (*D. petechia*) with interior riparian habitats of Oregon and Washington (Johnson and O'Neal 2001). Cedar waxwings showed an affinity to riparian areas, and are associated both with open woodlands and riparian areas, especially in arid areas (Witmer et al. 1997), but our relatively few detections provide weak support for cedar waxwings as a strong riparian indicator. The veery, warbling vireo, and yellow warbler are well-known riparian associates (Lowther et al. 1999, Gardali and Ballard 2000, Bevier et al. 2004). A less well-defined association with riparian areas has been reported for the western flycatcher (Lowther 2000), but our data show a relatively strong affinity for riparian areas. The red-naped sapsucker (*Sphyrapicus nuchalis*) likewise is considered closely associated with interior riparian areas (Walters et al. 2002), even though we found it to be a weak indicator of riparian habitat, probably because of low statistical power from relatively few detections.

Our results also suggest strong riparian associations in dry forests for the western wood pewee, black-capped chickadee (*Parus atricapillus*), Swainson's thrush, MacGillivray's warbler, song sparrow (*Melospiza melodia*), and black-headed grosbeak. These species are considered to be only generally, but not closely, associated with interior riparian habitats (Johnson and O'Neal 2001). The strong riparian indicator values that we quantified are supported by close associations of most species with deciduous or shrub habitats (Smith 1993, Hill 1995, Arcese et al. 2002, Walters et al. 2002). Although Swainson's thrush has been generally associated with wet coniferous forest in the Pacific Northwest, its

Table 5. Indicator value of terrestrial bird species in low-elevation dry and mesic upland forest and riparian forest of the eastern Washington Cascade Range, USA, during 1998 and 1999. Values are a function of the frequency of occurrence and relative abundance (detection indices) at sample points according to Dufrene and Legendre (1997).

Species	Upland forest		Riparian forest	*P*-value[a]
	Dry	Mesic		
Townsend's solitaire	72**[b]	14	2	0.010
Mountain chickadee	67**	32	0	0.012
Chipping sparrow	62**	26	8	0.006
Spotted towhee	58**	17	25	0.029
Purple finch	48*	27	16	0.140
Yellow-rumped warbler	46*	37	14	0.155
Western tanager	43*	40	17	0.107
Northern flicker	39*	21	0	0.211
Hermit thrush	5	76**	7	0.002
Brown creeper	12	73**	8	0.005
Red-breasted nuthatch	30	60**	7	0.002
Townsend's warbler	19	57**	24	0.013
Golden-crowned kinglet	16	57**	24	0.022
Chestnut-backed chickadee	6	56**	22	0.069
Dark-eyed junco	35	46**	19	0.033
Cassin's finch	43	49*	6	0.212
Song sparrow	0	0	100**	0.001
Cedar waxwing	0	0	100**	0.001
Swainson's thrush	1	4	86**	0.002
Yellow warbler	0	0	82**	0.002
Warbling vireo	10	11	78**	0.001
Veery	1	2	77**	0.010
Black-capped chickadee	7	7	76**	0.003
Western flycatcher	12	13	65**	0.037
Macgillivray's warbler	12	26	59**	0.001
Red-naped sapsucker	4	0	38*	0.194
Orange-crowned warbler	0	9	36*	0.217

[a] We calculated *P*-value as the proportion of 1,000 randomized trials with indicator value equal to or exceeding the observed indicator value. $P = (1 +$ no. of runs $\geq$ obs$)$ / $(1 +$ no. of randomized runs$)$.

[b] ** indicates strong indicator value $P \leq 0.10$; * indicates weak indicator value $P \leq 0.25$.

association with riparian vegetation in our dry forests is consistent with its use of riparian areas in the dry southerly part of its range in California, USA (Evans-Mack and Yong 2000). Density of the western wood pewee was highest in the riparian areas, but it was also dense in the open dry forest and did not show an indicator value (based on detection indices) for riparian areas. The species is known as a widespread habitat generalist of open forests that often is associated with riparian woodlands (Bemis and Rising 1999), so it likely would be a poor riparian-indicator species.

Hammond's and dusky flycatchers collectively were relatively abundant and represented an important component of the bird community. Their combined relative abundance across forest types totaled 10.5 detections per point per 10 visits per year, ranking fifth among species. Long-term (1994–2001) data from similar mixed-conifer forest north of the study area recorded Hammond's flycatcher as the third most abundant species, and dusky flycatchers to be moderately abundant as well (Huff and Brown 2006). Our combined-species detections were 2–5 times greater in riparian areas (6.17 detections/point/10 visits/yr) than in dry forest (3.00 detections/point/10 visits/yr) and mesic forest (1.33 detections/point/10 visits/yr). That pattern of abundance suggests that most of the detections were dusky flycatchers, which typically use shrubby riparian areas and open forests (Sedgwick 1993), versus Hammond's flycatchers, which typically are most abundant in mesic closed-canopy conifer forests (Sedgwick 1994). Regional monitoring confirms that Hammond's flycatchers are nearly 3 times more abundant than dusky flycatchers in mixed-conifer forest in the Okanogan Highlands north of the study area; whereas, dusky flycatchers were 15 times more abundant than Hammond's flycatchers in open ponderosa pine forest of northeastern Oregon (Huff and Brown 2006). Ongoing field studies in north-central Washington are attempting to clarify differences in upland forest use between these species (J. F. Lehmkuhl, United States Forest Service, personal communication).

Bird assemblages in mesic upland forest differed from those in dry forests but were not richer and more diverse as we hypothesized. Avian diversity across the upland forest was enhanced by those differences. The indicator value of Townsend's solitaire (*Myadestes townsendi*), mountain chickadee, and chipping sparrow in dry forest is consistent with the density data and life histories of those species (Kaufman 1996). The spotted towhee also was a strong indicator of dry forest, where its density was highest, but it also was found in relatively high density in riparian areas. Our results closely match Smith et al.'s (1997) description of spotted towhee habitat in eastern Washington as dry forest and the fringes of riparian areas at low elevations and Greenlaw's (1996) description of interior mountain habitat as riparian thickets and open slopes. Marginally lower shrub cover, with which spotted towhees are typically associated (Greenlaw 1996), in dry forest (20%) compared to other forest types (23–29%) appeared to have little effect on spotted towhee habitat use. Species we identified from relative abundance data as weak indictor species for dry forest (i.e., purple finch, yellow-rumped warbler, western tanager) were found to be forest generalist species with the more reliable density analysis, which is consistent with their life histories (Kaufman 1996). The designation of purple finch as a dry or generalist forest bird is further complicated by 2 issues. First, the status of the species is uncertain in the study area, which is peripheral to the species' main distribution in wet forests of western Washington, where it nevertheless favors patchy forested openings similar to our dry forests (Smith et al. 1997). Second, it is difficult in the field to differentiate purple finches from Cassin's finches (K. Z. Woodruff, Okanogan and Wenatchee National Forests, personal communication), which have been shown to favor open thinned forests in nearby areas (Gaines et al. 2007).

Density data and life histories (Kaufman 1996) are consistent for 6 of the 7 species we identified as strong indicators of mesic forest. Although density data support the dark-eyed junco as a strong indicator of mesic forest, the species' density in dry forest was relatively high and its breadth of habitat use is high (Nolan et al. 2002). As with the weak indicator species in dry forest, Cassin's finch abundance did not differ among the dry and mesic forest; hence, the species should be considered a generalist for the study area. Gaines et al. (2007), however, found Cassin's finch more abundant in open-canopy thinned forests than in closed-canopy forests. Our results for both dry and mesic forest suggest that the idea of a weak indicator species, as defined by a liberal (high) probability of Type I error, has little value for describing indicator values in our study area.

MANAGEMENT IMPLICATIONS

Our data show that riparian buffer zones created under current standards or guidelines for these types of streams would act as refuges that maintain bird assemblages characteristic of the narrow riparian zone and the adjacent uplands. Riparian buffer standards for National Forest lands under the Northwest Forest Plan (U.S. Department of Agriculture and U.S. Department of Interior 1994) are 100 m on either side of the stream. Recommended buffers for other forested areas within Washington State are 61 m wide on each side of the stream (Washington Department of Fish and Wildlife 1996). Those buffer widths would include a substantial area of upland forest, in many cases $\geq$50% of the buffer width on these third- and fourth-order streams, which also would accommodate a corridor function for upland species (Machtans et al. 1996, Wiebe and Martin 1998, Mosley et al. 2006). Most upland species also used the narrow riparian zone, so a corridor function would not be solely dependent on inclusion of upland forests. The value of buffer-zone corridors would be relatively low in these dry forests where upland forest management focuses on thinning for fuel reduction (mainly federal lands) versus areas where clear-cut harvesting may be practiced (mainly private lands).

Our density data and indicator species will help forest managers assess and monitor the wildlife impacts of dry

forest thinning or prescribed fire projects that aim to reduce ground and canopy fuels and reestablish natural fire regimes (Graham et al. 1999, Agee and Skinner 2005). Some of our indicator species are included in a group of focal species (Lambeck 1997) proposed by the international Partners In Flight (PIF) program for monitoring the impacts of dry forest management (Altman 2000). Some species in the PIF focal species group are uncommon or difficult to monitor, thus making implementation and measurement of management success problematic. Among those species, however, our data confirm that the chipping sparrow, brown creeper, and hermit thrush are good indicators (i.e., characteristic) of these forest types and abundant enough for reliable monitoring. The other PIF focal species for our region (white-headed woodpecker [*Picoides albolarvatus*], pygmy nuthatch [*Sitta pygmaea*], Lewis' woodpecker [*Melanerpes lewis*], Williamson's sapsucker [*Sphyrapicus thyroideus*], flammulated owl [*Otus flammeolus*], olive-sided flycatcher [*Contopus borealis*]) were relatively uncommon or poorly sampled by our point-transect method. Monitoring our indicator species might be an efficient and reliable adjunct to focal species monitoring of dry forest management impacts.

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Appendix. Key functions and series expansions used to model detection functions of breeding bird species in dry and mesic upland forest and riparian forest in 6 low-elevation stream reaches of the eastern Washington Cascade Range, USA, during 1998 and 1999. We listed only birds with sufficient captures for density estimation with Program DISTANCE.

Species	Upland forest		Riparian forest
	Dry	Mesic	
Western wood-pewee	Haz-rate poly[a]	Half-norm cos[b]	Haz-rate poly
Western flycatcher	Half-norm cos	Haz-rate poly	Half-norm cos
Cassin's vireo	Haz-rate poly	Haz-rate poly	Haz-rate poly
Warbling vireo	Haz-rate poly	Haz-rate poly	Half-norm cos
Mountain chickadee	Haz-rate poly	Haz-rate poly	Haz-rate poly
Red-breasted nuthatch	Haz-rate poly	Half-norm cos	Haz-rate poly
Golden-crowned kinglet	Haz-rate poly	Haz-rate poly	Haz-rate poly
Veery	Haz-rate poly	Haz-rate poly	Half-norm cos
Swainson's thrush	Haz-rate poly	Haz-rate poly	Haz-rate poly
Hermit thrush	Haz-rate poly	Haz-rate poly	Haz-rate poly
American robin	Haz-rate poly	Haz-rate poly	Haz-rate poly
Nashville warbler	Haz-rate poly	Haz-rate poly	Haz-rate poly
Yellow-rumped warbler	Haz-rate poly	Half-norm cos	Haz-rate poly
Townsend's warbler	Half-norm cos	Half-norm cos	Haz-rate poly
MacGillivray's warbler	Haz-rate poly	Haz-rate poly	Haz-rate poly
Western tanager	Haz-rate poly	Haz-rate poly	Haz-rate poly
Spotted towhee	Half-norm cos	Haz-rate poly	Half-norm cos
Chipping sparrow	Haz-rate poly	Haz-rate poly	Haz-rate poly
Dark-eyed junco	Haz-rate poly	Haz-rate poly	Haz-rate poly
Black-headed grosbeak	Half-norm cos	Half-norm cos	Half-norm cos
Brown-headed cowbird	Haz-rate poly	Haz-rate poly	Haz-rate poly
Purple finch	Haz-rate poly	Haz-rate poly	Haz-rate poly

[a] Hazard-rate key function with simple polynomial series expansion.
[b] Half-normal key function with cosine series expansion.