QUANTIFYING HABITAT RELATIONSHIPS OF SONGBIRDS IN QUAKING

ASPEN (*Populus tremuloides*) AND OTHER MONTANE COMMUNITIES

OF THE JARBIDGE MOUNTAINS, NEVADA

by

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The following individuals read and discussed the thesis submitted by student Kevin Patrick Glueckert, and they evaluated his presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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DEDICATION

This body of work is dedicated to my Mother and Father, Virginia and Richard Glueckert, for their exemplary inspiration throughout my life.

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ABSTRACT

Quaking aspen (*Populus tremuloides*) woodlands are expected to be sensitive to climate change, and have declined in parts of the West. Great Basin mountain ranges may be near the limits of aspen's climatic threshold, in terms of temperature and aridity, and thus are particularly vulnerable to climate change. Birds associating with aspen are likely to undergo regional population fluctuations and changes in distribution as a result of changes in aspen availability or distribution. Thus, understanding the habitat relationships of avian communities in aspen and other montane cover types is important for tracking the impacts of future landscape change. The mountainous terrain of the Humboldt-Toiyabe National Forest in northern Elko County, NV, supports a patchy array of aspen and conifer forest and shrubland distributed across 2,755 km^2. I quantified avian abundance using point count sampling over two breeding seasons (2010 – 2011) at 389 point locations in or near systematically selected stands of aspen (n = 135). For common species, I compared the mean abundance per stand in aspen to that in conifer, mixed aspen-conifer, and montane sage, using both paired and partially-paired t-tests. Most focal species were significantly more abundant in aspen than conifer (22 of 37 species) or montane sage (30 of 39 species) in the partially-paired comparisons. In paired comparisons, 4 of 15 species were significantly more common in aspen than conifer, and 19 of 24 were significantly more common in aspen than montane sage, but most comparisons with both conifer and mixed aspen-conifer were non-significant due to small sample sizes. I then used mixed-effects multiple regression, with stand and observer crew

as random effects, to identify key habitat and physiographic parameters driving species' abundance. For 8 of 11 aspen associates in mixed-effects models, abundance increased with an increase in aspen within 75 m; abundance also decreased with an increase in conifer for three aspen associates. For three of five conifer associates, abundance increased with an increase in 75-m conifer; abundance also increased with an increase in mixed aspen-conifer for three conifer associates. The results of my study underscore the ecological importance of aspen for montane passerine communities–aspen is preferred by most species over other available habitats, and abundance of most aspen-associated species increased as the proportion of aspen within 75 m increased. A reduction in aspen distribution in the Great Basin is likely to result in a decrease in abundance and distribution of a host of aspen-associated species and could have long-term effects on montane passerine communities. I suggest that management activities promoting aspen's persistence and resilience to climate change be considered as a means for maintaining abundance and species composition of montane bird communities in the island ranges of the Great Basin.

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Introduction

Quaking Aspen (*Populus tremuloides*) communities are of ecological and
conservation interest in the western U.S. because they are biologically diverse, ranked
only behind riparian ecosystems (Winternitz 1980, Rumble et al. 2001). Because aspen is
often the primary deciduous woodland occurring in western montane systems, the
ecological integrity of these areas may be considered dependent on this woodland type
(Kay 1997). When aspen-dominated landscapes transition to either sagebrush (*Artemisia*
spp.) or coniferous forest, there is a noticeable change in plant and animal species
richness and community composition (Bartos 2001). In fact, because of its ecological
importance (Flack 1976), aspen is likely a keystone species (Bartos 2001). Keystone
species carry significant weight in their associated communities, with disproportionate
(and often, indirect) influence on other species (Paine 1995). Additionally, aspen
woodlands provide ecosystem services (Kuhn et al. 2011) such as water table recharge,
soil water retention (DeByle 1985), increased plant, animal, and insect diversity (DeByle
1985, Jones et al. 1985, Chong et al. 2001), and added aesthetic value to mountain
viewsheds (Johnson et al. 1985). As a mesic system, these stands often function as
natural firebreaks (Fechner and Barrows 1976). Disturbance and succession-related
dynamics that historically affected aspen's distribution may be in a state of flux, in part

due to climate change. For ecologists and land managers to comprehend the dynamics affecting aspen, it is useful to consider the historical role of these processes and the outcome of predictive models that forecast long-term trends. Because of substantial environmental variability across the range of aspen communities in North America, research and management of aspen woodlands is best conducted at the local to regional scale (Wiens 1989, Romme et al. 2001).

The sensitivity of quaking aspen to perturbations in the western U.S. has been well documented. Drought, disease, insects, disruption of natural fire regimes, and browsing by wildlife and livestock have all been shown to reduce vitality of aspen communities (Bartos and Campbell 1998, Worrall et al. 2008). In particular, fire suppression likely contributes to long-term reduction in coverage of aspen woodlands (Rehfeldt et al. 2009). Wildfires often effectively renew the early stages of forest community succession in which aspen thrives, but conditions may exist in which aspen re-establishment is precluded due to the effectiveness of conifer re-seeding (Strand et al. 2009). Typically, with long enough intervals between fires, aspen-conifer communities can reach late successional stages, which may result in exclusion of aspen (Bartos 2001, Frey et al. 2004, Di Orio et al. 2005, Kuhn et al. 2011, St. Clair et al. 2013). Although approximately two-thirds of aspen stands in the western U.S. are thought to be seral (Mueggler 1989), many stands in the Great Basin may be nonseral (Mueggler 1989, Shinneman et al. 2013). Nonseral stands are not necessarily fire-dependent, and they often have sufficient regeneration to be self-replacing in the absence of disturbance (Mueggler 1989, Shepperd et al. 2006). Shinneman et al. (2013) described at least five

possible aspen fire regime types in the western U.S., ranging from highly fire-dependent, seral aspen-conifer to fire-independent, stable, pure aspen.

Hanna and Kulakowski (2012) emphasize the importance of research in those forest systems considered to be most at risk because of increasing climatic stressors (IPCC 2007), in part because changes in forest systems result in cascading effects to fauna, communities, and biomes (Hansen et al. 2001). Aspen ecologists seem to be in agreement that changes in the frequency and intensity of landscape disturbances that are predicted to occur as a result of climate change will affect aspen's persistence (Morelli and Carr 2011). As a result, research on aspen communities has become increasingly important (Rogers et al. 2013).

Drought is a major cause of the rapid decline in aspen recently observed in much of the West–a phenomenon known as sudden aspen decline, where stand mortality occurs in as little as 1-2 years (Hogg et al. 2008, Worrall et al. 2008, Rehfeldt et al. 2009). Decreases in annual precipitation and snowpack, and warmer summers, are expected in the western U.S., despite expected increases in precipitation globally (Cayan et al. 2008). Given that the distribution of aspen is in part influenced by temperature and available moisture (Worrall et al. 2008), suitable environments for aspen are likely to shift in distribution and potentially decline in abundance (Rehfeldt et al. 2009). Indeed, models that project change in aspen coverage across the landscape, based on future climate scenarios, show a major decline in aspen by the year 2060 (Rehfeldt et al. 2009, Worrall et al. 2013). Aspen is considered most susceptible to dieback at the edge of its climatic tolerance range, especially at lower elevations where moisture-stress is generally highest (Rehfeldt et al. 2009). Despite the seemingly logical outcomes of these modeling efforts,

predictions of aspen's response to current and projected climatic variability are made with uncertainty (Morelli and Carr 2011). In fact, in some areas, aspen could expand its distribution, especially under fire regimes that decrease competition with conifers (Kulakowski et al. 2013). Thus, inferences from model projections should be made with care across different spatial and temporal scales (Kulakowski et al. 2013).

Fauna currently associated with aspen may follow aspen's trajectory of decline or movement on the landscape due to succession or climate change, or the species may exhibit plasticity in niche breadth and habitat preference. Lack and Venables (1939) noted that while some avian species have specific habitat requirements, others are generalists or demonstrate flexibility in habitat requirements. On a larger scale, not only local patches (Rotenberry and Wiens 1980, Rotenberry 1985), but also the surrounding habitat matrix and the extent of landscape connectivity could be playing a significant role in the distribution and dynamics of avian populations (Wiens 1989, Knick and Rotenberry 1995, Rodewald and Yahner 2001). In riparian cottonwood (*Populus angustifolia*) corridors, Saab (1999) found that occurrence of most avian species was better explained by landscape characteristics than by local habitat patches. Lawler and Edwards (2006) also provide a strong case for approaching habitat association modeling at different scales. Thus, attempts to understand the use of aspen by avian communities should simultaneously consider their use of other habitats in the vicinity.

Avian abundance and species richness is known to be high in aspen in the Great Basin, and the distribution of some avian species may be tied to the distribution of aspen in this predominately shrubsteppe landscape (Dobkin and Wilcox 1986, Dobkin et al. 1995, Earnst et al. 2012). However, few studies have directly compared avian

communities in aspen and other habitats anywhere in the western U.S., and most of those have quantified species richness or diversity rather than abundance. Aspen had higher avian species richness (Rumble et al. 2001) and diversity (Griffis-Kyle and Beier 2003) than ponderosa pine (*Pinus ponderosa*), higher species richness than conifer (Turchi et al. 1995) and higher species diversity than mixed aspen-conifer or conifer (Hollenbeck and Ripple 2007). Griffis-Kyle and Beier (2003) quantified abundance, and found higher relative abundance of all bird detections in aspen compared to ponderosa pine in northern Arizona. Mills et al. (2000) also identified several species that were more abundant in mixed aspen-birch forests than ponderosa pine. In the Great Basin, the Nevada Breeding Bird Atlas (Floyd et al. 2007) describes general patterns of bird occurrence, but not abundance, in 4-km^2 blocks, and there are few survey blocks in aspen of the Jarbidge region. My study is the first to compare avian abundance in aspen to other cover types in the Great Basin, and the first to compare abundance in aspen to fir-dominated conifer woodlands and shrubsteppe in the western U.S.

Given that the distribution of aspen is influenced by available moisture and topographic setting (Worrall et al. 2008), and birds may also be directly affected by those factors, it is interesting to model avian abundance with respect to topographic parameters as well as vegetation. Climate change is also likely to affect birds directly, as well as indirectly via its anticipated effects on aspen. Climate change has influenced changes in avian species' distribution (Thomas and Lennon 1999, Hitch and Leberg 2006, Paprocki et al. 2014), and the timing of migration (Butler 2003, Cotton 2003, Moller et al. 2006) and breeding (Winkel and Hudde 1997, Dunn and Winkler 1999, Moller 2008, Heath et al. 2012). The pattern of change is expected to differ across regions (Marra et al. 2005),

depending, in part, on altitude (Inouye et al. 2000), and latitude and longitude (Tottrup et al. 2010). In some cases, an avian species' preferred elevational niche has become uninhabitable due to climatic changes and subsequent changes in plant communities (Sekercioglu et al. 2008, Fleishman and Dobkin 2009). Similarly, bird species of montane systems in California tracked their climatic niche over the past century, with respect to temperature, precipitation, or both (Tingley et al. 2009). The situation is further complicated by the likelihood that avian communities, and the plant communities on which they depend, will track their respective climatic niches at different rates or in different ways, and that birds will be significantly affected by shifts in distribution of both biotic and abiotic dimensions of their niche (Martin 2001, Auer and Martin 2009).

The Jarbidge and Mountain City Ranger Districts of the Humboldt-Toiyabe National Forest are comprised of nearly 9% aspen and 9% conifer woodlands, and both are primarily surrounded by montane shrublands (Beaty et al. 2004). The interdispersion of these co-occurring cover types presents an optimal setting in which to compare avian abundance in aspen to that in other cover types. Understanding habitat relationships of aspen-associated avian communities is particularly interesting in the montane islands of the Great Basin high desert, where aspen may be near its climatic threshold and thus particularly susceptible to climate change. To understand the potential effects of climate change on aspen-associated avian communities, it is important to quantify their use of both aspen and the non-aspen cover types that are likely to replace, or be replaced by, aspen in the future landscape.

The goal of my research is to quantify the relative importance of aspen and other mesic montane habitats to commonly breeding birds (hummingbirds, woodpeckers, and

passerines) of the Jarbidge region. Specifically, I use avian point counts to compare the abundance of species and nesting guilds in aspen to that in adjacent habitats. I also model avian abundance relative to the proportionate availability of aspen and other cover types, and relative to topographic gradients. In addition to modeling abundance of common species, I model abundance of nesting guilds because they identify predictor variables important to the guild as a whole, and incorporate the responses of less common species that were not modeled as individual focal species (Mac Nally et al. 2008).

Habitat associations of a given species may differ across the species' range, across latitudinal or elevational gradients, and may depend on the particular cover types available in a given study area. For example, Violet-green Swallows (*Tachycineta thalassina*) breed near sea level in the northern part of their range, while usually nesting at elevations greater than 2,000 m in the south (Brown et al. 1992). Similarly, the four major groups of subspecies of the broadly distributed Fox Sparrow (*Passerella iliaca*) show unique habitat preferences (reviewed in Weckstein et al. 2002). Despite these caveats, a review of the literature leads to several predictions about habitat associations of species expected to be present on the Jarbidge study area. The literature review is based primarily on Floyd et al. 2007, Poole 2005, and references therein.

I tested the following predictions within each research objective:

Objective 1. I compared abundance of focal species in aspen to that in each of three common cover types that occur in similar topographic settings: mixed aspen-conifer, conifer, and montane sage.

- Prediction 1.1. I predicted that the following species are more abundant in aspen than conifer: Red-naped Sapsucker (*Sphyrapicus nuchalis*), Downy Woodpecker (*Picoides*

pubescens), Western Wood-Pewee (*Contopus sordidulus*), Warbling Vireo (*Vireo gilvus*), Tree Swallow (*Tachycineta bicolor*), House Wren (*Troglodytes aedon*), Mountain Bluebird (*Sialia currucoides*), Swainson's Thrush (*Catharus ustulatus*), European Starling (*Sturnus vulgaris*), Orange-crowned Warbler (*Oreothlypis celata*), Yellow Warbler (*Setophaga petechia*), Song Sparrow (*Melospiza melodia*), and Brown-headed Cowbird (*Molothrus ater*).

- Prediction 1.2. I predicted that the following species are more abundant in conifer than aspen: Hammond's Flycatcher (*Empidonax hammondii*), Mountain Chickadee (*Poecile gambeli*), Red-breasted Nuthatch (*Sitta canadensis*), Ruby-crowned Kinglet (*Regulus calendula*), Yellow-rumped Warbler (*Setophaga coronata*), Western Tanager (*Piranga ludoviciana*), Chipping Sparrow (*Spizella passerina*), Cassin's Finch (*Haemorhous cassinii*), and Pine Siskin (*Spinus pinus*).

- Prediction 1.3. I predicted that the following species are similarly abundant in aspen and conifer: Hairy Woodpecker (*Picoides villosus*), Northern Flicker (*Colaptes auratus*), Dusky Flycatcher (*Empidonax oberholseri*), Violet-green Swallow, Hermit Thrush (*Catharus guttatus*), American Robin (*Turdus migratorius*), Dark-eyed Junco (*Junco hyemalis*), and Black-headed Grosbeak (*Pheucticus melanocephalus*).

- Prediction 1.4. I predicted that the following species is more abundant in mixed aspen-conifer than aspen: Cordilleran Flycatcher (*Empidonax occidentalis*).

- Prediction 1.5. I predicted that the following species are more abundant in montane sage than aspen: Rock Wren (*Salpinctes obsoletus*), MacGillivray's Warbler (*Geothlypis tolmiei*), Green-tailed Towhee (*Pipilo chlorurus*), Brewer's Sparrow (*Spizella breweri*), Vesper Sparrow (*Pooecetes gramineus*), Fox Sparrow, White-crowned Sparrow (*Zonotrichia leucophrys*), and Lazuli Bunting (*Passerina amoena*).

Objective 2. Using a subset of points that contain aspen, I constructed habitat association models of focal species' abundance using the following major predictors: a) cover type composition within the 75-m count circle; b) cover type composition within 300 m; and c) topographic parameters.

- <u>Prediction 2.1.</u> I predicted that the proportion of aspen within the 75-m count circle is a significant predictor of abundance for any species that is significantly more abundant in aspen than other cover types (as determined by comparisons described in Objective 1).

- <u>Prediction 2.2.</u> I predicted that the proportion of a given non-aspen cover type within the 75-m count circle is a significant predictor of abundance for any species that is significantly more abundant in that cover type than in aspen (as determined by comparisons described in Objective 1).

Methods

<u>Study Area</u>

Located in Elko County, NV, my study area was entirely within the Mountain City and Jarbidge Ranger Districts of Humboldt-Toiyabe National Forest, managed by U.S. Department of Agriculture. The study area perimeter spans approximately 98 km from west to east and 55 km from south to north, encompassing 2,755 sq. km at its minimum extent (longitude: -115.00'00" to -116.07'30" degrees; latitude: 41.30'00" to 41.56'00" degrees N). Much of the perimeter of the study area is high desert managed by U.S. Department of Interior – Bureau of Land Management, but some privately-owned ranches and Native American tribal lands also share its boundary. Aside from an excluded portion of the Mountain City Ranger District in the Independence Mountains, the study area perimeter matches that of the National Forest ranger districts. Some private holdings and state-owned parcels lie within the study area perimeter.

Physiographic features are diverse, from deep canyons to alpine peaks, and most of the terrain is remote and mountainous. The study area includes all or parts of the Bull Run Mountains, Mahogany Range, Copper Mountains, Jarbidge Range, and Elk

Mountain. Watersheds include parts of the Bruneau, North Fork Humboldt, Salmon Falls, South Fork Owyhee, Upper Humboldt, and Upper Owyhee.

Vegetation within the study area has been described in a digital vegetation cover type map obtained from USDA Forest Service (Beaty et al. 2004), and this map is used as the basis for the following description. The study area is primarily comprised of shrub communities (Beaty et al. 2004). Xeric shrub communities comprise 61% of the study area and are predominantly mixtures of mountain big sagebrush (*Artemisia tridentata vaseyana*), little sagebrush (*Artemisia arbuscula*), antelope bitterbrush (*Purshia tridentata*), rubber rabbitbrush (*Ericameria nauseosa*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), basin big sagebrush (*Artemisia tridentata tridentata*), and Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). Mesic shrub communities occupy 13% of the study area and include mixtures of mountain big sagebrush, mountain snowberry (*Symphoricarpos oreophilus*), wax currant (*Ribes cereum*), chokecherry (*Prunus virginiana*), saskatoon serviceberry (*Amelanchier alnifolia*), and snowbrush ceanothus (*Ceanothus velutinus*). Riparian areas comprise 2.5% of the study area and include willows (*Salix* spp.), gray alder (*Alnus incana*), cottonwood (*Populus* spp.), red osier dogwood (*Cornus sericea*), and wet meadows with some quaking aspen.

Woodlands comprise a minority of the study area (21.9%). Quaking aspen and conifer forests each account for about 9% of land cover. Conifer forest primarily consists of subalpine fir (*Abies lasiocarpa*), but also white fir (*Abies concolor*), limber pine (*Pinus flexilis*), whitebark pine (*Pinus albicaulis*), and small amounts of pinyon pine (*Pinus monophylla*). The Jarbidge Wilderness contains 62% of the conifer cover type on the study area (14,725 ha), approximately 90% of which is subalpine fir. Mixed aspen-

conifer comprises 0.3% of the study area. Mountain mahogany (*Cercocarpus ledifolius*) and juniper (*Juniperus* spp.) are dry woodland species that comprise 4% and 0.2% of the study area, respectively.

Large wildfires have burned 58,528 ha (21.2% of study area) since 2000 (unpublished data, USDOI – BLM – Nevada State Office – Mapping Sciences, 2008). Fires in 2000 burned 3,750 ha near the eastern edge of the study area and 11 ha on the western edge. The Snow Canyon fire (1,529 ha) occurred on the western flank of the Independence Mts. in 2006. The Elk Mountain fire (32,574 ha) of the Murphy Complex of 2007, covered much of the eastern portion of Mountain City Ranger District. In 2008, the East Slide Rock Ridge fire (20,664 ha) burned across the northern third of Jarbidge Wilderness and north to within 3 km of the Idaho border. The amount of aspen area affected by these wildfires is 12.4% (2,991/24,087 ha).

The climate of the study area varies with geographic position and can be described using data from SNOTEL (i.e., Snow Telemetry) stations, which record meteorological and snowpack data throughout the western U.S. (USDA – Natural Resources Conservation Service, Snow Survey and Water Supply Forecasting Program). Among the eight SNOTEL sites in my study area and the six years I considered (2006-2011), mean annual precipitation ranged from 36 to 127 cm. Lower elevations are typically warmer and drier than higher elevations. When elevation is held constant, annual precipitation appears to decrease from west to east. For example, mean annual precipitation was 100 cm at the Bear Creek SNOTEL site (elev. 2,450 m), compared to 58 cm at the Pole Creek SNOTEL site (elev. 2,538 m), located 19 km to the east (east of the Jarbidge crest). Similarly, mean annual precipitation for the same period was 73 cm at

the Laurel Draw SNOTEL site, compared to 47 cm at the Big Bend SNOTEL site, located 29 km to the east (elevation of both is approximately 2,042 m). Additionally, for any given SNOTEL location, annual precipitation varies greatly between years (e.g., at Bear Creek, 84 cm in 2007 and 127 cm in 2011, a difference of 34%).

Mean annual temperatures from SNOTEL sites at similar elevations are quite comparable. For example, mean annual temperature in 2010 and 2011 was 5.57°C and 5.45°C at Laurel Draw and 5.85°C and 5.79°C at Big Bend (both at approximately 2,042 m). Mean annual temperature in 2010 and 2011 was 3.30°C and 3.02°C at Bear Creek (2,450 m) and 3.23°C and 2.95°C at Pole Creek (2,538 m) (USDA – Natural Resources Conservation Service, Snow Survey and Water Supply Forecasting Program).

The study area is fragmented by Nevada state highway 225, gravel roads, unimproved roads, and ATV trails. Centers of human activity include the unincorporated communities of Jarbidge and Mountain City (year-round populations of 12 and 70, respectively). Developed sites include five campgrounds and five USDA-Forest Service administrative sites. A few gold mines are still active east of the town of Jarbidge, as well as in the central and western portions of the study area. Sheep and cattle grazing occur over most of the area. Other types of disturbance include fences, power transmission lines, stock ponds, water troughs, and historic, abandoned homesteads and abandoned small mines.

Sampling Design

Stand Selection

To select aspen stands in which I would conduct bird count sampling, I used a digital vegetation cover type layer obtained from USDA Forest Service (Beaty et al. 2004), in which aspen stands are categorized as riparian aspen, non-riparian aspen, or mixed aspen-conifer. For the purpose of stand selection, I pooled mixed aspen-conifer and non-riparian aspen but later separated these cover types based on field vegetation measurements. I only considered stands $\geq$ 4 ha in size because a 4-ha stand could fully contain a 100-m radius point count circle. For riparian stands embedded within non-riparian stands, the criterion for total stand size was also $\geq$ 4 ha.

Because bird survey locations are accessed prior to daylight and surveys are conducted during a 4-hour window of the early morning, I incorporated accessibility by truck, ATV, or foot travel in the sampling plan. Access routes included improved and unimproved roads, ATV trails, and hiking trails. To efficiently survey the area and minimize transit time, I limited the population of aspen stands available for selection to those containing area within 200 m of an access route, and limited survey stations available for sampling to those within 1 km of the access route. Areas near roads were not excluded from sampling because most roads were primitive, remote, and rarely used during the breeding bird season.

Of the 2,979 aspen stands on the study area, 397 (13.3%) met the size and access selection criteria. For available stands, I used systematic random selection to choose a sample of riparian and non-riparian stands with a relatively even geographic distribution. I used the stand's feature identification number (FID), derived in ArcGIS 9.3 (ESRI,

Redlands, California), that corresponds to the stand's geographic location, and drew a systematic sample from the list of numerically sorted feature identification numbers. I then randomly assigned half of the 148 selected stands to be sampled in 2010 and half in 2011. Minor adjustments were made to stand selection to obtain a set of stands that could be surveyed by a two-person crew within a survey morning (i.e., <5% of originally chosen stands were moved between survey years or dropped from selection). Just over half (1,518/2,979, 51%) of all stands on the study area were smaller than the minimum size criteria of 4 ha. Despite the lack of roads and relatively small amount of aspen within the Jarbidge Wilderness, sampling effort was spread fairly evenly across wilderness and non-wilderness areas. Of the 381 stands in the Jarbidge Wilderness, 32 (8.1%) met the selection criteria, and crews sampled 10 of those. Sampling effort was also well distributed across elevations. Aspen occurred on the study area at elevations between 1,619 and 2,849 m; elevations of stands available for selection were 1,860 to 2,683 m; and elevations of selected stands were 1,910 to 2,604 m.

Point Selection

Using ArcGIS, I placed a grid of 100-m radius, contiguous, non-overlapping circles over each selected stand, such that the number of interior circles (i.e., 100% aspen) was maximized. The remaining edge circles contained portions of aspen and other cover types, and I only considered edge circles for sampling if they contained at least 50% aspen. For most stands, I sampled all available interior circles plus two edge circles. For stands with more than four available interior circles, I randomly chose four contiguous interior circles and two contiguous edge circles.

Locations of point count stations were established within ArcGIS prior to field work. I did not adjust locations of point count stations in the field, except for six points that were each moved 20 m further from a stream to decrease potential effects of stream noise on observers' ability to detect birds.

Paired Design

To compare bird abundance in aspen and non-aspen cover types, I used a paired design in which point count locations were placed in aspen stands and adjacent non-aspen cover type patches. A non-aspen cover type patch was suitable for inclusion if it occupied the majority of an aspen stand's edge on the cover type map in ArcGIS, and if it were large enough to encompass at least two 100-m radius circles placed $\geq$ 150 m from the edge of the aspen stand. Crews initially sampled 58 aspen stands and associated non-aspen patches as part of the paired comparison – 20 paired with conifer patches, 24 with montane shrub, and 14 with sage. Paired stands were distributed fairly evenly across the spatial extent of the study area. This paired approach is statistically powerful because observer, date of survey, location, elevation, aspect, and slope are identical or very similar within each pairing–the paired analysis effectively removes shared variance due to these confounding factors and thus strengthens the comparison of interest, which is bird abundance in aspen vs. non-aspen.

During the analysis of paired points, I used only those points meeting the point count type definitions based on field descriptions and orthoimagery from NAIP (National Agricultural Imagery Program). The definitions are given under NAIP Habitat Classification and Point Type Classification. Classifying points in this manner also made it possible to add some paired points to the analysis, especially because presumed aspen

points were sometimes re-classified as mixed aspen-conifer or conifer. New pairings were included only if aspen and non-aspen points were in adjacent polygons, and if avian surveys were conducted by the same field crew on the same date. To avoid pseudoreplication, non-aspen points were paired with only one aspen stand, and vice-versa. The final paired analysis included 38 aspen stands, 10 stands paired with conifer points, 9 paired with mixed aspen-conifer points, and 22 paired with montane shrub or sagebrush cover types.

Avian Survey Technique

I employed a standard 100-m, fixed radius point count protocol of 10-minute duration (Ralph et al. 1993). Observers conducted surveys between 15 minutes prior to sunrise and 10:00 a.m., a period corresponding to peak singing activity. Surveys were not conducted in rain or high wind (> 19 km/hr), as these conditions may negatively affect singing rate and detection probability. Crews flagged count stations during the first bout of surveys, and navigated with GPS to facilitate their relocation. Prior to each point count, observers waited quietly for one minute to allow birds to acclimate to human presence. At each point, observers oriented to the four cardinal directions using a declinated compass, and estimated distance to singing birds and landmarks using a laser rangefinder.

Crews estimated wind speed using the Beaufort Wind Scale (National Meteorological Library 2010), and obtained ambient temperature in a shaded location. Crews estimated stream noise using the following criteria: 0 = Yellow-rumped Warbler song can be heard at distances > 75 m from the observer, 1 = Yellow-rumped Warbler song cannot be heard 75 m away but can be heard 50 m away, 2 = Yellow-rumped

Warbler song cannot be heard 50 m away but can be heard 25 m away, 3 = Yellow-rumped Warbler song cannot be heard 25 m away. This method, rather than a simple ranking of stream noise from 0 to 3, provided more standardization among observers, streams, and days. I selected the song of Yellow-rumped Warbler because a) observers were likely to encounter it most days and thus have its loudness in the forefront of memory, and b) the song is of intermediate loudness and is often discernable near streams.

Observers recorded the following: number of individuals within observation (flocks only), sex (male, female, unknown), age class (adult, juvenile, unknown), paired status (observed with mate or not), initial detection type (song, call, drum, visual), time interval (1 = 0 to 3 minutes, 2 = 3 to 5 minutes, 3 = 5 to 10 minutes), distance category from point center (1 = 0 to 25 m, 2 = 25 to 50 m, 3 = 50 to 75 m, 4 = 75 to 100 m, 5 = hunting or foraging in the airspace over the count circle). Observers did not record birds observed outside the 100-m count radius, or those flying through without foraging. Observers used countdown timers to track time intervals. Observers employed rangefinders to acquire distances to individuals when practical (i.e., open line of sight). Individuals were plotted on a diagram with four cardinal quadrants and concentric circles representing the four distance bands. Observers plotted detections to reduce the potential for double counting individuals, which would inflate relative abundance. During surveys, observers rotated the direction they were facing to facilitate equal sampling of the count circle.

In 2010, crews surveyed 59% of all points (n = 389), and surveyed the remaining 41% in 2011. Each point count station was sampled twice during the respective breeding

season (late May to early July), once by each of two observers that comprised a crew. I balanced surveys across observers within a crew to help offset potential sampling bias caused by observer differences. I also attempted to balance cover types across crews so that different crews surveyed similar proportions of aspen, conifer, and montane sage points. Point counts were primarily conducted by two crews in each year, each consisting of two observers, except that an additional single-person team sampled 2.6% (10/389) of all points in 2010. Between years, crews were different, except that one observer (KG) was a member of a crew in both years and the single observer in 2010 was also a member of a two-person crew in 2011.

Prior to analyses, survey data were truncated to 75-m (i.e., distance band 4 was excluded) because detectability of birds is higher closer to the observer and it avoids any bias that observers might have had to include birds at the edge of the 100-m radius used in the field. I excluded survey points from analysis that had excessive stream noise (16 points with a stream noise level of 3 during one of the two surveys), recent wildfire (35 points), or mountain mahogany as the majority cover type (4 points). I based evidence of recent fire as scorched leaves, or charring on live trees, snags, or coarse woody debris.

NAIP Habitat Classification

Observers used 1-m digital NAIP orthoimagery to help locate unique habitat patches within a 75-m radius of the point count center (USDA-FSA-APFO 2006). Habitat patches for most points (78.9 %, 307/389) were classified during field work, but habitat patches of a few points (n=82) were classified in the laboratory based on NAIP imagery and a comparison with nearby points (see below). Observers identified and delineated unique habitat patches ≥ 625 m^2 (25 m x 25 m), and assigned a cover type classification.

In addition to shrub and woodland community types, polygons could be defined as Grass/Sedge/Forb, Bare/Rock/Scree, or Water. Gaps $\leq$ 625 m^2 in size were not mapped.

For polygons classified as shrub cover types in the field, observers recorded an ocular estimate of the percent of shrub canopy cover occupied by each of the three most common species. In polygons classified as woodland cover types in the field, observers recorded an ocular estimate of percent of total stems of all tree species for the three most common tree species. The definition of tree for this purpose included any woody plant > 1.5 m in height.

I classified shrub communities into three types:

1. Xeric shrub: any mixture of shrubs associated with xeric conditions such as mountain big sagebrush, Wyoming big sagebrush, basin big sagebrush, little sagebrush, antelope bitterbrush, yellow rabbitbrush, or rubber rabbitbrush. The xeric shrub definition also stipulated that shrubs associated with mesic conditions could not comprise > 5% of total shrub cover.
2. Montane shrub: any mixture of mesic and xeric shrubs, where mesic shrubs comprised > 5% of total shrub cover.
3. Riparian shrub: any mixture of mesic shrubs associated with a water source, often with willow or alder present.

I classified woodland communities into the following types:

1. Aspen: > 90% overstory stems are aspen.
2. Conifer: > 90% overstory stems are conifer species.
3. Mixed Aspen-Conifer: mixture of conifer species and aspen, where aspen comprises > 10% and < 90% of overstory stems, and where conifer species comprise > 10% and < 90% of overstory stems.
4. Willow: > 90% overstory stems are willow.

5.   Willow-Aspen: mixture of willow and/or other riparian shrubs, and aspen, where aspen comprises > 10% and < 90% of overstory stems, and where willow and/or other riparian shrubs comprise > 10% and < 90% of overstory stems.

Using tools in ArcGIS 9.3, I digitized cover type polygons from field maps and calculated the percent area for each cover type within each 75-m radius point count circle. For the 82 points where cover types were not mapped in the field, I delineated cover type boundaries in ArcGIS using NAIP imagery and the Forest Service cover type layer. To help identify cover types, I compared the images of these points to nearby count circles for which cover types had been mapped in the field. In addition, for many of these points, I had personal knowledge of cover types from prior site visits.

Prior to analysis, I pooled some infrequently encountered polygon types with more common types that were of similar habitat structure: Riparian Shrub was combined with Willow, and Willow-Aspen was combined with Aspen. In addition to defining cover types, I ground-truthed riparian designations by documenting the presence or absence of available water and the type of water source (i.e., stream, spring, pond, other standing water) within a plot.

Point Type Classification

For the purpose of comparing avian abundance in aspen and non-aspen cover types (see Data Analysis -- Paired and Partially-paired Comparisons), I used the NAIP Habitat Classification (see previous section) and the following scheme to further classify points into four types:

1. Aspen is the most common cover type and comprises > 85% of the point count circle.

2. Conifer is the most common cover type and comprises > 75% of the point count circle, and the sum of aspen and mixed aspen-conifer cover types comprises < 15%.

3. Mixed Aspen-Conifer is the most common cover type, and the aspen cover type comprises < 15%.

4. Montane Shrub is the most common cover type, and the sum of aspen and mixed aspen-conifer cover types comprises < 15%.

b. Sage is the most common cover type, and there are no aspen, mixed aspen-conifer, or willow-aspen cover types within the point count circle. Sagebrush and montane shrub were then pooled into a new category called montane sage because of structural similarities and small samples of each.

Data Analysis

Paired and Partially-Paired Comparisons

I used paired t-tests in SAS v9.2 software to compare mean differences in abundance of focal species in aspen vs. conifer, aspen vs. mixed aspen-conifer, and aspen vs. montane sage cover types. Stand means were derived from points within stands, and point type means and standard errors were then calculated from means across stands within point types. I tested for normality using the Shapiro-Wilk test (SAS Institute 2011).

I also used partially-paired t-tests to compare abundance of focal species among cover types (aspen vs. conifer = 125 stands, aspen vs. mixed aspen-conifer = 130, aspen vs. montane sage = 134). The partially-paired comparison retains some of the advantages

of the paired approach because both paired and unpaired data are used, and it has the advantage of using over twice the sample size as the paired analysis (n = 169 vs. 79 stands). In partially-paired comparisons, the mean abundance per cover type and difference between cover types is calculated using all points in each cover type that met the point type definition (i.e., pairing is ignored), but the standard error of the difference is adjusted to properly account for the covariance between aspen and non-aspen types within the paired data (Bart et al. 1998, p. 74, equations 3.6 and 3.7).

For both paired and partially-paired analyses, I adjusted p-values for multiple comparisons, using Benjamini and Hochberg's false discovery rate (Benjamini and Hochberg 1995). This adjustment holds the false discovery rate, i.e., the rate at which rejected hypotheses are rejected falsely, at $p = 0.05$ and provides more statistical power than holding the family-wise error rate at $p = 0.05$ (Westfall et al. 1999). Adjusted p-values < 0.05 were considered statistically significant. Throughout the text, I use the term preference to indicate that a species' relative density (i.e., abundance per point count) is significantly higher in one cover type compared to another.

I limited analyses to passerines, woodpeckers, and hummingbirds. For paired and partially-paired comparisons, I restricted focal species to those occurring on at least seven stands within each comparison (e.g., 7/10 paired stands in the paired aspen-conifer comparison, and 7/125 stands in the partially-paired aspen-conifer comparison, of which 111 were aspen and 14 were conifer stands). The number of focal species meeting this restriction for paired and partially paired comparisons, respectively, was 15 and 38 for aspen vs. conifer, 14 and 38 for aspen vs. mixed aspen-conifer, and 24 and 40 for aspen vs. montane sage. Except Brown-headed Cowbird, I assigned each species (whether focal

or not) to one of three nesting guilds: overstory, ground/understory, or cavity. I pooled species' abundances within each guild and compared abundance of each guild across cover types using the same approach as for species.

Mixed Model Regression

I used mixed model regression to investigate the effect of vegetative cover type and topographic parameters on a species' abundance. I used the original points systematically placed within selected aspen stands and that field observations confirmed contained aspen (n = 324). I did not include any conifer or montane sage points that had been added to the design for the paired comparison. I conducted species-specific regression models for those species with a sum of $\geq$ 2 individuals on > 10% of points (where sum is the sum of counts from the two visits to a point). Because many aspen associates met this definition, I modeled only the two most abundant species within the overstory-, understory-, and ground-nesting aspen guilds. I modeled all five cavity-nesting aspen-associates because this group is of particular conservation interest. In total, I present models for 11 aspen associates, five conifer associates, one montane sage associate, three aspen-associated nesting guilds, and three conifer-associated nesting guilds.

For regression models, I divided each of the three nesting guilds into conifer- or aspen-associated nesting guilds based on results of the partially-paired comparison. Species more common in aspen at a p-value < 0.10 were assigned to the appropriate aspen-associated nesting guild; species more common in either conifer or mixed-aspen conifer at p < 0.10 were assigned to the respective conifer-associated nesting guild.

I used general linear mixed models to build species-specific bird-habitat relationship models and used the sum of counts for each bird species from the two visits to a point as the response variable. I used either negative binomial and poisson distribution for a given species; both distributions are appropriate for count data such as mine (Littell et al. 2006). Negative binomial is a more generalized case of poisson; negative binomial does not require the assumption that the mean equals the variance and it uses a scale parameter to account for overdispersion, i.e., the extent to which the variance is greater than the mean (Littell et al. 2006). I used negative binomial distribution for all models of a species when the coefficient of the scale parameter was significant in the univariate, fixed-effect model with either aspen, conifer, or montane sage (for aspen-, conifer-, or montane sage- associates), and used poisson distribution when the coefficient was not significant (Littell et al. 2006). In some cases (i.e., for four species) it was necessary to switch to poisson rather than negative binomial distribution when models did not converge upon the addition of random effects. I used the GLIMMIX procedure in SAS v9.2 because it supports the use of these non-normal distributions in mixed-effect models (Littell et al. 2006, SAS Institute 2011). I used mixed-effects models so that stand identity and observation crew could be added as random effects to account for the covariance between points within the same stand or surveyed by the same crew. Degrees of freedom were based on the Kenward-Roger method (SAS Institute 2011).

I used a hierarchical model-building process consisting of four stages (see Table A.1) designed to address the following questions: Does cover type composition within 75-m, or the presence of water in combination with cover types, explain bird abundance (Stage 1)? Does cover type composition at the 300-m scale explain any variation in

addition to what is explained by cover type composition at the 75-m scale (Stage 2)? Do topographic parameters, and indices derived from those parameters, explain any variation in addition to what is explained by cover type composition at 75-m and 300-m scales (Stage 3)? Does the addition of timing of the survey within the season explain additional variance in addition to that explained by cover types and topography (Stage 4)? At the end of each stage, I carried the best model subset forward to the next stage, using Akaike's Information Criterion (AIC) to identify best model subsets (Burnham and Anderson 2002). Although other approaches, such as evaluation of all possible combinations of all parameters, might have led to models with lower AIC values, my specific goal was to evaluate hypotheses, not to obtain the model with the lowest AIC. Fixed-effect models were evaluated without the addition of random effects so that models could be readily compared using AIC values. In models with poisson or negative binomial distributions, likelihoods are based on pseudo-likelihoods, causing AICs and other model comparison techniques to be invalid (Littell et al. 2006). After fixed-effect model building was complete, the two random effects, stand identification and crew, were added to the best subset of fixed-effect models.

In Stages 1 and 2, fixed effects included percent of 75-m and 300-m radius circles occupied by aspen (Asp75 and Asp300), mixed aspen-conifer (MixAC75 and MixAC300), conifer (Con75 and Con300), and montane sage (Mtsg75 and Mtsg300). Presence or absence of water (Rip) was included as a categorical variable at the 75-m scale. At the 300-m scale, I used the derived parameter Nasp300 to describe the relative contribution of montane sage and conifer to the non-aspen cover type matrix around aspen stands, defined as Mtsg300/(Mtsg300 + Con300). Similarly, Ncon300 was used to

describe the relative contribution of montane sage and aspen to the non-conifer matrix; it is defined as Mtsg300/(Mtsg300 + Asp300). To describe the relative contribution of conifer and aspen to the non-montane sage matrix, I used Nmtsg300, defined as Con300/(Con300 + Asp300). I also used the edge-to-area ratio (E2A) of aspen at 300-m, where edge (in meters) and area (in hectares) were calculated using tools in ArcGIS. Squared terms for cover type parameters at the 75-m and 300-m scales were included as potential fixed effects to allow non-linear relationships between the species' abundance and percent cover type. I used NAIP imagery to derive 75-m parameter values, and the Forest Service cover type layer for 300-m parameters.

At Stage 3, I considered the following six topographic parameters that I derived from digital elevation maps using tools available in ArcGIS (ESRI 2013) and the Geomorphometry and Gradient Metrics Toolbox (Evans 2012).

1. Elevation is mean altitude (m) within 75-m point count radius as calculated using tools in ArcGIS (ESRI 2013) and 20-m resolution digital elevation models (DEMs).

2. Southwestness (SW) is a measure of transformed aspect at the point count center with the highest values at SW aspects and the lowest at NE aspects, ranging from 2.0 (225 degrees) to 0.0 (45 degrees). SW was calculated using tools in ArcGIS (ESRI 2013) based on the formula in Beers et al. (1966): SW = cos(45-Aspect) + 1.

3. Slope is mean percent incline within 75-m point count radius, as obtained from 9-m resolution continuous floating point raster grid, and was calculated using tools in ArcGIS (ESRI 2013).

4. Heat Load Index (HLI) is an aspect-adjusted and slope-adjusted value of solar radiation, with the highest values at SW aspects and the lowest at NE aspects. HLI was calculated using tools in Evans (2012) and is explained more fully in McCune and Keon (2002).

5.   Compound Topographic Index (CTI) is an assessment of steady state soil moisture, based on slope and surrounding upstream physiography, which influences flow accumulation. Values increase as slope decreases and area of upstream flow accumulation increases. CTI was calculated using tools in Evans (2012) and is explained more fully in Gessler et al. (1995).

6.   Precipitation (Prec) is projected mean annual precipitation based on a model that spatially interpolates weather station data from 1981-2010 and accounts for physiographic influences such as rain shadows from mountain ranges (PRISM Climate Group 2012). The Prec value for a point count station was the value of the 800-m resolution raster cell in which it occurs.

At Stage 4 of model-building, I asked whether date of first survey (Day) improved upon the cover type and topographic model, where Day was coded as the number of days past April 30 that the first survey was conducted at a point (e.g., May 21 has the value "21"). The day of the first survey was investigated because it might have been near the arrival date for some species at some elevations. The second survey was well within the breeding period of species considered here.

I used different modeling schemes for aspen-, conifer-, and montane sage associates (see Table A.1). To determine which scheme to use for a given species, I used univariate linear regression to determine which cover type at the 75-m scale was a significant, positive predictor of abundance (Asp75, Con75, MixAC75, or Mtsg75). If more than one cover type was a significant positive predictor in univariate models (as was true for one species), both modeling schemes were used. The conifer scheme was used for species having either Con75 or MixAC75 as a significant, positive univariate predictor. If none of the cover types was a significant predictor (i.e., the null model was

the best model), the species was assigned to a scheme based on results of the paired t-test. I removed some of the more complex models (i.e., those with a squared term for one cover type combined with a second cover type at the same scale, and those with interaction terms) from the conifer and montane sage modeling schemes due to a smaller sample size of points dominated by those cover types.

To avoid multicollinearity, I did not allow the following highly correlated parameters ($r > 0.70$) to occur in the same model (Kleinbaum and Kupper 1978): Asp75 and MixAC75 ($r = -0.76$), Asp300 and Ncon300 ($r = -0.85$), and Nasp300 and Con300 ($r = -0.94$). As an exception to this rule, I included E2A and Asp300 ($r = -0.78$) in the same model because I preferred the ecological interpretation of E2A as edge-to-area when the effect of area is also in the model. In addition, I did not allow base parameters and parameters derived from them to be used in the same model. As a result, HLI, CTI, and precipitation were tested independently and none were used in combination with slope, aspect, or elevation.

I used an information-theoretic approach (Burnham and Anderson 2002), with modifications by Arnold (2010), to select the best subset of models for each species. At the end of each stage, either the simplest model with the lowest AIC was selected as the most parsimonious, or a more complex model was selected if it was >2 AIC units lower for every parameter increase over the simpler model. The best model subset for a given stage included the most parsimonious model and any within 4 AIC units of it, except that following Arnold (2010), I did not include models < 2 AIC units from the most parsimonious model that differed from it by one parameter (or <4 AIC if differing by two parameters). This approach helps to limit interpretation to truly competitive models and

to parameters that explain important additional variance (Burnham and Anderson 2002:170, Arnold 2010). At the end of Stage 4, I removed parameters that were not statistically significant ($p > 0.05$) from models in the best model subset and compared resulting models to originals to obtain the final best model subset. The final best model subset included the most parsimonious model and any models within 4 AIC units of it. For species having more than one competitive model in the best model subset, I used Akaike weights (w_i) as a measure of the relative likelihood that model i was the best predictive model (Burnham and Anderson 2002).

After fixed-effect model-building was complete, I added stand and crew as random effects to the best fixed-effects model for each species. Stand was a categorical variable serving as a unique identifier for each aspen stand (stands with only one point count station were merged with adjacent stands). Crew was a categorical variable indicating which observation crew (two each in 2010 and 2011) collected the data at a given point. In four cases in which the mixed-effects model with stand and crew as random effects did not converge, I used only stand as the random effect. The addition of random effects appropriately adjusts the coefficients and standard errors of fixed effects to account for shared variance among observations within stands and crews. Throughout Results and Discussion, I report and interpret fixed effect coefficients and standard errors that resulted from mixed-effect models. Only significant predictors ($p < 0.05$) in best model subsets are interpreted (Arnold 2010).

I also report the statistical significance of random effects to examine whether the addition of stand and crew improved the fixed-effects model. The statistical significance of random effects is based on likelihood ratio tests which use pseudo-likelihoods (Littell

et al. 2006). I considered using year of survey rather than crew (each crew surveyed in only one year, so year is a subset of crew), however, the crew parameter more effectively accounts for observer differences, and the ecological interpretation of year and crew models were identical in interim results (i.e., the values of fixed-effect coefficients were similar and their statistical significance did not differ).

Results

Description of Vegetation at Sampled Points

By design, the aspen cover type was present on all points used in multiple regression analyses; it comprised >50% of the count circle at 72% of points, and it was the only cover type at 10% of points (Table C.1). The conifer cover type was present on 16% and montane sage on 76% of count circles used in multiple regression analyses, and rarely did either comprise >50% of the count circle. For points at which species composition was recorded in the field, aspen was the most common tree recorded (83% of points; Table C.2). At conifer points used in the paired and partially-paired comparisons, fir was the most common tree at 80.0% and pine at 20% (Table C.3). At mixed aspen-conifer points, fir was the most common tree at 67% and aspen at 33%. Willow also occurred on 37% of mixed aspen-conifer points. Big sagebrush was one of the three most common shrubs on 95% of montane sage points, mountain snowberry on 62%, and serviceberry and chokecherry on 33% each (Table C.4).

Paired Comparisons

Most focal species (77%, 30 of 39 species) were more abundant in aspen than in montane shrub (Table 2; Fig. 2 to 5), and results were consistent across nesting guilds –

ground-understory-, overstory-, and cavity-nesting guild (all species pooled within each) were each significantly more common in aspen than montane shrub. The results were similar in the analysis of paired stands, in which 79% (19 of 24) of focal species were more common in aspen (Table 3). Three species (Green-tailed Towhee, Brewer's Sparrow, and Vesper Sparrow) all of which were ground or understory nesters were significantly more common in montane shrub than in aspen in both the paired and partially-paired comparisons.

Most focal species (59%, 22 of 37 species) were more common in aspen than conifer stands (Table 4; Fig. 6 to 9). The ground-understory-nesting guild (all species pooled) and most (80%, 12 of 15) ground-understory-nesting focal species were significantly more common in aspen than in conifer stands. Likewise, the cavity-nesting guild (all species pooled) and many cavity-nesting focal species (55%, 6 of 11 species) were more common in aspen than in conifer stands. In contrast, slightly more overstory-nesting focal species were more common in conifer (4 of 10 species) than in aspen (3 of 10 species), and three overstory-nesting species did not differ. In results from paired stands, four species were more common in aspen than in conifer, Ruby-crowned Kinglet was more common in conifer, and 10 species did not differ, in part due to the small sample size in paired comparisons (Table 5). Among species significantly preferring conifer over aspen, three were ground-understory nesters (Hermit Thrush, Chipping Sparrow, Dark-eyed Junco) and two were cavity nesters (Mountain Chickadee, Red-breasted Nuthatch).

Six of nine species that were more abundant in conifer than aspen were also more common in mixed aspen-conifer than aspen (Table 6; Figs. 10 to 12). However, of the 22

species that preferred aspen over conifer, only 12 (55%) preferred aspen over mixed aspen-conifer. The remaining 10 species showed no preference (Table 6). Species more abundant in mixed aspen-conifer were primarily overstory nesters (5 of 7 species). In paired comparisons of aspen versus mixed aspen-conifer, none of the 14 focal species showed a significant preference (Table 7).

Predictions were met for 22 of the 31 species that were predicted to prefer one cover type over another. Predictions were met for most species (12/13) expected to be more common in aspen than conifer, and most species (7/9) expected to be more common in conifer than aspen. Abundance of Downy Woodpecker, Hammond's Flycatcher, and Pine Siskin was not different in aspen and conifer. Of the eight species expected to not differ in abundance between aspen and conifer, the Dusky Flycatcher, Northern Flicker, American Robin, and Black-headed Grosbeak were more common in aspen, and the Hermit Thrush and Dark-eyed Junco were more common in conifer. Cordilleran Flycatchers were predicted to have higher abundance in mixed aspen-conifer but this difference was not statistically significant. Of the eight species expected to be more common in montane shrub than aspen, only Green-tailed Towhee, Brewer's Sparrow, and Vesper Sparrow were more common in montane shrub, while MacGillivray's Warbler, Fox Sparrow, and Lazuli Bunting were more common in aspen.

Avian-habitat Relationship Models

As the amount of aspen within a 75-m radius of the count center increased, abundance increased significantly for 8 of 11 aspen associates (Tables 8 to 10). For three of these aspen associates (Red-naped Sapsucker, House Wren, MacGillivray's Warbler), aspen-squared was an important predictor indicating the slope of the relationship between

abundance and amount of aspen varied as the amount of aspen increased (Fig. 13). Both Red-naped Sapsucker and House Wren abundance appeared to increase more steeply at higher percentages of aspen, while MacGillivray's Warbler abundance appeared highest at intermediate amounts of aspen. These three species were also the only species with percent aspen at 300-m as an important predictor in the best model subset (Fig. 14)–a negative predictor of Red-naped Sapsucker and House Wren abundance, and a marginally significant positive predictor of MacGillivray's Warbler abundance ($p = 0.081$).

Three aspen associates decreased in abundance as percent of conifer within 75-m increased, including two species with 75-m aspen as an important positive predictor (House Wren and Yellow Warbler) and one species without aspen (Orange-crowned Warbler) (Fig. 15). Yellow Warbler abundance was higher, and Orange-crowned Warbler abundance was lower, in riparian areas relative to non-riparian areas (Fig. 16). Northern Flicker and American Robin best model subsets did not include any cover type parameters (Table 11).

For most aspen associates (9 of 11 species), best model subsets included topographic or climatic parameters (Tables 8 to 11). Dusky Flycatchers increased, and House Wrens decreased, with elevation gain (Fig. 17). The squared elevation term was important in Yellow Warbler models and visual interpretation of the data suggests that abundance increased somewhat with elevation at lower elevations and declined at higher elevations (Fig. 17). Mountain Bluebird abundance decreased as slope increased (Fig. 18). American Robin abundance also decreased as slope increased in the most parsimonious model ($\omega_i = 0.62$), and abundance decreased as elevation increased in the alternate model ($\omega_i = 0.38$) (Fig. 17 and 18). Tree Swallow abundance increased as

compound topographic index increased, indicating that this species preferred areas at the bottom of drainages (Fig. 19). Northern Flicker, Warbling Vireo, and Orange-crowned Warbler abundance declined with increasing precipitation, indicating that these species preferred drier topographies (Fig. 20). Orange-crowned Warbler abundance also increased with later date of first survey.

For each of the three aspen nesting guilds, abundance increased with increasing aspen (Fig. 13) and declined with increasing conifer at the 75-m scale. For overstory nesters, visual inspection indicates that abundance increased with percent aspen more steeply at higher percentages of aspen. For understory nesters, the relationship between abundance and percent aspen appeared to plateau at higher percentages of aspen. For cavity-nesters, abundance declined with increasing aspen at the 300-m scale (Fig. 14). For understory nesters, abundance increased as the proportion of montane sage relative to conifer increased (i.e., Nasp300) (Table 10). Among the three competitive models for overstory nesters, riparian was a significant positive predictor in two ($p = 0.03$ and 0.05, $\sum \omega_i = 0.76$), precipitation was a significant negative predictor in two ($p = 0.03$ and 0.02, $\sum \omega_i = 0.77$), elevation was a marginally significant negative predictor in one ($p = 0.08$, $\omega_i = 0.23$), and day of first survey was non-significant in one ($p = 0.28$, $\omega_i = 0.24$) (Table 10).

For 3 of 5 conifer associates (Mountain Chickadee, Ruby-crowned Kinglet, Yellow-rumped Warbler), abundance increased with increasing amount of conifer at 75 m and increasing amount of mixed aspen-conifer at 75 m (Tables 12 to 14, Fig. 21 and 22). For Cassin's Finch, mixed aspen-conifer squared was an important predictor and visual inspection indicated that abundance increased more steeply at low and high

amounts of mixed aspen-conifer than at intermediate amounts (Fig. 22). Dark-eyed Junco abundance was lower in riparian relative to non-riparian areas, and decreased as the proportion of montane sage relative to aspen increased at the 300-m scale (i.e., Ncon300) (Table 14).

For most conifer associates (4 of 5 species), abundance increased with elevation (Fig. 23, Tables 12 to 14). Elevation was a significant or marginally significant positive predictor of abundance for Cassin's Finch ($p = 0.004$) and Dark-eyed Junco ($p = 0.06$), and for Yellow-rumped Warbler ($p = 0.01$) and Ruby-crowned Kinglet ($p = 0.06$) in the most parsimonious model of their best model subsets ($\omega_i = 0.37$ and 0.77, respectively). In alternate models, rather than increasing with elevation, Yellow-rumped Warbler abundance marginally decreased with either increasing heat load index ($p = 0.08$, $\omega_i = 0.34$) or increasing slope ($p = 0.08$, $\omega_i = 0.29$), and Ruby-crowned Kinglet abundance decreased with increasing heat load index ($\omega_i = 0.23$). Dark-eyed Junco abundance increased with day of survey.

For each of the three conifer-nesting guilds, abundance increased with increasing mixed aspen-conifer at the 75-m scale (Tables 13 and 14). Conifer-associated cavity and overstory nester abundance also increased with increasing conifer at the 75-m scale. Elevation squared was an important predictor for both overstory and understory nesters ($p = 0.07$ and $p = 0.0095$, respectively). Conifer-associated understory nesters were less abundant in riparian relative to non-riparian areas, declined in abundance with an increasing proportion of montane sage relative to aspen at the 300-m scale (i.e., Ncon300), and increased with later day of first survey.

The montane sage modeling scheme was used for Green-tailed Towhees because they had montane sage as a significant, positive predictor in univariate regression (Table B.1). For Green-tailed Towhees, in each of the three competitive models, abundance increased with increasing amount of montane sage at 75 m (Fig. 24), and was lower in riparian relative to non-riparian areas (Tables 15 and 16). The three models differed in whether Green-tailed Towhee abundance increased from northeasterly to southwesterly aspects ($\omega_i = 0.54$), increased with slope ($\omega_i = 0.25$), or increased with heat load index ($\omega_i = 0.21$) (Table 16). Because MacGillivray's Warblers had both aspen and montane sage within 75 m as significant, positive, univariate predictors (Tables B.1 and B.2), both modeling schemes were used (Table A.1). The montane sage model ($\omega_i = 0.17$) provided some evidence that MacGillivray's Warblers increased with intermediate amounts of montane sage within 75 m and with day of survey (Fig. 24, Tables 15 and 16).

Consequences of Random Effects

When stand and crew were added as random effects, stand was significant or marginally significant in nearly all cases (29 of 32 models) (Table D.1). Crew was significant or marginally significantly in only 15 of the 28 models that converged. Mixed-effect models did not converge, or the G-matrix was not positive definitive, for Mountain Chickadee, Orange-crowned Warbler, Cassin's Finch, and the conifer-associated cavity-nesting guild. Adding crew and stand as random effects to a model rarely changed the interpretation of its fixed effects. Fixed effects became non-significant in only three of the 32 mixed-effect models (Tables 11, 14, and 16). The fixed effect "day" was the parameter that most often became non-significant (two models) or marginally significant (four models). Other parameters became marginally significant in 11 models.

Aspen associates appear to treat mixed aspen-conifer differently than do conifer associates. Most species (12/22, 55%) that preferred aspen over conifer also preferred aspen over mixed aspen-conifer and none preferred mixed aspen-conifer over aspen. In contrast, most species (6/9, 67%) with higher abundance in conifer over aspen also had higher abundance in mixed aspen-conifer over aspen. In addition, most species (6/7) that were more common in mixed aspen-conifer than in aspen were conifer associates, and none were aspen associates. These findings are consistent with several prior studies that note a decline in species richness in the transition from aspen to conifer (Turchi et al. 1995, Mills et al. 2000, Rumble et al. 2001, Griffis-Kyle and Beier 2003).

Avian-habitat Relationship Models

Aspen Associates -- Overview

As predicted, most (8 of 11) aspen-associated species increased as aspen cover within 75-m increased in multiple regression models. Northern Flicker, American Robin, and Orange-crowned Warbler lacked 75-m aspen in their best models and appeared to respond primarily to topographic and climatic parameters, although both the Northern Flicker and Orange-crowned Warbler increased with increasing aspen in univariate models. House Wrens exhibited a positive change in the slope of the relationship as the amount of aspen increased, and MacGillivray's Warblers preferred intermediate amounts of aspen. Best models for House Wren and Yellow Warbler included both 75-m aspen (positive) and 75-m conifer (negative).

Yellow Warbler was the only aspen associate to increase in abundance with the presence of a water source within 75-m. Presence of water was also a positive predictor for all aspen associates pooled. Orange-crowned Warbler decreased in abundance with

the presence of water. These results may have differed if I had defined riparian on a larger scale (e.g., presence of water within 150 m or 300 m rather than within 75 m).

I found only moderate evidence that surrounding cover types (i.e., those outside the 75-m count circle) influenced avian abundance within the 75-m circle. For one, the ground- and understory-nesting guild of aspen associates (pooled) increased in abundance as the proportion of shrub cover relative to conifer within 300 m increased. Also, House Wrens and Red-naped Sapsuckers both decreased significantly with 300-m aspen, despite their positive response to 75-m aspen. A combined positive response to 75-m aspen and negative response to 300-m aspen may indicate a preference for relatively small stands in an open landscape, or for stands with substantial openings or edge. However, for all but one aspen associate, 300-m aspen did not provide more explanatory power than 75-m aspen alone, indicating that aspen within the greater landscape had little additional influence. Only MacGillivray's Warblers increased in abundance with increasing 300-m aspen; however, this result was only marginally significant, which suggests that large stands are not considerably better than small stands for most of the species studied. While my study does not directly address the effects of stand size, stand size is an ecologically relevant parameter that warrants further investigation.

Elevation influenced abundance of four aspen-associated species. Dusky Flycatchers increased in abundance as elevation increased, while House Wren and American Robin abundance decreased as elevation increased. For House Wrens, this may be a function of an increase in conifer cover at higher elevations. Yellow Warblers appeared to be most common at intermediate elevations with a strong decrease in abundance at higher elevations. The curvilinear nature of the relationship may partially

result from low abundance in the relatively small sample of low-elevation aspen stands (< 2,000 m).

Three aspen associates responded negatively to increasing mean precipitation: Northern Flicker, Warbling Vireo, and Orange-crowned Warbler. Precipitation is likely tied to both elevation and cover type to some extent. One interpretation of these models is that higher precipitation is correlated with more conifer cover and thus decreased abundance of aspen associates. Univariate results confirm that these three species decreased in abundance with both increasing conifer and precipitation. Precipitation in xeric landscapes is a parameter of interest, since higher avian species richness has been found to be driven by annual precipitation and net primary productivity (van Rensburg et al. 2002). Similarly, Lawler et al. (2004) found higher avian species richness in areas with higher annual precipitation and lower mean July temperatures.

Three out of four ground-nesters exhibited a positive response to advancing first day of survey, and two of them are aspen associates: Orange-crowned Warbler and MacGillivray's Warbler. I interpret this to be a function of receding snowpack and the resulting phenology of grasses, forbs, and shrubs, which provide concealment for ground nests.

Conifer Associates -- Overview

As predicted, most conifer associates increased in abundance as conifer increased (3 of 5); the exceptions were Cassin's Finch and Dark-eyed Junco. Most conifer associates (4 of 5) also increased in abundance with increasing proportion of mixed aspen-conifer. Species increasing in abundance with both parameters were Mountain Chickadee, Ruby-crowned Kinglet and Yellow-rumped Warbler. Cavity and overstory

nesting guilds of conifer associates also increased in abundance with both of these cover types. Dark-eyed Junco was the only conifer species for which neither conifer nor mixed-aspen conifer remained in the best model subset, and the only conifer associate with riparian designation and the proportion of shrub relative to aspen within 300 m to remain in the best model subset.

Elevation was a positive predictor of abundance for four of five conifer associates. To some extent, this positive response to elevation may reflect the distribution of conifer, which constitutes a greater proportion of vegetative cover at higher elevations. Elevation and 300-m conifer cover were moderately correlated ($r = 0.50$).

Day of first survey was a significant positive predictor of Dark-eyed Junco abundance. This may be a function of more snow-free areas later in the spring, especially at high elevations (which this species prefers), and thus more growth of herbaceous cover for this ground-nesting species.

Ruby-crowned Kinglet abundance was highest in areas of lower heat load index (HLI), suggesting that combinations of aspect and slope that have high solar radiation (McCune and Keon 2002) are not favorable for this species. With this response to heat load index, there appears to be microclimatic differences within conifer stands that affect Ruby-crowned Kinglets, as well as Yellow-rumped Warblers (result was marginally significant).

Montane Sage Associates -- Overview

As predicted, montane sage was a significant positive predictor of both Green-tailed Towhee and MacGillivray's Warbler abundance. Green-tailed Towhee abundance

decreased significantly with the presence of a water source in all models, and increased in the three competitive models with southwest aspect, increasing slope, or increasing HLI. Together, these models indicate that Green-tailed Towhees prefer montane sage in a fairly xeric, upslope micro-topographic setting. In contrast, MacGillivray's Warblers were more common at points with intermediate amounts of aspen in one model and more common with intermediate amounts of montane sage in the other competitive model. At the elevations where MacGillivray's Warblers were common, most points were comprised of aspen and montane sage, thus both models are consistent with an interpretation of MacGillivray's Warblers preferring the shrub-aspen interface. Further analysis is necessary to assess whether the two species prefer different shrub species compositions within montane shrub.

Because my study was designed to understand aspen-associated species, sampling units for multiple regression were points in aspen stands. As a result, most species that nest in montane sage were not abundant enough to meet my criteria for model-building. Still, montane sage has been demonstrated to be an important breeding habitat for many species (Knick and Rotenberry 1995, 1999, Rotenberry and Knick 1999).

Habitat Relationships of Understory and Overstory Nesting Aspen Associates

Warbling Vireos were more common in aspen than in conifer, mixed aspen-conifer, or montane sage cover types, and their abundance in aspen stands was related to 75-m aspen (+), precipitation (-), and first day of survey (+). Findings for Warbling Vireo are reasonably consistent with the literature. Warbling Vireos are known to be common breeders in aspen in the western U.S. (Turchi et al. 1995, Mills et al. 2000, Rumble et al. 2001, Griffis-Kyle and Beier 2003, Heltzel and Earnst 2006, Earnst et al. 2012).

Warbling Vireos may be found even where small patches (as small as a single tree) of deciduous trees occur within conifer stands (reviewed in Gardali and Ballard 2000). Richardson and Heath (2004) found decreasing abundance with increasing conifer cover in the eastern Sierra Nevada. In the southern Sierra Nevada, Warbling Vireos nested in deciduous trees more often than expected based on availability, but often nested at sites without deciduous trees (Purcell 2007). Because conifer cover is higher in areas of higher precipitation in my study area, the negative relationship with precipitation may reflect Warbling Vireos' preference for aspen over conifer cover. I did not find a positive association with riparian areas, as described by Salt (1957), Marzluff and Lyon (1983), Purcell (2007), and Gardali and Ballard (2000), either in the best model subset or in the univariate model for riparian designation. In some regions, this species' association with riparian areas appears due to the deciduous overstory occurring there (Marzluff and Lyon 1983). Day of first survey was a marginally significant positive predictor and is presumed to reflect advancing stages of aspen leaf-out at later dates and related increases in insect availability.

Yellow Warblers were more common in aspen than in conifer, mixed aspen-conifer, or montane sage, and their abundance in aspen stands was related to 75-m aspen (+), 75-m conifer (-), presence of water (+), and elevation^2 (-). These habitat relationships are comparable to those in the literature. Yellow Warblers are common breeders in aspen in the Great Basin (Heltzel and Earnst 2006, Earnst et al. 2012) and western U.S. (Salt 1957). Raphael et al. (1987) found them to be absent from mature conifer in the Sierra Nevada, and similarly, I found a significantly negative relationship with conifer. It is well known that Yellow Warblers are associated with riparian areas in the western U.S.

(reviewed in Heath 2008). In my study, riparian designation includes any water source within the 75-m circle, and its positive effect on Yellow Warblers is likely due, in part, to the presence of small patches of willow, alder, or other riparian shrubs near water. I found abundance steadily decreased with increasing elevation over most of the range of aspen I sampled (above 2,000 m). However, at a small sample of stands (n = 24) at elevations <2,000 m, abundance was much lower than at intermediate elevations.

Yellow Warblers are typically associated with habitats that include a prominent shrub component (reviewed in Lowther et al. 1999), including in western landscapes such as the northern Sierra Nevada, where they are more common in chapparal than surrounding mixed conifer forests (Siegel and DeSante 2003, Heath 2008, Humple and Burnett 2010). Total shrub cover was a significant positive predictor of Yellow Warbler abundance in chapparal, where the primary shrub species were greenleaf manzanita (*Arctostaphylos patula*), mountain whitethorn (*Ceanothus cordulatus*), and bush chinquapin (*Chrysolepis sempervirens*) (Humple and Burnett 2010). Similarly, abundance of breeding Yellow Warblers was highest in areas dominated by shrubs (primarily snowbrush ceanothus) where mixed-conifer forest was re-establishing 21-25 years post-fire, compared to earlier years following fire (Raphael et al. 1987). I suspect that understory mesic shrubs within aspen stands, or willows interspersed with aspen in riparian areas, increased Yellow Warbler abundance in my study, and I plan to examine the effect of understory composition and stand structure on bird abundance in future analyses. However, on my semi-arid study area where the montane shrub cover type is more xeric than the shrub cover found in the northern Sierra Nevada, I did not find that Yellow Warblers associated with the montane shrub cover type.

Dusky Flycatchers were more common in aspen than in conifer, mixed aspen-conifer, or montane sage cover types, and their abundance in aspen stands was affected by 75-m aspen (+), elevation (+), and day of first survey (-). Habitat preferences of Dusky Flycatchers vary regionally in the western U.S., and they are common breeders in aspen in the Intermountain West (reviewed in Sedgwick 1993, Mills et al. 2000, Heltzel and Earnst 2006, Earnst et al. 2012). The Nevada Breeding Bird Atlas suggests they are most common in montane shrub and montane woodlands with a shrub understory (Floyd et al. 2007). Other studies also suggest that Dusky Flycatchers are associated with shrub-dominated cover types or shrub understories. For example, in selectively-logged mixed conifer sites in central Idaho, Dusky Flycatchers placed territories in areas with more mesic shrub cover, particularly mountain maple (*Acer glabrum*), ninebark (*Physocarpus* spp.), and snowbrush ceanothus (Kroll and Haufler 2010). In western Wyoming, foliar cover around nests, particularly between 1-5 m in height, was the best predictor of Dusky Flycatcher habitat selection in an open mixed-conifer forest with a big sagebrush understory (Kelly 1993). My finding that Dusky Flycatcher abundance increased with elevation and decreased with earlier survey dates is consistent with other studies that found this species to be common at high elevations (reviewed in Sedgwick 1993, Floyd et al. 2007, Pereyra 2011) and to adjust the timing of breeding to match snow melt, plant phenology, and insect emergence (Pereyra 2011).

MacGillivray's Warblers were more common in aspen than either conifer or montane sage, and their abundance in aspen was influenced by 75-m aspen^2 (-), 300-m aspen (+), and day of first survey (+) in the most supported model, and by 75-m montane sage^2 (-) and day of first survey (+) in the alternate model. The squared terms, and visual

inspection of Figs. 13 and 24, indicate that MacGillivray's Warblers were more common at intermediate amounts of aspen or intermediate amounts of montane sage. Because all sampled points used in regression models were at least partially within aspen stands, I interpret the two models as indicating a preference for the aspen-shrubsteppe interface. Day of first survey was a positive predictor of MacGillivray's Warbler abundance, and may be related to timing of snow-free conditions and the phenology of ground cover that conceals early nesting attempts.

Several studies support the assertion that MacGillivray's Warblers are found in areas of high (and typically mesic) shrub density. In early-successional Douglas fir (*Pseudotsuga menziesii*), MacGillivray's Warblers were positively associated with deciduous shrub cover, primarily vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), salmonberry (*Rubus spectabilis*), and thimbleberry (*Rubus parviflorus*), and negatively associated with deciduous tree cover, primarily red alder (*Alnus rubra*) (Morrison 1981). In the same area, Morrison and Meslow (1983) found this species increasing in density as low vegetative cover (< 1.0 m) increased, but also as deciduous tree cover increased. Similarly, MacGillivray's Warbler density increased with increasing shrub cover in chaparral in the northern Sierra Nevada (Humple and Burnett 2010). In central Nevada mountains where primary cover types were aspen, willow, and big sagebrush, the probability of occupancy of MacGillivray's Warblers increased with increasing frequency of riparian shrubs and with increasing proportion of riparian plants such as willow, chokecherry, and elderberry (*Sambucus cerulean*) in the canopy (Dickson et al. 2009). Floyd et al. (2007) and Ryser (1985) also describe this species' preference

for riparian areas in the Great Basin, but I did not find them to be more common at sites with water present in either multiple or univariate regression models.

Orange-crowned Warblers were more common in aspen than in conifer or montane sage, and their abundance in aspen was influenced by 75-m conifer (-), presence of water (-), precipitation (-), and first day of survey (+). In univariate models, Orange-crowned Warblers were more common at intermediate amounts of aspen within 75 m, and also increased with increasing amounts of montane sage. However, the avoidance of conifer proved to be a better predictor in multiple regression models and was the only cover type predictor in the best model subset. Taken together, I interpret these results as indicating that this species is most common at the aspen-montane sage interface.

Orange-crowned Warblers are known to breed in aspen and riparian areas in the Great Basin (Earnst et al. 2012) and elsewhere (Dieni and Anderson 1999, review in Gilbert et al. 2010). The difference between my finding that Orange-crowned Warblers avoid riparian areas within aspen stands and the literature is likely related to scale. While my definition of riparian was presence of water within 75 m, and regression results come from points in aspen stands, other studies likely refer to a larger riparian buffer and are comparing riparian areas to primarily unsuitable cover types (rather than restricting the comparison to one cover type known to be suitable – aspen). Day of first survey was also a significant positive predictor of abundance and may be related to timing of snow-free conditions and the phenology of ground cover that conceals nests.

American Robins were more common in aspen than in conifer or montane sage in partially-paired comparisons. However, in regression analyses, the null cover type model performed better than any single cover type model, and the best model subset contained

only slope (-), and day of first survey (-). In the alternate model, robin abundance decreased as elevation increased. Robins are typically considered habitat generalists (reviewed in Sallabanks and James 1999), but specific habitat associations have been identified in some regions. In Wisconsin, robins preferred mixed deciduous-conifer forest tracts containing an abrupt edge with alder shrub cover (Hawrot and Niemi 1996). In the western U.S. and northern Great Basin, robins are common nesters in aspen (Turchi et al. 1995, Mills et al. 2000, Rumble et al. 2001, Heltzel and Earnst 2006, Earnst et al. 2012) and in a variety of conifer forest types (reviewed in Sallabanks and James 1999, Sallabanks et al. 2002). In conifer forests, increasing stem density of trees has a significant negative effect on robin density (Hansen et al. 1995), which suggests a preference for more open conifer stands.

Habitat Relationships of Cavity-Nesting Aspen Associates

The keystone role of Northern Flickers and Red-naped Sapsuckers as primary cavity excavators makes understanding their habitat relationships a conservation priority, in part because of implications for a suite of secondary cavity nesters (Martin et al. 2004). Indeed, populations of secondary cavity nesters may be limited by availability of cavities (Newton 1994, Dobkin et al. 1995, Aitken and Martin 2008). Red-naped Sapsuckers are integral in shaping avian communities in aspen woodlands (Dobkin and Wilcox 1986, Ehrlich and Daily 1988, Fleury 2000) and create significantly more cavities than other primary excavators in some locations (Daily et al. 1993). However, in British Columbia, secondary cavity-nesters used Red-naped Sapsucker cavities proportionately less, and Northern Flicker cavities proportionately more, than predicted by availability (Aitken and Martin 2004). Northern Flickers accounted for nearly half of cavity excavations, and just

over half of those were occupied by primary or secondary cavity nesters (Aitken and Martin 2004). Northern Flickers, which are described as weak excavators (Harestad and Keisker 1989), nested in snags proportionately more than live trees in aspen stands of Hart Mountain, Oregon, while Red-naped Sapsuckers nested in live trees and snags in proportion to their availability (Dobkin et al. 1995). Because aspen stands contain more live than dead trees, and cavities created in live aspen trees remain available over twice as long as those in dead trees (Edworthy et al. 2012), it is possible that Red-naped Sapsuckers are providing a longer term benefit for secondary cavity nesters. Both Red-naped Sapsuckers and Northern Flickers preferentially excavate in trees with heartwood decay which is commonly created by shelf fungi (*Fomes* spp.) (Crockett and Hadow 1975, Harestad and Keisker 1989, Daily 1993).

Because of the keystone role these primary excavators have in structuring communities, as well as population declines in Northern Flickers (Sauer et al. 2000) and the restricted range of Red-naped Sapsuckers (Rich et al. 2004), further research is warranted on these species. In particular, Sauer et al. (2000) emphasize the importance of understanding causes of population declines and identifying management solutions, and Warren et al. (2005) emphasize the need for research on landscape-scale habitat relationships of all cavity nesters. Li and Martin (1991) point out that loss of aspen could decrease availability of suitable cavity substrate and increase competition for cavities.

Northern Flickers were more common in aspen than conifer or montane sage, and marginally more common in aspen than mixed aspen-conifer. However, the best regression model contained mean precipitation as the only predictor, and indicated that Northern Flicker abundance in aspen was higher in areas of lower mean precipitation.

This finding is consistent with evidence that drier areas may have higher availability of ants, a major food source for Northern Flickers (Elchuk and Wiebe 2002). The finding of lower abundance in areas with higher mean precipitation may also result, in part, from one or more of the following relationships: 1) decreasing abundance with an increase in elevation (which the univariate model supports), 2) decreasing abundance with an increase in conifer cover (which the univariate model supports), 3) decreasing abundance with an increase in conifer cover relative to aspen cover and a concomitant decrease in forest-edge habitat. Indeed, when precipitation, vegetative cover, and elevation layers are overlaid in GIS, the positive correlation between them is evident. At sampled points, there is considerable correlation between precipitation and elevation ($r = 0.62$), precipitation and conifer cover within 300 m ($r = 0.58$), and elevation and conifer cover within 300 m ($r = 0.50$).

My finding that Northern Flickers were more abundant in aspen is consistent with much of the literature. Northern Flickers are typically more common in aspen than montane conifer forests (Turchi et al. 1995, Mills et al. 2000, Rumble et al. 2001, Griffis-Kyle and Beier 2003). Additionally, in boreal areas, Northern Flickers associated with early seral aspen (Kirk et al. 1996), and in western North America, aspen trees were commonly selected as nest sites in forests where conifer species occur in far greater proportion (Li and Martin 1991, Martin and Eadie 1999, Wiebe 2001, Martin et al. 2004). In general, Northern Flicker nest site characteristics vary greatly, but must be located near suitable foraging habitat (Conner and Adkisson 1977). For example, in British Columbia, Northern Flickers preferred home ranges with a greater proportion of non-wooded habitat for foraging, and the spatial configuration of their foraging sites

influenced home range size and shape (Elchuk and Wiebe 2003). At this site, home ranges were comprised largely of grassland, edges of forest patches (aspen, lodgepole pine (*Pinus contorta*), Douglas-fir), and edges of ponds and lakes. In managed mixed deciduous, deciduous-conifer, and mixed conifer forest of New Brunswick, Warren et al. (2005) found that Northern Flicker occupancy was influenced by stem density, forest type, and stand age at various spatial scales (i.e., 100-m, 300-m, and 1,000-m). Based on their model, they suggest maintenance of open areas at local and 300-m scale would benefit Northern Flickers.

Red-naped Sapsuckers were more abundant in aspen than in conifer, mixed-aspen conifer, or montane sage, and their abundance in aspen stands was influenced by 75-m aspen^2 (+) and 300-m aspen (-). Sapsucker preference for aspen relative to conifer in the western U.S. has been documented by several prior studies (Turchi et al. 1995, Mills et al. 2000, Rumble et al. 2001, Griffis-Kyle and Beier 2003). My finding that sapsucker abundance was highest at intermediate amounts of 75-m aspen and decreased with 300-m aspen could suggest a preference for stand edges or smaller stands. In the Uinta Mountains of Utah, Red-naped Sapsucker nesting habitat was typically near stand edges adjacent to open areas, and usually not in stands encompassed by conifer forest (Lawler and Edwards 2002). Crockett and Hadow (1975) found that aspen were required for Red-naped Sapsucker nesting in three study areas, where 100% of nests were in aspen stands and adjacent conifer stands were used for foraging. Other studies have also documented this species commonly breeding in aspen (Smith 1982, Daily et al. 1993, Dobkin et al. 1995, Earnst et al. 2012).

Tree Swallows were more common in aspen than either conifer or montane sage, and their abundance within aspen was related to 75-m aspen (+), compound topographic index (+), and day of first survey (-). The preference for aspen is consistent with several studies in western North America (Salt 1957, Winternitz 1980, Dobkin et al. 1995, Turchi et al. 1995, Lawler and Edwards 2002, Aitken and Martin 2008) and may be driven by co-occurrence with Red-naped Sapsuckers. Elsewhere in the Great Basin, a majority (over two-thirds) of Tree Swallow nest cavities were excavated by sapsuckers (Dobkin et al. 1995), and this preference for sapsucker cavities is thought to be related to entrance dimension and avoidance of competition with European Starlings (Rendell and Robertson 1989). Furthermore, in Colorado, Daily et al. (1993) found that Tree Swallows only bred in aspen stands occupied by Red-naped Sapsuckers, which favored stands near (<50 m) or including willow. In contrast, in mixed aspen-conifer stands in British Columbia, Aitken and Martin (2004) found that Tree Swallows used flicker-excavated cavities more, and sapsucker-excavated cavities less, than expected based on availability.

Tree Swallows appear to avoid nest cavities near the edge of aspen stands, possibly as a means of avoiding competition with House Wrens (Rendell and Robertson 1990). Alternatively, Tree Swallows may also be reducing costs of brood-rearing by nesting close to forest edges that are adjacent to open habitats used for foraging (Aitken et al. 2002). My finding that Tree Swallow abundance in aspen stands increased with increasing values of compound topographic index (CTI) indicates a preference for valley bottoms or low-lying areas. It is likely that the abundance of aerial insects is higher in these low-lying areas, especially if they contain water (reviewed by Winkler et al. 2011). Lastly, day of first survey was a marginally significant, negative predictor in the best

model and may be related to fewer visual observations with advanced aspen leaf-out, as many Tree Swallow detections are visual.

House Wrens were more common in aspen than in conifer or montane sage, and their abundance within aspen stands was influenced by 75-m aspen^2 (+), 75-m conifer (-), 300-m aspen (-), and elevation (-). The higher abundance at intermediate amounts of aspen within 75 m and in landscapes with less aspen within 300 m suggests a preference for medium-sized stands or possibly stand edges. Similarly, in forests in mid-Atlantic states, Robbins et al. (1989) found lower probability of House Wren occurrence as forest area increased, especially in tracts exceeding 100 ha. Likewise, smaller stands of aspen were found to be commonly used in Saskatchewan (Johns 1993). My finding that House Wren abundance in aspen stands decreases with elevation may be related to higher elevations having more conifer, a cover type that I found them to avoid. House Wrens are known to be common breeders in aspen in the Great Basin (Earnst et al. 2012) and western U.S. (Salt 1957, Turchi et al. 1995, Griffis-Kyle and Beier 2003) but an avoidance of conifer has not been previously reported (reviewed in Johnson 1998). The availability of nest cavities is likely a factor in House Wrens' preference for aspen in my study area and elsewhere, where primary excavators are more common in aspen. Dobkin et al. (1995) suggest that House Wren life history traits, especially their ability to re-nest readily and raise two broods, may facilitate their disproportionate use of available cavities and cause a subsequent negative effect on other cavity nesters.

Mountain Bluebirds were more common in aspen than in conifer, mixed aspen-conifer, or montane sage cover types, and their abundance in aspen stands was influenced by 75-m aspen (+) and slope (-). An association with aspen by Mountain Bluebirds has

been shown in the Black Hills of South Dakota (Rumble et al. 2001) and the Teton

Mountains of Wyoming (Salt 1957). However, most documentation of this species'

habitat preferences are for edge, openings, and recently burned areas (reviewed in Power

and Lombardo 1996, Aitken et al. 2002), in diverse montane habitats (Floyd et al. 2007).

Limited availability of nest cavities may be driving the Mountain Bluebird's habitat

selection at local scales (Dobkin et al. 1995). In aspen woodlands at Hart Mountain,

Oregon, Dobkin et al. (1995) found this species using Northern Flicker cavities more

often than Red-naped Sapsucker cavities. In British Columbia, the Mountain Bluebird's

preference for nest cavities in aspen over conifer may be a result of aspen's frequent

occurrence near edges of mixed aspen-conifer forests (Aitken et al. 2002). Mountain

Bluebirds are not restricted to montane forest types but instead also occur in high desert

habitat with suitable nest sites. For example, along a gradient of shrub-steppe to late-

successional juniper, Mountain Bluebirds were significantly more common in old-growth

juniper (Reinkensmeyer et al. 2007).

Habitat Relationships of Conifer Associates

Yellow-rumped Warblers were more common in conifer and mixed aspen-conifer

than in aspen, and their abundance in aspen stands was affected by 75-m conifer (+) in all

models, by elevation (+) in one model, by 75-m mixed aspen-conifer (+) and heat load

index (-) in a second competing model, and by 75-m mixed aspen-conifer (+) and slope (-

) in a third competing model. The literature also describes Yellow-rumped Warblers as

being associated with conifer (Snyder 1950, Douglas et al. 1992, Mills et al. 2000) and

mixed-aspen conifer cover types (Schieck et al. 1995, Kirk et al. 1996). Likewise,

Yellow-rumped Warblers increased with an increase in mature conifer cover in boreal

forests of western Canada (Kirk et al. 1996). Yellow-rumped Warblers have also been found to be more common in older stands of aspen (> 120 years old) that are transitioning to late seral communities with conifer (Schieck et al. 1995, Schieck and Nietfield 1995, Kirk et al. 1996). My finding that Yellow-rumped Warblers increased with increasing elevation could be related to the greater extent of conifer cover and/or cooler microclimate at higher elevations. Similarly, the finding that Yellow-rumped Warbler abundance decreased with increasing heat load index suggests that Yellow-rumped Warblers may be seeking cooler microclimates in conifer forest.

Cassin's Finches were more common in conifer and mixed aspen-conifer than in aspen, and their abundance in aspen stands was affected by mixed aspen-conifer^2 (+) and elevation (+). The squared mixed aspen-conifer term reflects a steeper increase in abundance at lower amounts of mixed aspen-conifer (0 – 40%) than at higher amounts. Unlike the other conifer associates, Cassin's Finches increased with increasing amount of mixed aspen-conifer rather than conifer. The literature confirms this species' use of various conifer forest types, including mixed aspen-conifer (Behle et al. 1985, Ryser 1985, review by Hahn 1996). The increase in abundance with elevation that I found is consistent with prior studies of Cassin's Finches (reviewed in Hahn 1996).

Dark-eyed Juncos were more common in conifer and mixed aspen-conifer than aspen, and their abundance in aspen stands was influenced by presence of water (-), ratio of shrub-to-aspen at 300-m (-), elevation^2 (+), and day of first survey (+). In univariate regression models, conifer and mixed aspen-conifer were significant positive predictors, and aspen was a significant negative predictor, of Dark-eyed Junco abundance. However in multiple regression models, neither conifer nor mixed aspen-conifer was a better

predictor than absence of a water source. Because Dark-eyed Juncos use a wide array of cover types during the breeding season (reviewed in Nolan et al. 2002), including riparian and snow-pocket aspen stands (Earnst et al. 2012) and forest edges (pers. obs., and Ryser 1985), it is not surprising that the regression model did not include a specific cover type. Although the negative response to a water source within 75 m at first seems inconsistent with Ryser's (1985) observation that they occur along forest edges associated with riparian corridors, the issue may be one of scale (i.e., the edge of the riparian vegetation may often be more than 75 m from water) or a result of forest edges not associated with riparian corridors being common on the Jarbidge study area. In addition, this ground-nesting species may be avoiding dense riparian shrub cover or avoiding encounters with nest predators that might use riparian corridors as travel routes.

The higher Dark-eyed Junco abundance in areas where the non-conifer matrix at 300-m contained proportionately more aspen than montane sage is consistent with their preference for aspen over montane sage in partially-paired comparisons. The increase in abundance with elevation is consistent with other studies that show them breeding across a wide elevational gradient (e.g., reviewed in Nolan et al. 2002, Bears et al. 2009). The increased abundance at later dates of first survey may be related to more snow-free areas or increased time since snowmelt, and thus more grass and forb cover for this ground-nesting species.

Mountain Chickadees were more common in conifer and mixed aspen-conifer than in aspen, and their abundance in aspen stands was influenced by 75-m conifer (+) and 75-m mixed aspen-conifer (+). This is consistent with qualitative descriptions of their

association with conifer and aspen (Ryser 1985) or mixed conifer (Turchi et al. 1995), and their use of conifers for foraging (Douglas et al. 1992, McCallum et al. 1999).

Ruby-crowned Kinglets were more common in conifer and mixed aspen-conifer than aspen, and their abundance in aspen stands was affected by 75-m conifer (+) and 75-m mixed aspen-conifer (+). In addition, elevation-squared was a positive predictor of abundance in the most supported model and heat load was a negative predictor in the alternate model. A preference for cooler areas (those with a lower heat load) is consistent with a preference for higher elevations, where this species is known to commonly breed (Marshall et al. 2003). My finding that Ruby-crowned Kinglets are more common in conifer and mixed aspen-conifer than in aspen is consistent with descriptions of this species being in older stands of conifer (Turchi et al. 1995) and mixed aspen-conifer (Snyder 1950, Kirk et al. 1996). Similarly, in Saskatchewan, Ruby-crowned Kinglets were more common in older aspen with more conifers and shrubs than in other aspen stands (Hobson and Bayne 2000), and more common in older stands (100+ years) than younger stands of mixed conifer-deciduous forest (Cumming and Diamond 2002). In northeast Oregon, Ruby-crowned Kinglet density was higher in managed than old-growth mixed-conifer forests (Mannan and Meslow 1984). This finding was unexpected, according to the authors, and probably related to the closed canopy in the old-growth stands, where tree species composition was otherwise favorable.

Habitat Relationship of Montane Sage Associates

Green-tailed Towhees were more common in montane sage than aspen, and their abundance in aspen stands was related to 75-m montane sage (+) and presence of water (-). Alternate models also included either southwest aspect (+), slope (+), or heat load

index (+). Several studies describe Green-tailed Towhee as a shrubsteppe associate (Braun et al. 1976, Wiens and Rotenberry 1981, Sedgwick 1987, Knopf et al. 1990), but Reinkensmeyer et al. (2007) found it to be a grassland associate in central Oregon. Green-tailed Towhees breed in diverse sagebrush communities ranging from those that include mountain mahogany and chokecherry (Knopf et al. 1990), to those that include antelope bitterbrush and green rabbitbrush (Wiens and Rotenberry 1981). Green-tailed Towhees also breed in post-disturbance, early seral montane conifer and mixed shrub habitats (reviewed in Dobbs et al. 2012) and chapparal (Humple and Burnett 2010). Although Berry and Bock (1998) found that Green-tailed Towhee presence in northern Colorado was negatively associated with shrub cover at 50-m, they attribute this to avoidance of vegetative cover with low diversity. The presence of water as a negative predictor in my models, and either increasing slope, southwesterly aspect, or increasing heat load index as positive predictors in alternate models is consistent with descriptions of Green-tailed Towhees occurring on dry slopes (Ryser 1985, Hutto 1995).

Other Considerations Affecting Interpretation

Observer Differences and Detectability

Studies using point count surveys to estimate avian abundance often employ multiple observers and thus should take observer differences into account (Kendall et al. 1996). Observers may differ in their ability to detect birds (Robbins et al. 1986, Sauer et al. 1994, Nichols et al. 2000), to distinguish between species (Scott and Ramsey 1981) and to distinguish between individuals within a species (Bart and Schoultz 1984). An observer's ability to detect an individual bird may be influenced by the distance and density of singing individuals, as well as habitat structure (Emlen 1971, Bart and

Schoultz 1984). In my study, I took the following steps to minimize observer effect: 1) selection of experienced observers that had at least three months of experience conducting singing bird surveys, 2) one week of intensive field training that included observers conducting simultaneous point counts and comparing results, 3) use of rangefinders to obtain distance of bird locations (Alldredge et al. 2007), 4) truncation of data to 75-m radius (Buckland et al. 2001), 5) two visits to each point count circle, each by a different observer, 6) an overall design that balanced cover types among crews, and for some questions, a paired design in which the same observers surveyed both cover types of the pair, and 7) pooling observations within a two-person crew and using crew as a random effect in mixed models. Adding both crew and stand as random effects to a model rarely changed the interpretation of fixed effects (i.e., fixed effects became non-significant in only three species-specific mixed-effect models).

Importantly, my research compares relative abundance among cover types and across topographic gradients, and does not attempt to estimate population size. Thus, the only observer or detection issues of importance would be those that resulted in a higher detection rate in one cover type than another. Although most detections are auditory rather than visual, differences between habitats in visibility of birds could produce different detection rates between habitats. For example, visual detection rates might be lower in structurally complex aspen, conifer, and mixed aspen-conifer forests than in montane sage, and thus removing this potential bias would result in the difference in bird abundance in aspen vs. montane sage being greater than reported here.

Inferences about Conifer and Montane Sage Associates

As the emphasis of my study was to quantify the relative importance of aspen to songbirds and to identify habitat relationships within aspen stands, a large number of point count stations were placed in systematically chosen aspen stands. As a result, the estimates of avian abundance in aspen are statistically robust. For comparison to aspen stands, points were also placed in conifer or montane sage patches 150 m to 650 m from aspen stands. For some aspen associates, this design might somewhat overestimate their abundance in non-aspen if they frequent the edges but not the interiors of non-aspen patches. Removing this potential bias would only strengthen my conclusion that the abundance of these species is greater in aspen than non-aspen. On the other hand, for some non-aspen associates, this design might somewhat underestimate their abundance in non-aspen if they avoid edges and favor the interiors of non-aspen patches. If this potential bias was removed, some species that showed no preference between aspen and non-aspen might be shown to be more common in non-aspen (e.g., Hairy Woodpecker and Hammond's Flycatcher in conifer, and White-crowned Sparrow in montane sage). Likewise, a larger sample of conifer and montane sage points would have provided more statistical power to detect a difference between abundance in aspen and these non-aspen cover types, and I might have been able to conduct analyses on some additional fairly common non-aspen species, such as Black-billed Magpie (*Pica hudsonia*), Clark's Nutcracker (*Nucifraga columbiana*), Brown Creeper (*Certhia americana*), and Western Meadowlark (*Sturnella neglecta*).

The multiple regression study was designed to identify important predictors of avian abundance within aspen stands, and thus, the sample of points was restricted to

those with aspen present. As post-hoc analyses, I also modeled abundance of some conifer and montane sage associates. For these non-aspen associates, models should be interpreted as identifying predictors of abundance within (or partially within) an aspen stand. These predictors might be different than those within non-aspen or across the landscape as a whole.

Parameters not Measured

Although use of coarse-scale vegetative cover types, such as those available from GIS layers, are a standard tool in building avian-habitat relationship models (Lawler and Edwards 2002), I recognize that habitat parameters that I have not measured (i.e., stand structure, extent of understory shrub cover) could be important in defining avian habitat relationships.

Abundance as an Indicator of Habitat Quality

It is valid to ask whether mean abundance (the response variable in my study), as opposed to productivity, is a useful indicator of habitat quality (Van Horne 1983). For example, nonbreeders that cannot obtain a territory in prime habitat may congregate in suboptimal habitat (Van Horne 1983) or a species' abundance may reflect former, rather than current, habitat conditions (Knick and Rotenberry 2000). The latter may be of particular concern in heavily human-altered landscapes (Bock and Jones 2004). However, often the same factors that produce high quality breeding habitat, such as high food availability (Lyons 2005), also support a high density of breeders (Brown 1969). Indeed, Bock and Jones (2004) find in their meta-analysis that density of breeding individuals is

often a reliable indicator of habitat quality, and thus, estimates of avian abundance are an adequate tool for assessing habitat preferences.

Implications of Climate and Landscape Change

Cover types on the Jarbidge study area may shift from current proportions due to climate-related stressors such as drought, or other disturbances such as wildfire, insects, or forest pathogens (Littell et al. 2010, Worrall et al. 2013). Although some forecasted climate changes, such as warmer temperatures and more frequent fires, may favor aspen over conifer at some points in time, the negative effects of more severe and prolonged drought are expected to over-ride the former (reviewed in Morelli and Carr 2011, Kulakowski et al. 2013). Because most aspen stands are surrounded by shrubsteppe communities in the Jarbidge and much of the Great Basin, and because xeric shrub communities are more likely to do well in future hot and arid climates, shrubsteppe communities are the most likely to replace aspen in future climates. Models that project change in aspen cover across the landscape, based on future climate scenarios, show a major decline in aspen over the next 50 to 100 years (Rehfeldt et al. 2009, Worrall et al. 2013, Yang et al., in review). Models by Yang et al. (in review) also show a reduction in conifer and an increase in shrubsteppe communities. Avian species are certain to vary in their resilience to these potential changes due to inherent differences in life history, physiology, genetic diversity, and phenotypic plasticity (Weathers 1979, Pulido and Berthold 2004, Tottrup et al. 2010). Knowledge of a species' current habitat relationships, and the specificity of those relationships, will aid in predicting its response to changes in vegetation induced by climate change.

The 22 species that I identified as being substantially more common in aspen than conifer are expected to be the most vulnerable to any replacement of aspen by conifer in the Jarbidge study area. Seven of these species were completely absent from conifer: Western Wood-Pewee, Swainson's Thrush, European Starling, Orange-crowned Warbler, White-crowned Sparrow, Lazuli Bunting, and Brown-headed Cowbird. An additional 12 species were at least twice as common in aspen than conifer (ratio of abundance in aspen to conifer given in parentheses, Table E.1): Yellow Warbler (68.5), Black-headed Grosbeak (15.5), Warbling Vireo (10.0), Tree Swallow (9.1), MacGillivray's Warbler (8.8), Northern Flicker (8.7), Dusky Flycatcher (7.4), and Red-naped Sapsucker (5.3), Fox Sparrow (4.6), House Wren (4.5), Mountain Bluebird (3.1), and American Robin (2.0). For aspen associates that decreased with increasing conifer cover in regression models, such as House Wren, Yellow Warbler, and Orange-crowned Warbler, any shift toward a conifer-dominated landscape could prove detrimental even if aspen cover did not change. Similarly, I identified 30 species that were more common in aspen than montane sage and thus expected to be vulnerable to any replacement of aspen by montane sage.

My study was designed to identify aspen-associated avian species and describe their habitat relationships within aspen. Thus, I do not have as large a sample in conifer and montane sage as in aspen. Nonetheless, I identified nine avian species that are substantially more common in conifer than aspen and are thus expected to be vulnerable to any replacement of conifer by aspen (listed from highest to lowest ratio of abundance in conifer to aspen): Red-breasted Nuthatch, Chipping Sparrow, Ruby-crowned Kinglet, Mountain Chickadee, Hermit Thrush, Dark-eyed Junco, Western Tanager, Cassin's

Finch, and Yellow-rumped Warbler. Similarly, the three species substantially more common in montane shrub communities than in aspen include Brewer's Sparrow, Vesper Sparrow, and Green-tailed Towhee.

Patch size, connectivity, and landscape composition affect avian abundance in deciduous woodlands (Saab 1999, Lawler and Edwards 2002) and may be affected by climate change, especially if different sized patches of vegetation have different vulnerabilities and abilities to persist (e.g., reviewed in Kefi et al. 2011). My literature review did not reveal any studies that examined whether smaller aspen stands have lower tolerance thresholds, and thus higher vulnerability, to climate change, but I suggest that this is an important topic for future research. In the Jarbidge study area, approximately half of aspen stands are smaller than 4 ha, and most are surrounded by shrub communities. Because the amount of 300-m aspen only improved the model over 75-m aspen for one aspen associate, the importance of small stands should not be understated. Similarly, aspen patch size did not affect nest success of common breeders elsewhere in the Great Basin (Heltzel and Earnst 2006). Therefore, I suggest that small stands may be as important, or more important, in maintaining avian abundance and diversity as large stands, and that the loss of smaller stands should be a management concern.

Climate change is predicted to reduce the seasonal availability of water sources and associated vegetation due to changes in the hydrologic cycle (Breshears et al. 2005, Stewart et al. 2005). For example, in the northern Great Basin, the timing of snowmelt and related peak streamflow occurred over one week earlier in 2002 than in 1948 (Stewart et al. 2005). This trend is in part due to an increase in winter and spring temperatures, a trend predicted to continue (Dettinger and Cayan 1995, Mote et al. 2005).

Although total precipitation has only slightly increased since 1916 (Hamlet et al. 2007), mostly at higher elevations (Stewart 2009), the proportion of precipitation falling as snow has declined (Knowles et al. 2006). A decrease in snowpack is likely to negatively affect aspen (LaMalfa and Ryle 2008, Anderegg et al. 2013) and thus negatively affect the 22 avian species shown to be associated with aspen in my study. Changes to stream flow may also directly affect species described to be riparian associates such as Yellow Warblers, Warbling Vireos, and MacGillivray's Warblers (Marzluff and Lyon 1983, Floyd et al. 2007, Earnst et al. 2012). Early snowmelt may also initiate an unexpected cascade of effects. For example, in central Arizona, Martin (2007) found that earlier snowmelt led to increased elk browsing, reduced cover of deciduous vegetation, increased nest predation and substantial declines in Orange-crowned Warblers, MacGillivray's Warblers, and Green-tailed Towhees.

Avian species whose abundance is increasing with elevation could be responding to a number of factors such as cover type, stand structure, understory vegetation, seasonal phenology, or micro-climate. Climate change may affect each of these factors and the interactions among them. For example, aspen distribution is expected to move upslope as suitable temperature and precipitation conditions also move upslope (Kelly and Goulden 2008). Similarly, avian species may also track their preferred cover type across elevations or latitudes (reviewed in Sekercioglu et al. 2008). For instance, the 22 aspen-associated avian species identified in this study might be expected to track any elevational shifts in aspen distribution, and to track shifts in relevant aspects of stand structure or understory vegetation.

Avian species may also track changes in the abiotic dimensions of their niche, such as temperature and precipitation, across elevation (Tingley et al. 2012, Tingley and Beissinger 2013). The literature suggests that high elevation species may respond more strongly to changes in temperature while lower elevation species may respond more strongly to changes in precipitation (Tingley et al. 2009). Rising temperature is expected to push species upslope while increased precipitation pulls them downslope, but climatic factors also combine to create varied responses (Tingley et al. 2012). These fairly simple predictions, combined with the results of my regression analyses, allows for species-specific predictions for my study area. Species that I found to be more common at high elevations in my study area, and thus most likely to be affected by the predicted rise in temperature, are Dusky Flycatcher, Ruby-crowned Kinglet, Yellow-rumped Warbler, Dark-eyed Junco, and Cassin's Finch. Species that I found to be more common at low elevations, and thus most likely to be affected by the predicted increase in precipitation, are House Wren, American Robin, and Yellow Warbler. Other species that might be expected to respond to changes in precipitation under climate change are those found to be less common in areas of high precipitation in my study area–Northern Flicker, Warbling Vireo, and Orange-crowned Warbler. Although this is a useful framework, reality is likely to be more complicated. For example, species are expected to differ in their sensitivity to temperature and precipitation, and local differences in climate patterns are likely to cause a species to move upslope in one region and downslope in another (Tingley et al. 2012). Also, Tingley et al. (2012) found that the combination of predictions based on temperature and precipitation were much better than those based on either temperature or precipitation alone. In addition, some species, like Dark-eyed

Juncos (Bears et al. 2009), that exhibit plasticity in reproductive and life-history

strategies across elevational gradients, may be more able than others to track the abiotic

dimensions of their niche across elevation.

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Table 1. Results of hypotheses tested for focal species in partially-paired comparisons and multiple regression. The expected habitat association in the Mountain West is based on literature. The observed association is based on partially-paired t-tests; parentheses indicate marginal significance (0.05< p <0.10). The "Predictor?" column indicates whether the relevant cover type parameter (e.g. Asp75 for aspen associates; Con75 for conifer associates, etc.) is a significant predictor in the best model subset (Y = yes, N = no, --- = no model built for this species).

Species	Expected	Observed	Predictor?
Aspen vs. Conifer			
Swainson's Thrush	aspen	aspen	---
Orange-crowned Warbler	aspen	aspen	N
Yellow Warbler	aspen	aspen	Y
Song Sparrow	aspen	aspen	---
Western Wood-Pewee	aspen	aspen	---
Warbling Vireo	aspen	aspen	Y
Red-naped Sapsucker	aspen	aspen	Y
Downy Woodpecker	aspen	no difference	---
Tree Swallow	aspen	aspen	Y
House Wren	aspen	aspen	Y
Mountain Bluebird	aspen	aspen	Y
European Starling	aspen	aspen	---
Brown-headed Cowbird	aspen	aspen	---
Chipping Sparrow	conifer	conifer	---
Hammond's Flycatcher	conifer	no difference	---
Ruby-crowned Kinglet	conifer	conifer	Y
Yellow-rumped Warbler	conifer	conifer	Y
Western Tanager	conifer	conifer	---
Cassin's Finch	conifer	conifer	N
Pine Siskin	conifer	(conifer)	---
Mountain Chickadee	conifer	conifer	Y
Red-breasted Nuthatch	conifer	conifer	---
Dusky Flycatcher	no difference	aspen	Y
Hermit Thrush	no difference	conifer	---
Dark-eyed Junco	no difference	conifer	N
Black-headed Grosbeak	no difference	aspen	---
American Robin	no difference	aspen	N
Hairy Woodpecker	no difference	no difference	---
Northern Flicker	no difference	aspen	N
Violet-green Swallow	no difference	no difference	---
Aspen vs. Mixed Aspen-Conifer			
Cordilleran Flycatcher	aspen-conifer	(aspen-conifer)	---

Aspen vs. Montane Sage			
MacGillivray's Warbler	montane sage	aspen	Y
Green-tailed Towhee	montane sage	montane sage	Y
Brewer's Sparrow	montane sage	montane sage	---
Vesper Sparrow	montane sage	montane sage	---
Fox Sparrow	montane sage	aspen	---
White-crowned Sparrow	montane sage	no difference	---
Lazuli Bunting	montane sage	aspen	---
Rock Wren	montane sage	(montane sage)	---

Table 2.   Mean difference in abundance in aspen minus montane sage. Statistics based on t-tests for partially-paired data. P-values are prior to adjustment for multiple comparisons. Asterisks and habitat association are based on significance post-adjustment (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). N = 111 aspen and 23 montane sage stands.

Species or Nesting Guild	Mean Diff.[a] (ind. per point)	Standard Error[b]	t-value	p-value	Association[c]
Ground/Understory[d]	3.33	0.80	4.19	<0.001***	aspen
Hummingbirds	0.20	0.04	5.59	<0.001***	aspen
Empidonax spp.	0.23	0.04	5.57	<0.001***	aspen
Dusky Flycatcher	1.91	0.14	13.35	<0.001***	aspen
Rock Wren	-0.18	0.10	-1.75	0.08(*)	(shrub)
Swainson's Thrush	0.14	0.04	3.92	<0.001***	aspen
Hermit Thrush	0.21	0.04	4.88	<0.001***	aspen
Orange-crowned Warbler	0.95	0.10	9.36	<0.001***	aspen
Yellow Warbler	1.30	0.14	9.15	<0.001***	aspen
MacGillivray's Warbler	0.92	0.10	9.07	<0.001***	aspen
Green-tailed Towhee	-1.67	0.48	-3.48	<0.001**	shrub
Chipping Sparrow	<0.01	0.07	-0.04	0.97	n.s.
Brewer's Sparrow	-1.96	0.43	-4.60	<0.001***	shrub
Vesper Sparrow	-0.45	0.15	-3.02	0.003**	shrub
Fox Sparrow	0.64	0.09	7.48	<0.001***	aspen
Song Sparrow	0.14	0.04	3.35	0.001**	aspen
White-crowned Sparrow	0.08	0.17	0.49	0.63	n.s.
Dark-eyed Junco	0.58	0.09	6.83	<0.001***	aspen
Black-headed Grosbeak	0.31	0.04	7.51	<0.001***	aspen
Lazuli Bunting	0.18	0.07	2.70	0.008*	aspen
Overstory[d]	7.65	0.43	17.94	<0.001***	aspen
Western Wood-Pewee	0.71	0.10	6.84	<0.001***	aspen
Hammond's Flycatcher	0.06	0.02	2.39	0.02*	aspen
Cordilleran Flycatcher	0.17	0.04	3.96	<0.001***	aspen
Warbling Vireo	2.48	0.13	19.50	<0.001***	aspen
Ruby-crowned Kinglet	0.31	0.08	3.80	<0.001***	aspen
American Robin	1.63	0.19	8.50	<0.001***	aspen
Yellow-rumped Warbler	0.95	0.09	10.93	<0.001***	aspen
Western Tanager	0.34	0.07	4.93	<0.001***	aspen
Cassin's Finch	0.69	0.10	6.83	<0.001***	aspen
Pine Siskin	0.21	0.06	3.42	<0.001**	aspen
Cavity[d]	6.49	0.34	19.09	<0.001***	aspen
Red-naped Sapsucker	0.37	0.06	6.68	<0.001***	aspen
Downy Woodpecker	0.07	0.02	3.38	<0.001**	aspen
Hairy Woodpecker	0.25	0.04	5.82	<0.001***	aspen
Northern Flicker	0.48	0.12	4.03	<0.001***	aspen
Tree Swallow	0.51	0.12	4.31	<0.001***	aspen
Violet-green Swallow	-0.02	0.09	-0.26	0.79	n.s.
Mountain Chickadee	0.34	0.05	6.81	<0.001***	aspen
Red-breasted Nuthatch	0.05	0.02	2.38	0.02*	aspen
House Wren	4.02	0.19	20.94	<0.001***	aspen
Mountain Bluebird	0.21	0.11	2.00	0.05(*)	(aspen)
European Starling	0.12	0.05	2.45	0.02*	aspen
Brood Parasite					
Brown-headed Cowbird	0.12	0.06	1.90	0.06(*)	(aspen)

[a]Mean abundance in aspen minus mean abundance in montane shrub. For each cover type, points within stands were averaged prior to analysis. A significant positive mean difference for a species indicates higher abundance in aspen.

[b]Standard Error of the difference calculated using formula for partially-paired samples.

[c]Associations in parentheses indicate differences that were marginally significant (i.e., $0.05 < p < 0.10$) after adjustment for multiple comparisons; n.s. denotes non-significance.

[d]Guild means calculated by summing individuals across all species within the guild, including some that did not meet the focal species criteria.

Table 3. **Mean difference in abundance in aspen minus montane sage. Statistics based on t-tests for paired data. P-values are prior to adjustment for multiple comparisons. Asterisks and habitat association are based on significance post-adjustment (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). N = 22 paired aspen and montane sage stands.**

Species or Nesting Guild	Mean Diff.[a] (ind. per point)	Standard Error[b]	t-value	p-value	Association[c]
Ground/Understory[d]	3.40	0.68	4.99	<0.001***	aspen
Hummingbirds	0.28	0.07	3.80	0.001**	aspen
Dusky Flycatcher	1.89	0.29	6.42	<0.001***	aspen
Hermit Thrush	0.35	0.14	2.55	0.02*	aspen
Orange-crowned Warbler	0.86	0.18	4.87	<0.001***	aspen
Yellow Warbler	1.04	0.20	5.14	<0.001***	aspen
MacGillivray's Warbler	0.98	0.22	4.42	<0.001***	aspen
Green-tailed Towhee	-1.32	0.47	-2.80	0.01*	shrub
Brewer's Sparrow	-2.06	0.44	-4.68	<0.001***	shrub
Vesper Sparrow	-0.49	0.16	-3.16	0.005**	shrub
Fox Sparrow	0.54	0.12	4.49	<0.001***	aspen
White-crowned Sparrow	0.16	0.13	1.23	0.23	n.s.
Dark-eyed Junco	0.52	0.12	4.30	<0.001***	aspen
Black-headed Grosbeak	0.48	0.09	5.46	<0.001***	aspen
Overstory[d]	6.38	0.49	12.95	<0.001***	aspen
Western Wood-Pewee	0.44	0.17	2.60	0.02*	aspen
Warbling Vireo	2.74	0.32	8.48	<0.001***	aspen
American Robin	1.09	0.24	4.63	<0.001***	aspen
Yellow-rumped Warbler	0.90	0.13	6.73	<0.001***	aspen
Cassin's Finch	0.43	0.11	4.02	0.001**	aspen
Cavity[d]	5.70	0.48	11.88	<0.001***	aspen
Red-naped Sapsucker	0.28	0.08	3.46	0.002**	aspen
Hairy Woodpecker	0.13	0.04	3.47	0.002**	aspen
Northern Flicker	0.31	0.13	2.31	0.03*	aspen
Tree Swallow	0.48	0.12	3.88	0.001**	aspen
Mountain Chickadee	0.36	0.11	3.37	0.003**	aspen
House Wren	3.62	0.34	10.78	<0.001***	aspen
Mountain Bluebird	0.07	0.12	0.61	0.55	n.s.

[a]Mean abundance in aspen minus mean abundance in montane shrub. For each cover type, points within stands were averaged prior to analysis. A significant positive mean difference for a species indicates higher abundance in aspen.

[b]Standard Error of the difference calculated using formula for paired samples.

[c]Associations in parentheses indicate differences that were marginally significant (i.e., $0.05 < p < 0.10$) after adjustment for multiple comparisons; n.s. denotes non-significance.

[d]Guild means calculated by summing individuals across all species within the guild, including some that did not meet the focal species criteria.

Table 4. **Mean difference in abundance in aspen minus conifer. Statistics based on t-tests for partially-paired data. P-values are prior to adjustment for multiple comparisons. Asterisks and habitat association are based on significance post-adjustment (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). N = 111 aspen and 14 conifer stands.**

Species or Nesting Guild	Mean Diff.[a] (ind. per point)	Standard Error[b]	t-value	p-value	Association[c]
Ground/Understory[d]	4.69	0.68	6.85	<0.001***	aspen
Hummingbirds	0.20	0.04	5.59	<0.001***	aspen
Empidonax spp.	0.20	0.05	3.58	<0.001	aspen
Dusky Flycatcher	1.73	0.15	11.55	<0.001***	aspen
Swainson's Thrush	0.14	0.04	3.92	<0.001***	aspen
Hermit Thrush	-0.71	0.18	-3.92	<0.001***	conifer
Orange-crowned Warbler	0.97	0.10	9.99	<0.001***	aspen
Yellow Warbler	1.35	0.14	9.77	<0.001***	aspen
MacGillivray's Warbler	0.86	0.12	7.00	<0.001***	aspen
Green-tailed Towhee	0.32	0.12	2.59	0.011*	aspen
Chipping Sparrow	-0.61	0.17	-3.49	<0.001**	conifer
Brewer's Sparrow	0.04	0.02	2.46	0.02*	aspen
Fox Sparrow	0.50	0.15	3.33	0.001**	aspen
Song Sparrow	0.14	0.04	3.35	0.001**	aspen
White-crowned Sparrow	0.30	0.06	5.27	<0.001***	aspen
Dark-eyed Junco	-1.26	0.46	-2.77	0.007**	conifer
Black-headed Grosbeak	0.29	0.05	5.83	<0.001***	aspen
Lazuli Bunting	0.22	0.06	3.90	<0.001***	aspen
Overstory[d]	-1.41	1.16	-1.22	0.23	n.s.
Western Wood-Pewee	0.71	0.10	6.84	<0.001***	aspen
Hammond's Flycatcher	-0.19	0.16	-1.23	0.22	n.s.
Cordilleran Flycatcher	-0.34	0.27	-1.24	0.22	n.s.
Warbling Vireo	2.25	0.21	10.87	<0.001***	aspen
Ruby-crowned Kinglet	-1.58	0.23	-6.80	<0.001***	conifer
American Robin	0.99	0.37	2.66	0.009*	aspen
Yellow-rumped Warbler	-0.80	0.27	-2.98	0.004**	conifer
Western Tanager	-0.73	0.29	-2.52	0.01*	conifer
Cassin's Finch	-0.87	0.32	-2.71	0.008*	conifer
Pine Siskin	-0.52	0.28	-1.85	0.07(*)	(conifer)
Cavity[d]	2.77	0.61	4.54	<0.001***	aspen
Red-naped Sapsucker	0.30	0.07	4.18	<0.001***	aspen
Downy Woodpecker	0.00	0.07	0.01	0.99	n.s.
Hairy Woodpecker	-0.14	0.23	-0.63	0.53	n.s.
Northern Flicker	0.54	0.10	5.41	<0.001***	aspen
Tree Swallow	0.57	0.10	5.49	<0.001***	aspen
Violet-green Swallow	0.03	0.04	0.62	0.54	n.s.
Mountain Chickadee	-1.28	0.36	-3.56	<0.001***	conifer
Red-breasted Nuthatch	-0.81	0.19	-4.24	<0.001***	conifer
House Wren	3.14	0.37	8.39	<0.001***	aspen
Mountain Bluebird	0.24	0.08	2.83	0.005**	aspen
European Starling	0.12	0.05	2.45	0.02*	aspen
Brood Parasite					
Brown-headed Cowbird	0.18	0.03	5.25	<0.001***	aspen

[a]Mean abundance in aspen minus mean abundance in conifer. For each cover type, points within stands were averaged prior to analysis. A significant positive mean difference for a species indicates higher abundance in aspen.

[b]Standard Error of the difference calculated using formula for partially-paired samples.

[c]Associations in parentheses indicate differences that were marginally significant (i.e., $0.05 < p < 0.10$) after adjustment for multiple comparisons; n.s. denotes non-significance.

[d]Guild means calculated by summing individuals across all species within the guild, including some that did not meet the focal species criteria.

Table 5. **Mean difference in abundance in aspen minus conifer. Statistics based on t-tests for paired data. P-values are prior to adjustment for multiple comparisons. Asterisks and habitat association are based on significance post-adjustment (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). N = 10 paired aspen and conifer stands.**

Species or Nesting Guild	Mean Diff.[a] (ind. per point)	Standard Error[b]	t-value	p-value	Association[c]
Ground/Understory[d]	3.52	0.78	4.53	0.001*	aspen
Dusky Flycatcher	1.85	0.25	7.43	<0.001***	aspen
Hermit Thrush	-0.33	0.25	-1.31	0.22	n.s.
Orange-crowned Warbler	0.92	0.24	3.84	0.004*	aspen
MacGillivray's Warbler	0.77	0.40	1.91	0.09	n.s.
Dark-eyed Junco	-0.68	0.48	-1.43	0.19	n.s.
Overstory[d]	-0.08	0.67	-0.12	0.90	n.s.
Warbling Vireo	1.43	0.48	2.96	0.02*	aspen
Ruby-crowned Kinglet	-1.07	0.36	-2.98	0.02*	conifer
American Robin	0.53	0.57	0.93	0.37	n.s.
Yellow-rumped Warbler	-0.03	0.35	-0.10	0.93	n.s.
Western Tanager	-0.03	0.36	-0.09	0.93	n.s.
Cassin's Finch	-0.43	0.21	-2.08	0.07	n.s.
Pine Siskin	0.20	0.39	0.51	0.62	n.s.
Cavity[d]	2.40	1.22	1.97	0.08	n.s.
Hairy Woodpecker	0.40	0.45	0.88	0.40	n.s.
Mountain Chickadee	-1.13	0.53	-2.12	0.06	n.s.
House Wren	2.42	0.73	3.30	0.009*	aspen

[a]Mean abundance in aspen minus mean abundance in conifer. For each cover type, points within stands were averaged prior to analysis. A significant positive mean difference for a species indicates higher abundance in aspen.

[b]Standard Error of the difference calculated using formula for paired samples.

[c]Associations in parentheses indicate differences that were marginally significant (i.e., $0.05 < p < 0.10$) after adjustment for multiple comparisons; n.s. denotes non-significance.

[d]Guild means calculated by summing individuals across all species within the guild, including some that did not meet the focal species criteria.

Table 6. **Mean difference in abundance in aspen minus mixed aspen-conifer. Statistics based on t-tests for partially-paired data. P-values are prior to adjustment for multiple comparisons. Asterisks and habitat association are based on significance post-adjustment (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). N = 111 aspen and 19 mixed aspen-conifer stands.**

Species or Nesting Guild	Mean Diff.[a] (ind. Per point)	Standard Error[b]	t-value	p-value	Association[c]
Ground/Understory[d]	2.39	0.64	3.74	<0.001**	aspen
Hummingbirds	-0.01	0.10	-0.13	0.90	n.s.
Empidonax spp.	<0.01	0.11	0.04	0.97	n.s.
Dusky Flycatcher	1.11	0.25	4.39	<0.001***	aspen
Swainson's Thrush	-0.09	0.15	-0.58	0.56	n.s.
Hermit Thrush	-0.30	0.16	-1.90	0.06(*)	(aspen-conifer)
Orange-crowned Warbler	0.78	0.14	5.58	<0.001***	aspen
Yellow Warbler	1.08	0.18	5.83	<0.001***	aspen
MacGillivray's Warbler	0.38	0.21	1.76	0.08	n.s.
Green-tailed Towhee	0.35	0.10	3.61	<0.001**	aspen
Chipping Sparrow	-0.21	0.12	-1.65	0.10	n.s.
Brewer's Sparrow	0.04	0.02	2.46	0.02*	aspen
Fox Sparrow	-0.32	0.23	-1.37	0.17	n.s.
Song Sparrow	0.03	0.11	0.30	0.76	n.s.
White-crowned Sparrow	0.12	0.11	1.09	0.28	n.s.
Dark-eyed Junco	-0.81	0.25	-3.17	0.002**	aspen-conifer
Black-headed Grosbeak	0.20	0.08	2.44	0.02*	aspen
Lazuli Bunting	0.17	0.08	2.18	0.03(*)	(aspen)
Overstory[d]	-5.23	0.78	-6.70	<0.001***	aspen-conifer
Western Wood-Pewee	0.45	0.19	2.36	0.02*	aspen
Hammond's Flycatcher	-0.16	0.12	-1.33	0.18	n.s.
Cordilleran Flycatcher	-0.55	0.25	-2.20	0.03(*)	(aspen-conifer)
Warbling Vireo	1.04	0.21	4.96	<0.001***	aspen
Ruby-crowned Kinglet	-1.79	0.22	-8.07	<0.001***	aspen-conifer
American Robin	-0.24	0.37	-0.63	0.53	n.s.
Yellow-rumped Warbler	-0.41	0.17	-2.36	0.02*	aspen-conifer
Western Tanager	-0.64	0.24	-2.63	0.01*	aspen-conifer
Cassin's Finch	-2.11	0.33	-6.36	<0.001***	aspen-conifer
Pine Siskin	-0.66	0.22	-3.02	0.003*	aspen-conifer
Cavity[d]	1.06	0.77	1.37	0.17	n.s.
Red-naped Sapsucker	0.30	0.08	3.57	<0.001**	aspen
Downy Woodpecker	0.07	0.02	3.38	<0.001**	aspen
Hairy Woodpecker	-0.01	0.11	-0.13	0.90	n.s.
Northern Flicker	0.26	0.14	1.89	0.06(*)	(aspen)
Tree Swallow	0.41	0.15	2.71	0.008*	aspen
Violet-green Swallow	0.04	0.04	1.04	0.30	n.s.
Mountain Chickadee	-1.12	0.24	-4.70	<0.001***	aspen-conifer
Red-breasted Nuthatch	-0.14	0.07	-1.93	0.06(*)	(aspen-conifer)
House Wren	0.91	0.60	1.53	0.13	n.s.
Mountain Bluebird	0.24	0.09	2.70	0.008*	aspen
European Starling	0.12	0.05	2.45	0.02*	aspen
Brood Parasite					
Brown-headed Cowbird	0.13	0.06	2.04	0.04(*)	(aspen)

[a]Mean abundance in aspen minus mean abundance in mixed aspen-conifer. For each cover type, points within stands were averaged prior to analysis. A significant positive mean difference for a species indicates higher abundance in aspen.

[b]Standard Error of the difference calculated using formula for partially-paired samples.

[c]Associations in parentheses indicate differences that were marginally significant (i.e., $0.05 < p < 0.10$) after adjustment for multiple comparisons; n.s. denotes non-significance.

[d]Guild means calculated by summing individuals across all species within the guild, including some that did not meet the focal species criteria.

Table 7.   Mean difference in abundance in aspen minus mixed aspen-conifer. Statistics based on t-tests for paired data. P-values are prior to adjustment for multiple comparisons. Asterisks and habitat association are based on significance post-adjustment (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). N = 9 paired aspen and mixed aspen-conifer stands.

Species or Nesting Guild	Mean Diff.[a] (ind. per point)	Standard Error[b]	t-value	p-value	Association[c]
Ground/Understory[d]	2.19	1.15	1.91	0.09	n.s.
Dusky Flycatcher	0.33	0.34	0.98	0.36	n.s.
Fox Sparrow	0.22	0.37	0.59	0.57	n.s.
Dark-eyed Junco	0.31	0.48	0.64	0.54	n.s.
Overstory[d]	-0.67	1.97	-0.34	0.74	n.s.
Cordilleran Flycatcher	-0.25	0.46	-0.54	0.60	n.s.
Warbling Vireo	0.99	0.51	1.96	0.09	n.s.
Ruby-crowned Kinglet	-0.90	0.62	-1.46	0.18	n.s.
American Robin	0.39	0.58	0.68	0.52	n.s.
Yellow-rumped Warbler	-0.30	0.36	-0.83	0.43	n.s.
Western Tanager	0.04	0.48	0.08	0.94	n.s.
Cassin's Finch	-0.58	0.47	-1.22	0.26	n.s.
Cavity[d]	0.10	1.09	0.09	0.93	n.s.
Red-naped Sapsucker	0.69	0.24	2.83	0.02	n.s.
Mountain Chickadee	-1.03	0.32	-3.27	0.01	n.s.
House Wren	0.24	0.82	0.29	0.78	n.s.
Mountain Bluebird	0.40	0.23	1.71	0.12	n.s.

[a]Mean abundance in aspen minus mean abundance in mixed aspen-conifer. For each cover type, points within stands were averaged prior to analysis. A significant positive mean difference for a species indicates higher abundance in aspen.

[b]Standard Error of the difference calculated using formula for paired samples.

[c]Associations in parentheses indicate differences that were marginally significant (i.e., $0.05 < p < 0.10$) after adjustment for multiple comparisons; n.s. denotes non-significance.

[d]Guild means calculated by summing individuals across all species within the guild, including some that did not meet the focal species criteria.

Table 8. Coefficients and standard errors (in parentheses) of parameters in best model subsets for aspen-associated species in the overstory- and ground/understory-nesting guilds. For species having more than one model in the best model subset, model weights are given as footnotes. Model selection was based on fixed-effects models; coefficients, standard errors, and significance are from mixed-effects models (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; (*) $p < 0.10$, and ns for $p > 0.10$). N = 324 points.

Parameter	Warbling Vireo	American Robin[a]	American Robin[b]	Dusky Flycatcher	Yellow Warbler	MacGillivray's Warbler[c]	Orange-crowned Warbler
Asp75	0.007 (0.002)***			0.009 (0.002)***	0.008 (0.003)*	0.03 (0.01)**	
Asp75^2						-0.0003 (0.00008)**	
Con75					-0.03 (0.02)*		-0.03 (0.01)*
Rip					0.69 (0.15)***		-0.36 (0.15)*
Asp300						0.008 (0.004)(*)	
Elev			-0.01 (0.004)*	0.009 (0.003)**	0.64 (0.21)**		
Elev^2					-0.002 (0.0005)**		
Slope		-0.01 (0.005)*					
Prec	-0.01 (0.005)**						-0.03 (0.008)***
Day	0.01 (0.008)(*)	-0.02 (0.01)(*)		-0.007 (0.008)ns		0.02 (0.01)(*)	0.03 (0.01)*

[a] $w_i = 0.62$;   [b] $w_i = 0.38$;   [c] $w_i = 0.83$;

Table 9. **Coefficients and standard errors (in parentheses) of parameters in best model subsets for aspen-associated species in the cavity-nesting guild. Model selection was based on fixed-effects models; coefficients, standard errors, and significance are from mixed-effects models (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10, and ns for p > 0.10). N = 324 points.**

Parameter	Red-naped Sapsucker	Northern Flicker	Tree Swallow	House Wren	Mountain Bluebird
Asp75	0.09 $(0.04)^*$		0.01 $(0.004)^{**}$	-0.008 $(0.005)^{ns}$	0.008 $(0.003)^*$
Asp75^2	-0.0005 $(0.0003)^{(*)}$			0.0001 $(0.00004)^{**}$	
Con75				-0.009 $(0.004)^*$	
Asp300	-0.02 $(0.007)^*$			-0.005 $(0.002)^*$	
Elev				-0.008 $(0.003)^{**}$	
Slope					-0.04 $(0.01)^{**}$
CTI			0.52 $(0.13)^{***}$		
Prec		-0.04 $(0.009)^{***}$			
Day			-0.04 $(0.02)^{(*)}$		

Table 10. Coefficients and standard errors (in parentheses) of parameters in best model subsets for aspen-associated species in each of the pooled nesting guilds. For guilds having more than one model in the best model subset, model weights are given as footnotes. Model selection was based on fixed-effects models; coefficients, standard errors, and significance are from mixed-effects models (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; (*) $p < 0.10$, and ns for $p > 0.10$). N = 324 points.

Parameter	Ground and Understory	Overstory[a]	Overstory[b]	Overstory[c]	Cavity
Asp75	0.01 (0.004)**	-0.005 (0.004)ns	-0.005 (0.004)ns	-0.005 (0.004)ns	0.008 (0.001)***
$Asp75^2$	-0.00008 (0.00003)**	0.00008 (0.00004)*	0.00008 (0.00004)*	0.00007 (0.00004)*	
Con75	-0.01 (0.003)***	-0.007 (0.003)*	-0.007 (0.003)*	-0.008 (0.003)*	-0.01 (0.004)**
Rip		0.13 (0.06)*	0.12 (0.06)(*)		
Asp300					-0.006 (0.002)**
Nasp300	0.007 (0.002)**				
Elev			-0.004 (0.002)(*)		
Prec		-0.007 (0.003)*		-0.009 (0.004)*	-0.007 (0.004)(*)
Day	0.01 (0.006)*			0.007 (0.006)ns	

[a] $w_i = 0.53$; [b] $w_i = 0.23$; [c] $w_i = 0.24$

Table 11. Model selection statistics for best model subsets (i.e., those $\leq$ 4 AIC of best) for aspen-associated species.

Species or Guild[a]	Model[b]	AIC	ΔAIC	w_i
Overstory nesters				
Overstory-nesting Guild_1	-Asp75$^{(ns)}$ + Asp75^2 - Con75 + Rip - Prec	1485.1	0	0.53
Overstory-nesting Guild_2	-Asp75$^{(ns)}$ + Asp75^2 - Con75 - Prec + Day$^{(ns)}$	1486.6	1.54	0.24
Overstory-nesting Guild_3	-Asp75$^{(ns)}$ + Asp75^2 - Con75 + Rip$^{(m)}$ - Elev$^{(m)}$	1486.8	1.70	0.23
Warbling Vireo	+Asp75 - Prec + Day$^{(m)}$	1153.5	0	1.00
American Robin_1	-Slope - Day$^{(m)}$	1149.0	0	0.62
American Robin_2	-Elev	1150.0	0.98	0.38
Understory/ground nesters				
Ground/understory-nestingGuild	+Asp75 -Asp75^2 - Con75 + Nasp300 + Day	1671.6	0	1.00
Dusky Flycatcher	+Asp75 + Elev - Day$^{(ns)}$	1078.4	0	1.00
Orange-crowned Warbler	-Con75 - Rip - Prec + Day	785.9	0	1.00
Yellow Warbler	+Asp75 - Con75 + Rip + Elev - Elev^2	844.4	0	1.00
MacGillivray's Warbler_1	+Asp75 - Asp75^2 + Asp300$^{(m)}$ + Day$^{(m)}$	829.3	0	0.83
Cavity nesters				
Cavity-nesting Guild	+Asp75 - Con75 - Asp300 - Prec^{ns}	1640.4	0	1.00
Red-naped Sapsucker	+Asp75 - Asp75$^{2(m)}$ - Asp300	391.3	0	1.00
Northern Flicker	-Prec	586.9	0	1.00
Tree Swallow	+Asp75 + CTI - Day$^{(m)}$	612.9	0	1.00
House Wren	-Asp75$^{(ns)}$ + Asp75^2 - Con75 - Asp300 - Elev	1418.8	0	1.00
Mountain Bluebird	+Asp75 - Slope	463.4	0	1.00

[a] "_1", "_2", etc. indicate alternate models for the same species or guild; [b] Model selection based on fixed-effect models; parameter significance based on mixed-effect models. Parameters are significant except those which became non-significant (ns) or marginally significant (m) upon addition of random effects.

Table 12. Coefficients and standard errors (in parentheses) of parameters in best model subsets for conifer-associated species in the overstory-nesting guild. For species having more than one model in the best model subset, model weights are given as footnotes. Model selection was based on fixed-effects models; coefficients, standard errors, and significance are from mixed-effects models (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; (*) $p < 0.10$, and ns for $p > 0.10$). N = 324 points.

Parameter	Ruby-crowned Kinglet[a]	Ruby-crowned Kinglet[b]	Yellow-rumped Warbler[c]	Yellow-rumped Warbler[d]	Yellow-rumped Warbler[e]	Cassin's Finch
MixAC75	0.02 (0.003)***	0.03 (0.003)***		0.006 (0.002)*	0.005 (0.002)*	0.04 (0.009)***
MixAC75^2						-0.0002 (0.0001)*
Con75	0.03 (0.006)***	0.03 (0.006)***	0.01 (0.004)*	0.01 (0.004)**	0.01 (0.004)**	
Elev	0.46 (0.24)(*)		0.01 (0.005)**			0.02 (0.007)**
Elev^2	-0.001 (0.0005)(*)					
Slope					-0.01 (0.006)(*)	
HLI		-0.001 (0.0004)*		-0.0005 (0.0003)(*)		

[a] $w_i = 0.77$; [b] $w_i = 0.23$; [c] $w_i = 0.37$; [d] $w_i = 0.34$; [e] $w_i = 0.29$

Table 13.   **Coefficients and standard errors (in parentheses) of parameters in best model subsets for conifer-associated species in the ground/understory- and cavity-nesting guilds, and for each of the pooled nesting guilds. Model selection was based on fixed-effects models; coefficients, standard errors, and significance are from mixed-effects models (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10, and ns for p > 0.10). N = 324 points.**

Parameter	Mountain Chickadee	Dark-eyed Junco	Ground and Understory	Overstory	Cavity
MixAC75	0.02 $(0.003)^{***}$		0.004 $(0.003)^{ns}$	0.01 $(0.002)^{***}$	0.02 $(0.003)^{***}$
Con75	0.03 $(0.006)^{***}$			0.02 $(0.004)^{***}$	0.03 $(0.005)^{***}$
Rip		-0.53 $(0.17)^{**}$	-0.46 $(0.14)^{**}$		
NCon300		-0.01 $(0.005)^{**}$	-0.01 $(0.004)^{**}$		
Elev		0.37 $(0.18)^{*}$	0.44 $(0.16)^{**}$	0.18 $(0.09)^{*}$	
$Elev^2$		-0.0008 $(0.0004)^{(*)}$	-0.0009 $(0.0003)^{**}$	-0.0004 $(0.0002)^{(*)}$	
Day		0.04 $(0.02)^{*}$	0.04 $(0.01)^{**}$		

Table 14.   Model selection statistics for best model subsets (i.e., those $\leq$ 4 AIC of best) for conifer-associated species.

Species or Guild[a]	Model[b]	AIC	ΔAIC	w_i
Overstory nesters				
Overstory-nesting Guild	$+\text{Con75} + \text{MixAC75} + \text{Elev} - \text{Elev}^{2(m)}$	1343.5	0	1.00
Ruby-crowned Kinglet_1	$+\text{Con75} + \text{MixAC75} + \text{Elev}^{(m)} - \text{Elev}^{2(m)}$	522.6	0	0.77
Ruby-crowned Kinglet_2	$+\text{Con75} + \text{MixAC75} - \text{HLI}$	525.1	2.43	0.23
Yellow-rumped Warbler_1	$+\text{Con75} + \text{Elev}$	886.8	0	0.37
Yellow-rumped Warbler_2	$+\text{Con75} + \text{MixAC75} - \text{HLI}^{(m)}$	887.0	0.15	0.34
Yellow-rumped Warbler_3	$+\text{Con75} + \text{MixAC75} - \text{Slope}^{(m)}$	887.3	0.46	0.29
Cassin's Finch	$+\text{MixAC75} - \text{MixAC75}^{2} + \text{Elev}$	777.1	0	1.00
Understory/ground nesters				
Ground/understory-nesting Guild	$+\text{MixAC75}^{(ns)} - \text{Rip} - \text{Ncon300} + \text{Elev} - \text{Elev}^2 + \text{Day}$	855.0	0	1.00
Dark-eyed Junco	$-\text{Rip} - \text{Ncon300} + \text{Elev} - \text{Elev}^{2(m)} + \text{Day}$	680.9	0	1.00
Cavity nesters				
Cavity-nesting Guild	$+\text{Con75} + \text{MixAC75}$	634.7	0	1.00
Mountain Chickadee	$+\text{Con75} + \text{MixAC75}$	578.8	0	1.00

[a] "_1", "_2", etc. indicate alternate models for the same species or guild.

[b] Model selection based on fixed-effect models; parameter significance based on mixed-effect models. Parameters are significant except those which became non-significant (ns) or marginally significant (m) upon addition of random effects.

Table 15. Coefficients and standard errors of parameters in best model subsets for montane sage-associated species. For species having more than one model in the best model subset, model weights are given as footnotes. Model selection was based on fixed-effects models; coefficients, standard errors, and significance are from mixed-effects models (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; (*) $p < 0.10$, and ns for $p > 0.10$). N = 324 points.

Parameter	MacGillivray's Warbler[a]	Green-tailed Towhee[b]	Green-tailed Towhee[c]	Green-tailed Towhee[d]
Mtsg75	0.03 $(0.01)^*$	0.04 $(0.005)^{***}$	0.03 $(0.005)^{***}$	0.03 $(0.005)^{***}$
$Mtsg75^2$	-0.0003 $(0.0002)^{ns}$			
Rip		-0.69 $(0.20)^{***}$	-0.56 $(0.19)^{**}$	-0.61 $(0.19)^{**}$
SW		0.39 $(0.16)^*$		
Slope			0.02 $(0.009)^*$	
HLI				0.0006 $(0.0003)^{(*)}$
Day	0.03 $(0.01)^*$			

[a] $w_i = 0.17$; [b] $w_i = 0.54$; [c] $w_i = 0.25$; [d] $w_i = 0.21$

Table 16.   Model selection statistics for best model subsets (i.e., those $\leq$ 4 AIC of best) for montane sage-associated species.

Species[a]	Model[b]	AIC	ΔAIC	w_i
MacGillivray's Warbler_2	+Mtsg75 - Mtsg$^{2(ns)}$ + Day	832.5	3.22	0.17
Green-tailed Towhee_1	+Mtsg75 - Rip + SW	565.0	0	0.54
Green-tailed Towhee_2	+Mtsg75 - Rip + Slope	566.6	1.59	0.25
Green-tailed Towhee_3	+Mtsg75 - Rip + HLI$^{(m)}$	566.9	1.89	0.21

[a] "_1", "_2", etc. indicate alternate models for the same species.

[b] Model selection based on fixed-effect models; parameter significance based on mixed-effect models. Parameters are significant except those which became non-significant (ns) or marginally significant (m) upon addition of random effects.
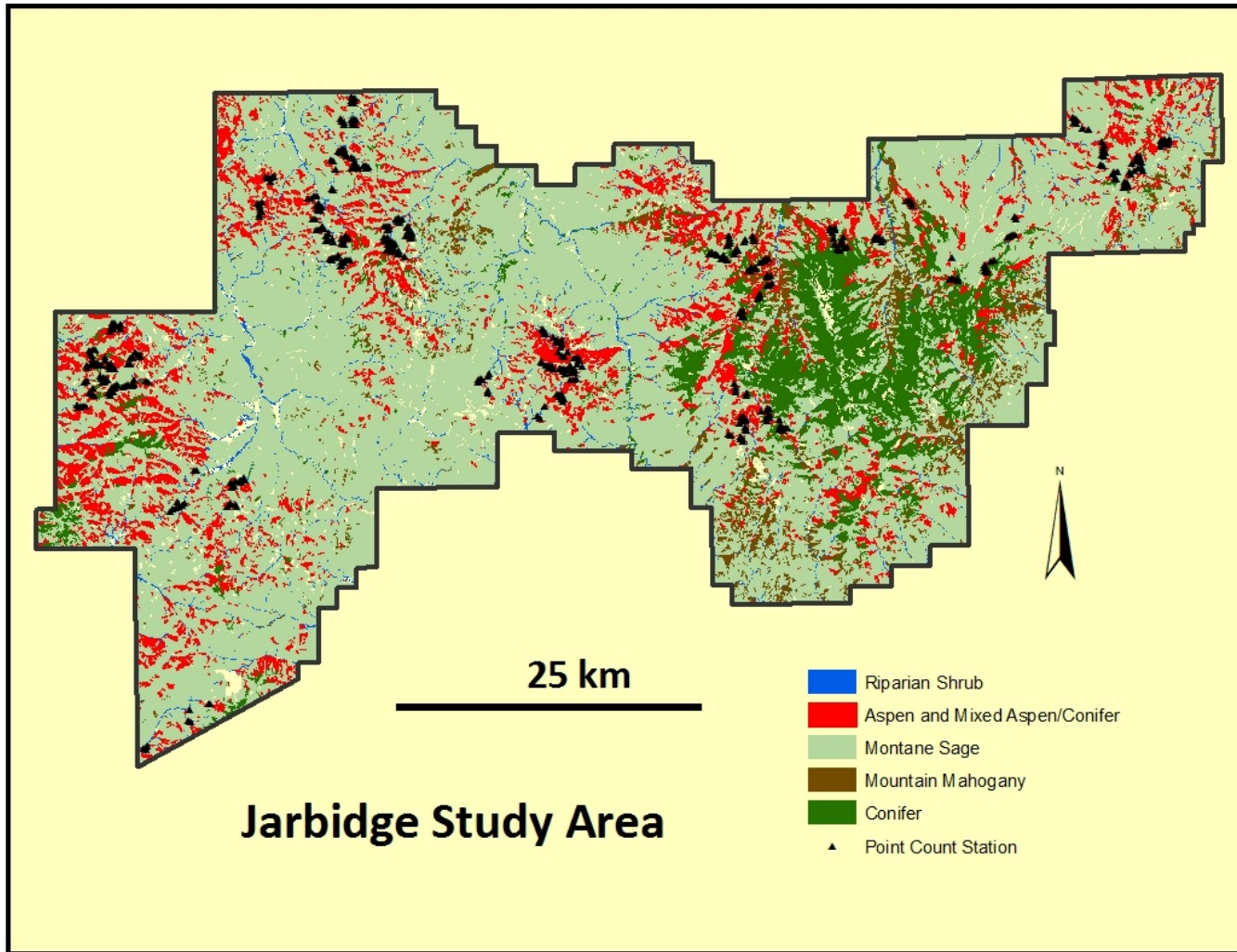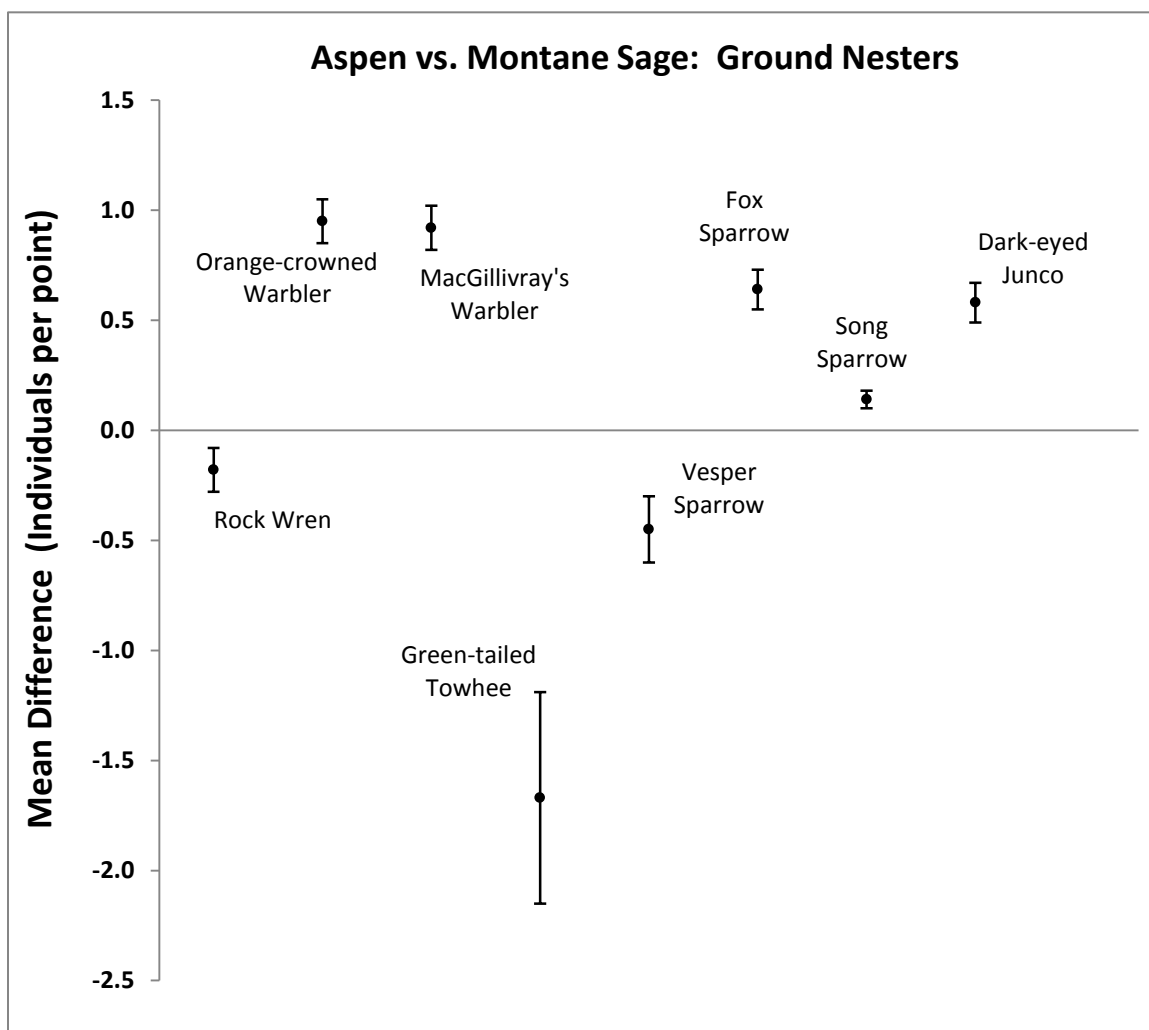
Figure 1. **Jarbidge Study Area, Humboldt-Toiyabe National Forest, Elko County, NV.**
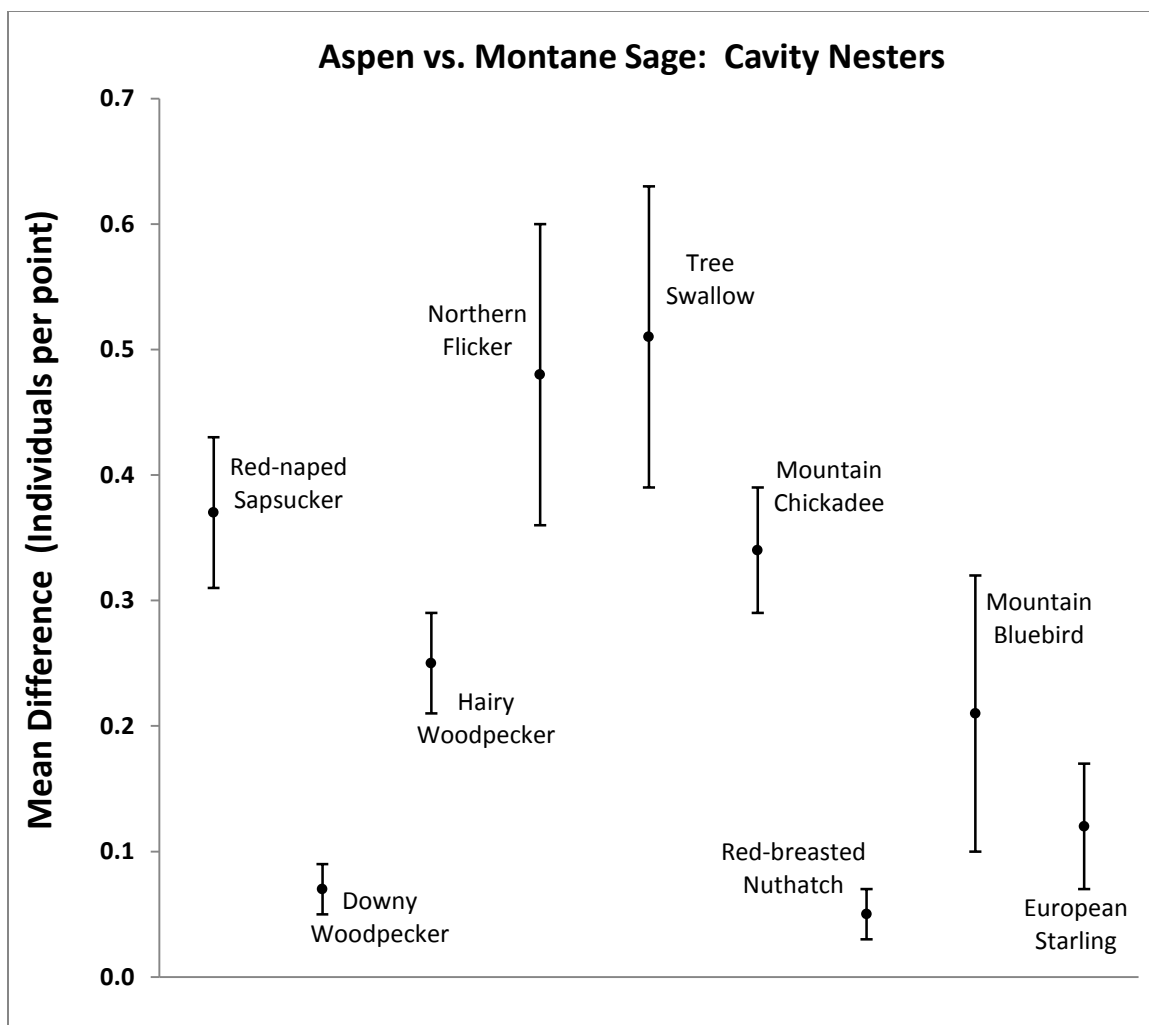
Figure 2. **Mean differences for ground-nesting species in aspen minus montane sage (N = 111 aspen and 23 montane sage stands). Differences for species shown are significant after adjustment for multiple comparisons, except for Rock Wren which is marginally significant. Results based on partially-paired t-tests. See Table 2 for complete results.**
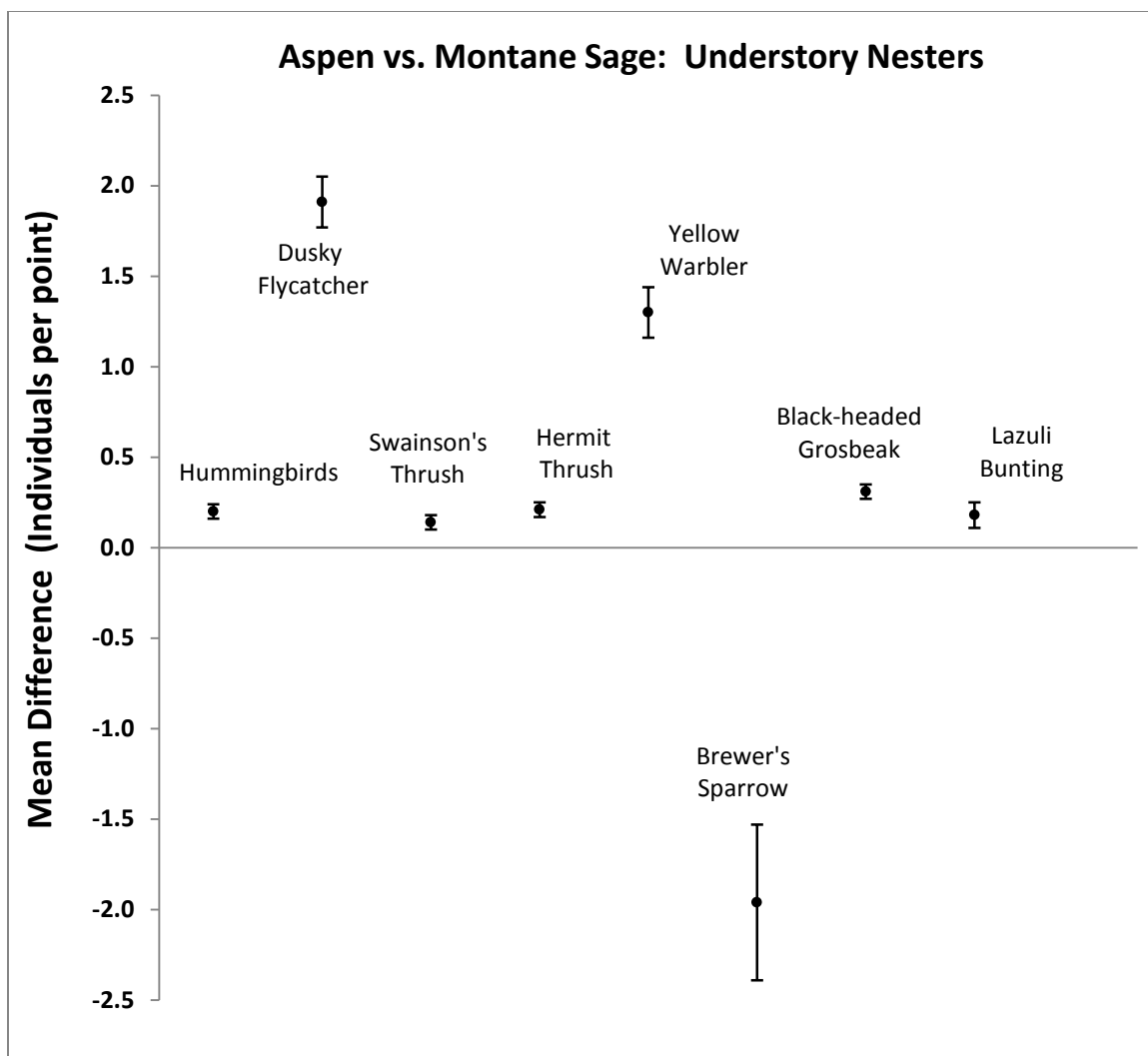
Figure 3. **Mean differences for understory-nesting species in aspen minus montane sage (N = 111 aspen and 23 montane sage stands). Differences for species shown are significant after adjustment for multiple comparisons. Results based on partially-paired t-tests. See Table 2 for complete results.**
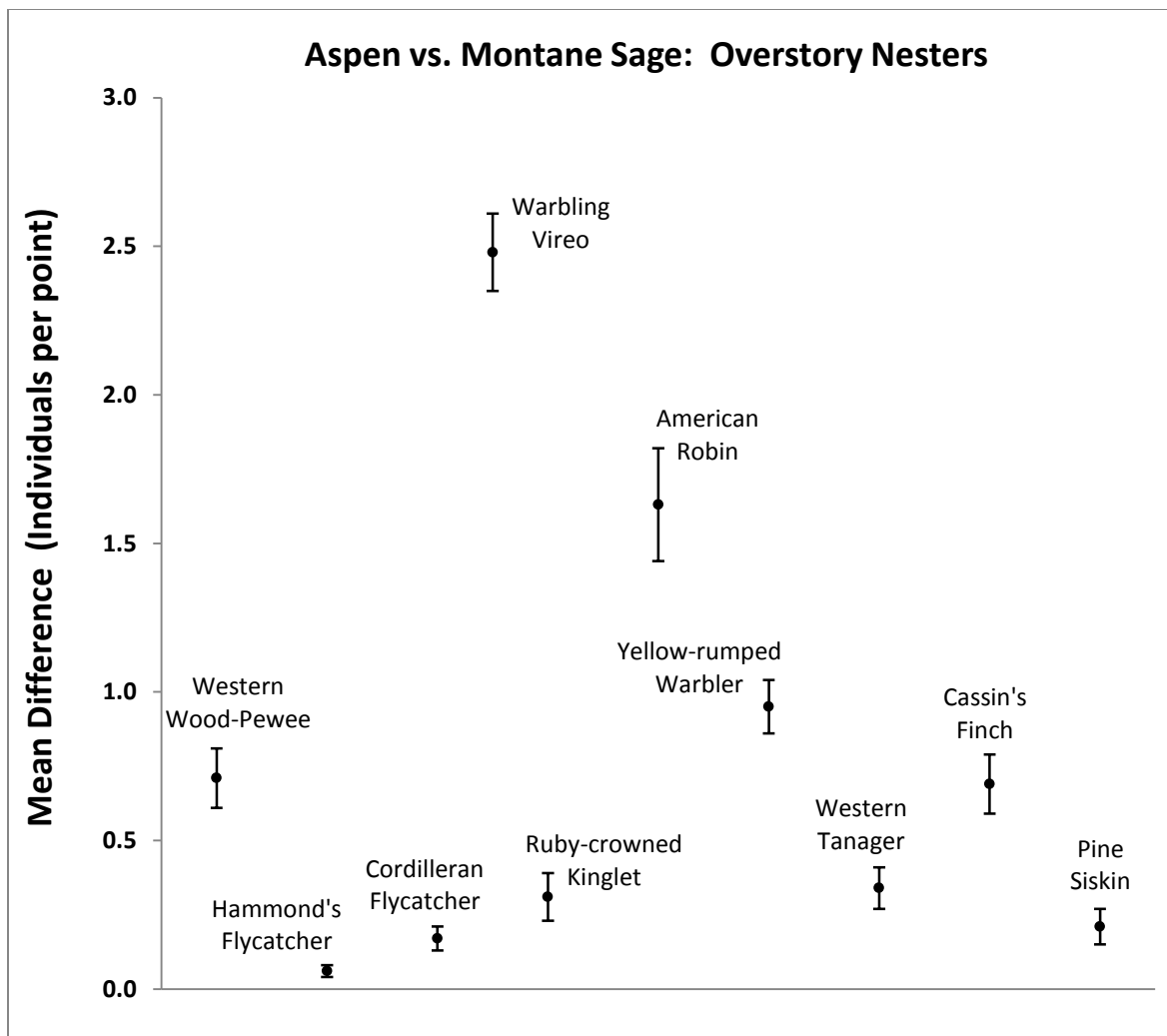
Figure 4. **Mean differences for overstory-nesting species in aspen minus montane sage (N = 111 aspen and 23 montane sage stands). Differences for species shown are significant after adjustment for multiple comparisons. Results based on partially-paired t-tests. See Table 2 for complete results.**
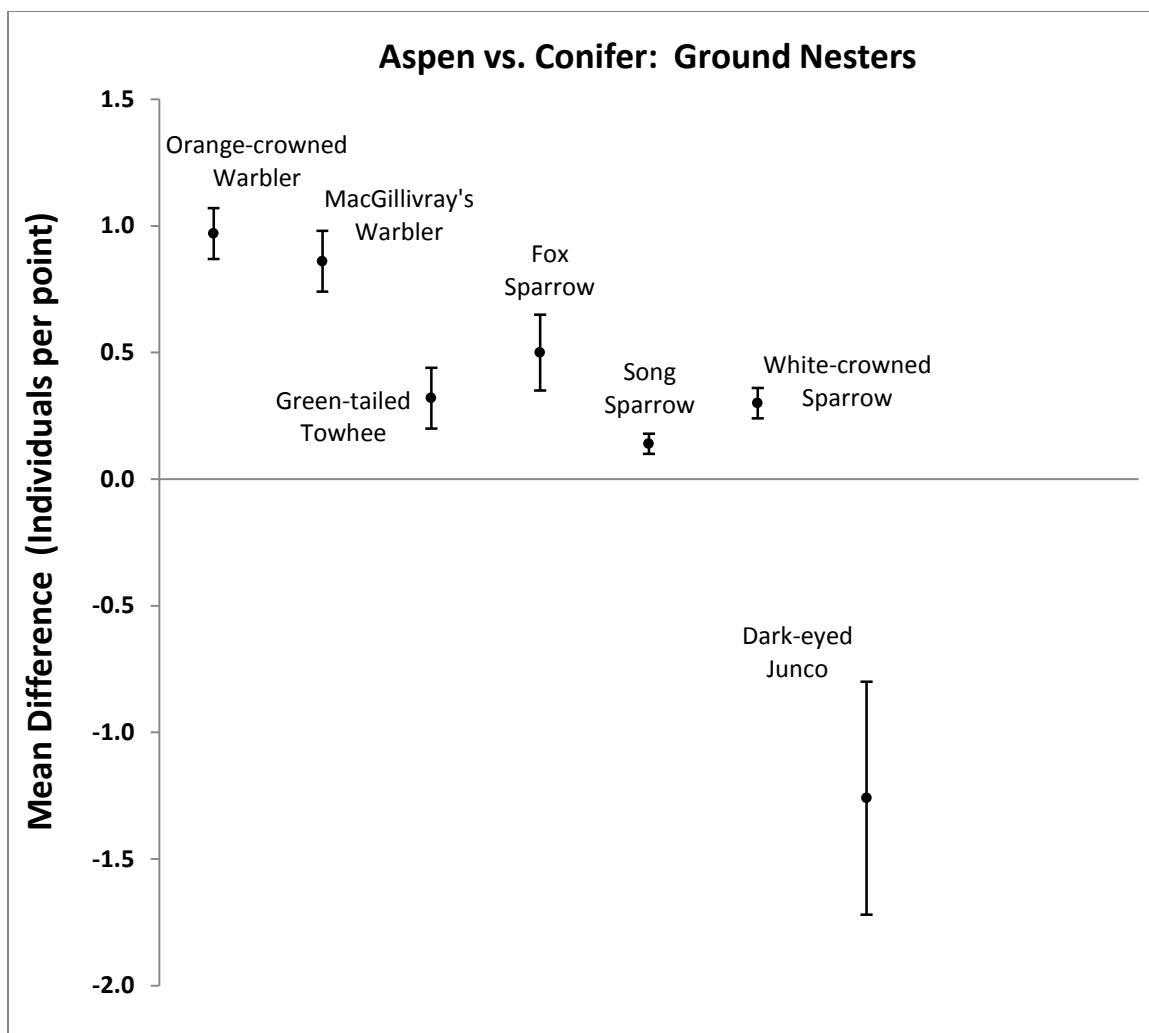
Figure 5. **Mean differences for cavity-nesting species in aspen minus montane sage (N = 111 aspen and 23 montane sage stands). Differences for species shown are significant after adjustment for multiple comparisons, except for Mountain Bluebird which is marginally significant. Results based on partially-paired t-tests. Mean difference for House Wren (not shown) is + 4.02 ($\pm$ 0.19)[***]. See Table 2 for complete results.**

Figure 6. **Mean differences for ground-nesting species in aspen minus conifer (N = 111 aspen and 14 conifer stands). Differences for species shown are significant after adjustment for multiple comparisons. Results based on partially-paired t-tests. See Table 4 for complete results.**
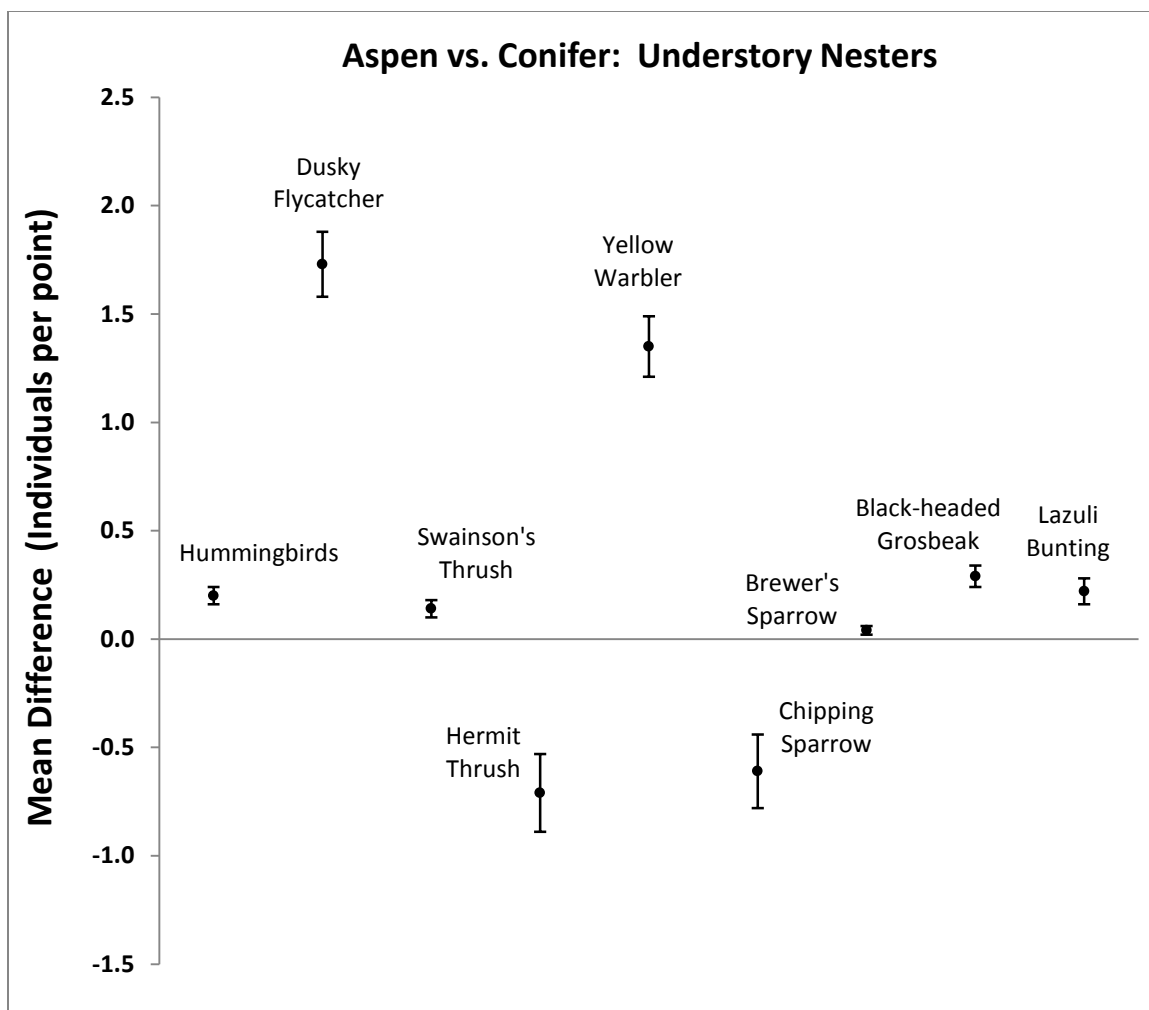
Figure 7. **Mean differences for understory-nesting species in aspen minus conifer (N = 111 aspen and 14 conifer stands). Differences for species shown are significant after adjustment for multiple comparisons. Results based on partially-paired t-tests. See Table 4 for complete results.**
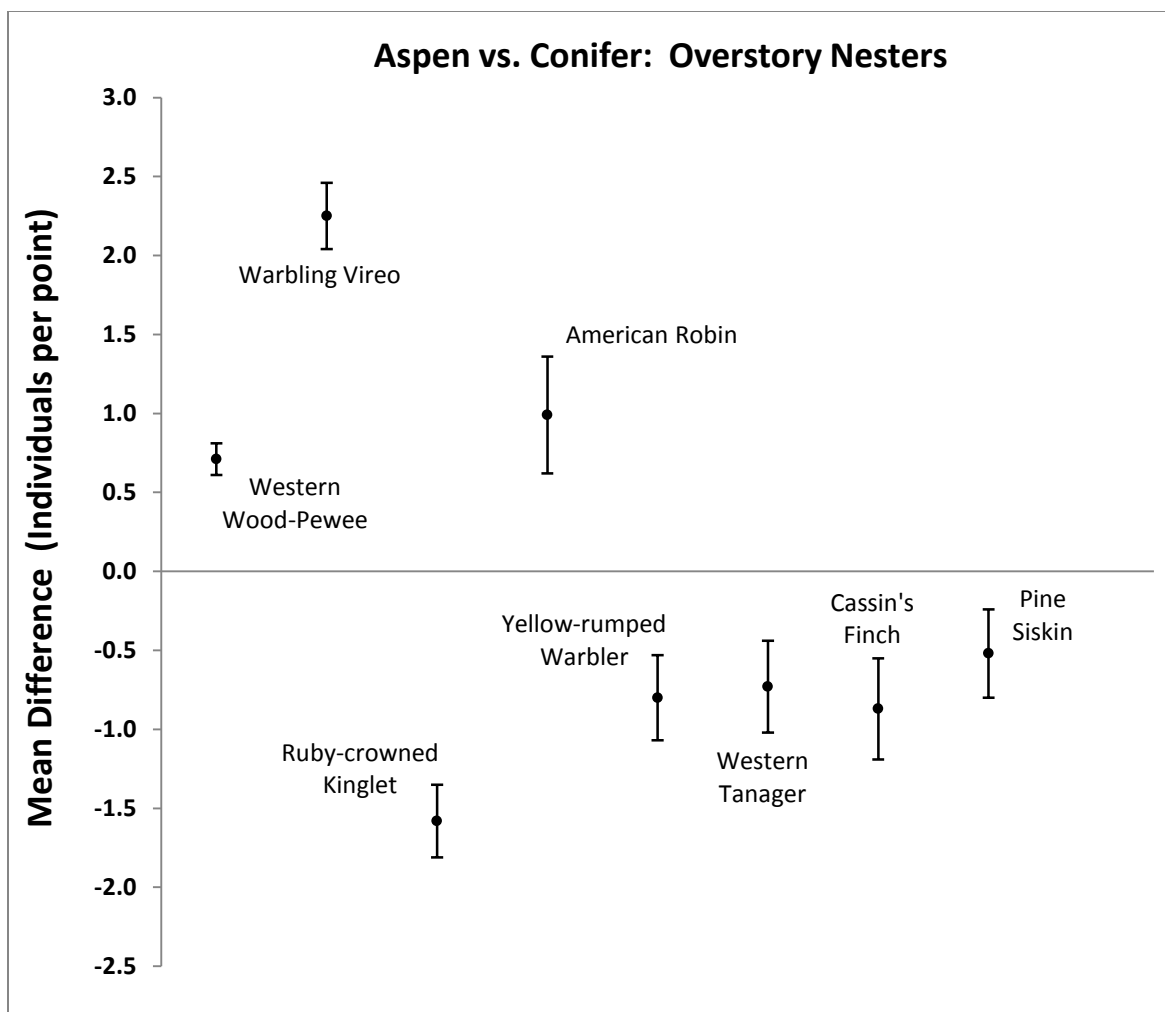
Figure 8. **Mean differences for overstory-nesting species in aspen minus conifer (N = 111 aspen and 14 conifer stands). Differences for species shown are significant after adjustment for multiple comparisons, except for Pine Siskin which is marginally significant. Results based on partially-paired t-tests. See Table 4 for complete results.**

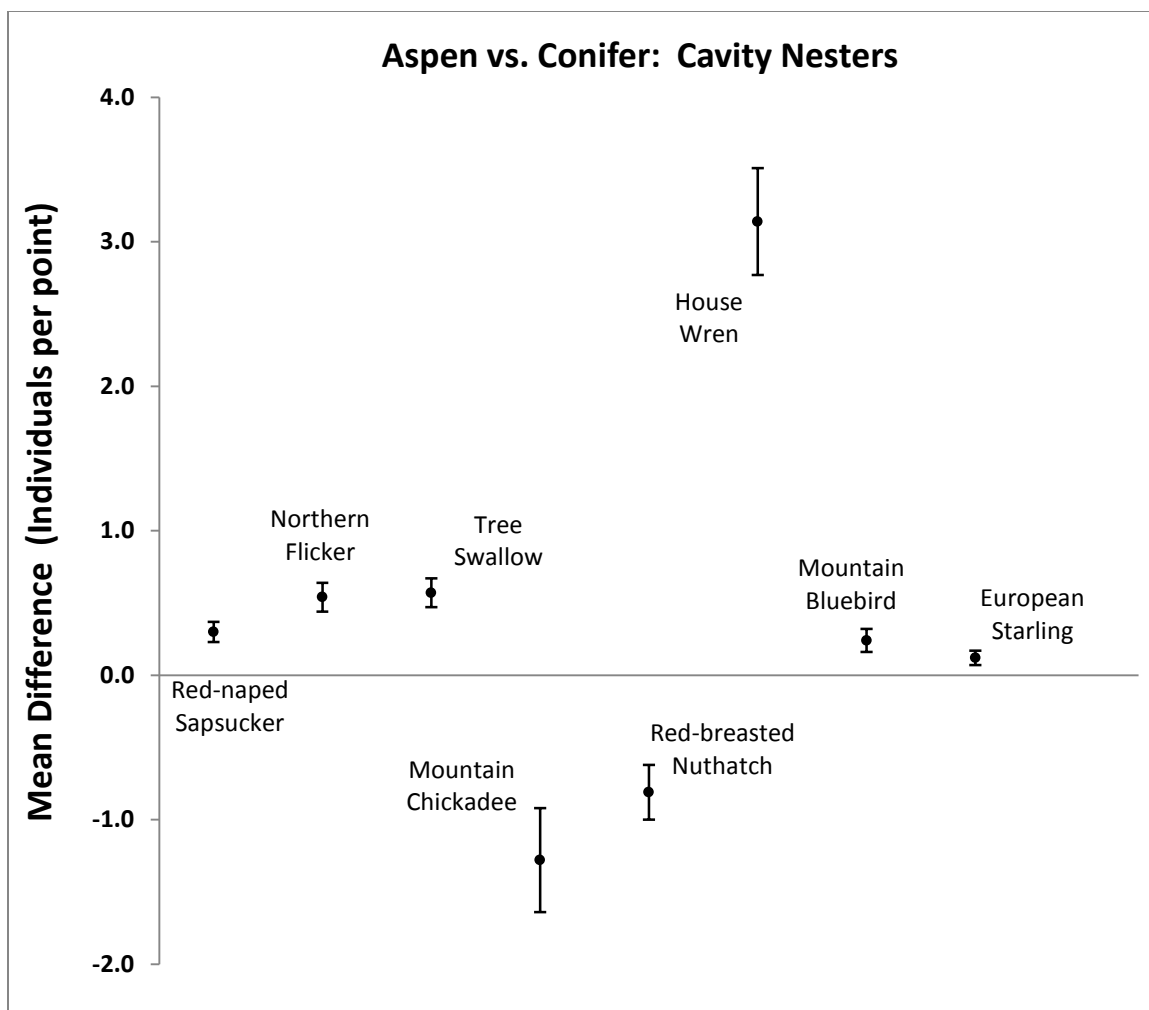**Aspen vs. Conifer: Cavity Nesters**

Figure 9.   **Mean differences for cavity-nesting species in aspen minus conifer (N = 111 aspen and 14 conifer stands). Differences for species shown are significant after adjustment for multiple comparisons. Results based on partially-paired t-tests. See Table 4 for complete results.**
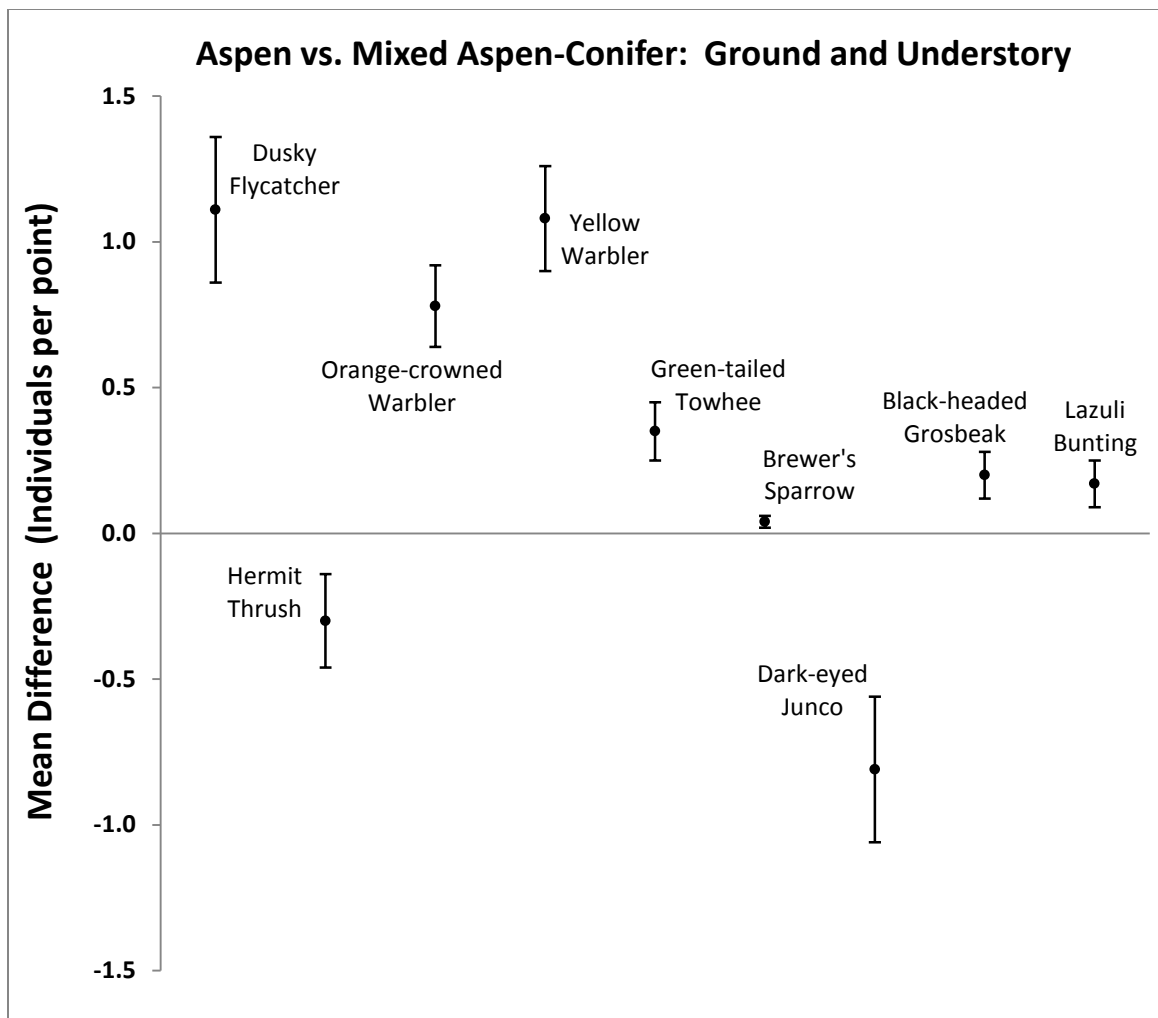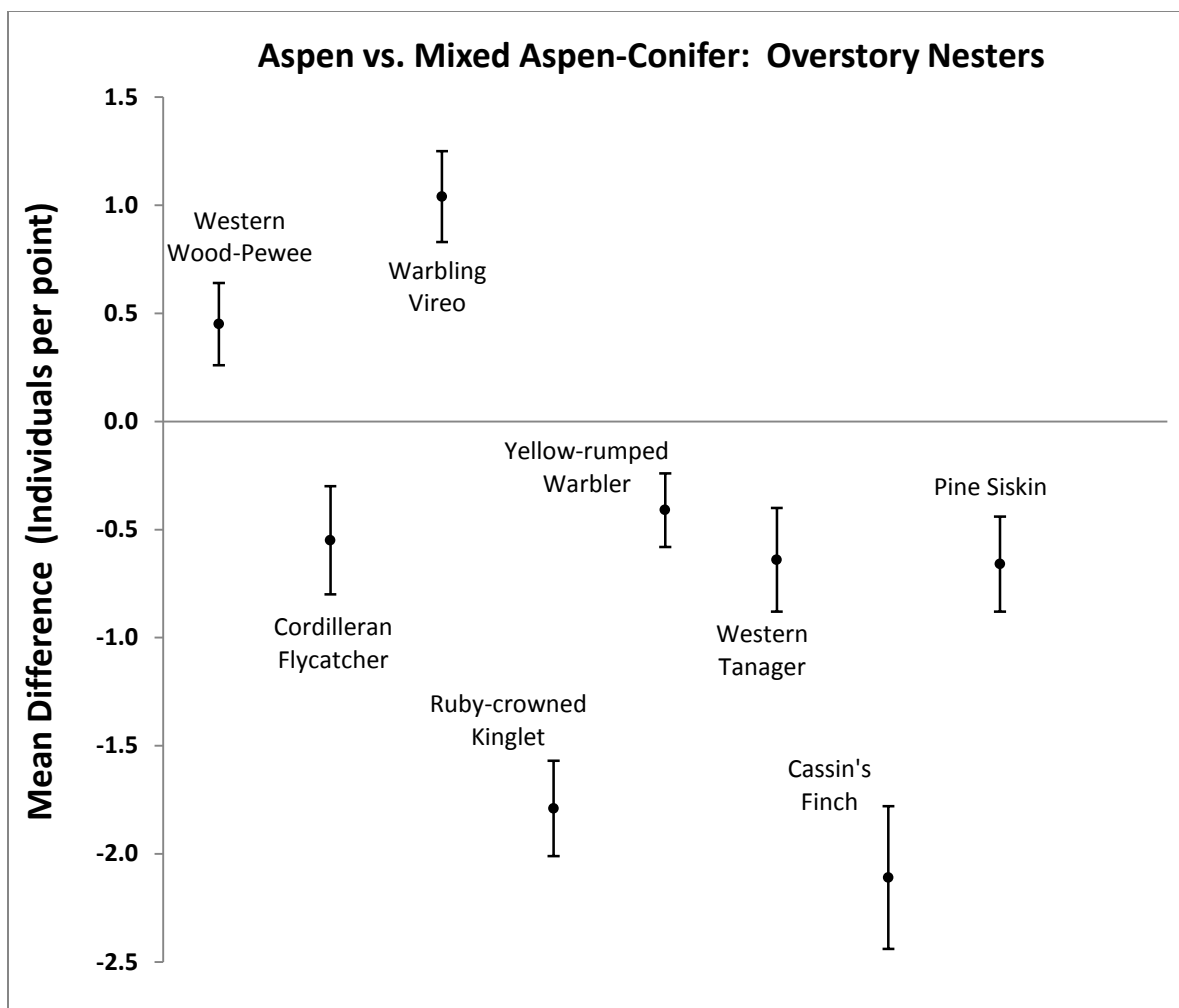
Figure 10. **Mean differences for ground- and understory-nesting species in aspen minus mixed aspen-conifer (N = 111 aspen and 19 mixed aspen-conifer stands). Differences for species shown are significant after adjustment for multiple comparisons, except for Hermit Thrush and Lazuli Bunting, which are marginally significant. Results based on partially-paired t-tests. See Table 6 for complete results.**

Figure 11. **Mean differences for overstory-nesting species in aspen minus mixed aspen-conifer (N = 111 aspen and 19 mixed aspen-conifer stands). Differences for species shown are significant after adjustment for multiple comparisons, except for Cordilleran Flycatcher which is marginally significant. Results based on partially-paired t-tests. See Table 6 for complete results.**
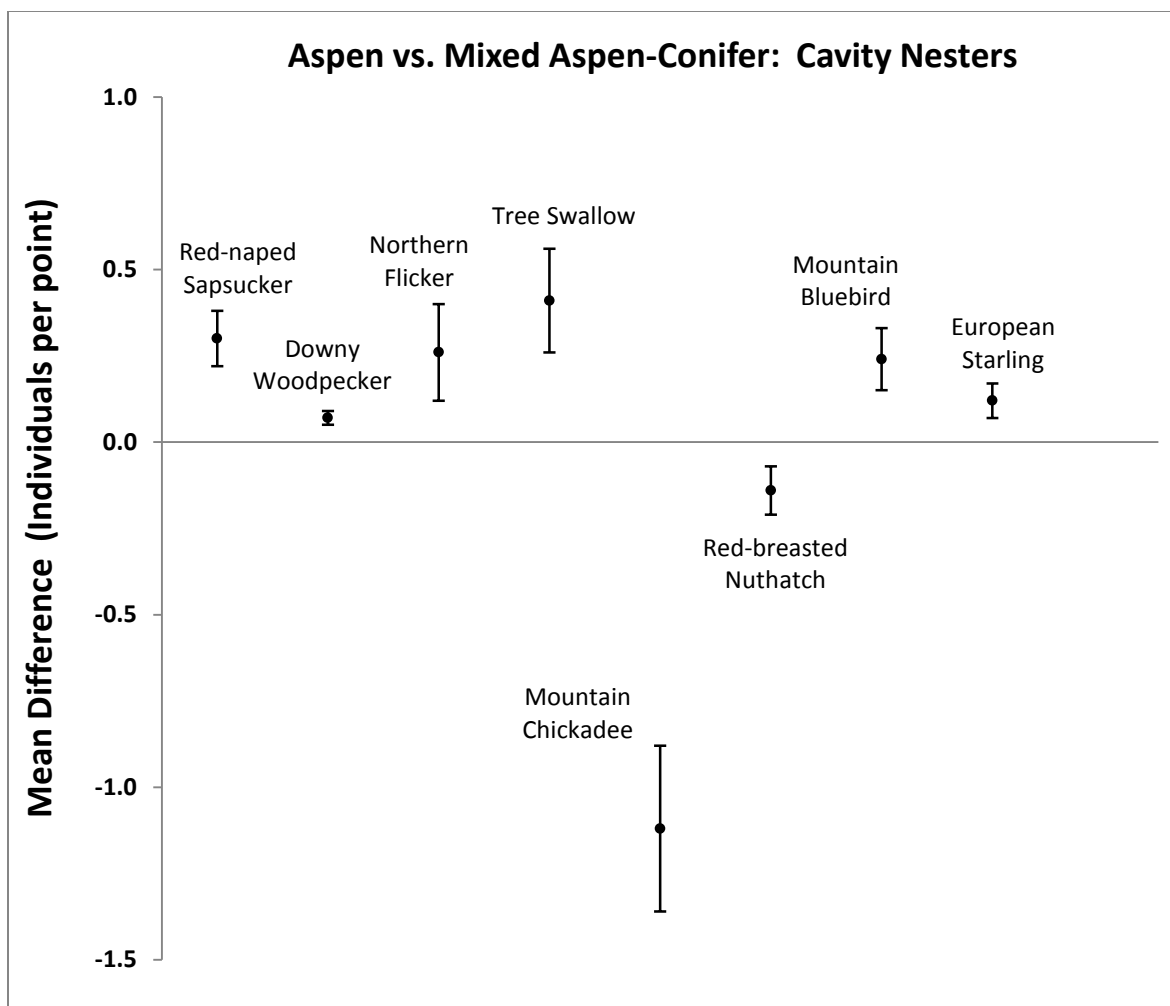
Figure 12. **Mean differences for cavity-nesting species in aspen minus mixed aspen-conifer (N = 111 aspen and 19 mixed aspen-conifer stands). Differences for species shown are significant after adjustment for multiple comparisons, except for Northern Flicker and Red-breasted Nuthatch, which are marginally significant. Results based on partially-paired t-tests. See Table 6 for complete results.**
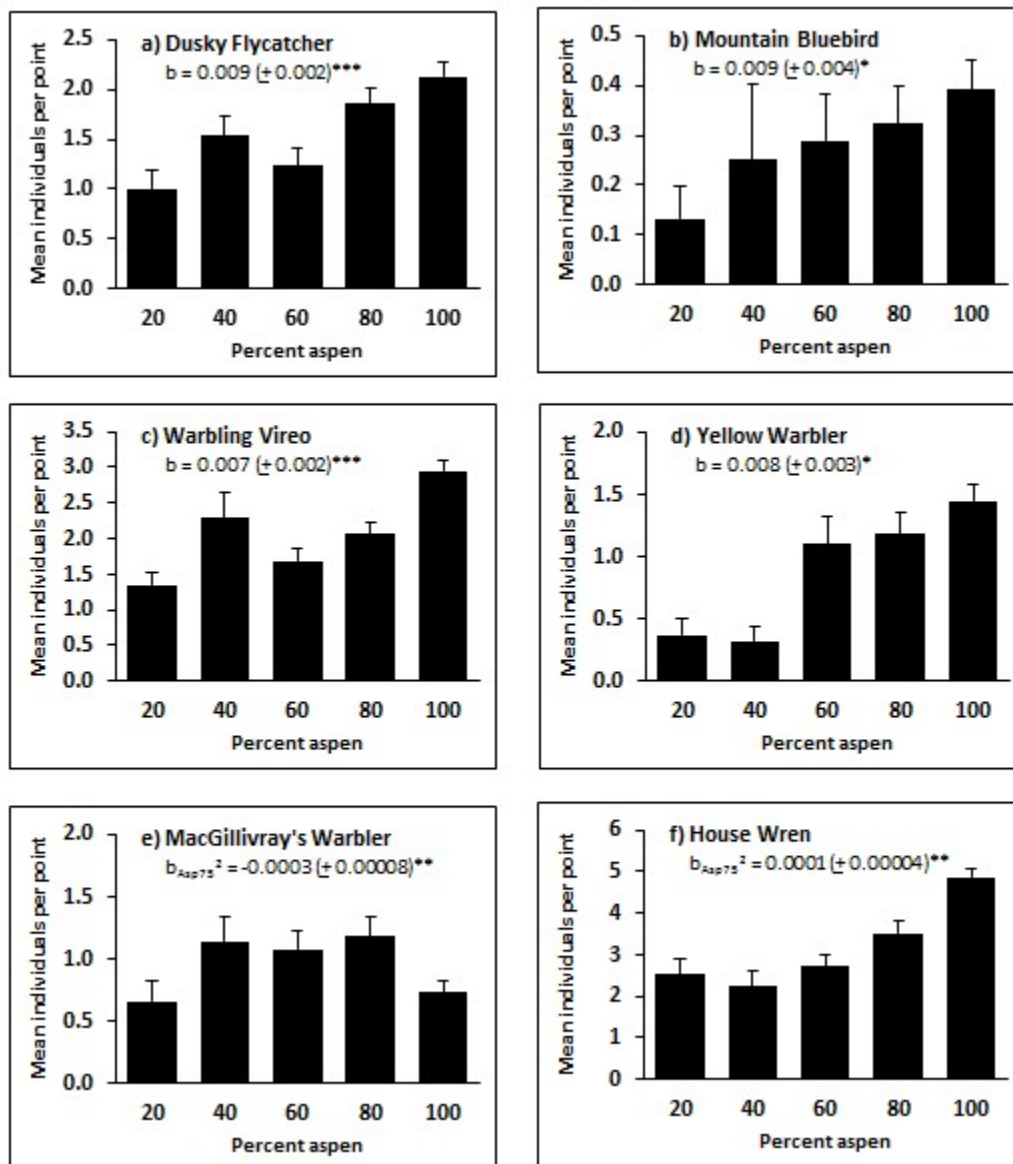
Figure 13. Mean abundance per point for aspen associates with a significant response to proportion of aspen within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect rather than squared term unless noted otherwise, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of percent 75-m aspen are 38, 28, 52, 68, 138, respectively.

Figure 13 (continued).

Figure 14. Mean abundance per point for aspen associates with a significant response to proportion of aspen within 300 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect rather than squared term unless noted otherwise, and are from mixed-effect models with random effects of stand and observer crew (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; (*) $p < 0.10$). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of percent 300-m aspen are 21, 122, 129, 45, 7, respectively.

Figure 15. Mean abundance per point for aspen associates with a significant response to proportion of conifer within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect rather than squared term unless noted otherwise, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of percent 75-m conifer are 295, 17, 10, 1, 1, respectively.
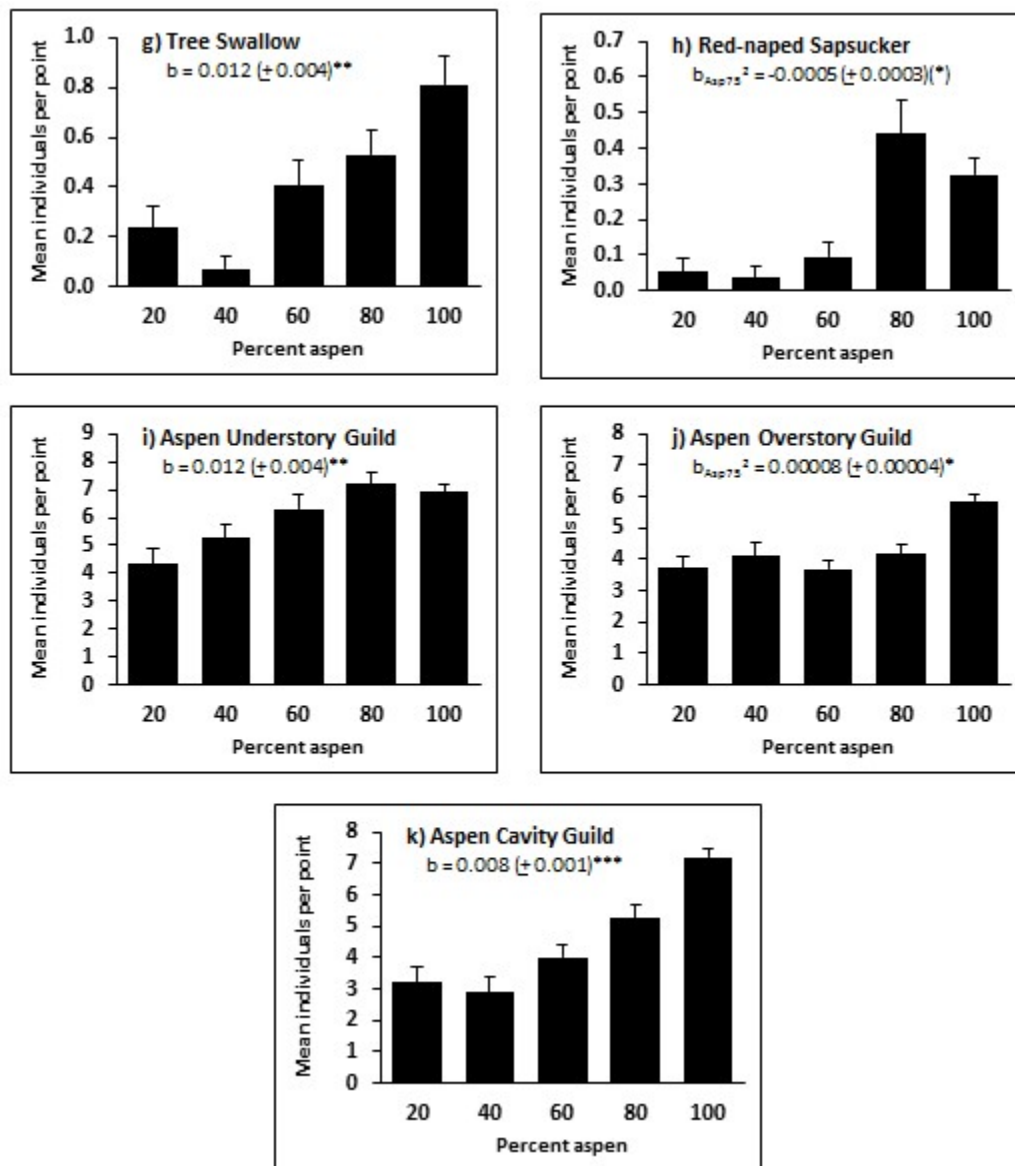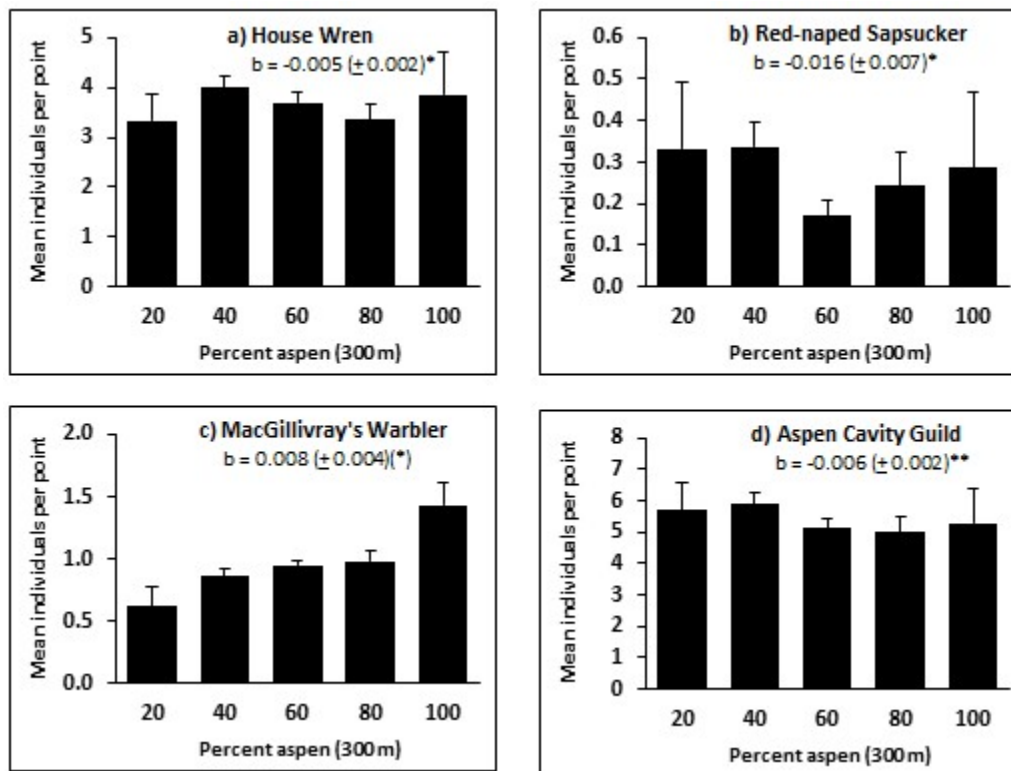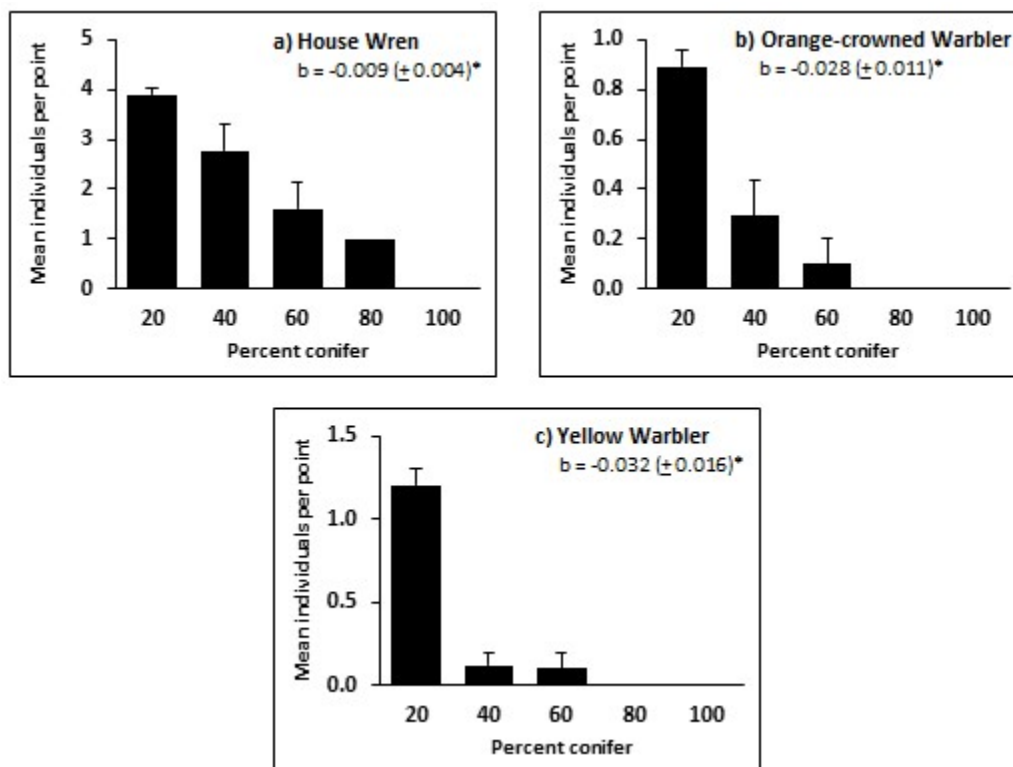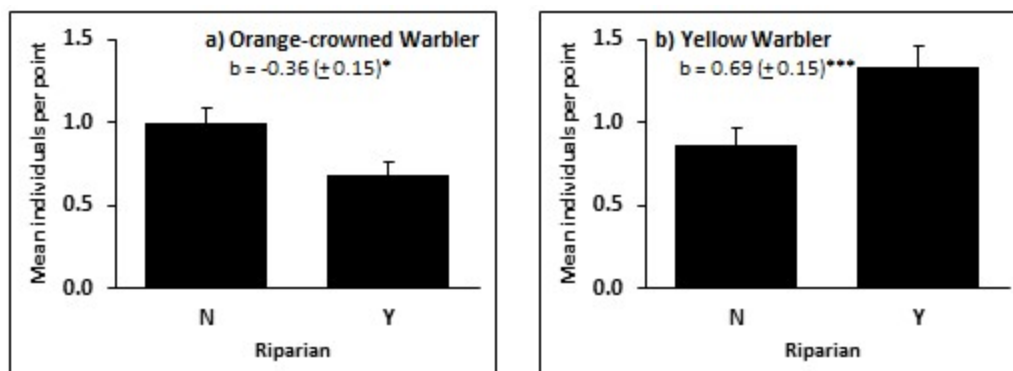
Figure 16. **Mean abundance per point for aspen associates with a significant response to riparian designation within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Riparian categories indicate presence/absence of a water source (i.e. Y/N). Sample sizes for each category of riparian designation are (N) 154, (Y) 170.**
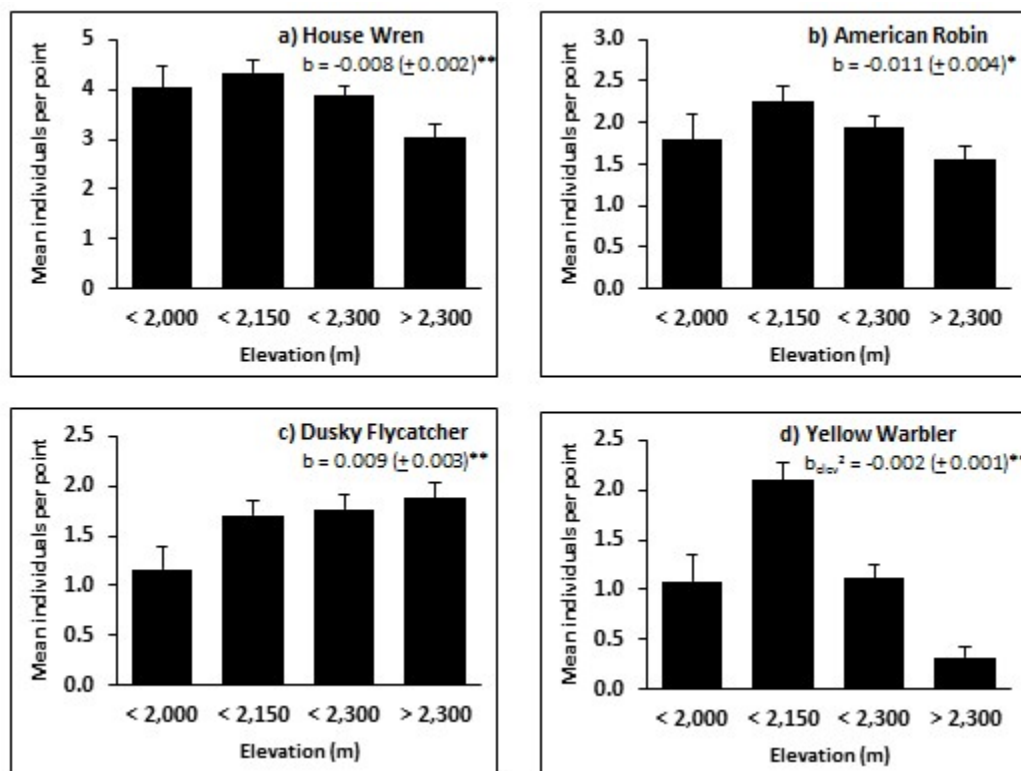
Figure 17. **Mean abundance per point for aspen associates with a significant response to mean elevation within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect rather than squared term unless noted otherwise, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of mean elevation are 24, 81, 118, 101, respectively.**
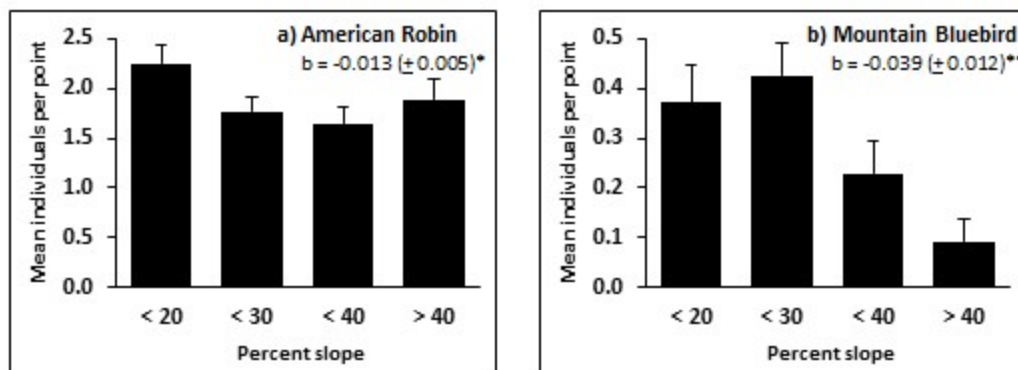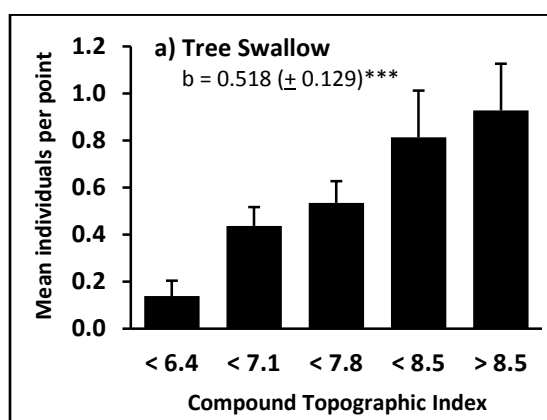
Figure 18. **Mean abundance per point for aspen associates with a significant response to mean slope within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of mean slope are 89, 113, 79, 43, respectively.**

Figure 19. **Mean abundance per point for Tree Swallows vs. Compound Topographic Index (CTI) within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of CTI are 29, 94, 114, 59, 28, respectively.**
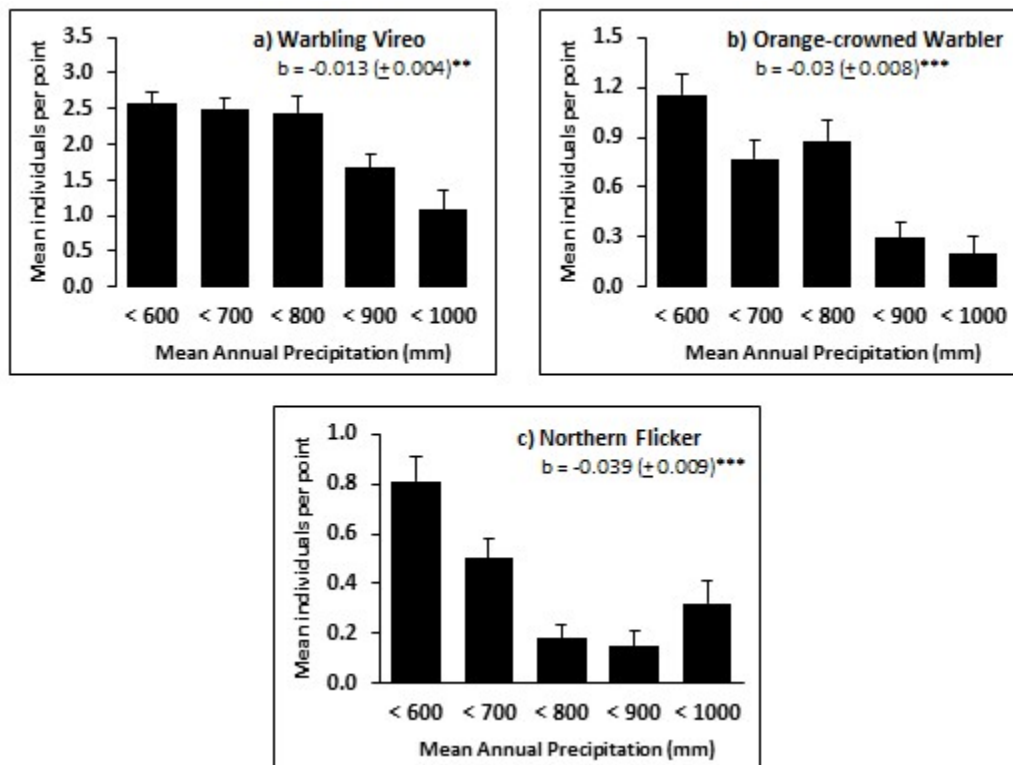
Figure 20. Mean abundance per point for aspen associates with a significant response to estimated mean annual precipitation at the survey point (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of mean precipitation are 110, 88, 67, 34, 25, respectively.

Figure 21. Mean abundance per point for conifer associates with a significant response to proportion of conifer within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect rather than squared term unless noted otherwise, and are from mixed-effect models with random effects of stand and observer crew (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; (*) $p < 0.10$). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of percent 75-m conifer are 295, 17, 10, respectively.
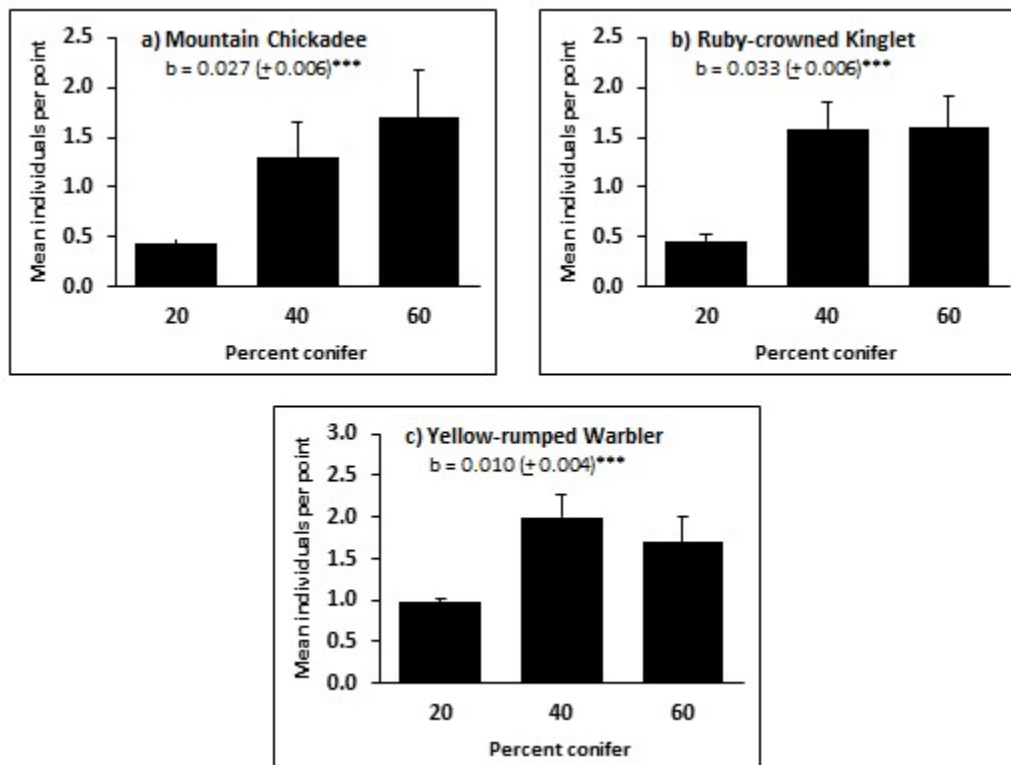
Figure 22. Mean abundance per point for conifer associates with a significant response to proportion of mixed aspen-conifer within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect rather than squared term unless noted otherwise, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of percent 75-m mixed aspen-conifer are 256, 19, 20, 12, 17, respectively.

Figure 23. **Mean abundance per point for conifer associates with a significant response to mean elevation within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect rather than squared term unless noted otherwise, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of mean elevation are 24, 81, 118, 101, respectively.**
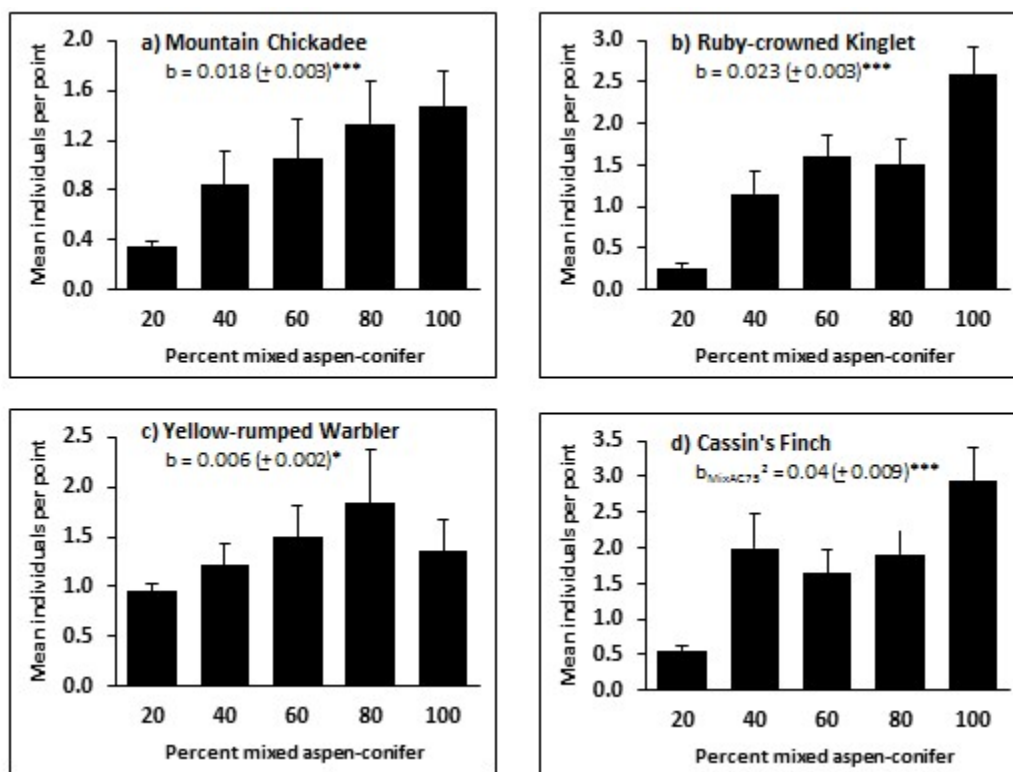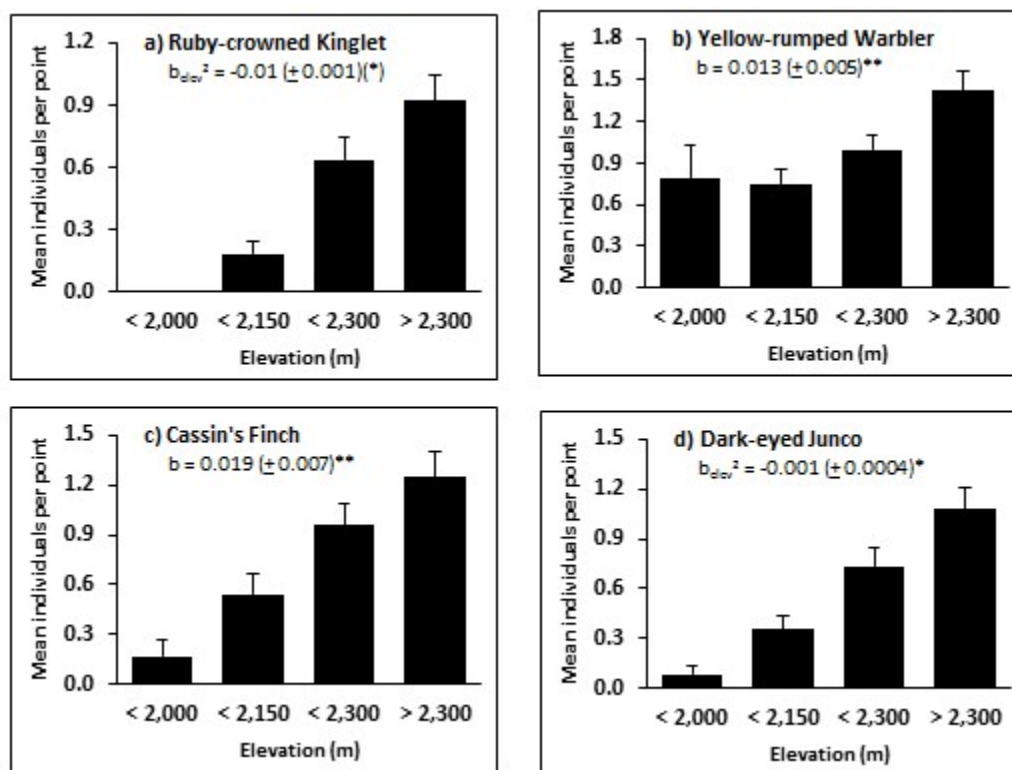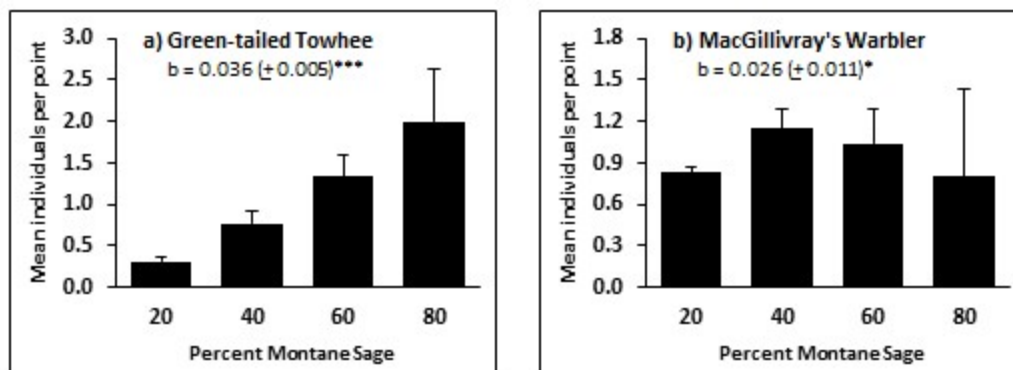
Figure 24. Mean abundance per point for montane sage associates with a significant response to proportion of montane sage within 75 m (N = 324). Regression coefficient (b), its SE (in parentheses), and significance are for the main effect rather than squared term unless noted otherwise, and are from mixed-effect models with random effects of stand and observer crew (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10). Mean abundance is based on the sum of two visits. Standard error bars do not incorporate random effects. Sample sizes for each category of percent 75-m montane sage are 231, 61, 27, 5, respectively.

APPENDIX A

Hierarchical Modeling Scheme of Fixed-effect Parameters used for Aspen-,

Conifer-, and Montane Sage-associated Avian Species

Table A.1. Hierarchical modeling scheme of fixed-effect parameters used for aspen-, conifer-, and montane sage-associated avian species. Stages 1 and 2 add 75-m and 300-m cover type parameters, respectively; Stage 3 adds topographic parameters, and Stage 4 adds day. Only models in the best model subset were carried to the next stage. Models with squared terms or interactions also included the corresponding main effects.[a]

Stage	Aspen associates	Conifer associates	Montane sage associates
1	Asp75	Con75	Mtsg75
	$Asp75^2$	$Con75^2$	$Mtsg75^2$
	Asp75 + Con75	Con75 + MixAC75	Mtsg75 + Con75
	Asp75 + Rip	Con75 + Rip	Mtsg75 + Rip
	Asp75 + Con75 + Rip	Con75 + MixAC75 + Rip	Mtsg75 + Con75 + Rip
	$Asp75^2$ + Con75	$Con75^2$ + Rip	Mtsg75 + MixAC75 + Rip
	$Asp75^2$ + Rip	MixAC75	$Mtsg75^2$ + Rip
	$Asp75^2$ + Con75+ Rip	$MixAC75^2$	Mtsg75 + MixAC75
		MixAC75 + Rip	
		$MixAC75^2$ + Rip	
2	Stage 1	Stage 1	Stage 1
	Stage 1 + Asp300	Stage 1 + Con300	Stage 1 + Mtsg300
	Stage 1 + Nasp300	Stage 1 + Ncon300	Stage 1 + Nmtsg300
	Stage 1 + $Asp300^2$	Stage 1 + $Con300^2$	Stage 1 + $Mtsg300^2$
	Stage 1 + Asp300 + Nasp300	Stage 1 + Con300 + Ncon300	Stage 1 + Mtsg300 + Nmtsg300

Table A.1. Continued.

2	Stage 1 + Asp300*Nasp300		
	Stage 1 + Asp300 + E2A		
	Stage 1 + Asp300 + Nasp300 + E2A		
	Stage 1 + Asp300^2 + E2A		
3	Stage 2	Stage 2	Stage 2
	Stage 2 + Elev	Stage 2 + Elev	Stage 2 + Elev
	Stage 2 + SW	Stage 2 + SW	Stage 2 + SW
	Stage 2 + Slope	Stage 2 + Slope	Stage 2 + Slope
	Stage 2 + Elev^2	Stage 2 + Elev^2	Stage 2 + Elev^2
	Stage 2 + Prec	Stage 2 + Prec	Stage 2 + Prec
	Stage 2 + HLI	Stage 2 + HLI	Stage 2 + HLI
	Stage 2 + CTI	Stage 2 + CTI	Stage 2 + CTI
4	Stage 3	Stage 3	Stage 3
	Stage 3 + Day	Stage 3 + Day	Stage 3 + Day

[a] Parameter abbreviations are as follows: Asp (aspen), Con (conifer), MixAc (mixed aspen-conifer), Mtsg (montane sage), Rip (riparian), Nasp (non-aspen matrix), Ncon (non-conifer matrix), Nmtsg (non-montane sage matrix), E2A (edge:area ratio), Elev (elevation), SW (southwestness), Slope, HLI (heat load index), CTI (compound topographic index), Prec (precipitation), Day (day of first survey). The 75 and 300 suffixes to cover types indicate measurements within 75- or 300-m radius of the point count circle. Parameters are further defined in Methods.

APPENDIX B

Significant Univariate Predictors for Aspen-,

Conifer-, and Montane Sage-associated Avian Species

Table B.1. Statistically significant (p < 0.05) positive (+) and negative (-) univariate predictors for conifer- and montane sage-associated species. Parentheses indicate marginal significance; 0.10 < p < 0.05. N = 324 points.

Parameter	Ruby-crowned Kinglet	Yellow-rumped Warbler	Cassin's Finch	Mountain Chickadee	Dark-eyed Junco	MacGillivray's Warbler	Green-tailed Towhee
Asp75	-		-	-	-		
MixAC75	+	+	+	+	+		-
Con75	+	+		+	+		
Mtsg75	-	-	-	-	-	+	+
Rip					-		-
Asp300					+		(-)
Con300	+	+	+	+	+		
Nasp300	-	-	-	-	-		
Ncon300	-		-	(-)	-		+
Elev	+	+	+	+	+		-
Slope			-			+	+
HLI	(-)	-					+
CTI			+				-
Prec	+	+	+	+	+		-
Day	+	+	+	+	+	+	(-)

Table B.2.   **Statistically significant (p < 0.05) positive (+) and negative (-) univariate predictors for aspen-associated species. Parentheses indicate marginal significance; 0.10 < p < 0.05. N = 324 points.**

Parameter	Warbling Vireo	American Robin	Dusky Flycatcher	Yellow Warbler	Mac-Gillivray's Warbler	Orange-crowned Warbler	Red-naped Sapsucker	Northern Flicker	Tree Swallow	House Wren	Mountain Bluebird
Asp75	+		+	+		+	+	+	+	+	+
MixAC75	-		-	-		-	-	-	-	-	
Con75	-	(-)	-	-		-	-	-	-	-	-
Mtsg75	-		(-)		+	+				-	
Rip			(-)	+		-					
Asp300							-				
E2A300		+					(+)				
Con300	-		-	-		-	(-)	-	-	-	
Nasp300	+		+	+		+	+	+	+	+	
Ncon300		+		+			+	+		+	(+)
Elev	(-)	-	(+)	-				-		-	
Slope		-			(+)				-		-
HLI			(-)								
CTI						-			+		
Prec	-			-		-	-	-	-	-	
Day		-	+	-	+				-	-	

APPENDIX C

Vegetative Cover Type and Tree and Shrub Species Composition at Sampled Points

Table C.1.   Cover type composition of all points used in multiple regression (N = 324). By design, all had the aspen cover type present. Cell contents are number of points (percent of all 324 points).

Composition (%)	Aspen	Mixed Aspen-Conifer	Conifer	Montane Sage
>0%	324 (100)	92 (28)	53 (16)	246 (76)
>50%	234 (72)	39 (12)	4 (1)	16 (5)
100%	31 (10)	7 (2)	0	0

Table C.2.   Tree species composition of a subset of points used in multiple regression for which species composition was recorded in the field (N = 254). By design, all had the aspen cover type present. Cell contents are number of points with percent of column total in parentheses.

	Most Common Tree Species[a]	
Second Most Common Tree Species[b]	Aspen	Fir
Aspen	68 (32)[c]	25 (89)
Fir	45 (21)	0
Willow	42 (20)	0
Serviceberry	29 (14)	0
Chokecherry	20 (10)	0
Gray alder	6 (3)	0
Mountain mahogany	1 (1)	0
Pine	0	3 (11)
Total [b]	211	28

[a] Additional points not included in this table are those with the following species as most common: 3 with willow, 2 with pine, and 14 with serviceberry, chokecherry, alder, or mountain mahogany as the most common.

[b] For the purpose of tree species composition, a tree was defined as an individual > 1.5 m in height. Scientific names are as follows: Aspen (*Populus tremuloides*), Fir (*Abies* spp.), Willow (*Salix* spp.), Serviceberry (*Amelanchier alnifolia*), Chokecherry (*Prunus virginiana*), Gray alder (*Alnus incana*), Mountain mahogany (*Cercocarpus ledifolius*).

[c] Aspen was the only tree species recorded on 68 points.

Table C.3.   Most common tree species recorded at conifer (N = 20) and mixed aspen-conifer (N = 27) points used in the paired and partially-paired comparisons and for which species composition was recorded in the field.

| | Number of Points (% within cover type) | | | |
| | Conifer (N = 20) | | Mixed Aspen-Conifer (N = 27) | |
	Most Common	Present	Most Common	Present
Fir	16 (80)	20 (100)	18 (67)	27 (100)
Pine	4 (20)	12 (60)	0	5 (19)
Aspen	0	0	9 (33)	27 (100)
Willow	0	0	0	10 (37)
Alder	0	0	0	2 (7)

Table C.4.   The three most common shrub species recorded at a subset of montane sage points (N = 21) used in the paired and partially-paired comparisons and for which species composition was recorded in the field.

Species	Number of Points	Percent of Points (N = 20)
Big sagebrush	20	95
Mountain snowberry	13	62
Serviceberry	7	33
Chokecherry	7	33
Yellow rabbitbrush	6	29
Snowbrush ceanothus	2	10
Rubber rabbitbrush	2	10
Antelope bitterbrush	2	10
Wax currant	2	10

APPENDIX D

Coefficients and Standard Errors of Random Effects for Aspen-, Conifer-,

and Montane Sage-associated Avian Species

Table D.1. Coefficients and standard errors (in parentheses) of random effects for focal species and nesting guilds. Asterisks indicate p-values of random effects[a] (* p <0.05; ** p <0.01; *** p <0.001; (*) p <0.10; [ns] p >0.10). N = 324 points.

Cover Type	Species or Nesting Guild	Crew	Stand
Aspen	*Ground/Understory[b]*		0.05 (0.02)***
	Dusky Flycatcher	0.23 (0.19)***	0.005 (0.02)[ns]
	Orange-crowned Warbler[b]		0.17 (0.10)*
	Yellow Warbler	0.22 (0.21)***	0.27 (0.12)**
	MacGillivray's Warbler_1	0.02 (0.04)[ns]	0.19 (0.10)*
	Overstory_1	0.01 (0.02)*	0.04 (0.02)**
	Overstory_2	0.02 (0.02)*	0.04 (0.02)**
	Overstory_3	0.01 (0.01)*	0.04 (0.02)**
	Warbling Vireo	0.02 (0.02)*	0.04 (0.03)*
	American Robin_1	0.02 (0.03)[ns]	0.20 (0.06)***
	American Robin_2	0.03 (0.04)[ns]	0.20 (0.06)***
	Cavity	0.01 (0.02)[ns]	0.06 (0.03)**
	Red-naped Sapsucker	0.006 (0.04)[ns]	0.08 (0.18)[ns]
	Northern Flicker	0.04 (0.06)[ns]	0.18 (0.11)*
	Tree Swallow	0.20 (0.22)*	0.31 (0.15)**
	House Wren	0.01 (0.02)*	0.04 (0.03)*
	Mountain Bluebird	0.008 (0.06)[ns]	0.32 (0.17)**
Conifer	*Ground/Understory*	0.03 (0.05)[ns]	0.21 (0.10)**
	Dark-eyed Junco	0.02 (0.06)[ns]	0.26 (0.12)**
	Overstory	0.02 (0.03)(*)	0.11 (0.05)**
	Ruby-crowned Kinglet_1	0.07 (0.12)[ns]	0.38 (0.19)**
	Ruby-crowned Kinglet_2	0.08 (0.13)[ns]	0.42 (0.18)**
	Yellow-rumped Warbler_1	0.04 (0.05)*	0.08 (0.07)[ns]
	Yellow-rumped Warbler_2	0.04 (0.05)*	0.09 (0.07)(*)
	Yellow-rumped Warbler_3	0.04 (0.05)	0.11 (0.07)(*)
	Cassin's Finch[b]		0.26 (0.11)**
	Cavity[b]		0.29 (0.12)***
	Mountain Chickadee[b]		0.26 (0.13)**
Montane Sage	*Ground/Understory[c]*	--	--
	MacGillivray's Warbler_2	0.02 (0.04)[ns]	0.23 (0.09)***
	Green-tailed Towhee_1	0.10 (0.13)(*)	0.33 (0.14)**
	Green-tailed Towhee_2	0.14 (0.16)*	0.33 (0.14)**
	Green-tailed Towhee_3	0.10 (0.13)(*)	0.34 (0.14)**

[a] P-values are from likelihood ratios based on pseudo-likelihoods. Models also contain the fixed effects identified in Tables 11, 14, and 16.

[b] Blank cells for a random effect indicate that the model did not converge or the G-matrix was not positive definitive.

[c] Nesting guilds were not modeled for montane-sage associates

APPENDIX E

Mean Number of Individuals per Point for Aspen-, Conifer-,

and Montane Sage-Associated Avian Species

Table E.1. **Mean number of individuals per point for aspen, mixed aspen-conifer, conifer, and montane sage; based on sum of two visits per point. Means and standard errors are based on stand as the primary sampling unit (i.e., data averaged within stands and then across stands). N = 111 aspen stands, 19 mixed aspen-conifer, 14 conifer, and 23 montane sage stands.**

Species or Nesting Guild	Aspen	Mixed Aspen-Conifer	Conifer	Montane Sage
Ground/Understory[a]	9.01 (0.30)	6.62 (0.57)	4.32 (0.66)	5.67 (0.81)
Hummingbirds	0.20 (0.04)	0.21 (0.10)	0.00	0.00
Empidonax spp.	0.23 (0.04)	0.23 (0.10)	0.04 (0.04)	0.00
Dusky Flycatcher	2.00 (0.13)	0.89 (0.24)	0.27 (0.08)	0.09 (0.06)
Rock Wren	0.02 (0.01)	0.00	0.00	0.20 (0.10)
Swainson's Thrush	0.14 (0.04)	0.23 (0.14)	0.00	0.00
Hermit Thrush	0.21 (0.04)	0.51 (0.15)	0.92 (0.18)	0.00
Orange-crowned Warbler	0.97 (0.10)	0.20 (0.12)	0.00	0.02 (0.02)
Yellow Warbler	1.37 (0.14)	0.29 (0.13)	0.02 (0.02)	0.07 (0.05)
MacGillivray's Warbler	0.97 (0.09)	0.59 (0.19)	0.11 (0.08)	0.04 (0.04)
Green-tailed Towhee	0.46 (0.08)	0.11 (0.06)	0.14 (0.10)	2.13 (0.50)
Chipping Sparrow	0.08 (0.03)	0.29 (0.12)	0.69 (0.18)	0.09 (0.06)
Brewer's Sparrow	0.04 (0.02)	0.00	0.00	2.00 (0.43)
Vesper Sparrow	0.03 (0.01)	0.00	0.00	0.48 (0.15)
Fox Sparrow	0.64 (0.09)	0.96 (0.23)	0.14 (0.14)	0.00
Song Sparrow	0.14 (0.04)	0.11 (0.11)	0.00	0.00
White-crowned Sparrow	0.30 (0.06)	0.18 (0.09)	0.00	0.22 (0.18)
Dark-eyed Junco	0.58 (0.09)	1.39 (0.26)	1.85 (0.47)	0.00
Black-headed Grosbeak	0.31 (0.04)	0.11 (0.07)	0.02 (0.02)	0.00
Lazuli Bunting	0.22 (0.06)	0.05 (0.05)	0.00	0.04 (0.04)
Overstora[a]	8.01 (0.40)	13.25 (0.87)	9.43 (1.16)	0.37 (0.15)
Western Wood-Pewee	0.71 (0.10)	0.25 (0.16)	0.00	0.00
Hammond's Flycatcher	0.06 (0.02)	0.21 (0.12)	0.25 (0.16)	0.00
Cordilleran Flycatcher	0.17 (0.04)	0.72 (0.25)	0.51 (0.28)	0.00
Warbling Vireo	2.50 (0.12)	1.46 (0.17)	0.25 (0.16)	0.02 (0.02)
Ruby-crowned Kinglet	0.31 (0.08)	2.10 (0.23)	1.89 (0.22)	0.00
American Robin	1.98 (0.14)	2.21 (0.38)	0.99 (0.34)	0.35 (0.15)
Yellow-rumped Warbler	0.95 (0.09)	1.36 (0.16)	1.75 (0.27)	0.00
Western Tanager	0.34 (0.07)	0.98 (0.24)	1.07 (0.29)	0.00
Cassin's Finch	0.69 (0.10)	2.81 (0.36)	1.56 (0.33)	0.00
Pine Siskin	0.21 (0.06)	0.87 (0.21)	0.73 (0.27)	0.00
Cavity[a]	6.99 (0.30)	5.93 (0.75)	4.23 (0.56)	0.50 (0.19)
Red-naped Sapsucker	0.37 (0.06)	0.08 (0.06)	0.07 (0.05)	0.00
Downy Woodpecker	0.07 (0.02)	0.00	0.07 (0.07)	0.00
Hairy Woodpecker	0.25 (0.04)	0.26 (0.10)	0.39 (0.22)	0.00
Northern Flicker	0.61 (0.07)	0.34 (0.13)	0.07 (0.07)	0.13 (0.10)
Tree Swallow	0.64 (0.08)	0.23 (0.13)	0.07 (0.07)	0.13 (0.10)
Violet-green Swallow	0.06 (0.02)	0.03 (0.03)	0.04 (0.04)	0.09 (0.09)
Mountain Chickadee	0.34 (0.05)	1.46 (0.24)	1.62 (0.35)	0.00
Red-breasted Nuthatch	0.05 (0.02)	0.19 (0.07)	0.86 (0.19)	0.00
House Wren	4.04 (0.19)	3.12 (0.57)	0.89 (0.32)	0.02 (0.02)
Mountain Bluebird	0.34 (0.05)	0.11 (0.07)	0.11 (0.08)	0.13 (0.10)
European Starling	0.12 (0.05)	0.00	0.00	0.00
Brood Parasite				
Brown-headed Cowbird	0.18 (0.03)	0.05 (0.05)	0.00	0.07 (0.05)

[a]Guild means calculated by summing individuals across all species within the guild, including some that did not meet the focal species criteria.