



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.

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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-García 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, sub-alpine, 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,

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