EFFECTS OF CONIFERS ON ASPEN-BREEDING BIRD COMMUNITIES IN THE SIERRA NEVADA

T. WILL RICHARDSON,[1] Biological Resources Research Center, Mail Stop 314, University of Nevada, Reno, NV 89557, USA

SACHA K. HEATH, PRBO Conservation Science, 4990 Shoreline Hwy, Stinson Beach, CA 94970, USA

ABSTRACT: We examined bird-habitat relationships within and across a range of aspen habitats in four major watersheds in the eastern Sierra Nevada mountains of California and Nevada to identify habitat features of importance to aspen-breeding birds. Using point counts and vegetation assessments from 462 individual stations between 2001 and 2003 allowed us to investigate important habitat features at watershed and regional scales. Several trends were found: bird species richness and abundance were positively correlated with lower percent conifer cover, increased herbaceous cover, and lower shrub-class aspen cover. Dusky Flycatcher (*Empidonax oberholseri*) presence and abundance were positively correlated with increased percent shrub-class aspen cover and lower percent tree-class cover of all conifers or individual coniferous species. Warbling Vireo (*Vireo gilvus*) presence and abundance were positively correlated with increased percent tree-class aspen cover. The results suggest that mature aspen stands with healthy herbaceous communities and limited or no conifer intrusion are optimal habitats for aspen-breeding birds in the eastern Sierra Nevada. To maximize bird species richness and bird abundance, management actions in aspen stands should concentrate on conifer removal, where conditions warrant, and the promotion of a healthy herbaceous layer. Conservation planning for birds in aspen habitats of the Sierra Nevada is discussed.

Key words: aspen, conifer encroachment, Dusky Flycatcher, *Empidonax oberholseri, Populus tremuloides*, Sierra Nevada, species richness, *Vireo gilvus*, Warbling Vireo

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The importance of quaking aspen (*Populus tremuloides*) to birds and other wildlife in western North America has long been appreciated by biologists (Salt 1957, Flack 1976, DeByle 1985b). Many studies from this region have demonstrated that aspen habitats typically support much greater diversity, richness, and abundance of birds than adjacent habitats (Flack 1976, Winternitz 1980, Mills et al. 2000, Griffis-Kyle and Beier 2003, Heath and Ballard 2003), and several bird species have shown a strong affinity with aspen, including Northern Goshawk (*Accipiter gentilis*), Red-naped and Red-breasted Sapsuckers (*Sphyrapicus nuchalis/ruber*), Dusky Flycatcher (*Empidonax oberholseri*), Warbling Vireo (*Vireo gilvus*), Swainson's Thrush (*Catharus ustulatus*), and MacGillivray's Warbler (*Oporornis tolmiei*) (Salt 1957, Flack 1976, Finch and Reynolds 1988, Heath and Ballard 2003).

The obvious benefits to birds breeding in aspen stands are many. Ground-nesting birds benefit from an exceedingly thick herbaceous layer and deep leaf litter, which aids in potential for nest concealment (Flack 1976, DeByle 1985b). Both primary and secondary cavity nesters benefit from aspen's susceptibility to heart rot and an associated abundance of cavity-bearing trees (DeByle 1985b, Daily et al. 1993). It is highly likely that one of the main benefits to all birds breeding in aspen stands is the increased abundance and diversity of invertebrate prey (Winternitz 1980).

However, this habitat may become greatly reduced for birds in the foreseeable future. Because western aspen primarily reproduce through vegetative suckering, generally following a disturbance of some kind, whole stands may succumb to conifer succession within a few hundred years if no disturbance occurs (e.g., fire suppression). Much of the aspen in the western United States is threatened in this manner, and much, if not most, of the historic aspen coverage in western states has already been lost (Kay 1997, Bartos and Campbell Jr. 1998, Bartos 2001). The current extent and condition of aspen in the Sierra Nevada Mountains of California and Nevada has yet to be fully inventoried.

In light of the threatened status of aspen habitat, it is also important to highlight the documented population declines and tenuous status of some aspen-associated bird species in the west. Western Warbling Vireo population declines are well documented (Gardali et al. 2000, Ballard et al. 2003), and Swainson's Thrushes are declining or have been extirpated from much of their historic breeding range in the Sierra Nevada (Verner and Boss 1980, Gaines 1988, Siegel and DeSante 1999). Northern

ASPEN SYMPOSIUM

[1] E-mail: trichard@unr.nevada.edu

Goshawk is a California Bird Species of Special Concern and a United States Forest Service, Region 5 Sensitive Species (USFS 2001, CDFG and PRBO 2001). Clearly, the losses incurred on both aspen habitats and associated bird species warrants an investigation into the relationship between the two.

As the most widespread native North American tree (and second most widespread tree in the world), the enormous ecological amplitude of aspen must be considered in the interpretation of ecological studies of aspen (Campbell Jr. and Bartos 2001, Romme et al. 2001). Even at the regional or local scale, aspen's ability to occur in a broad environmental context makes generalizations difficult. Within the Sierra Nevada, aspen may occur in a variety of riparian habitats, in association with wet or dry meadows, as isolated or connected patches within a matrix of conifer-dominated forest, as stand-alone groves in snowpockets or along avalanche paths, or in large networks of climax stands. For these reasons Romme et al. (2001) urged the need for more local case studies on aspen ecology.

In a habitat type as wide-ranging yet locally varied as aspen, it is important to consider the habitat features important to bird populations at several spatial scales. Results derived from large scale avian and habitat studies may have little biological meaning or application to local conditions (Meents et al. 1983). Conversely, extrapolating locally derived results to wide ranging or disparate locations can be inappropriate (Wiens 1981, Knopf and Samson 1994). Thus, bird and habitat relationship studies are most instructive when approached at several spatial scales (Knopf and Samson 1994, Saab 1999).

We examined bird-habitat relationships within and across a range of aspen habitats in four major watersheds in the eastern Sierra Nevada Mountains of California and Nevada to identify habitat features of importance to aspen-breeding birds. This approach allowed investigation of regional trends across the eastern Sierra Nevada as well as potential differences between watersheds. We identify habitat characteristics that predict overall bird species richness (BSR) and total abundance (TBA) of aspen-breeding birds, as well as the occurrence and abundance of two species that have a demonstrated association with aspen over much of their respective ranges: Dusky Flycatcher and Warbling Vireo (Finch and Reynolds 1988, Mills et al. 2000).

METHODS

Study Area

Study sites were located along a 360-km stretch of the eastern Sierra Nevada, in the Owens River, Mono Lake, East Walker, and West Walker River watersheds (Inyo and Mono Counties, California) and the Truckee River watershed (El Dorado, Placer, and Sierra Counties, California; Carson City, Douglas, and Washoe Counties Nevada; Fig. 1). All Inyo and Mono County sites were situated within riparian habitat, along 23 streams of the four major watersheds. The Truckee River sites were associated with meadow edges, streams, avalanche slide paths, or in large forest stands. Elevation of point count stations ranged from approximately 2030 to 2840 m.

Point count stations used for these analyses were drawn from larger data sets, selected by having aspen cover in at least one of the three major vegetation layers (see Habitat Assessments, below, for explanation). For the entire study area, 83% of all stations (n = 383) had a conifer component in the canopy layer. A full 98% of Truckee River stations (n = 172) had conifers in the canopy. The canopy at study sites consisted primarily of aspen, Jeffrey and lodgepole pine (*Pinus jefferyi* and *P. contorta*), and fir trees (*Abies concolor* and *A. magnifica*). Red fir (*A. magnifica*) only occurred in Truckee River sites. Shrub layers at the sites consisted primarily of willow species (*Salix* spp.), alder (*Alnus incana*), snowberry (*Symphoricarpos rotundifolius*), and immature aspen and coniferous trees. Across the study area, the herbaceous layer was highly variable, ranging from being dominated by low grasses and sedges at meadow edges, to *Wyethia mollis* at drier sites, to a full complement of tall, lush vegetation at moist forest sites. The latter, typically including species such as *Veratrum californicum*, *Heracleum lanatum*, *Osmorhiza occidentalis*, *Hackleia nervosa*, *Delphinium glaucum*, and *Thalictrum fendleri*. Adjacent vegetation communities were comprised primarily of big sage (*Artemisia tridentata*), conifer species, non-aspen riparian species, or montane and subalpine meadow species.

Point Counts

We conducted 5-min, 50-m, fixed-radius point counts at 462 independent stations following the guidelines of Ralph et al. (1993, 1995). We placed stations at least 250 m apart to avoid double counting of territorial birds and to assure independence of stations. We recorded all birds observed and type of detection (song, call, or visual), and denoted whether the individual was within or outside of the 50-m radius census plot. All counts were conducted two times during the peak songbird breeding season, 22 May to 10 July. Visits to individual stations were spaced at least seven days apart. Inyo and Mono County sites were surveyed 2001 to 2003. Point counts at Truckee River sites were conducted in 2002 and 2003.

Habitat Assessments

We collected vegetation data at Inyo and Mono County sites in 2001 and at Truckee River sites in 2002. Our habitat estimates followed a modified version of the relevé technique (Ralph et al. 1993). In short, for a 50-m radius plot, centered on each point count station, we estimated percentage cover for every species of plant for each of three height categories: "herb" (0.0 - 0.5 m), "shrub" (0.5 - 5 m), and "tree" (>5 m).

Data Analysis

We calculated mean annual bird species richness (BSR) and mean annual total bird abundance (TBA) for each station, based on annual totals summed over two visits in each of two or three years, using the program PointCnt 2.75 (Ballard 2002). We restricted our data set to detections within 50 m and further limited the indices to include species most reliably censused with the point count method. We therefore removed nocturnal species (e.g., *Strigidae*), known post-breeding dispersers, va-

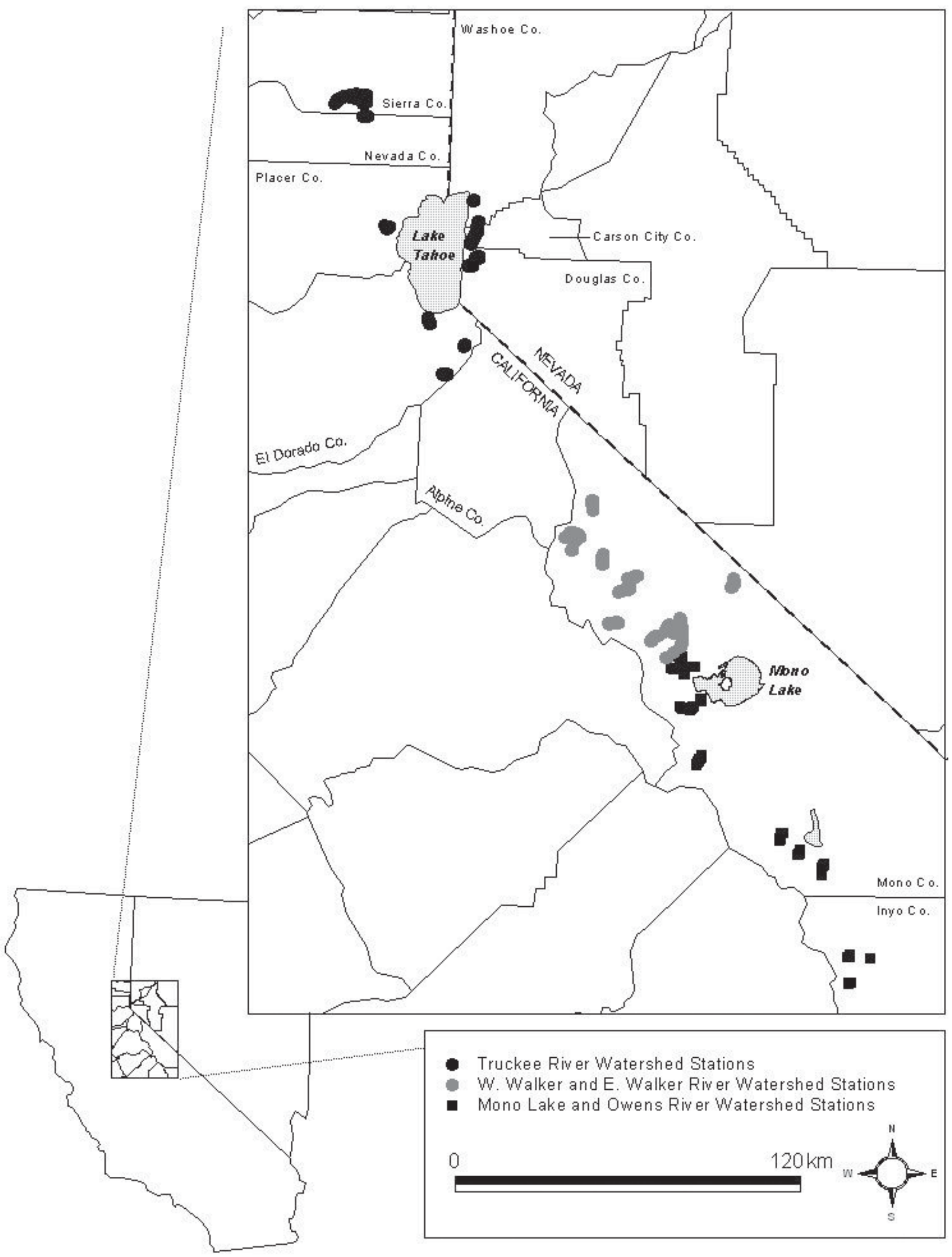

Figure 1. Point count stations in aspen habitat of the eastern Sierra Nevada mountains, California and Nevada, 2001-2003.

grants, and migrants (e.g., *Selasphorus rufus*), non-territorial or colonial species (e.g., *Laridae*), and species with territories typically too large to ensure independence of individual point count stations (e.g., *Anseriformes*, *Falconiformes*). A complete list of common and Latin names for all species used in analysis is presented in Appendix A. ANOVA tests were performed to compare BSR and TBA indices between watersheds. Due to small sample sizes of the Mono Lake and Owens River drainages, a simple t-test was used to determine suitability of combining data from these adjacent watersheds for habitat models.

Of the hundreds of potential vegetation and environmental variables available, we selected fifteen that we felt would best contribute to models predicting BSR, TBA, and Dusky Flycatcher and Warbling Vireo occurrence or abundance on a regional scale; three additional variables were utilized in model selection restricted to data from Truckee River watershed sites (Table 1). We looked for highly correlated variables when building full models in an attempt to reduce dimensionality, but in no cases found correlations high enough to warrant exclusion of parameters from the full model. Variance inflation factors were examined for each parameter in the reduced models to ensure that no highly correlated variables were causing problems associated with multicollinearity. BSR and TBA model selection was performed using the maximum R^2 improvement (MAXR) technique, as implemented in the SAS macro REGDIAG (Fernandez 2003). Optimal models were selected based on a combination of lowest Akaike's information criterion (AIC) score and Mallows' statistic (C_p).

We constructed habitat models predicting BSR and TBA using four regional groupings of the data: (1) the entire study area, (2) Truckee River sites, (3) Walker River sites, and (4) Mono Lake / Owens River sites. At Truckee River sites, we also calculated mean annual Dusky Flycatcher and Warbling Vireo abundance for each station, based on means of annual total detections, summed over two visits in each of two years. Neither abundance nor occurrence of these species was normally distributed across non-Truckee River sites. We therefore restricted data to 2002-3, and constructed models predicting Dusky Flycatcher and Warbling Vireo occurrence over the entire

Table 1. Environmental and habitat variables used in model selection to predict bird species richness, bird abundance, and presence of Dusky Flycatcher and Warbling Vireo from point count data, eastern Sierra Nevada mountains.

Habitat Variable	Units	Habitat Variable	Units
Absolute tree-class cover	%	Ab. shrub-class willow (*Salix*) cover	%
Ab. tree-class aspen cover	%	Ab. herbaceous cover	%
Ab. tree-class conifer cover	%	Maximum tree height	m
Ab. tree-class Jeffrey pine cover		Maximum aspen height[a]	m
Ab. tree-class lodgepole pine cover	%	Maximum tree dbh	cm
Ab. tree-class fir (*Abies*) cover		Maximum aspen dbh[a]	cm
Ab. shrub-class cover	%	Canopy cover[a]	%
Ab. shrub-class aspen cover	%	Tree species richness	#
Ab. shrub-class conifer cover	%	Shrub species richness	#

[a]Variable only used in model selection restricted to Truckee River watershed.

study area and for the remaining regional groupings. These models predicted occurrence against the fifteen variables using a forward selection technique on a randomly assigned training data set (approximately 67% of point count stations) and were validated with an independent validation data set (remaining 33% of stations), as implemented in the SAS macro LOGISTIC (Fernandez 2003). Predicted event classification probability was fixed at $P = 0.5$.

Potentially influential extreme outliers (standardized values falling outside ± 3.5) were excluded from analyses. All statistical tests were performed using SAS (SAS 1999). Model significance was designated at $P < 0.05$.

RESULTS

Breeding Bird Species Richness

Entire Study Area.- For the entire study area, mean BSR was 7.71 (± 2.38) species and ranged from 2 to 16 species. Results from the ANOVA test showed highly significant differences in BSR between the four watersheds ($F_{3,459} = 39.58$, $P < 0.001$), with the Truckee River sites demonstrating the greatest species richness (Figure 2A). The optimal habitat model was highly significant ($F_{7,452} = 29.05$, Adj. $R^2 = 0.30$, $P < 0.001$) and retained tree-class conifer cover, herbaceous cover, maximum tree height, tree-class aspen cover, shrub-class aspen cover, shrub species richness, and shrub cover (Table 2A).

Truckee River.-A model built from data for the Truckee River watershed had the highest predictive power ($F_{5,167} = 21.42$, Adj. $R^2 = 0.37$, $P < 0.001$). BSR for Truckee River sites ranged from 2 to 16 species, with a mean of 8.45 (± 2.86) species (Table 2A). Variables retained in this model included herbaceous cover, tree-class aspen cover, maximum aspen DBH, shrub-class willow cover, and tree-class lodgepole pine cover.

Walker River.-BSR at Walker River sites had a mean of 5.63 (± 2.20) species and ranged from 1.67 to 13 species. The optimal model built for these data was highly significant ($F_{6,163} = 13.48$, Adj. $R^2 = 0.30$, $P < 0.001$). The most highly predictive variables retained in this model were tree species richness, shrub cover, herbaceous cover, tree-class fir cover, tree-class aspen cover, and shrub species richness (Table 2A).

Mono Basin/Owens River.-We found no difference in BSR between Mono Basin and Owens River sites ($P = 0.494$), and thus combined these data for further analyses. BSR at Mono/Owens sites had a mean of 6.24 (± 2.01) species and ranged from 2.33 to 10.33 species. The optimal model built for these data was highly significant ($F_{6,107} = 9.24$, Adj. $R^2 = 0.30$, $P < 0.001$) and retained herbaceous cover, maximum tree DBH, tree-class conifer cover, tree-class fir cover, shrub-class aspen cover, and tree cover (Table 2A).

Total Breeding Bird Abundance

Entire Study Area.- For the entire study area, mean TBA was 12.92 (± 5.23) individuals and ranged from 2 to 31 individuals. Results from the ANOVA test showed

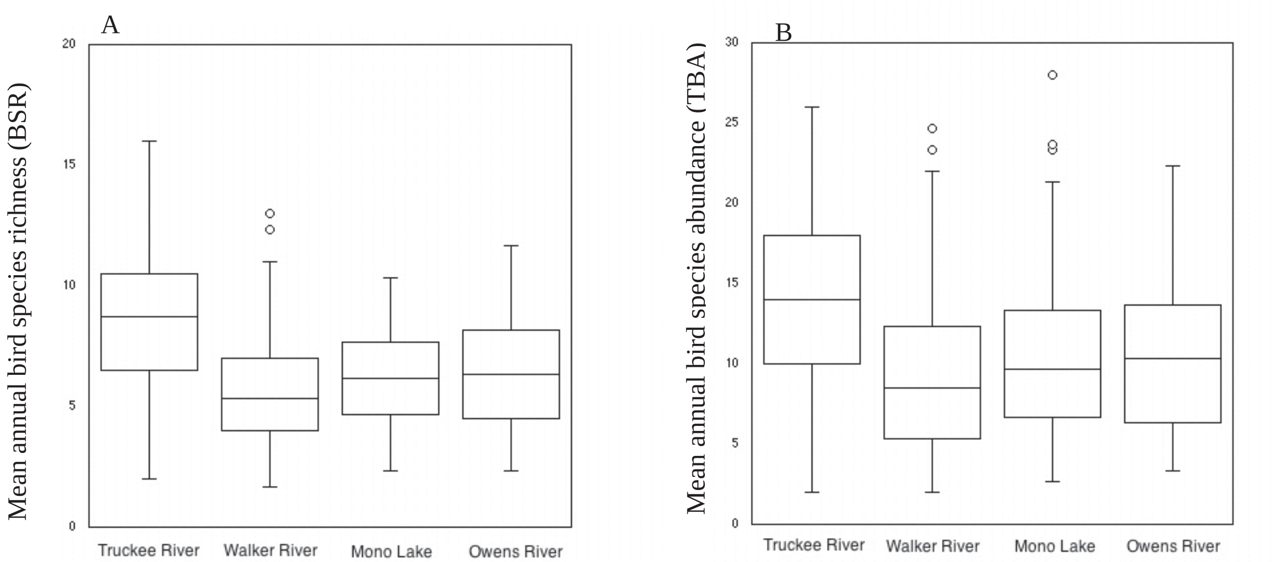

Figure 2. Box-plots representing (A) BSR and (B) TBA of point count stations in aspen habitat in four major drainages in the eastern Sierra Nevada Mountains: Truckee River ($n = 175$), Walker River ($n = 170$), Mono Lake ($n = 74$), and Owens River ($n = 43$).

highly significant differences in TBA between the four watersheds ($F_{3,459}$ = 25.19, $P < 0.001$), with the Truckee River sites demonstrating the greatest abundance (Figure 2B). The optimal habitat model was highly significant ($F_{7,452}$ = 36.27, Adj. $R^2 = 0.35$, $P < 0.001$) and retained tree-class conifer cover, herbaceous cover, tree cover, shrub species richness, maximum tree height, shrub-class aspen cover, and tree-class fir cover (Table 2B).

Truckee River.-Mean TBA at northern sites was 13.77 (± 5.59) individuals, with a range of 2 to 26 individuals. The optimal model selected for these data was highly significant ($F_{4,168}$ = 41.85, Adj. $R^2 = 0.49$, $P < 0.001$) and retained maximum aspen height, herbaceous cover, tree-class aspen cover, and tree-class conifer cover as the most influential variables (Table 2B).

Walker River.-Mean TBA at Walker River sites was 9.04 (± 4.73) individuals, with a range of 2 to 24.67 individuals. The optimal model selected for these data retained tree species richness, tree-class aspen cover, herbaceous cover, shrub species richness, shrub-class aspen cover, tree-class fir cover, and shrub-class willow cover, and was highly significant ($F_{8,160}$ = 11.02, Adj. R^2 = 0.32, $P < 0.001$).

Mono Lake/Owens River.- We found no difference in TBA between Mono Lake and Owens River sites (P = 0.863), and thus combined these data for further analyses. Bird abundance at Mono/Owens sites had a mean of 10.47 (± 5.02) individuals and ranged from 2.67 to 28 individuals. The optimal model built for these data was highly significant ($F_{6, 108}$ = 10.00, Adj. $R^2 = 0.32$, $P < 0.001$) and retained herbaceous cover, maximum tree DBH, shrub-class aspen cover, tree-class lodgepole pine cover, shrub species richness, and shrub-class conifer cover (Table 2B).

Occurrence and Abundance of Aspen-associated Species

Dusky Flycatcher.-For the entire study area, Dusky Flycatchers were present at 47.8 % of point count stations. Presence of Dusky Flycatcher was most accurately predicted by a combination of maximum tree height, shrub-class aspen cover, tree-class conifer cover, shrub species richness, and shrub cover (Table 3A). This model accurately predicted Dusky Flycatcher presence at 70.3% of stations (Brier scores: training = 0.19, validation = 0.18). Dusky Flycatchers occurred at 27.1% of Walker River stations. A combination of shrub-class aspen cover and shrub cover, along with tree-class fir cover correctly predicted Dusky Flycatcher occurrence at 71.6% of Walker River stations (Brier scores: training = 0.16, validation = 0.20, Table 3A). Dusky Flycatchers occurred at 23.1% of Mono/Owens stations. Different criteria appeared to be important for these flycatchers, as herbaceous cover and tree-class lodgepole pine cover best predicted their occurrence. This model correctly predicted Dusky Flycatcher occurrence at 84.3% of Mono/Owens stations (Brier scores: training = 0.12, validation = 0.27).

For Truckee River sites, annual Dusky Flycatcher abundance ranged from 0 to 5 individuals per station (mean = 1.51 ± 1.14). An optimal model built for these data was highly significant ($F_{4,170}$ = 10.04, Adj. $R^2 = 0.17$, P < 0.001) and retained tree-class conifer cover, maximum aspen height, shrub species richness, and shrub-class aspen cover (Table 2C).

Warbling Vireo.-For the entire study area, Warbling Vireo was present at 68.7% of stations. The occurrence of this species was most accurately predicted by a combination of tree-class aspen cover, tree-class conifer cover, and herbaceous cover (Table 3B). This model accurately predicted the occurrence of Warbling Vireos at 69.5% of stations (Brier scores: training = 0.18, validation = 0.19). Warbling Vireos occurred at 57.6 % of Walker River stations. Here, Warbling Vireo presence was accurately predicted by a combination of tree-class aspen cover and shrub cover (Table 3B). This model predicted Warbling Vireo occurrence at 70.6% of point count stations (Brier scores: training = 0.18, validation =0.29). Mono/Owens Warbling Vireos occurred at 60.7% of stations. Presence of the species at Mono/Owens sites was also best predicted by tree-class aspen cover, this time in combination with herbaceous cover (Table 3B). This model correctly predicted vireo presence at 68.6% of Mono/Owens stations (Brier scores: training = 0.18, validation = 0.22).

For Truckee River watershed sites, annual Warbling Vireo abundance ranged from 0 to 7.5 individuals per station (mean = 2.45 ± 1.67). An optimal model built for these data retained tree-class aspen cover, tree-class conifer cover, herbaceous cover, maximum aspen height, maximum aspen DBH, shrub-class aspen cover, and shrub-class willow cover (Table 2D). This model was highly significant ($F_{4,169}$ = 17.62, Adj. $R^2 = 0.40$, $P < 0.001$).

DISCUSSION

Both bird species richness (BSR) and bird abundance (TBA) were significantly different between watersheds. These differences may be due to unexplored potential differences between drainages in elevation, precipitation, or adjacent habitats. It is important to consider that for many of these analyses, several models were often highly competitive, and only the optimal models for these particular data are reported here. Thus, relatively minor changes in the data (as would be expected through further data collection or narrowing or possibly broadening our definition of “aspen sites”) would likely result in retention of different variables in the optimal models selected. Nonetheless, few major differences are apparent between the watersheds. While each of these models retained a slightly different set of parameters that best predicted their response variable, several common threads may be found, and all suggest positive relationships between birds and mature, pure aspen stands.

While absolute percent of tree-class aspen cover was retained as a positive effect in many of the models for BSR and TBA, all models demonstrated negative relationships between coniferous trees in the canopy and the response variable. Also, tree-class cover of all conifers or individual coniferous species was always retained in models predicting presence or abundance of Dusky Flycatchers and half of the Warbling Vireo models. In several models, tree-class conifer cover was the most influential parameter. It is reasonable to think that the addition of conifers into a pure aspen stand would benefit the avian community by adding structural complexity as well as adding bird species associated with conifers otherwise not found in a pure aspen environment (DeByle 1985b). However, our results suggest that whatever benefits these additions may bring to the avian community are outweighed by the negative impacts of conifer encroachment. These findings mirror those of studies in Colorado (Finch and Reynolds 1988) and South Dakota (Rumble et al. 2001).

Conifer encroachment is the greatest threat to aspen stand survival and condition throughout much of the Sierra Nevada (D. Burton, Aspen Delineation Project, pers. comm.), but the encroachment of conifers may have a direct negative effect on aspen-breeding birds themselves. One possible explanation for the negative relationships between bird numbers and conifer cover is the increased availability of insect prey found in pure aspen habitats. Schimpf and MacMahon (1985) found that insect abun-

Table 2. Habitat parameters retained in optimal regression models predicting (A) BSR and (B) TBA in aspen habitats, eastern Sierra Nevada. Variables are listed in descending order of influence, based on standardized regression coefficients (STB). P-values are from test that parameter = 0.

Variable	STB	P	
A. Breeding Bird Species Richness			
Entire Study Area			
Tree-class conifer cov.	- 0.416	< 0.001	**
Herbaceous cov.	0.264	< 0.001	**
Max. tree DBH	0.212	< 0.001	**
Tree-class aspen cov.	0.187	< 0.001	**
Shrub-class aspen cov.	- 0.131	0.007	**
Shrub species richness	- 0.120	0.007	**
Shrub cov.	0.083	0.106	
Truckee River			
Herbaceous cov.	0.377	< 0.001	**
Tree-class aspen cov.	0.232	< 0.001	**
Max. aspen DBH	0.156	0.014	*
Shrub-class willow cov.	0.117	0.066	†
Tree-class lodgepole pine cov.	- 0.113	0.077	†
Walker River			
Tree species richness	- 0.235	0.002	**
Shrub cov.	0.165	0.019	*
Herbaceous cov.	0.155	0.036	*
Tree-class fir cov.	- 0.155	0.027	*
Tree-class aspen cov.	0.129	0.072	†
Shrub species richness	- 0.128	0.107	
Mono Lake/Owens River			
Herbaceous cov.	0.382	< 0.001	**
Max. tree DBH	- 0.269	0.002	**
Tree-class conifer cov.	- 0.239	0.013	*
Tree-class fir cov.	- 0.193	0.017	*
Shrub-class aspen cov.	- 0.191	0.035	*
Tree cov.	0.161	0.092	†

Table 2. (continued) Habitat parameters retained in optimal regression models predicting (A) BSR and (B) TBA in aspen habitats, eastern Sierra Nevada. Variables are listed in descending order of influence, based on standardized regression coefficients (STB). P-values are from test that parameter = 0.

Variable	STB	P	
B. Breeding Bird Abundance			
Entire Study Area			
Herbaceous cov.	0.314	< 0.001	**
Tree-class conifer cov.	- 0.235	< 0.001	**
Tree cov.	0.192	< 0.001	**
Shrub species richness	- 0.136	0.001	**
Max. tree height	0.125	0.003	**
Shrub-class aspen cov.	- 0.124	0.005	**
Tree-class fir cov.	- 0.087	0.065	†
Truckee River			
Max. aspen height	0.314	< 0.001	**
Herbaceous cov.	0.294	< 0.001	**
Tree-class aspen cov.	0.192	0.005	**
Tree-class conifer cov.	- 0.123	0.043	*
Walker River			
Tree species richness	- 0.246	0.002	**
Tree-class aspen cov.	0.201	0.014	*
Herbaceous cov.	0.176	0.018	*
Shrub species richness	- 0.162	0.041	*
Shrub-class aspen cov.	- 0.155	0.060	†
Tree-class fir cov.	- 0.123	0.076	†
Shrub-class willow cov.	- 0.112	0.092	†
Mono Lake/Owens River			
Herbaceous cov.	0.390	< 0.001	**
Max. tree DBH	- 0.283	0.001	**
Shrub-class aspen cov.	- 0.238	0.004	**
Tree-class lodgepole pine cov.	- 0.234	0.005	**
Shrub species richness	- 0.139	0.107	
Shrub-class conifer cov.	- 0.136	0.097	†
C. Dusky Flycatcher Abundance[a]			
Tree-class conifer cov.	- 0.234	0.002	**
Shrub-class aspen cov.	0.167	0.033	*
Shrub species richness	- 0.154	0.034	*
Max. aspen height	0.140	0.066	†
D. Warbling Vireo Abundance[a]			
Max. aspen DBH	0.181	0.074	†
Tree-class aspen cov.	0.164	0.055	†
Max. aspen height	0.142	0.144	
Shrub-class willow cov.	0.135	0.031	*
Tree-class conifer cov.	- 0.132	0.050	*
Shrub-class aspen cov.	0.130	0.079	†
Herbaceous cov.	0.088	0.236	

** Parameter highly significant (P = 0.001)
* Parameter significant (P = 0.05)
† Parameter marginally significant (P = 0.1)
[a] Abundance models of these species restricted to data from Truckee River sites

dance and species richness were greater in both the aspen understory and canopy than in adjacent coniferous habitats. We speculate that this may be due in part to aspen's ability to remain moist throughout the summer months. DeByle (1985a) provides an overview of the mechanics behind this phenomenon, all of which are compromised by intrusion of conifers into the stand.

Absolute herbaceous cover is an important habitat variable in almost every model. It is unclear whether herbaceous cover provides direct benefits to aspen-breeding birds or if it is merely associated with hidden factors that we failed to measure or parameterize (e.g., moisture, abundance of invertebrates). In these analyses it was often highly positively correlated with a high percentage of aspen in the canopy and negatively correlated with a coniferous overstory. At many sites, release from conifer encroachment through thinning or natural disturbance may stimulate herbaceous growth by increasing both available moisture and sunlight needed by these plants. The herbaceous community experiences significant decreases in species richness and diversity with succession to conifer in the canopy (Harper 1973, Korb and

Table 3. Maximum likelihood estimates, Wald Chi-square statistics, and significance for parameters selected from multiple logistic regression models predicting occurrence of (A) Dusky Flycatcher and (B) Warbling Vireo in aspen habitats, eastern Sierra Nevada. Models built using forward selection on randomly assigned training dataset (67% of stations) and tested against independent validation dataset. Results of overall model are expressed as percent of stations correctly classified.

Variable	Estimate	Wald Chi-sq.	P
A. Dusky Flycatcher			
Entire study area: $P < 0.001$			
Correctly classified: 70.3%			
Max. tree height	0.1054	26.4345	< 0.001
Shrub-class aspen cov.	4.0491	12.8165	< 0.001
Tree-class conifer cov.	- 2.5822	10.3568	0.001
Shrub species richness.	- 0.1804	6.6656	0.010
Shrub cov.	- 0.0214	6.6170	0.010
Walker River: P < 0.001			
Correctly classified: 71.6%			
Shrub-class aspen cov.	5.2093	9.6882	0.007
Shrub cov.	- 0.0450	7.3924	0.007
Tree-class fir cov.	- 0.2491	2.8717	0.090
Mono Basin/Owens River: $P < 0.001$			
Correctly classified: 84.3%			
Herbaceous cov.	0.0643	11.2698	0.001
Tree-class lodgepole pine cov.	-0.0785	2.7640	0.096
B. Warbling Vireo			
Entire study area: P < 0.001			
Correctly classified: 69.5%			
Tree-class aspen cov.	4.3643	14.0831	< 0.001
Herbaceous cov.	0.0129	4.2470	0.039
Tree-class conifer cov.	- 1.2693	3.4388	0.064
Walker River: P < 0.001			
Correctly classified: 70.6%			
Shrub cov.	0.0453	9.9396	0.002
Tree-class aspen cov.	5.8459	9.2959	0.002
Mono Lake/Owens River: $P < 0.001$			
Correctly classified: 68.6%			
Herbaceous cov.	0.0480	10.0439	0.002
Tree-class aspen cov.	4.2001	6.4195	0.011

Ranker 2001), and Harper (1973) found that understory production decreased by 50% where the canopy was composed of a high percentage of conifers (>50%).

Plant species richness in the tree and shrub strata often demonstrated a negative relationship with response variables. As aspen is typically the only hardwood reaching the canopy throughout much of its range in the Sierra Nevada, tree species richness on these sites is increased primarily through the addition of coniferous species. The shrub layer in pure aspen stands tends to consist only of snowberry, willow, and immature aspens. Immature coniferous trees penetrating into these stands tended to increase shrub species richness. Stations along narrow riparian corridors, especially at Mono/Owens sites, tended to host additional shrub species from adjacent, comparatively bird-poor sagebrush or coniferous vegetation communities. In the Truckee River watershed, drier forest sites succumbing to conifer encroachment tended to have the most complex shrub layer, including several species each of *Ceanothus* and *Arctostaphylos*, *Artemisia tridentata*, and the full complement of immature coniferous trees. Such sites typically had few live aspen trees remaining and hosted few birds.

Shrub-class aspen generally demonstrated a negative relationship with BSR and TBA. It is doubtful that birds are avoiding young aspen outright. Indeed the opposite appears to be true for at least one species (Dusky Flycatcher, see below), but two common scenarios help to explain this result. The highest density of shrub-class aspen occurs at stations that are recovering from recent disturbance and therefore undergoing high-output vegetative reproduction (e.g. avalanche paths). These young sites can be choked with a virtual monoculture of uniformly shrub-sized aspen, providing shrub-class aspen cover as high as 97% and typically hold far less diversity than mature sites. These results corroborate those of Scott and Crouch (1998) who found that in Colorado, BSR and TBA was higher in mature aspen than in 6- to 10-year-old clearcuts. Alternatively, the interior of mature aspen stands with a completely closed canopy had far fewer shrub-class aspens in the understory, and stations in this habitat typically had the highest BSR and TBA.

For Dusky Flycatchers, all models demonstrated negative relationships between flycatchers and conifers in the canopy, and increased shrub-class aspen cover was an important predictor of either Dusky Flycatcher presence or abundance in three of the four models for these watersheds. Dusky Flycatchers will use a variety of nesting substrates, including conifer branches, but at these sites they seem to prefer to nest in upright forks of tall shrubs, especially small aspen trees: at Mono, Owens, and Truckee sites, Dusky Flycatcher nests averaged 1.44 m above the ground (n=66), and 70% were located in aspen (unpublished PRBO Conservation Science/Biological Resources Research Center data). Increased shrub-class aspen cover thus equates to an increase in preferred nesting substrate for this species, and lack of preferred nesting substrate may be limiting at stations with a low percent of shrub-class aspen. The Mono/Owens model for Dusky Flycatcher presence had a completely unique set of parameters, suggesting that flycatchers in this part of their range may be selecting for slightly different habitat criteria. However, a considerable discrepancy in the Brier scores between training and validation data suggests that this may not be the optimal model for these data.

Absolute tree-class aspen cover was retained as an important predictor of all Warbling Vireo models. While shrub cover and herbaceous cover may have dropped out first in the forward-selection procedures of the Walker River and Mono/Owens analyses respectively, tree-class aspen cover has a much higher estimate in both cases (Table 3B). Because these variables all measure absolute percent cover, we are confident in the assessment that tree-class aspen cover has the highest influence on vireo presence. arbling Vireo has demonstrated an association with *Populus* species throughout its range (Gardali and Ballard 2000) and is considered an aspen-associated species throughout the western United States (Finch and Reynolds 1988, Mills et al. 2000, Heath and Ballard 2003). Flack (1976) described Warbling Vireo as the "most abundant and frequently encountered bird in aspen forests throughout western mountains," and, despite their widespread presence in other western habitats (e.g., post timber-harvest shrub fields, cottonwoods) Warbling Vireo are more likely to be found in aspen (Hutto and Young 1999). While anecdotal and without comparison of available nesting sites at these locations, it is no less notable that at Mono/Owens and Truckee River study sites, 88 of 91 Warbling Vireo nests were in aspen trees (unpublished PRBO Conservation Science /Biological Resources Research Center data). That presence of both Dusky Flycatcher and Warbling Vireo had significantly negative relationships with tree-class conifer cover is also worth note, as these species are known to breed in purely coniferous stands.

MANAGEMENT IMPLICATIONS

Management Recommendations

Encroachment into aspen stands by conifers has negative impacts on herbaceous cover (Harper 1973, Korb and Ranker 2001), stand moisture (DeByle 1985a), insect abundance (Schimpf and MacMahon 1985), and bird species richness and abundance. Removal of conifers not only helps to ensure long-term persistence of the stand itself, it can be a critical factor in the preservation of the stand's ecological function. We believe that conifer removal in at-risk stands, performed outside of the avian breeding season, may increase bird species richness and abundance overall, and increase the likelihood of occurrence and abundance of aspen-associated species such as Dusky Flycatcher and Warbling Vireo in the Sierra Nevada. Any successful management plan designed to maintain or improve the purity, area, and function of mature aspen stands will almost certainly have positive effects on aspen-breeding bird population levels.

Efforts should be made to manage aspen stands for a healthy herbaceous community. Aspen stands are often very wet or in a true riparian context, and Potter (1998) considered the Quaking Aspen/Corn Lily (*Veratrum californicum*) plant association to be one of the more fragile habitats in the Sierra Nevada. Thus, any conifer-thinning treatment must consider its impact on the soil and its seedbank as well as local hydrological considerations. Also, excessive livestock grazing in aspen stands can degrade the quality of herbaceous cover, alter the hydrological conditions that allow for a vigorous herbaceous understory, and limit aspen regeneration (Bartos and Campbell Jr. 1998).

Efforts should also be made to increase the area, age complexity, and regeneration of aspen habitats at the landscape scale to ensure long-term persistence of aspen in the Sierra Nevada. However, land managers must consider the immediate effects of these actions on bird populations. For example, clear-cutting aspen to promote vegetative regeneration would have an immediate negative impact on most aspen-breeding birds. Repopulation of the stand might be swift for many species, but woodpeckers and other cavity nesters, canopy nesters such as Warbling Vireo, and some forest-interior ground nesting species may not be able to re-colonize the stand for over ten years following treatment (Scott and Crouch 1998). A mosaic of age classes on the landscape should ensure that mature stands are available as refugia for these species.

Aspen and Avian Conservation Planning

Many authors have repeated the statement that, in the semi-arid west, aspens are second only to riparian habitats in terms of biodiversity and importance as wildlife habitat (Kay 1997). This leads to somewhat faulty thinking, however, as aspens and riparian habitat are often the same. Further, evidence from the Sierra Nevada suggests that riparian aspen actually hosts greater bird diversity than other types of riparian habitat (Heath and Ballard 2003). Current California Partners in Flight (CalPIF) Bird Conservation Plans (BCP) present objectives and broad management guidelines for bird conservation in riparian ecosystems. The two potential CalPIF BCPs that might address aspen (Sierra Nevada, Riparian) essentially ignore aspen as an important bird habitat-type (Siegel and DeSante 1999, RHJV 2004). The broad Sierra Nevada Bird Conservation Plan (Siegel and DeSante 1999) lists two priority habitats for conservation of which aspen can be a major component, montane meadows and non-meadow riparian habitat, but aspen is never mentioned explicitly. The Riparian Bird Conservation Plan (RHJV 2004) devotes a brief paragraph to a description of aspen's geographic range and vegetation associations in the state, and little else. Neither plan addresses the importance of aspen habitat on California's birds explicitly. More importantly, a great many aspen stands in the Sierra Nevada are not in a riparian or montane meadow context. Thus, many important aspen habitats fall through the cracks under the current CalPIF BCP framework. We believe that California's bird conservation planning community may be underestimating the importance of aspen. Further, long-term persistence of aspen in the Sierra Nevada, where stands have probably always been restricted to a patchy distribution on limited portions of the landscape, may be no less-threatened than riparian, montane meadow, coastal scrub, blue-oak woodland, or other priority habitats, especially in the face of global climate change (Campbell Jr. and Bartos 2001, Hogg 2001). A CalPIF BCP dedicated to aspen habitats would necessarily overlap with other BCPs, but would allow for the importance of non-riparian, non-montane meadow aspen habitat to receive the attention that it deserves.

Warbling Vireos provide an interesting example of where this need exists. Recent evidence suggests that Warbling Vireo populations are experiencing a significant decline, although the mechanisms are not currently understood (Gardali et al. 2000, Gardali and Jaramillo 2001, Ballard et al. 2003). Warbling Vireo is addressed as a riparian focal species under the current CalPIF framework, but aspen is not specifically addressed in management guidelines for the species (RHJV 2004). In eastern Sierra Nevada riparian habitats, aspen cover was found to be the most highly correlated predictor of vireo occurrence (Heath and Ballard 2003). Conservation and restoration of aspen habitats, riparian or otherwise, in the Sierra Nevada may help to offset or possibly reverse this negative trend at a regional scale.

An added difficulty in conservation planning for aspen explicitly is the wide variety of ecological roles aspen can play, depending on the environmental context. For example, what are the differences between seral and climax aspen communities in terms of importance to breeding birds? Wherever aspen occurs, it is likely to be a keystone species, especially in terms of its effect on local soil, hydrology, and vascular plants, but also birds and other wildlife. Certain generalizations would likely apply to any management guidelines for bird conservation (e.g. herbaceous cover is good for birds in Sierra Nevada aspen stands). However, because of aspen's ecological amplitude, management actions should always be locally prescriptive and not based solely on regional or broader-scale generalizations.

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APPENDIX A. Bird species observed during 5-minute point counts at eastern Sierra Nevada aspen habitat, 2001-2003. Only those species utilized for analyses are included (see Methods for details).

Common Name	*Scientific Name*
Blue Grouse	*Dendragapus obscurus*
Mountain Quail	*Oreortyx pictus*
California Quail	*Callipepla californica*
Band-tailed Pigeon	*Columba fasciata*
Mourning Dove	*Zenaida macroura*
Calliope Hummingbird	*Stellula calliope*

Common Name	*Scientific Name*
Broad-tailed Hummingbird	*Selasphorus platycerus*
Lewis' Woodpecker	*Melanerpes lewis*
Red-naped Sapsucker	*Sphyrapicus nuchalis*
Red-breasted Sapsucker	*S. ruber*
Williamson's Sapsucker	*S. thyroideus*

Common Name	*Scientific Name*
Downy Woodpecker	*Picoides pubescens*
Hairy Woodpecker	*P. villosus*
White-headed Woodpecker	*P. albolarvatus*
Black-backed Woodpecker	*P. arcticus*
Red-shafted Flicker	*Colaptes auratus collaris*
Olive-sided Fycatcher	*Contopus cooperi*
Western Wood-Pewee	*C. sordidulus*
Willow Flycatcher	*Empidonax traillii*
Hammond's Flycatcher	*E. hammondii*
Dusky Flycatcher	*E. oberholseri*
Gray Flycatcher	*E. wrightii*
Pacific-Slope Flycatcher	*E. difficilis*
Cordilleran Flycatcher	*E. occidentalis*
Cassin's Vireo	*Vireo cassinii*
Warbling Vireo	*V. gilvus*
Steller's Jay	*Cyanocitta stelleri*
Clark's Nutcracker	*Nucifraga columbiana*
Black-billed Magpie	*Pica pica*
Tree Swallow	*Tachycineta bicolor*
Mountain Chickadee	*Poecile gambeli*
Bushtit	*Psaltriparus minimus*
Red-breasted Nuthatch	*Sitta canadensis*
White-breasted Nuthatch	*S. carolinensis*
Pygmy Nuthatch	*S. pygmaea*
Brown Creeper	*Certhia americana*
Rock Wren	*Salpinctes obsoletus*
Bewick's Wren	*Thryomanes bewickii*
Winter Wren	*Troglodytes troglodytes*
House Wren	*T. aedon*
Golden-crowned Kinglet	*Regulus satrapa*
Ruby-crowned Kinglet	*R. calendula*
Western Bluebird	*Sialia mexicana*
Mountain Bluebird	*S. currucoides*
Townsend's Solitaire	*Myadestes townsendi*
Swainson's Thrush	*Catharus ustulatus*
Hermit Thrush	*C. guttatus*
American Robin	*Turdus migratorius*
Sage Thrasher	*Oreoscoptes montanus*

Common Name	*Scientific Name*
European Starling	*Sturnus vulgaris*
Orange-crowned Warbler	*Vermivora celata*
Nashville Warbler	*V. ruficapilla*
Virginia's Warbler	*V. virginiae*
Yellow Warbler	*Dendroica petechia*
Audubon's Warbler	*D. coronata auduboni*
Black-throated Gray Warbler	*D. nigrescens*
Hermit Warbler	*D. occidentalis*
MacGillivray's Warbler	*Oporornis tolmiei*
Common Yellowthroat	*Geothlypis trichas*
Wilson's Warbler	*Wilsonia pusilla*
Western Tanager	*Piranga ludoviciana*
Green-tailed Towhee	*Pipilo chlorurus*
Spotted Towhee	*P. maculatus*
Chipping Sparrow	*Spizella passerina*
Brewer's Sparrow	*S. breweri*
Sage Sparrow	*Amphispiza belli*
Savannah Sparrow	*Passerculus sandwichensis*
Fox Sparrow	*Passerella iliaca*
Song Sparrow	*Melospiza melodia*
Lincoln's Sparrow	*M. lincolnii*
Mountain White-crowned Sparrow	*Zonotrichia leucophrys oriantha*
Oregon Junco	*Junco hyemalis thurberi*
Black-headed Grosbeak	*Pheucticus melanocephalus*
Lazuli Bunting	*Passerina amoena*
Red-winged Blackbird	*Agelaius phoeniceus*
Western Meadowlark	*Sturnella neglecta*
Brewer's Blackbird	*Euphagus cyanocephalus*
Brown-headed Cowbird	*Molothrus ater*
Bullock's Oriole	*Icterus bullockii*
Pine Grosbeak	*Pinicola enucleator*
Cassin's Finch	*Carpodacus cassinii*
House Finch	*C. mexicanus*
Red Crossbill	*Loxia curvirostra*
Pine Siskin	*Cardeulis pinus*
Lesser Goldfinch	*C. psaltria*
Evening Grosbeak	*Coccothraustes vespertinus*