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The conservation value of high elevation habitats to North American migrant birds

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ABSTRACT

The basic patterns of faunal community composition and habitat associations of high elevation mountainous regions are poorly-known. This is true for the avifauna of western North America where our knowledge of high elevation use is primarily restricted to breeding assemblages. Here we report on systematic avian surveys of high elevation habitats over four years in British Columbia conducted during the post-breeding and fall migration periods (Aug–Oct). We detected a remarkable diversity of birds (95 species in 30 families) using alpine, subalpine, and montane forest, many of which used these habitats seasonally. One quarter of the species are on lists of conservation concern. Density, species richness, and community composition varied considerably between habitats and mountain ranges within the study area, especially between the western slope of the Coast range and other ranges. Most species exhibited strong temporal variation in patterns of abundance that were related to migratory behavior. From an extensive literature-based survey, we found that ~35% of North America's breeding bird species use high elevations, and that all primary high elevation habitats are important for full life-cycle conservation of this avifauna. Our findings highlight the importance of high elevation habitats to migrating birds from wide-ranging breeding distributions for at least three months of the year, a period equivalent to the length of the breeding season for most species. These results emphasize the need for effective conservation of fragile alpine and other high elevation habitats that are increasingly threatened by local, regional, and global anthropogenic disturbance.

1. Introduction

Mountain ranges are found on every continent of the world and account for 24% of terrestrial land area (Blyth et al., 2002). The relatively small pool of high elevation specialist species must cope with shorter growing seasons, colder and more extreme temperatures, and lower partial pressure of oxygen at the highest elevations (Körner, 2007). While such species are the focus of important studies of physiology (e.g., Cheviron and Brumfield, 2012; Dragon et al., 1999; Projecto-Garcia et al., 2013), and life history variation (Badyaev, 1997; Bears et al., 2009; Boyle et al., in press), we know comparatively little about high elevation animal communities outside the breeding season, and we have an incomplete understanding of the contributions of high elevations to regional and global biodiversity. Understanding the nature and extent of seasonal use of high elevations by mobile animals is critical to assessing and conserving year-round biodiversity in mountainous regions of the earth.

Mobile vertebrates have the opportunity to exploit mountain habitats seasonally, departing high elevations when conditions become unfavorable (Hahn et al., 2004; O'Neill and Parker, 1978). Birds are an excellent study taxa because they are relatively easy to detect on surveys, are taxonomically diverse, and engage in at least three types of seasonal use of high elevations; (1) as part of latitudinal migrations of varying lengths (e.g., short-distance and long-distance migrations), (2) via altitudinal migrations between breeding and non-breeding areas, and (3) short-term high altitude use during the post-breeding season not associated with either breeding or overwintering. In the first case, some latitudinal migrants regularly follow high elevation fall migration routes (Hoffman and Smith, 2003; La Sorte et al., 2014; Wilson and Martin, 2005). Colder temperatures and delayed snow melt at high elevation result in plant and arthropod prey phenology being typically shifted later in the season relative to lower elevations. Elevational differences in phenology shape the temporal variation in relative food availability with elevation (e.g., hummingbirds and flowering phenology; Phillips, 1975). Furthermore, shorter growing seasons and/or aridity gradients may result in larger peaks of prey availability relative to low elevations, especially during fall migration (DeLong et al., 2005). Consequently, many latitudinal migrants use high elevations pre-migration and during stop-over as high-quality fueling sites (Evans Ogden et al., 2013). The availability of fruits may be a key axis of fall habitat quality as birds can deposit fat rapidly on carbohydrate-rich diets (Parrish, 1997).

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The second type of seasonal use is altitudinal migration involving predictable, seasonal movements up and down slope between breeding and wintering ranges within the same geographic region. Diverse taxa engage in altitudinal migrations including mammals (Hebblewhite and Merrill, 2009; McGuire and Boyle, 2013), reptiles (Blake et al., 2012), insects (Haber and Stevenson, 2004; Stefanescu, 2001), and birds (Boyle, 2011; Gillis et al., 2008; Powell and Bjork, 2004). Altitudinal migration appears to be fairly common in western North American birds (e.g., mountain quail [*Oreortyx pictus*; Ormiston (1966)], American dipper [*Cinclus mexicanus*; Gillis et al. (2008); (Mackas et al., 2010)], and yellow-eyed junco [*Junco phaeonotus*; (Lundblad, 2014)]. A third type of seasonal use of high elevations is often characterized as post-breeding "dispersal" to high elevations by species that both breed and winter at lower elevations. Such species are usually not considered to depend on high elevations, but they likely take advantage of elevational gradients in phenology to molt and/or prepare for winter. These are the least well-characterized types of seasonal movements involving relatively short-term use of high elevation habitats. An example of such movements in British Columbia is the chestnut-backed chickadee (*Poecile rufescens*) that breeds at 0–1500 m and moves up to 2200 m in late summer (Campbell et al., 1997) but winters at lower elevations.

We know little either about how common seasonal elevational movements are, or the taxonomic or geographic patterns and drivers of such movements (Faaborg et al., 2010a). This gap in knowledge stems from the fact that, at least in North America, most large-scale bird sampling schemes (e.g., Breeding Bird Survey, bird observatories, migration monitoring stations) do not sample high elevation habitats effectively. Even eBird and other citizen-science distributional data suffer from reporting biases that underestimate avian use of high elevations due to relative inaccessibility (Snäll et al., 2011; Sullivan et al., 2009). Filling this knowledge gap is a high priority in avian migration research due to the importance of the post-breeding season in shaping key vital rates, and the recognition that habitat quality experienced by migrants during their journeys can substantially affect fitness (Faaborg et al., 2010b).

Previous research on Vancouver Island recorded surprisingly high avian diversity at high elevation sites, especially during late summer and fall (Martin and Ogle, 1998). In mainland British Columbia, latitudinal migrants exhibit considerable variation in habitat specialization, with the species selecting the highest elevation habitats also being those that most consistently breed in alpine habitats (Wilson and Martin, 2005). Additionally, coastal mountains in British Columbia are high quality migratory stop-over sites as evidenced by higher fattening rates at high relative to low elevation sites (Evans Ogden et al., 2013). Understanding the extent and nature of high elevation use by species not deemed to be high elevation specialists is an important step in understanding the value of mountains for avian conservation and assessing the generality of such patterns on broader spatial scales.

Our objectives were to describe avian use of high elevation habitats in multiple regions within British Columbia during post-breeding and migration seasons, and, more generally, to review avian use of mountain habitats in North America. We assessed the conservation value of British Columbia's high elevations by characterizing: (1) the number and frequency of bird species that use high elevation habitats in fall, (2) the species-level differences in the use of alpine, subalpine, and montane forest habitats, (3) the regional variation in the diversity, species composition, and abundance of birds using coastal and interior high elevation habitats among major mountain ranges, and (4) the temporal patterns of high elevation habitat use, both among years and within seasons, and whether temporal patterns vary with migratory strategy. To address these goals, we conducted surveys over four years at 10 sites in four biogeoclimatic regions of southern and central British Columbia. We then sought to (5) place these data in a continental context by collecting and summarizing published and unpublished data by experts on avian use of high elevation habitats during all seasons across the USA and Canada. No such continental perspective is currently available and this summary represents two decades of data compilation that complement the regional perspective offered by the field data.

2. Methods

2.1. Study sites

British Columbia is bisected by multiple mountain ranges oriented roughly NW–SE. We sampled 10 sites located in four mountain ranges representing different biogeoclimatic zones (Pojar et al., 1987): (1) three sites on the wet western slope of the Coast range; Seymour Mountain (SM), Cypress Mountain (CM), and Garibaldi Provincial Park (GA); (2) four sites on the drier interior slope of the Coast range; Stein Divide (ST), Shulaps Mountain (SH), Perkins Peak (PP), and Rainbow Ridge (RR); (3) two sites in the northern-most North Cascade mountains; Manning Provincial Park (MA) and Crater Mountain (CR); and (4) one site in the Cariboo mountains in the Columbia Range; Wells Gray Provincial Park (WG; Fig. 1). We provide a detailed description of sites in the electronic supplementary material.

We selected sites within the constraints of access, with the nearest transect being within a one-hour hike from a camping location. Prior to initiating the study we field-checked sites to confirm there was sufficient area to establish an average of five transects in each of alpine, subalpine, montane forest habitat types. Lines followed haphazard bearings constrained such that each transect remained within a habitat type, and spacing of lines was sufficient to avoid double counting birds. We located transect lines such that they crossed elevational and other physical or habitat gradients rather than following horizontally along the mountain side. Thus, all transects covered a cross-section of the vegetation and topographic features within each habitat. The elevation of most transects ranged from 800 to 2200 m above sea level. A detailed summary of our sampling effort is available in the electronic supplementary material (Table S1).

Within each site, we stratified sampling effort by habitat and located transects within each of three main high elevation vegetation types: *alpine* areas characterized by hardy perennial herbaceous plants, sub-shrubs and few or no trees (0–5% tree cover), *subalpine* meadows of herbaceous plants and shrubs interspersed with sparse patches of trees and krumholtz (5–50% tree cover), and *montane forests* consisting of relatively continuous, open-canopy forest of trees averaging 15 m or more in height (>50% tree cover). We verified habitat assignments by conducting detailed vegetation sampling and related these categories to quantitative metrics of cover by plant functional groups (Wilson and Martin, 2005).

2.2. Bird sampling

We established transects 400 m in length based on preliminary data that indicated we would typically detect ≥25 birds/survey, thus maximizing the number of replicates possible within habitats and sites. However, the constraints of topography and vegetation required us to truncate some transect lines. Observers surveyed multiple transects on each sampling day during two sampling periods: morning (06:30–12:00) or afternoon (13:00–20:23). We surveyed each transect at least once over five, ~2 week intervals during the late summer and fall, with 64% (660/1038) of the transect/interval/year combinations surveyed twice per interval (i.e., once in both morning and afternoon). Dates of the five intervals were: [1] 5–20 Aug. (no interval 1 surveys in 2000 due to high snow pack), [2] 21 Aug.–3 Sep., [3] 7–19 Sep., [4] 20 Sep.–3 Oct., and [5] 6–23 Oct. (no interval 5 surveys in 1999). We chose not to sample in July based on preliminary surveys at our study sites and other high elevations sites on Vancouver Island indicating that the main migratory period begins in August in this region. Nonetheless, the timing of our surveys may have precluded detecting peak abundances of some species. Observers walked an average of 1.1 km/h, counting and identifying every bird detected calling,

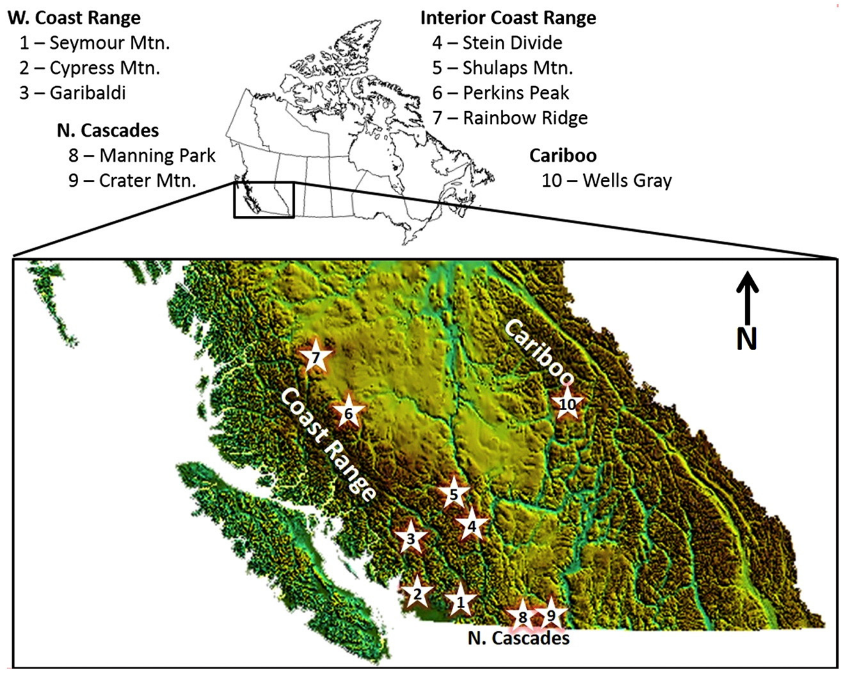

Fig. 1. Map of southern British Columbia depicting location of mountain ranges and study sites.

foraging, perched, or otherwise interacting with the habitat along the transect line. Birds that flew over without stopping ("flyovers") and birds detected beyond the ends of transects were recorded as present at the site but not used in density calculations. Thus, density estimates represent only individuals actively using the habitat. Observers estimated the angle and the distance (with rangefinders) to each bird and we calculated perpendicular distance from transect lines. Observers did not survey when wind exceeded 4 on the Beaufort scale. Starting temperatures ranged from −5 °C to 28 °C (mean 13.4 °C).

2.3. Analyses

We estimated densities of each species by mountain range, site, habitat, year, and time interval corrected for habitat-specific differences in detectability using the program DISTANCE (Buckland et al., 1993; Thomas et al., 2009). We treated birds as clusters because many detections consisted of multiple individuals, stratifying sites by year and habitat. We calculated effective strip widths (ESW; Buckland et al., 1993) with a standard set of detection functions and used Akaike's Information Criterion (AIC_c) to determine the one best fitting our observations. Because we did not have data from every year × site × habitat combination, we calculated detection functions by habitat and applied resulting ESWs to all years and sites (i.e., assumed no differences in detectability across years and sites). We used 2× the habitat-specific ESWs to calculate the effective area (in ha) surveyed and calculated density as *n* individuals detected/ha/survey.

We summarized abundances of species in three ways (objective 1). First, we calculated the mean density of each species across surveys within each of the three habitats. We then identified the maximum densities recorded for each species, including the site, habitat, year, and time interval during which those maxima occurred. Additionally, we tabulated the number and % of all surveys in which each species was detected in each habitat to assess spatial and temporal variation in habitat use.

To examine how patterns of use varied between groups of species (objective 2), we classified each species as either latitudinal short- or long-distance migrants, altitudinal migrants including short-term seasonal uses not associated with breeding or wintering, or non-migrants or based data in the Birds of North America Online (Poole, 2005). We considered a species resident if accounts included no references to seasonal latitudinal or altitudinal movements within western North America. We classified species as altitudinal migrants if BC-breeding populations were not known to make latitudinal migrations, but had been documented making either regular altitudinal migrations or short-term post-breeding uphill movements. We classified species as short-distance migrants when birds engaged in latitudinal movements, and the winter range included southern British Columbia or western regions lying north of the Oregon–California border, a group mostly consisting of species that overwinter primarily within North America. Long-distance migrants included any species whose entire wintering range lay south of 42°N (a minimum migration distance of 800 km). Most of these species' winter ranges extend into Central or South America. We acknowledge that individuals of species classified as "short" distance migrants may migrate >800 km if their breeding range extends far to the north of our study areas or some of their wintering range extends south of 42°N but no alternative standard definition currently exists. We also assessed high elevation use by species of conservation concern based on endangered or threatened (i.e., Red-listed) or special concern classification (i.e., Blue-listed) by Committee on the Status of Endangered Wildlife in Canada (COSEWIC), in British Columbia, or listed by Partners in Flight as a conservation priority (i.e., common species in steep decline or species of high tri-national concern; Berlanga et al., 2010).

To compare species richness among mountain ranges (objective 3), we calculated the Chao 1 estimate (Chao, 1984) and the Shannon diversity index (Magurran, 2004) using the program EstimateS (Colwell, 2013). Exploration of alternative methods to estimate species richness (e.g., Chao 2 (Chao, 1987), first- and second-order Jackknife (Burnham and Overton, 1979), Bootstrap (Smith and Vanbelle, 1984), and Michaelis–Menten means (Colwell et al., 2004)) all revealed comparable patterns. Thus, we present only the Chao 1 metric which we calculated by rarefying the number of surveys in all regions to 282, the total number of surveys conducted in the region with fewest surveys. We randomized survey order over 50 runs without shuffling individuals among samples. We compared species composition of the high elevation avifauna from different regions by calculating similarity indices based on presence–absence

Table 1
Abundance of 95 bird species observed between mid-August and early October at 10 sites over 4 years in British Columbia, Canada. The common names of all species noteworthy from a conservation perspective appear in bold font (see Section 2.3). We classified the migratory status (Mig status) of species in BC denoted as residents (r), altitudinal migrants (a), short-distance migrants (s), and long-distance migrants (l). Mean relative abundances are based on density estimates (individuals^{-ha}) averaged across all surveys within alpine (A), subalpine (S), and montane (M) forest habitats. Maximum relative abundance denotes the survey with the peak density estimate for each species, as well as the site, habitat, time interval, and year for the peak density record. Missing values in abundance data represent species only detected outside the effective strip widths or as fly-overs (see Section 2.2). The number and percent of surveys in which a species was detected is based on all detections including flyovers and incidental sightings. See Section 2.1, supplementary material, and table S1 for explanations of habitat and site codes.

Common name	Scientific name	Mig status	Mean rel. abundance			Maximum rel. abundance					N surveys detected			% of surveys detected		
			A	S	M	Ind/ha	Site	Habitat type	Time interval	Year	A	S	M	A	S	M
ANATIDAE																
Canada Goose[*1]	*Branta canadensis*	s	…	…	…	…	…	…	…	…	0	0	2	0.0	0.0	0.4
Mallard	*Anas platyrhynchos*	s	0.000	0.010	0.009	3.4	RR	S	1	1998	0	3	2	0.0	0.5	0.4
PHASIANIDAE																
Ruffed Grouse	*Bonasa umbellus*	r	0.000	0.000	0.002	0.7	CR	M	4	1998	0	0	2	0.0	0.0	0.4
Spruce Grouse	*Falcipennis canadensis*	a	0.000	0.001	0.013	0.8	SH	M	3	2001	0	2	13	0.0	0.3	2.6
Willow Ptarmigan	*Lagopus lagopus*	a	0.005	0.004	0.000	2.5	RR	A	3	1998	4	1	0	0.7	0.2	0.0
White-tailed Ptarmigan[§2]	*Lagopus leucura*	a	0.038	0.002	0.000	2.9	GA	A	1	1998	18	2	0	3.0	0.3	0.0
Dusky Grouse	*Dendragapus obscurus*	a	0.005	0.014	0.023	2.7	CR	M	2	1998	3	9	9	0.5	1.4	1.8
Sooty Grouse	*Dendragapus fuliginosus*	a	0.002	0.008	0.004	2.0	MA	S	1	2001	2	4	2	0.3	0.6	0.4
ACCIPITRIDAE																
Northern Harrier	*Circus cyaneus*	s	0.005	0.009	0.001	1.2	WG	S	1	1998	35	26	1	5.9	4.2	0.2
Sharp-shinned Hawk	*Accipiter striatus*	s	0.003	0.004	0.000	1.0	CR	A	4	1998	13	13	1	2.2	2.1	0.2
Cooper's Hawk	*Accipiter cooperii*	s	0.002	0.003	0.001	1.0	CR	S	2	1999	9	8	2	1.5	1.3	0.4
Northern Goshawk[*3]	*Accipiter gentilis*	s	0.000	0.001	0.002	0.7	CR	M	3	1999	1	2	2	0.2	0.3	0.4
Red-tailed Hawk	*Buteo jamaicensis*	s	0.000	0.004	0.000	0.7	WG	S	3	1999	5	14	2	0.8	2.3	0.4
Rough-legged Hawk[§]	*Buteo lagopus*	s	0.000	0.001	0.000	0.5	MA	S	4	2001	0	3	0	0.0	0.5	0.0
Golden Eagle	*Aquila chrysaetos*	s	0.001	0.001	0.000	0.7	CR	S	1	1999	6	4	0	1.0	0.6	0.0
FALCONIDAE																
American Kestrel	*Falco sparverius*	s	0.019	0.004	0.001	1.3	MA	A	2	1998	38	12	3	6.4	1.9	0.6
Merlin[§]	*Falco columbarius*	s	0.002	0.001	0.000	0.4	ST	S	3	2001	8	2	0	1.3	0.3	0.0
Peregrine Falcon[*4]	*Falco peregrinus*	s	…	…	…	…	…	…	…	…	0	1	0	0.0	0.2	0.0
Prairie Falcon[*]	*Falco mexicanus*	s	0.002	0.000	0.000	0.6	CR	A	2	1999	4	2	0	0.7	0.3	0.0
RALLIDAE																
American Coot	*Fulica americana*	s	0.000	0.000	0.001	0.4	RR	M	1	1998	0	0	1	0.0	0.0	0.2
CHARADRIIDAE																
Killdeer[§]	*Charadrius vociferus*	s	0.002	0.000	0.000	0.6	CR	A	1	2001	2	0	0	0.3	0.0	0.0
SCOLOPACIDAE																
Spotted Sandpiper	*Actitis macularius*	l	0.000	0.001	0.000	0.5	ST	S	1	1998	0	1	0	0.0	0.2	0.0
Greater Yellowlegs	*Tringa melanoleuca*	s	…	…	…	…	…	…	…	…	0	1	1	0.0	0.2	0.2
Baird's Sandpiper	*Calidris bairdii*	l	0.004	0.000	0.000	1.9	CR	A	1	2001	2	0	0	0.3	0.0	0.0
COLUMBIDAE																
Band-tailed Pigeon[§]	*Patagioenas fasciata*	s	0.000	0.009	0.001	2.7	CY	S	1	1998	0	7	5	0.0	1.1	1.0
APODIDAE																
Black Swift	*Cypseloides niger*	l	…	…	…	…	…	…	…	…	1	1	0	0.2	0.2	0.0
TROCHILIDAE																
Rufous Hummingbird	*Selasphorus rufus*	l	0.001	0.008	0.002	1.7	SE	S	1	1999	4	6	1	0.7	1.0	0.2
PICIDAE																
Red-naped Sapsucker	*Sphyrapicus nuchalis*	l	0.000	0.001	0.007	1.1	WG	M	1	1998	0	2	6	0.0	0.3	1.2
Red-breasted Sapsucker	*Sphyrapicus ruber*	s	0.000	0.002	0.014	1.7	SE	M	4	2001	0	2	10	0.0	0.3	2.0
Downy Woodpecker	*Picoides pubescens*	r	0.000	0.000	0.010	3.4	SE	M	3	1999	0	0	3	0.0	0.0	0.6
Hairy Woodpecker[§5]	*Picoides villosus*	a	0.000	0.001	0.012	1.7	WG	M	2	1998	0	1	5	0.0	0.2	1.0
American Three-toed Woodpecker	*Picoides dorsalis*	r	0.000	0.000	0.012	1.3	GA	M	3	1998	0	0	8	0.0	0.0	1.6
Northern Flicker	*Colaptes auratus*	r	0.001	0.021	0.018	2.2	SE	S	3	2001	9	38	19	1.5	6.1	3.8
Pileated Woodpecker	*Dryocopus pileatus*	a	…	…	…	…	…	…	…	…	0	0	1	0.0	0.0	0.2
TYRANNIDAE																
Olive-sided Flycatcher[§]	*Contopus cooperi*	l	0.000	0.000	0.001	0.6	WG	M	2	1998	0	0	2	0.0	0.0	0.4
Hammond's Flycatcher	*Empidonax hammondii*	l	0.001	0.001	0.003	1.1	WG	M	1	1998	1	2	2	0.2	0.3	0.4
Pacific-slope Flycatcher	*Empidonax difficilis*	l	0.000	0.000	0.003	1.7	SH	M	2	1999	0	0	1	0.0	0.0	0.2
VIREONIDAE																
Cassin's Vireo	*Vireo cassinii*	l	0.000	0.000	0.003	0.6	WG	M	1	1998	0	0	3	0.0	0.0	0.6
CORVIDAE																
Gray Jay	*Perisoreus canadensis*	r	0.012	0.119	0.129	5.0	MA	S	2	2001	14	77	68	2.4	12.4	13.6
Steller's Jay[§6]	*Cyanocitta stelleri*	a	0.000	0.001	0.011	1.1	SE	M	5	1998	0	6	10	0.0	1.0	2.0
Clark's Nutcracker	*Nucifraga columbiana*	a	0.017	0.028	0.046	4.2	SH	M	1	1998	39	59	50	6.6	9.5	10.0
Black-billed Magpie	*Pica hudsonia*	a	0.000	0.001	0.000	0.7	ST	S	5	1998	1	1	0	0.2	0.2	0.0
Northwestern Crow	*Corvus caurinus*	r	0.000	0.000	0.002	0.8	CR	M	4	1999	0	0	1	0.0	0.0	0.2
Common Raven	*Corvus corax*	r	0.008	0.014	0.020	5.0	SE	M	3	1999	33	66	35	5.6	10.6	7.0

Table 1 (*continued*)

Common name	Scientific name	Mig status	Mean rel. abundance			Maximum rel. abundance					N surveys detected			% of surveys detected		
			A	S	M	Ind/ha	Site	Habitat type	Time interval	Year	A	S	M	A	S	M
ALAUDIDAE																
Horned Lark[*7]	*Eremophila alpestris*	s	0.749	0.030	0.000	68.8	MA	A	3	2000	127	26	0	21.4	4.2	0.0
HIRUNDINIDAE																
Barn Swallow[§]	*Hirundo rustica*	l	…	…	…	…	…	…	…	…	0	0	1	0.0	0.0	0.2
PARIDAE																
Black-capped Chickadee	*Poecile atricapillus*	r	0.001	0.001	0.003	0.8	CY	M	4	1998	1	1	3	0.2	0.2	0.6
Mountain Chickadee	*Poecile gambeli*	a	0.009	0.061	0.181	5.9	CR	M	2	1999	11	51	73	1.9	8.2	14.6
Chestnut-backed Chickadee	*Poecile rufescens*	a	0.000	0.000	0.246	10.1	SE	M	2	1998	0	0	46	0.0	0.0	9.2
Boreal Chickadee	*Poecile hudsonicus*	r	0.000	0.005	0.025	0.7	SH	S	3	1998	0	4	10	0.0	0.6	2.0
SITTIDAE																
Red-breasted Nuthatch	*Sitta canadensis*	a	0.005	0.065	0.373	8.8	CY	M	3	2001	12	68	135	2.0	10.9	27.0
CERTHIIDAE																
Brown Creeper	*Certhia americana*	a	0.000	0.003	0.078	3.4	SE	M	2	2000	0	2	37	0.0	0.3	7.4
TROGLODYTIDAE																
Rock Wren	*Salpinctes obsoletus*	l	0.001	0.000	0.000	0.5	CR	A	3	1999	1	0	0	0.2	0.0	0.0
Pacific Wren	*Troglodytes pacificus*	a	0.001	0.047	0.196	3.4	SE	M	4	1998	2	49	97	0.3	7.9	19.4
CINCLIDAE																
American Dipper	*Cinclus mexicanus*	a	0.000	0.002	0.000	0.5	ST	S	3	2001	0	2	0	0.0	0.3	0.0
REGULIDAE																
Golden-crowned Kinglet[§]	*Regulus satrapa*	s	0.006	0.402	1.467	31.9	SE	M	4	2001	12	137	280	2.0	22.0	56.0
Ruby-crowned Kinglet	*Regulus calendula*	s	0.007	0.061	0.088	6.2	WG	M	1	1998	9	61	33	1.5	9.8	6.6
TURDIDAE																
Mountain Bluebird	*Sialia currucoides*	s	0.024	0.019	0.001	7.9	CR	S	4	2000	14	10	1	2.4	1.6	0.2
Townsend's Solitaire	*Myadestes townsendi*	a	0.003	0.020	0.003	2.2	CR	S	4	1998	6	18	3	1.0	2.9	0.6
Swainson's Thrush	*Catharus ustulatus*	l	0.000	0.000	0.008	1.7	SE	M	5	1998	0	0	4	0.0	0.0	0.8
Hermit Thrush	*Catharus guttatus*	s	0.000	0.010	0.026	2.7	CY	S	3	1998	0	10	15	0.0	1.6	3.0
American Robin	*Turdus migratorius*	s	0.013	0.102	0.108	10.3	SE	S	2	1998	25	75	35	4.2	12.1	7.0
Varied Thrush	*Ixoreus naevius*	s	0.001	0.041	0.153	11.2	SH	M	4	2001	2	25	42	0.3	4.0	8.4
MOTACILLIDAE																
American Pipit	*Anthus rubescens*	s	0.369	0.067	0.000	35.3	WG	A	2	2000	173	54	2	29.2	8.7	0.4
BOMBYCILLIDAE																
Bohemian Waxwing	*Bombycilla garrulus*	s	0.000	0.002	0.000	0.7	SH	S	3	1998	0	2	0	0.0	0.3	0.0
Cedar Waxwing	*Bombycilla cedrorum*	s	0.000	0.011	0.009	6.8	SE	S	3	2001	1	2	6	0.2	0.3	1.2
PARULIDAE																
Orange-crowned Warbler	*Oreothlypis celata*	l	0.000	0.006	0.001	0.9	SE	S	2	1998	0	6	1	0.0	1.0	0.2
Nashville Warbler	*Oreothlypis ruficapilla*	l	0.000	0.001	0.000	0.4	SH	S	1	1998	0	1	0	0.0	0.2	0.0
MacGillivray's Warbler	*Geothlypis tolmiei*	l	0.001	0.005	0.002	0.8	CY	M	2	2001	1	7	1	0.2	1.1	0.2
Yellow-rumped Warbler[§]	*Setophaga coronata*	s	0.078	0.330	0.126	11.2	SH	M	3	1999	84	153	59	14.2	24.6	11.8
Townsend's Warbler	*Setophaga townsendi*	l	0.004	0.023	0.036	2.9	CY	M	2	2001	4	19	14	0.7	3.1	2.8
Wilson's Warbler	*Cardellina pusilla*	l	0.006	0.042	0.010	4.3	WG	S	1	1999	7	27	3	1.2	4.3	0.6
EMBERIZIDAE																
Spotted Towhee	*Pipilo maculatus*	a	0.000	0.000	0.007	1.7	SE	M	4	1998	0	0	2	0.0	0.0	0.4
Chipping Sparrow	*Spizella passerina*	l	0.052	0.103	0.022	8.4	MA	S	1	2001	20	40	8	3.4	6.4	1.6
Vesper Sparrow[*]	*Pooecetes gramineus*	l	0.019	0.026	0.000	4.3	RR	A	2	1998	14	12	0	2.4	1.9	0.0
Savannah Sparrow	*Passerculus sandwichensis*	l	0.083	0.152	0.005	24.8	MA	S	3	2000	69	78	3	11.6	12.5	0.6
Fox Sparrow	*Passerella iliaca*	s	0.003	0.021	0.006	2.2	SH	M	4	2001	4	24	2	0.7	3.9	0.4
Song Sparrow	*Melospiza melodia*	a	0.000	0.015	0.000	2.0	WG	S	1	1998	1	12	0	0.2	1.9	0.0
Lincoln's Sparrow	*Melospiza lincolnii*	s	0.000	0.023	0.001	2.2	WG	S	3	2001	0	15	1	0.0	2.4	0.2
Swamp Sparrow	*Melospiza georgiana*	s	0.000	0.001	0.000	0.7	WG	S	2	2001	0	1	0	0.0	0.2	0.0
White-crowned Sparrow	*Zonotrichia leucophrys*	s	0.075	0.497	0.064	28.8	SH	S	3	1998	54	134	24	9.1	21.5	4.8
Golden-crowned Sparrow	*Zonotrichia atricapilla*	s	0.002	0.018	0.000	2.2	RR	S	1	1998	3	15	0	0.5	2.4	0.0
Dark-eyed Junco	*Junco hyemalis*	a	0.176	0.625	0.593	24.4	WG	A	1	1999	59	222	165	9.9	35.7	33.0
CARDINALIDAE																
Western Tanager	*Piranga ludoviciana*	l	0.000	0.000	0.001	0.6	SE	M	2	1998	0	0	1	0.0	0.0	0.2
ICTERIDAE																
Western Meadowlark[*]	*Sturnella neglecta*	s	…	…	…	…	…	…	…	…	0	1	0	0.0	0.2	0.0
Brewer's Blackbird	*Euphagus cyanocephalus*	s	0.000	0.001	0.000	0.4	ST	S	4	2001	2	2	0	0.3	0.3	0.0
FRINGILLIDAE																
Gray-crowned Rosy-Finch	*Leucosticte tephrocotis*	s	0.004	0.001	0.000	1.6	ST	A	4	2001	5	2	0	0.8	0.3	0.0
Pine Grosbeak[§8]	*Pinicola enucleator*	a	0.001	0.001	0.010	1.7	SH	M	3	2000	2	3	4	0.3	0.5	0.8
Cassin's Finch	*Carpodacus cassinii*	s	0.000	0.001	0.000	0.4	SH	S	1	1998	0	1	2	0.0	0.2	0.4
House Finch	*Carpodacus mexicanus*	s	0.000	0.000	0.003	1.7	SE	M	4	1998	0	0	1	0.0	0.0	0.2

(*continued on next page*)

Table 1 (*continued*)

Common name	Scientific name	Mig status	Mean rel. abundance			Maximum rel. abundance					N surveys detected			% of surveys detected		
			A	S	M	Ind/ha	Site	Habitat type	Time interval	Year	A	S	M	A	S	M
FRINGILLIDAE																
Red Crossbill	*Loxia curvirostra*	s	0.016	0.047	0.061	11.9	MA	S	2	2001	4	23	51	0.7	3.7	10.2
White-winged Crossbill	*Loxia leucoptera*	s	0.000	0.001	0.024	3.9	MA	M	3	2001	0	4	10	0.0	0.6	2.0
Pine Siskin	*Spinus pinus*	s	0.036	0.208	0.230	44.3	GA	S	1	1998	76	125	78	12.8	20.1	15.6
American Goldfinch	*Spinus tristis*	s	0.000	0.000	0.002	0.8	ST	M	3	1998	0	0	1	0.0	0.0	0.2
Evening Grosbeak	*Coccothraustes vespertinus*	s	…	…	…	…	…	…	…	…	3	1	2	0.5	0.2	0.4

* species considered endangered or threatened in BC (i.e., Red listed).
§ denotes species of special concern (i.e., Blue listed), and other species in bold font are considered common, but in steep decline, or are a species of high tri-national concern according to Partners In Flight.
[1] *occidentalis* subspecies Red listed in BC.
[2] *saxatilis* subspecies Blue listed in BC.
[3] *laingi* subspecies Red listed in BC.
[4] *anatum* subspecies Red listed in BC, *pealei* subspecies Blue listed in BC.
[5] *picoideus* subspecies Blue listed in BC.
[6] *carlottae* subspecies Blue listed in BC.
[7] *strigata* subspecies Red listed in BC, *merrilli* subspecies Blue listed in BC.
[8] *carlottae* subspecies Blue listed in BC.

in surveys as well as indices based on the relative abundance of species by region (i.e., Chao-Jaccard and Chao-Sorensen indices; Chao et al., 2005).

We examined how the combined densities of all bird species detected on transects varied spatially and temporally, and the degree to which regions, habitats, and time during the season predicted density by modeling variation in density in a generalized linear mixed model framework in R (R Core Team, 2015) using the glmer function in the lme4 package (Bates et al., 2014). We modeled the summed total of birds counted on each transect and included the area surveyed to account for variation among transects in length and detection probability. We examined fixed effects of habitat, mountain range, morning or afternoon survey times, and interval within the season. Additionally, we explored whether the relative densities in each habitat and/or the temporal patterns of high elevation use differed among ranges by including the habitat*range and interval*range interaction, and using AIC to the explanatory power of models including interactions. We included year, site, and individual transect line ID as random effects.

We described the temporal patterns of high elevation habitat use at the species level by restricting our dataset to only those species detected in ≥10 surveys (objective 4). We calculated the mean density (across all habitats and ranges) in each of the five intervals within the season, and plotted these species-level temporal patterns by family. We then classified temporal patterns according to whether abundance peaked early (i.e., intervals 1 or 2), mid-season (i.e., interval 3), late (increased throughout the season), or exhibited no clear seasonal abundance pattern.

2.4. Continental-scale patterns of avian use of high elevations

To put our results into a broader geographic context (objective 5), and to evaluate the value of high elevation habitat for North American birds more generally, we searched the literature for high elevation or mountain habitat use for individual species in the Birds of North America accounts (Poole and Gill, 2000), the Birds of British Columbia (Campbell et al., 1997), and with a thorough literature search for papers including avian use for well-known mountain parks and protected areas. We contacted ornithologists in the Yukon, British Columbia, and federal and state government personnel in the Western United States (including National and State Park agencies) for records of high elevation bird use throughout the year. We categorized each species as occurring in one or more of the following four habitat types designed to capture the broader range of vegetation communities present at the continental scale (and therefore differing somewhat from the habitat categories at our British Columbia sites): *alpine tundra* consisting of rocky, sparsely-vegetated habitat occurring above the treeline in mountains, sharing Arctic flora and fauna; *alpine meadows and krumholtz* consisting of dry meadows and grasslands at or above the treeline, with herbaceous plants, shrubs and small stunted trees; *upper montane forest* consisting of a mixture of forest and wet meadows or parkland; and *lower montane forest* consisting of contiguous high elevation forest usually composed of one or two dominant tree species. In a few cases we were unable to assign records of high elevation use to one or more of these habitat types but we included them as being present in unspecified high elevation habitats. Additionally, we coded each species according to whether or not it bred, wintered, and/or used the habitat for migration. We considered Arctic-tundra breeding species only if they also bred in alpine habitats on more southerly mountains (i.e., south of Alaska, Yukon and Northwest Territory borders). We summarized data by summing the species utilizing high elevation habitats collectively during the entire year, and during each of the breeding, wintering, or migration seasons. Throughout we follow the American Ornithologists' Union (1998); Chesser et al. (2012) for species names and taxonomic sequences.

3. Results

3.1. Avian use of high elevations in late summer and autumn

We surveyed 142 transects averaging 333 m in length (±91 m SD; range 75–550 m). Observers spent 717 h surveying over the four years resulting in 8347 detections of 18,965 individuals of 95 species in high elevation habitats (Table 1). Over 26% of the species ($n = 25$) detected on our surveys were birds listed by North American and local conservation planning and management agencies including five Red-listed and eight Blue-listed species or subspecies (Table 1). Of the 95 species, 22 were long-distance latitudinal migrants, 43 short distance latitudinal migrants, 21 altitudinal migrants, and nine were residents. Birds of different migratory strategies tended to differ in their abundance at high elevations with altitudinal and short-distance migrants being counted more commonly and in greater numbers than residents or long-distance migrants (n detections, $F_{3,91} = 1.9$, $P = 0.136$; n individuals counted, $F_{3,91} = 2.0$, $P = 0.126$). Maximum densities of most species occurred most frequently at the beginning of our survey period and in mid-September (intervals 1 and 3; Table 1). The complete dataset is available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.bf486.

3.2. How do birds differ in their use of alpine, subalpine, and montane forests?

Bird varied dramatically in habitat-specific detection frequency and mean and maximum abundances of individuals (Table 1). Of 95 species, 87 (92%) actively used high elevation habitats, and 8 species were detected only incidentally or as fly-overs (including 2 aerial insectivores not expected to "interact" with terrestrial habitats). We detected 48 species using alpine areas, 69 in subalpine, and 62 in montane forest. Montane forests contained the greatest numbers of both resident and migrant species detected in only that vegetation type. Species detected in all habitats typically varied dramatically in their abundance or frequency of detection among habitats. Many infrequently-detected species were occasionally quite abundant leading to low mean densities. Peak densities were more often recorded in montane forest (38 species) and subalpine (36 species) than in alpine vegetation (13 species). Migrants and residents tended to differ in the habitat in which we detected their peak abundance; none of the 9 resident species reached their highest abundances in alpine areas, whereas 23.1% of both altitudinal and long-distance migrants, and 53.8% of 43 short-distance migrants did.

3.3. Regional and temporal differences in diversity, species composition, and abundance

Estimated species richness based on Chao 1 species accumulation curves was highest in the interior Coast range (77 species) and lowest in the western slope of the Coast range (52 species; Fig. 2a). Species richness was highest in the interior Coast range and lowest in the western Coast range (Fig. 2b). Regional patterns of diversity as estimated by the Shannon index mirrored patterns of species richness indicating that patterns of dominance did not differ strongly among ranges. Both presence–absence indices (i.e., Jaccard and Sorensen indices) and relative abundance indices (Chao et al., 2005) revealed that the interior Coast range sites and the Cascades were most similar in species composition, while the Cariboo and the western Coast range were the least similar (Table 2). Despite their proximity, opposite sides of the Coast range were less similar than the distant Cariboo and interior Coast range sites.

Densities of birds differed among habitats (likelihood ratio $\chi^2 = 10.9$, df $= 2$, $P = 0.004$), morning or afternoon survey times (likelihood ratio $\chi^2 = 781.6$, df $= 1$, $P < 0.0001$), and interval in the season (likelihood ratio $\chi^2 = 8.3$, df $= 1$, $P = 0.004$) but not mountain range after accounting for random variation in year, site, and individual transect line ID). The model including interactions between mountain range and habitat, and mountain range and interval performed better than either model including no interactions (ΔAIC $= 60$), and better than models including only range*habitat (ΔAIC $= 11$) or range*interval (ΔAIC $= 35$). Thus, the relationships between density and both habitat and interval in the season varied among mountain ranges (habitat*range, likelihood-ratio $\chi^2 = 22.6$, df $= 6$, $P = 0.0001$; interval*range, likelihood-ratio $\chi^2 = 56.1$, df $= 3$, $P < 0.0001$). To visualize these interactions, we calculated the deviance residuals from a generalized linear model with the sum of birds counted as our response variable, and ha surveyed, morning or afternoon survey time, site, year, and transect line ID, and seasonal interval. Using the deviance residual from these models we plotted the least square means ($\pm$95% CI) for each combination of habitat*range (Fig. 3). We then repeated this procedure, replacing interval with habitat, and plotted residual abundance in each of the interval*range combinations (Fig. 4). The western slope of the Coast range differed most strongly in the abundance of birds among different habitat types with alpine areas in that region having the lowest densities of any combination of range and habitat (Fig. 3). At the beginning of the post-breeding season, densities were similar among ranges, but in the Cariboo range, abundance dropped sharply after interval 2, whereas in the western Coast range, densities were highest in the last two intervals in the season (Fig. 4).

3.4. Species-level temporal patterns of high elevation use

The range of patterns of seasonal abundance for the 48 species detected in ≥10 surveys (Appendix 2) are represented by 18 species in Fig. 5. We classified 14 species as being most abundant early in the season (e.g., Fig. 5a), 11 peaking mid-season (e.g., Fig. 5b), and 5 peaking late in the season (e.g., Fig. 5c). Fifteen species showed no clear seasonal pattern of abundance, including all species in the Corvidae and Paridae. We were unable to classify the patterns of three species; Band-tailed Pigeon (*Patagioenas fasciata*), Golden-crowned Sparrow (*Zonotrichia atricapilla*), and Red Crossbill (*Loxia curvirostra*) (Fig. 5d).

In the subset of 48 species detected in ≥10 surveys, 12.5% were long-distance migrants, compared to 23.2% of species in the full dataset (likelihood ratio $\chi^2 = 2.5$, $P = 0.485$). Over 45% of species using high elevations during this study were short-distance migrants. Timing of peak abundance differed among species of different migratory patterns (likelihood ratio $\chi^2 = 20.9$, $P = 0.013$). All species with peak abundance late in the season were either altitudinal or short-distance migrants, and all but one of the long-distance migrants (Savannah Sparrow, *Passerculus sandwichensis*) peaked at the beginning of the season (Fig. 5a).

3.5. Year-round avian use of North America's high elevations — continental context

We documented 246 bird species from mainland North America using high elevation habitats during some portion of their annual

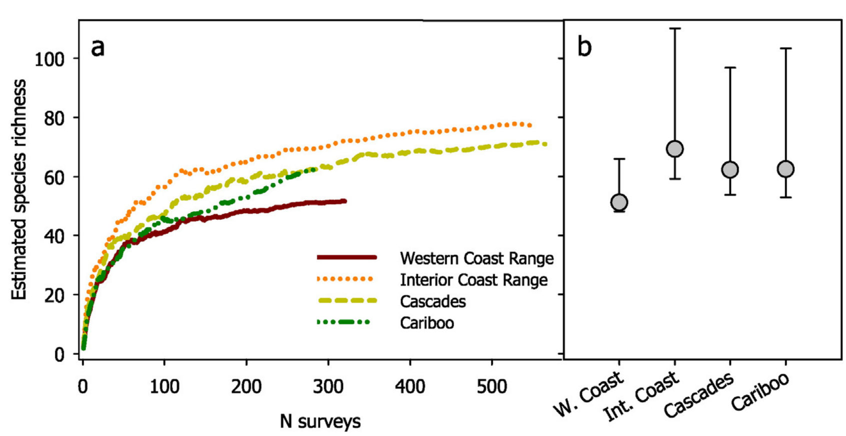

Fig. 2. Estimated species richness based on Chao's (2005) formula. Values represent the mean of 50 randomized runs for the number of surveys conducted in each range (panel a) and the mean $\pm$ 95% CI for each range rarefied to 282 surveys (the maximum conducted in the Cariboo range, panel b).

Table 2
Regional similarity based on classic presence-absence indices and indices based on abundance (i.e., the number of surveys in which each species was detected). Pairs of sites are arranged from least similar to most similar.

Range pairs	Chao-Jaccard	Chao-Sorensen	Jaccard classic	Sorensen classic
W. Coast – Cariboo	0.850	0.919	0.581	0.735
W. Coast range – Cascades	0.884	0.938	0.617	0.763
W. Coast – Interior Coast	0.894	0.944	0.587	0.739
Interior Coast – Cariboo	0.961	0.980	0.632	0.774
Cascades – Cariboo	0.965	0.982	0.690	0.817
Cascades – Interior Coast	0.969	0.984	0.710	0.830

cycle (Table 3). This constitutes 35% of the bird species breeding in continental North America (Richard Cannings, personal communication for tally of NA breeding bird species). While only 6 species are considered to be obligate alpine specialist breeders, 24 species (10%) use high elevations year round. Of the 244 species, 73% breed in high elevation habitats, 11% winter there, while 64% use high elevations during migration or during molt (note that these categories are not mutually-exclusive). As in British Columbia, alpine areas are used by the fewest species at the continental scale (Table 3). However, 164 species regularly use alpine tundra and/or alpine meadows and *krumholtz* at some point during the year, and the majority of these are migrants. While it was not possible to apply the same criteria to determine if these records represented long-distance, short-distance latitudinal, or altitudinal migrations as we did with the BC data, the larger dataset includes many species known to spend the non-breeding season within the continental USA and Canada.

4. Discussion

Our intensive regional sampling in British Columbia and our extensive literature survey for North America both demonstrate that a remarkable number of bird species commonly use high elevations during late summer and fall, confirming mounting evidence from other sites (Blake, 1984; Carlisle et al., 2012; Carlisle et al., 2009; Greenberg et al., 1974; Hutto, 1985b; Wightman et al., 2007). We detected 95 species from 30 families using alpine, subalpine, and montane habitats in British Columbia which represents over a third of the breeding bird species in the province (www.birdatlas.bc.ca). Furthermore, migrant birds use high elevations in large numbers. The number of species and abundance of short-distance migrants we detected suggest that mountains may be particularly important for species that over-winter within North America. Although more species were observed in montane and subalpine habitats than in alpine areas, over half (48) of the species we detected use alpine habitat, a surprising finding given that this habitat is typically thought of as being species-poor (Blyth et al., 2002).

Our study demonstrates that migrant birds are collectively using British Columbia's high elevations for at least three months of the year, a duration equivalent to the breeding season of many temperate-zone species. Although few species occupied these areas over the whole three month period, our results highlight the mounting evidence of the importance of high elevations to full life cycle conservation of North American birds (e.g., see also Carlisle et al., 2009; DeLong et al., 2013; Ruth et al., 2012). Our estimates of abundance represent minima because it is possible that our sampling may have missed some peak usage by long-distance migrants as we detected peak numbers of these migrants in the earliest interval, consistent with other migration phenology studies of long distance migrants in western North America (Carlisle et al., 2005b). Additionally, at the end of our survey period, we found that several species undertaking local altitudinal migrations increased in abundance through to the last time interval. The pattern of a late fall peak was also consistent with data from Vancouver Island where residents and altitudinal migrants persisted at high elevations into October when the onset of unfavorable weather likely limits their persistence (Martin and Ogle, 1998). Our regional results suggest that the Coast mountains or the Fraser River Valley may act as a natural migration corridor for birds during their southward migration. Additionally, the high abundance and distinct species assemblage present on the western slope of the Coast range suggest that a comparatively species-poor assemblage is able to exploit this very wet area of North America, but does so in relatively high densities. Strong temporal and regional patterns may reflect geographic variation in the phenology of migration or may reflect differences in the proportions of long- and short-distance migrants using high elevations in different mountain ranges suggesting that species-specific traits influence patterns of avian use of high elevations.

We detected fewer long-distance migrants than are commonly found at nearby lowland sites (K. Martin and L. J. Evans-Ogden, unpublished data), mirroring patterns at high elevations in Vermont (Rimmer and McFarland, 2000). The reasons for this are unclear. In British Columbia, high elevations can be highly profitable refueling sites during fall migration (Evans Ogden et al., 2013). Likewise, in S. Arizona, migrant insectivores were more abundant at high elevations in fall than spring, a pattern attributed to spatial and phenological patterns of

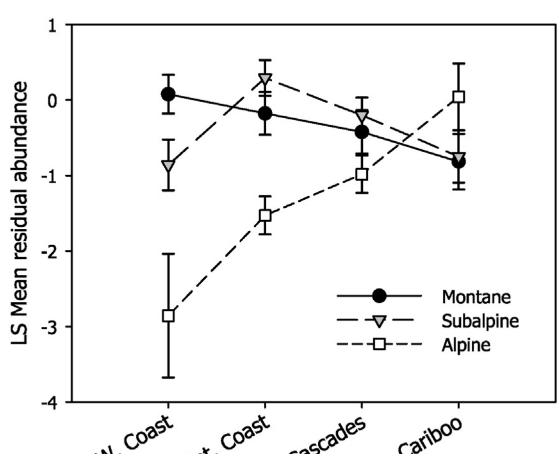

Fig. 3. Variation in bird densities by range and habitat. Symbols represent the least square mean (± SE) of the deviance residuals from a generalized linear model of bird abundance as a function of area surveyed, survey time (morning/afternoon), interval in the season, transect line ID, and year.

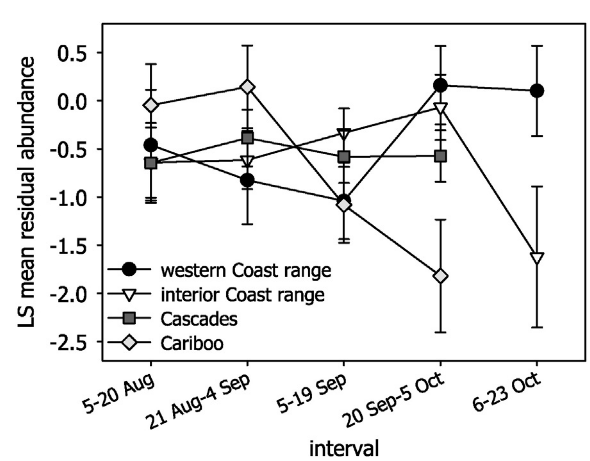

Fig. 4. Temporal patterns of densities by range and time interval during the season. Symbols represent the least square mean (± SE) of the deviance residuals from a generalized linear model of bird abundance as a function of area surveyed, survey time (morning/afternoon), habitat, transect line ID, and year.

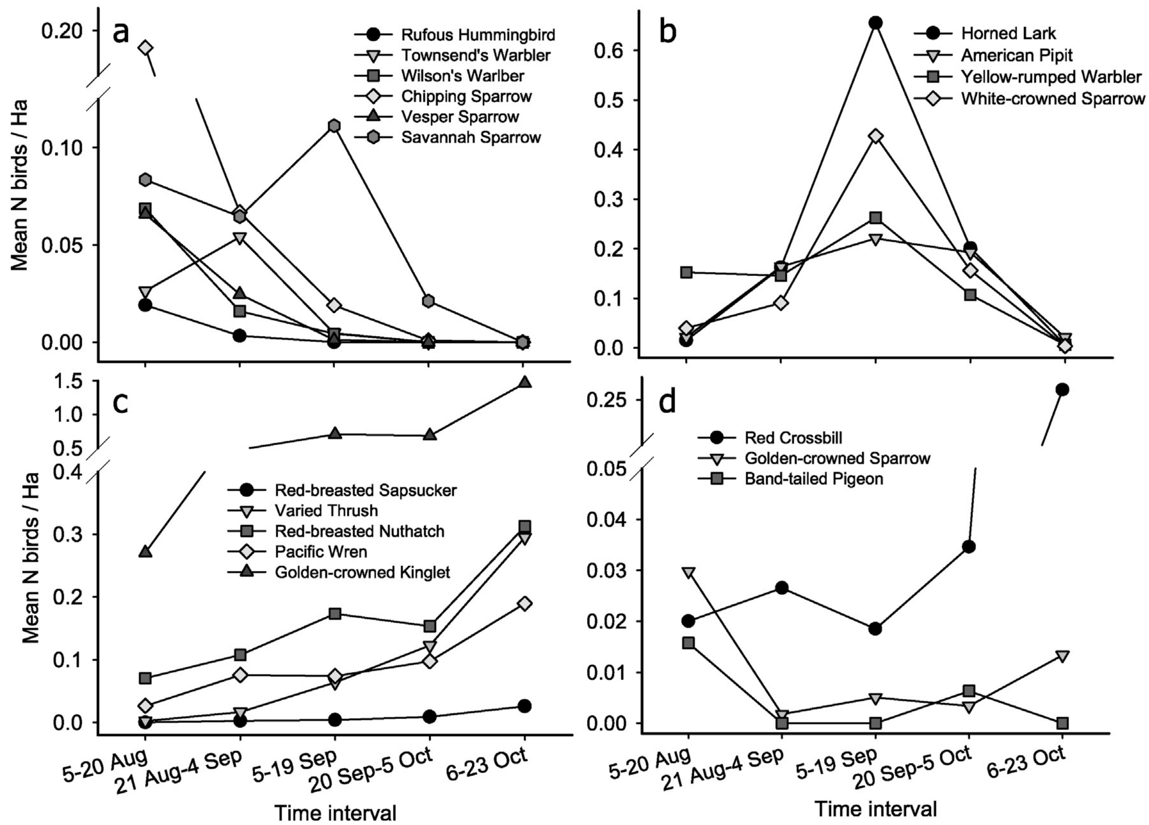

Fig. 5. Examples of species-level variation in temporal patterns of abundance between early August and late October. Panel a depicts the temporal patterns of abundance for all six long-distance migrant species detected in ≥10 surveys. Only one of these (Savannah Sparrow) did not peak in abundance early in the season. Panel b depicts four examples of mid-season peaking species, all of which were classified as short-distance migrants. Panel c depicts all five of the late-peaking species (two altitudinal migrants and three short-distance migrants). Panel d depicts patterns for the three species (short-distance migrants) that showed clear temporal variation in abundance, but did not fit the early-, mid-, and late-peaking patterns.

insect prey availability (Hutto, 1985b). However, high elevations may not be uniformly profitable for refueling of long-distance migrants in autumn (Rimmer and McFarland, 2000; Ruth et al., 2012). Future research should investigate the species-level traits (such as diet, geographic attributes of breeding and wintering ranges, or habitat preferences) shaping habitat selection by migrants.

Our continental-scale tabulations demonstrate that seasonal use of high elevations is remarkably widespread and may be typical of temperate mountains worldwide. Although we have known for decades that high elevation sites are important to migrant raptors (Bednarz et al., 1990; Hoffman and Smith, 2003), and that hummingbirds and other species move upslope post-breeding and some even establish feeding territories (Sutherland et al., 1982), the prevalence of high elevation use by migrant landbirds is generally under-appreciated. This underappreciation may be due to the ubiquitous decline in bird diversity with increasing elevation (McCain, 2009) that parallels diversity patterns in plant and other animal taxa (Rosenzweig, 1995). However, the inaccessibility of most high elevation areas, and lower concentration of bird monitoring schemes at high elevations may mean that short-term non-breeding use of high elevations has largely gone unnoticed. Partners in Flight (http://www.partnersinflight.org/) has identified studies such as ours that elucidate migration routes and timing of migration and stop-over as a priority need for achieving full life-cycle bird conservation and similar caveats ought to apply to community-level studies of other taxa.

We still know remarkably little about the individual-, population-, and species-level patterns of migratory behavior for many North American birds, in particular for those inhabiting mountain regions (but see La Sorte et al., 2014). The importance of filling these knowledge gaps increases given that high elevation environments are highly susceptible to global climate change (La Sorte and Jetz, 2010) and multiple other threats including natural resource extraction and recreation (Martin, 2012). We recommend the following steps to address gaps in knowledge. First, we need more systematic monitoring of high elevation habitats over broader spatial scales to understand the generality of the patterns presented here. A combination of methods capable of detecting many species over large areas (e.g., Hutto, 1985a) and individual marking (e.g., Carlisle et al., 2005a; DeLong et al., 2005) will be the most effective. In addition to site-focused monitoring of whole communities, we need targeted population-level studies to elucidate the patterns of movement for short-distance movements of birds and other animals within the continental USA and Canada.

Given the surprising diversity of a relatively well-studied taxon (i.e., birds) that we document seasonally utilizing high elevations habitats, we suspect that other less conspicuous mobile taxa such as mammals and flying insects may also exhibit similar patterns. Bat (McGuire and Boyle, 2013), ungulate (Mysterud et al., 2001), and butterfly (Shapiro, 1974) communities, in particular, may experience strong seasonal fluctuations in abundance and diversity at high elevations that would not be detected by current sampling. The threats to all high elevation taxa are numerous and severe, and include complex responses to changing climate (Inouye, 2008) and the interactions between multiple direct and indirect anthropogenic disturbances (Forister et al., 2010). Such disturbances in fragile temperate montane environments can take decades or more to recover (Curtin, 1995). We urge researchers to better document the ecological values of mountain habitats for the conservation of all taxa in North America and worldwide.

Acknowledgments

We are grateful to P. Collins, C. Conroy, B. Gowans, Y. Moresby, M. Mossop, S. Ogle, M. Preston, P. Ronalds, and S. Wilson for conducting

Table 3
Tabulation of all bird species using high elevations in North America derived from literature surveys, field surveys and consultation with experts. See Section 2.4 for description of high elevation habitat types. Periods of recorded use classified as B = breeding, W = winter, M = migration or at some other time of year. Unspecified high elevation habitat ("Unspec HE habitat") includes records of avian use of high elevation not assigned to a particular habitat. We summarized avian use of any high elevation habitat as occurring during breeding, winter, and/or migration/other periods. We highlight species using high elevations all year round with bold font Xs in the any HE habitat columns. Due to the special interest in alpine habitats, we include a column summarizing species that use the alpine at any time of the year ("Any alpine"). References are denoted by numbers listed below this table.

Scientific name	Common name	Alpine tundra			Alpine meadow-krumholz			Upper montane			Lower montane			Unspec HE habitat			Any HE habitat			Any alpine	References
		B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	Any time	
Anatidae																					
Anser albifrons	Greater White-fronted Goose	x		x													x		x	x	19
Chen caerulescens	Snow Goose	x		x													x		x	x	11, 31
Branta canadensis	Canada Goose	x		x									x				x		x	x	11, 19, 31
Anas strepera	Gadwall			x													x		x	x	13
Anas americana	American Wigeon	x					x										x		x	x	19, 31
Anas platyrhynchos	Mallard	x		x			x			x			x				x		x	x	19, 24, 31
Anas clypeata	Northern Shoveler	x		x													x		x	x	24
Anas acuta	Northern Pintail	x		x			x			x			x				x		x	x	24, 31
Anas crecca	Green-winged Teal						x			x			x						x	x	19, 24
Aythya collaris	Ring-necked Duck									x									x		19
Aythya marila	Greater Scaup	x		x													x		x	x	31
Aythya affinis	Lesser Scaup	x		x			x			x							x		x	x	19, 13, 31
Histrionicus histrionicus	Harlequin Duck							x			x						x				5, 6
Melanitta perspicillata	Surf Scoter	x															x			x	11, 31
Clangula hyemalis	Long-tailed Duck	x															x			x	11
Bucephala clangula	Common Goldeneye			x							x		x				x		x	x	11
Bucephala islandica	Barrow's Goldeneye			x			x			x	x		x				x		x	x	5, 11, 33
Mergus merganser	Common Merganser	x															x			x	31
Odontophoridae																					
Oreortyx pictus	Mountain Quail										x						x				18
Phasianidae																					
Bonasa umbellus	Ruffed Grouse				x					x	x						x		x	x	2, 5, 17, 19
Centrocercus urophasianus	Greater Sage-Grouse				x		x										x		x	x	
Falcipennis canadensis	Spruce Grouse							x	x	x	x	x	x				**x**	**x**	**x**		5, 19, 23
Lagopus lagopus	Willow Ptarmigan	x	x	x	x		x		x			x					**x**	**x**	**x**	x	5, 19, 31
Lagopus muta	Rock Ptarmigan	x	x	x	x		x		x			x					**x**	**x**	**x**	x	5, 26, 31
Lagopus leucura	White-tailed Ptarmigan	x	x	x	x	x	x			x			x				**x**	**x**	**x**	x	5, 19, 26
Dendragapus obscurus	Dusky Grouse			x	x		x	x		x	x						x		x	x	5, 9, 19, 20, 25
Dendragapus fuliginosus	Sooty Grouse			x	x		x	x		x	x						x		x	x	5, 9, 19, 20, 25
Tympanuchus phasianellus	Sharp-tailed Grouse									x			x						x		5
Gaviidae																					
Gavia stellata	Red-throated Loon	x															x			x	31
Gavia immer	Common Loon	x		x													x		x	x	11, 33
Podicipedidae																					
Podiceps nigricollis	Eared Grebe															x			x		13
Cathartidae																					
Cathartes aura	Turkey Vulture						x						x						x	x	20
Gymnogyps californianus	California Condor									x									x		18
Pandionidae																					
Pandion haliaetus	Osprey			x			x												x	x	19, 33
Accipitridae																					
Haliaeetus leucocephalus	Bald Eagle			x			x			x			x						x	x	5, 19
Circus cyaneus	Northern Harrier	x		x			x			x			x				x		x	x	5, 19, 24, 31
Accipiter striatus	Sharp-shinned Hawk			x			x	x		x	x		x				x		x	x	5, 7, 19, 20
Accipiter cooperii	Cooper's Hawk			x			x			x	x		x				x		x	x	5, 19
Accipiter gentilis	Northern Goshawk			x			x	x			x		x				x		x	x	5, 19, 26
Buteo lineatus	Red-shouldered Hawk									x			x						x		26
Buteo platypterus	Broad-winged Hawk									x			x						x		26
Buteo swainsoni	Swainson's Hawk			x			x												x	x	5, 20
Buteo jamaicensis	Red-tailed Hawk			x			x			x			x						x	x	13, 19
Buteo regalis	Ferruginous Hawk			x			x												x	x	24
Buteo lagopus	Rough-legged Hawk	x		x			x										x		x	x	19, 24
Aquila chrysaetos	Golden Eagle	x		x	x		x										x		x	x	17, 24, 31
Falconidae																					
Falco sparverius	American Kestrel			x			x			x									x	x	13, 19
Falco columbarius	Merlin	x		x			x			x	x		x				x		x	x	5, 19, 23
Falco rusticolus	Gyrfalcon	x		x													x		x	x	31
Falco peregrinus	Peregrine Falcon	x		x			x	x		x							x		x	x	19, 20, 24
Falco mexicanus	Prairie Falcon	x		x	x		x			x							x		x	x	19, 24
Rallidae																					
Fulica americana	American Coot												x						x		19
Gruidae																					
Grus canadensis	Sandhill Crane	x					x			x							x		x	x	5, 19

Table 3 (*continued*)

Scientific name	Common name	Alpine tundra			Alpine meadow-krumholz			Upper montane			Lower montane			Unspec HE habitat			Any HE habitat			Any alpine	References
		B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	Any time	
Charadriidae																					
Pluvialis fulva	Pacific Golden-Plover	x		x													x		x	x	5, 31
Charadrius semipalmatus	Semipalmated Plover	x		x			x										x		x	x	5, 31
Charadrius vociferus	Killdeer	x		x	x		x	x		x	x						x		x	x	5, 20, 31
Scolopacidae																					
Actitis macularius	Spotted Sandpiper	x		x	x		x	x		x	x		x				x		x	x	5, 18, 19, 26
Tringa solitaria	Solitary Sandpiper	x		x			x	x		x	x		x				x		x	x	5, 19, 24, 26, 31
Tringa incana	Wandering Tattler	x															x			x	31
Tringa melanoleuca	Greater Yellowlegs	x		x	x		x	x		x	x		x				x		x	x	5, 19
Tringa flavipes	Lesser Yellowlegs	x															x			x	31
Bartramia longicauda	Upland Sandpiper	x														x	x		x	x	3
Numenius phaeopus	Whimbrel	x															x			x	1
Numenius americanus	Long-billed Curlew															x			x		3
Limosa haemastica	Hudsonian Godwit	x															x			x	31
Limosa fedoa	Marbled Godwit			x															x	x	24
Calidris virgata	Surfbird	x															x			x	11
Calidris bairdii	Baird's Sandpiper	x		x													x		x	x	5, 19, 24
Calidris minutilla	Least Sandpiper	x		x													x		x	x	31
Calidris mauri	Western Sandpiper	x		x													x		x	x	31
Limnodromus griseus	Short-billed Dowitcher	x		x													x		x	x	31
Gallinago delicata	Wilson's Snipe	x			x			x			x						x			x	2, 20, 24, 31
Phalaropus lobatus	Red-necked Phalarope	x		x													x		x	x	5, 19
Stercorariidae																					
Stercorarius longicaudus	Long-tailed Jaeger	x		x													x		x	x	5
Laridae																					
Chroicocephalus philadelphia	Bonaparte's Gull	x		x	x		x	x		x							x		x	x	5, 31, 33
Leucophaeus pipixcan	Franklin's Gull			x			x												x	x	3, 24, 26
Larus canus	Mew Gull	x															x			x	31
Larus argentatus	Herring Gull	x															x			x	31
Sterna paradisaea	Arctic Tern	x															x			x	31
Columbidae																					
Patagioenas fasciata	Band-tailed Pigeon						x			x			x						x	x	5, 19
Zenaida macroura	Mourning Dove			x			x			x			x						x	x	2, 3, 24
Strigidae																					
Psiloscops flammeolus	Flammulated Owl										x						x				18
Bubo virginianus	Great Horned Owl	x		x			x	x			x	x	x				**x**	**x**	**x**	x	2, 3, 5, 24
Bubo scandiacus	Snowy Owl	x					x					x					**x**	**x**	**x**	x	5, 19
Surnia ulula	Northern Hawk Owl					x	x	x	x		x						**x**	**x**	**x**	x	5, 33
Glaucidium gnoma	Northern Pygmy-Owl						x	x	x	x	x	x	x				**x**	**x**	**x**	x	5, 19, 33
Strix nebulosa	Great Gray Owl									x			x						x		5, 20
Asio otus	Long-eared Owl			x			x	x		x	x		x				x		x	x	5, 19, 24
Asio flammeus	Short-eared Owl	x					x										x		x	x	5, 19, 31
Aegolius funereus	Boreal Owl							x	x	x	x	x	x				**x**	**x**	**x**		32, 33
Aegolius acadicus	Northern Saw-whet Owl						x	x			x						x		x	x	5, 19
Caprimulgidae																					
Chordeiles minor	Common Nighthawk	x		x	x		x			x			x				x		x	x	5, 19, 20, 24
Apodidae																					
Cypseloides niger	Black Swift			x			x			x	x		x				x		x	x	5,19
Chaetura pelagica	Chimney Swift			x			x			x									x	x	3, 23
Chaetura vauxi	Vaux's Swift			x			x			x	x		x				x		x	x	5, 19
Aeronautes saxatalis	White-throated Swift			x			x			x									x	x	18, 24
Trochilidae																					
Archilochus colubris	Ruby-throated Hummingbird			x			x	x			x						x		x	x	23
Archilochus alexandri	Black-chinned Hummingbird												x						x		18
Stellula calliope	Calliope Hummingbird						x	x		x	x						x		x	x	5, 8
Selasphorus platycercus	Broad-tailed Hummingbird			x			x			x			x						x	x	2, 3
Selasphorus rufus	Rufous Hummingbird	x		x	x		x	x		x	x		x				x		x	x	4, 5, 19
Alcedinidae																					
Megaceryle alcyon	Belted Kingfisher										x		x				x		x		5
Picidae																					
Melanerpes lewis	Lewis's Woodpecker									x			x						x		20
Sphyrapicus thyroideus	Williamson's Sapsucker							x		x	x						x		x		2, 18, 20
Sphyrapicus varius	Yellow-bellied Sapsucker												x						x		30
Sphyrapicus nuchalis	Red-naped Sapsucker							x		x	x		x				x		x		5, 19, 20
Sphyrapicus ruber	Red-breasted Sapsucker							x		x	x		x				x		x		2, 5, 19
Picoides pubescens	Downy Woodpecker										x		x				x		x		19, 23
Picoides villosus	Hairy Woodpecker									x	x		x				x		x		5, 19, 23, 28
Picoides albolarvatus	White-headed Woodpecker										x						x				18
Picoides dorsalis	American Three-toed Woodpecker							x			x	x	x				**x**	**x**	**x**		2, 3, 19, 28
Picoides arcticus	Black-backed Woodpecker							x			x	x	x				**x**	**x**	**x**		5, 20

(continued on next page)

Table 3 (*continued*)

Scientific name	Common name	Alpine tundra			Alpine meadow-krumholz			Upper montane			Lower montane			Unspec HE habitat			Any HE habitat			Any alpine	References
		B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	Any time	
Picidae																					
Colaptes auratus	Northern Flicker				x		x	x		x	x						x		x	x	5, 19, 21, 24
Dryocopus pileatus	Pileated Woodpecker										x	x	x				**x**	**x**	**x**		2, 19
Tyrannidae																					
Contopus cooperi	Olive-sided Flycatcher						x	x			x						x		x	x	5, 19,21, 23
Contopus sordidulus	Western Wood-Pewee										x						x				5, 19
Contopus virens	Eastern Wood-Pewee												x						x		23
Empidonax flaviventris	Yellow-bellied Flycatcher										x		x				x		x		23, 40
Empidonax minimus	Least Flycatcher												x						x		19
Empidonax hammondii	Hammond's Flycatcher							x		x	x						x		x		5, 18, 19
Empidonax oberholseri	Dusky Flycatcher				x			x		x	x						x		x	x	5, 8, 20, 26
Empidonax difficilis	Pacific-slope Flycatcher										x						x		x		5, 19, 21
Sayornis nigricans	Black Phoebe												x						x		18
Sayornis saya	Say's Phoebe	x		x	x		x	x									x		x	x	5, 13, 31
Tyrannus verticalis	Western Kingbird												x						x		3
Tyrannus tyrannus	Eastern Kingbird												x						x		2
Laniidae																					
Lanius ludovicianus	Loggerhead Shrike															x			x		3
Lanius excubitor	Northern Shrike	x		x			x										x		x	x	31
Vireonidae																					
Vireo cassinii	Cassin's Vireo										x		x				x		x		5, 19, 21, 27
Vireo gilvus	Warbling Vireo												x						x		21
Vireo olivaceus	Red-eyed Vireo										x		x				x		x		23
Corvidae																					
Perisoreus canadensis	Gray Jay			x	x		x	x			x	x	x				**x**	**x**	**x**	x	2, 3, 5, 19, 23
Cyanocitta stelleri	Steller's Jay			x			x	x		x	x	x	x				**x**	**x**	**x**	x	3, 5, 19, 30
Cyanocitta cristata	Blue Jay												x						x		23
Nucifraga columbiana	Clark's Nutcracker			x	x			x				x					**x**	**x**	**x**	x	5, 16
Pica hudsonia	Black-billed Magpie	x					x										x		x	x	19, 31
Corvus brachyrhynchos	American Crow															x			x		23
Corvus caurinus	Northwestern Crow			x			x												x	x	5, 19
Corvus corax	Common Raven	x	x	x	x	x	x	x	x	x	x	x	x				**x**	**x**	**x**	x	5, 19, 24, 31
Alaudidae																					
Eremophila alpestris	Horned Lark	x		x	x		x			x							x		x	x	5, 19, 26, 29
Hirundinidae																					
Progne subis	Purple Martin												x						x		23
Tachycineta bicolor	Tree Swallow	x		x			x			x			x				x		x	x	3, 24, 31
Tachycineta thalassina	Violet-green Swallow	x		x			x			x			x				x		x	x	2, 3, 19, 31
Stelgidopteryx serripennis	Northern Rough-winged Swallow									x			x						x		20
Riparia riparia	Bank Swallow															x			x		3
Petrochelidon pyrrhonota	Cliff Swallow	x		x	x		x										x		x	x	3, 5, 13
Hirundo rustica	Barn Swallow	x		x	x		x	x			x						x		x	x	5, 19, 31
Paridae																					
Poecile atricapillus	Black-capped Chickadee						x			x	x		x				x		x	x	5, 19, 23
Poecile gambeli	Mountain Chickadee			x			x	x	x	x	x	x	x				**x**	**x**	**x**	x	3, 5, 15
Poecile rufescens	Chestnut-backed Chickadee			x			x			x	x		x				x		x	x	5, 19, 21
Poecile hudsonicus	Boreal Chickadee							x	x	x	x	x	x				**x**	**x**	**x**		5, 19, 23
Aegithalidae																					
Psaltriparus minimus	Bushtit									x			x						x		14, 15
Sittidae																					
Sitta canadensis	Red-breasted Nuthatch			x			x	x		x	x	x	x				**x**	**x**	**x**	x	5, 19, 21, 30
Sitta carolinensis	White-breasted Nuthatch			x			x	x	x	x	x	x	x				**x**	**x**	**x**	x	17, 26
Sitta pygmaea	Pygmy Nuthatch										x	x	x				**x**	**x**	**x**		2, 15
Certhiidae																					
Certhia americana	Brown Creeper										x	x	x				**x**	**x**	**x**		5, 8, 18, 19
Troglodytidae																					
Salpinctes obsoletus	Rock Wren	x		x	x		x										x		x	x	3, 5, 19, 22, 24
Catherpes mexicanus	Canyon Wren															x			x		20
Troglodytes aedon	House Wren													x			x				2, 15
Troglodytes pacificus	Pacific Wren				x		x	x		x	x						x		x	x	5, 19, 21, 27
Troglodytes hiemalis	Winter Wren				x		x	x		x	x						x		x	x	5, 19, 21, 27
Polioptilidae																					
Polioptila caerulea	Blue-gray Gnatcatcher										x		x			x	x		x		3, 15
Cinclidae																					
Cinclus mexicanus	American Dipper	x		x	x		x	x		x	x						x		x	x	5, 19, 24
Regulidae																					
Regulus satrapa	Golden-crowned Kinglet						x	x	x	x	x	x	x				**x**	**x**	**x**	x	19, 21, 26
Regulus calendula	Ruby-crowned Kinglet						x	x		x	x		x				x		x	x	10, 19, 26
Turdidae																					
Sialia mexicana	Western Bluebird							x			x						x				5, 18, 20
Sialia currucoides	Mountain Bluebird	x		x	x		x	x		x	x		x				x		x	x	5, 19, 22, 24

Table 3 (*continued*)

Scientific name	Common name	Alpine tundra			Alpine meadow-krumholz			Upper montane			Lower montane			Unspec HE habitat			Any HE habitat			Any alpine	References
		B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	Any time	
Turdidae																					
Myadestes townsendi	Townsend's Solitaire	x		x	x		x	x		x	x		x				x		x	x	5, 8, 19, 21
Catharus minimus	Gray-cheeked Thrush	x			x			x			x						x			x	5, 31
Catharus bicknelli	Bicknell's Thrush				x			x			x						x			x	23, 27, 33
Catharus ustulatus	Swainson's Thrush						x	x		x	x		x				x		x	x	2, 5, 19
Catharus guttatus	Hermit Thrush	x			x		x	x		x	x		x				x		x	x	5, 19, 21, 31
Turdus migratorius	American Robin	x		x	x		x	x		x	x		x				x		x	x	5, 19, 24
Ixoreus naevius	Varied Thrush						x	x			x						x		x	x	5, 19, 21
Sturnidae																					
Sturnus vulgaris	European Starling															x			x		20
Motacillidae																					
Anthus rubescens	American Pipit	x		x	x		x	x		x							x		x	x	1, 3, 4, 17, 24
Bombycillidae																					
Bombycilla garrulus	Bohemian Waxwing						x			x	x		x			x	x		x	x	3, 5, 19, 31
Bombycilla cedrorum	Cedar Waxwing						x			x	x		x				x		x	x	5, 19, 26
Calcariidae																					
Calcarius lapponicus	Lapland Longspur			x															x	x	31
Calcarius ornatus	Chestnut-collared Longspur			x															x	x	4, 5
Calcarius pictus	Smith's Longspur	x															x			x	26, 31
Plectrophenax nivalis	Snow Bunting	x	x	x		x											**x**	**x**	**x**	x	19, 24, 31
Parulidae																					
Parkesia noveboracensis	Northern Waterthrush										x						x				23
Mniotilta varia	Black-and-white Warbler										x						x				23
Oreothlypis celata	Orange-crowned Warbler						x	x		x	x		x				x		x	x	2, 3, 12, 19, 26
Oreothlypis ruficapilla	Nashville Warbler									x	x		x				x		x		12, 19, 23
Oreothlypis virginiae	Virginia's Warbler												x						x		15
Geothlypis tolmiei	MacGillivray's Warbler						x	x		x	x		x				x		x	x	12, 13, 19
Setophaga ruticilla	American Redstart									x	x						x		x		23, 27
Setophaga magnolia	Magnolia Warbler							x			x						x				23
Setophaga castanea	Bay-breasted Warbler							x			x						x		x		23
Setophaga fusca	Blackburnian Warbler							x		x	x		x				x		x		23
Setophaga petechia	Yellow Warbler	x															x			x	31
Setophaga striata	Blackpoll Warbler				x			x			x						x			x	23
Setophaga caerulescens	Black-throated Blue Warbler												x						x		23
Setophaga pinus	Pine Warbler												x						x		23
Setophaga coronata	Yellow-rumped Warbler			x			x	x		x	x		x				x		x	x	12, 14, 19, 23
Setophaga graciae	Grace's Warbler									x			x						x		15
Setophaga nigrescens	Black-throated Gray Warbler										x		x				x		x		12
Setophaga townsendi	Townsend's Warbler						x	x		x	x		x				x		x	x	12, 14, 19
Setophaga occidentalis	Hermit Warbler							x		x	x		x				x		x		12, 14, 21, 26
Setophaga virens	Black-throated Green Warbler									x	x		x				x		x		23
Cardellina canadensis	Canada Warbler										x						x				23
Cardellina pusilla	Wilson's Warbler	x			x		x	x		x	x		x				x		x	x	2, 19, 21
Myioborus pictus	Painted Redstart										x						x				15
Emberizidae																					
Pipilo chlorurus	Green-tailed Towhee						x	x			x						x		x	x	2, 24
Pipilo maculatus	Spotted Towhee												x						x		19
Spizella arborea	American Tree Sparrow	x															x			x	31
Spizella passerina	Chipping Sparrow				x		x	x		x	x		x				x		x	x	8, 19, 21, 24
Spizella pallida	Clay-colored Sparrow															x			x		3, 24
Spizella breweri	Brewer's Sparrow	x			x												x			x	24, 31, 33
Pooecetes gramineus	Vesper Sparrow			x	x		x			x			x				x		x	x	2, 17, 19, 24
Artemisiospiza belli	Bell's Sparrow												x						x		18
Calamospiza melanocorys	Lark Bunting			x															x	x	3
Passerculus sandwichensis	Savannah Sparrow	x		x	x		x	x		x							x		x	x	19, 24, 26, 31
Passerella iliaca	Fox Sparrow	x			x		x	x		x	x		x				x		x	x	18, 19, 21
Melospiza melodia	Song Sparrow							x			x		x			x	x		x		2, 3, 19
Melospiza lincolnii	Lincoln's Sparrow	x			x		x	x		x	x		x				x		x	x	2, 13, 19, 21
Zonotrichia leucophrys	White-crowned Sparrow	x		x	x		x	x		x	x		x				x		x	x	8, 19, 26, 31
Zonotrichia atricapilla	Golden-crowned Sparrow	x		x	x		x	x		x	x		x				x		x	x	19, 26, 31
Junco hyemalis	Dark-eyed Junco	x		x	x		x	x		x	x		x				x		x	x	8, 19, 23, 24
Cardinalidae																					
Piranga flava	Hepatic Tanager												x						x		15
Piranga ludoviciana	Western Tanager									x	x		x				x		x		18, 19, 21
Pheucticus melanocephalus	Black-headed Grosbeak									x	x						x		x		15, 20, 21
Passerina amoena	Lazuli Bunting												x						x		18
Icteridae																					
Agelaius phoeniceus	Red-winged Blackbird						x												x	x	3, 24
Sturnella neglecta	Western Meadowlark				x		x	x		x							x		x	x	3, 17, 19, 24
Xanthocephalus xanthocephalus	Yellow-headed Blackbird						x												x	x	24

(continued on next page)

Table 3 (*continued*)

Scientific name	Common name	Alpine tundra			Alpine meadow-krumholz			Upper montane			Lower montane			Unspec HE habitat			Any HE habitat			Any alpine	References
		B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	B	W	M	Any time	
Icteridae																					
Euphagus carolinus	Rusty Blackbird			x															x	x	31
Euphagus cyanocephalus	Brewer's Blackbird			x			x												x	x	3, 17, 19, 24
Molothrus ater	Brown-headed Cowbird			x						x			x						x	x	19, 24
Icterus bullockii	Bullock's Oriole												x						x		18
Fringillidae																					
Leucosticte tephrocotis	Gray-crowned Rosy-Finch	x					x										x		x	x	4
Leucosticte atrata	Black Rosy-Finch	x					x										x		x	x	4
Leucosticte australis	Brown-capped Rosy-Finch	x					x										x		x	x	4
Pinicola enucleator	Pine Grosbeak						x	x		x	x	x	x				**x**	**x**	**x**	x	2, 3, 8, 19, 23
Haemorphis purpureus	Purple Finch												x						x		21, 27
Haemorphis cassinii	Cassin's Finch				x		x	x	x	x	x	x	x				**x**	**x**	**x**	x	2, 3, 19, 21, 24, 26
Loxia curvirostra	Red Crossbill				x	x	x	x	x	x	x	x	x				**x**	**x**	**x**	x	19, 21, 24
Loxia leucoptera	White-winged Crossbill						x			x	x	x	x				**x**	**x**	**x**	x	19, 21
Acanthis flammea	Common Redpoll	x		x													x		x	x	31
Spinus pinus	Pine Siskin						x			x	x		x				x		x	x	15, 19, 24, 26
Spinus tristis	American Goldfinch						x			x			x						x	x	23, 31
Coccothraustes vespertinus	Evening Grosbeak						x	x		x	x		x				x		x	x	19, 21

References for Table 3.[1] (Banfield, 1953), [2] (Behl and Ghiselin, 1958), [3] (Braun, 1969), [4] (Calder, 1897), [5] (Campbell et al., 1997), [6] (Clarke and Cowan, 1945), [7] (Cooper, 1994), [8] (DeSante, 1990), [9] (Edwards and Banko, 1976), [10] (Franzreb, 1984), [11] (Godfrey, 1986), [12] (Greenberg et al., 1974), [13] (Hendricks and Norment, 1986), [14] (Hutto, 1985b), [15] (Johnson, 1965), [16] (Johnson, 1974), [17] (Johnson, 1966), [18] (Lentz, 1993), [19] (Martin and Ogle, 1999, and Martin unpublished data), [20] (Martin, 2001), [21] (Manuwal et al., 1987), [22] (Miller, 1939), [23] (Palmer and Taber, 1946), [24] (Pattie and Verbeek, 1966), [25] (Pedersen and Adams, 1975), [26] (Poole, 2005), [27] (Sabo, 1980), [28] (Salt, 1957), [29] (Verbeek, 1967), [30] (Wagner, 1984), [31] (Weeden, 1960), [32] (Whelton, 1989), [33] Personal communication, various naturalists and scientists.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:http://dx.doi.org/10.1016/j.biocon.2015.10.008. These data include the Google map of the most important areas described in this article.

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