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*REVIEW*

# Altitudinal bird migration in North America

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**ABSTRACT**

Altitudinal bird migration involves annual seasonal movements up and down elevational gradients. Despite the fact that species from montane avifaunas worldwide engage in altitudinal migration, the patterns, causes, and prevalence of these movements are poorly understood. This is particularly true in North America where the overwhelming majority of avian migration research has focused on obligate, long-distance, temperate–tropical movements. Elsewhere in the world, most altitudinal migrants are partial migrants, making downhill movements to nonbreeding areas. However, spatial and temporal patterns, the prevalence and predictability of migration at individual and population levels, and the ultimate ecological factors selecting for movement behavior vary considerably among taxa and regions. I conducted a systematic survey of the evidence for altitudinal migration to fill gaps in our understanding of this behavior among the landbirds of North America and Hawaii. Altitudinal migration was as prevalent as in other avifaunas, occurring in >20% of continental North American and nearly 30% of Hawaiian species. Of the species wintering within the USA and Canada, ~30% engage in altitudinal migrations. Altitudinal migrants are far more common in the West, are taxonomically and ecologically diverse, and North American species exhibit patterns similar to altitudinal migrants elsewhere in the world. Because altitudinal migration systems are relatively tractable, they present excellent opportunities for testing hypotheses regarding migration generally. Altitudinal migration has likely been overlooked in North America due to contingency in the history of ornithological research. Our need to understand the patterns and causes of altitudinal migrations has never been greater due to emerging environmental threats to montane systems.

*Keywords:* alpine, altitudinal movements, elevational migration, facultative migration, high elevation, partial migration, post-breeding dispersal, nomadism

## Migración altitudinal de aves en América del Norte

La migración altitudinal refiere a movimientos estacionales a través de gradientes elevacionales. Aunque aves de altura por todo el mundo hacen migraciones altitudinales, los patrones, causas, y la prevalencia son poco conocidas comparando con la migración latitudinal de larga distancia. Se desconoce los patrones en particular para la avifauna de Norteamérica, donde la gran mayoría de investigaciones han enfocado en movimientos entre zonas templadas y tropicales. En otros partes del mundo, migraciones altitudinales tienden de ser parciales, y las aves bajan desde zonas altas donde anidan hacia zonas bajas donde pasan la época non-reproductiva. Sin embargo, existe mucha variación en los patrones espaciales y temporales, la prevalencia y previsibilidad de migración al nivel individual y poblacional, y los factores ecológicos que afecta a este comportamiento. Realicé una encuesta sistemática de la evidencia por la migración altitudinal en las aves terrestres de Norteamérica y Hawaii. La prevalencia de migración altitudinal era parecido con otros avifaunas, ocurriendo en más de 20% de las especies continentales y 30% de las especies de Hawái. De las especies que inviernan completamente o parcialmente en los EEUU o Canadá, ~30% migran altitudinalmente. Los migrantes son mucho más común en el oeste, son diversos en cuanto la taxonomía y ecología, y muestran patrones similares a migrantes altitudinales en otras partes del mundo. Como son relativamente fáciles de estudiar, son sistemas excelentes para probar hipótesis para la migración en general. Lo más posible es que la migración altitudinal se ha pasado por alto por azar o por idiosincrasias de la historia de investigaciones ornitológicas. Nos urge entender los patrones y causas de migración altitudinal en Norteamérica como en otras avifaunas frente los cambios ambientales que están amenazando a zonas de altura mundiales.

*Palabras clave:* alpina, movimiento altitudinales, movimiento elevational, migración facultativa, migración parcial, dispersión, nomadismo

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## INTRODUCTION

Birds are the most mobile of animal taxa. Their mobility has profoundly influenced every other aspect of their ecology and evolution. To paraphrase Dobzhansky's (1973) famous quote, nothing in ornithology makes sense except in light of movement strategies. The study of avian movements has focused on migration, a term which (in ornithological literature) refers to predictable, annual, return movements between breeding and nonbreeding ranges. Classic or "regular" bird migration involves long-distance movements of all individuals in a population between discrete breeding and wintering areas (Terrill and Able 1988) via movements that are often innately controlled (Berthold 1991). The overwhelming majority of avian migration studies have focused on obligate, innate, long-distance movements, from macro-ecological scales (e.g., Dingle 2008, Somveille et al. 2013) to field-intensive, population studies (e.g., Marra et al. 1998, Ydenberg et al. 2002, Stanley et al. 2012). These and hundreds of other studies have taught us a great deal about the implications of being migratory, especially for physiology, demography, and conservation.

While long-distance, obligate migrations may be "classic" examples, they may not be representative or even typical. Most species of avian migrants are probably partial migrants rather than complete migrants (Berthold 2001) meaning that not all individuals migrate. Differences in migratory tendency can occur at the population level (Berthold 1998, Jahn et al. 2012) or at the individual level (Ogonowski and Conway 2009, Hegemann et al. 2015). Many species exhibiting behavior at this "fuzzier" end of the spectrum of migratory behavior also migrate facultatively over shorter distances and exhibit less predictability in tendency, timing, and distance (Newton 2012). One such type of migratory behavior involves movements over elevational gradients. These *altitudinal migrations* often involve annual, return movements between breeding and nonbreeding ranges, justifying application of the term migration in an ornithological context. They are poorly understood, particularly within temperate avifaunas.

Ignoring altitudinal migrants and other facultative, short-distance movements has several consequences. First, our world view of migration is inherently biased, meaning that scientific perceptions of "normal" are flawed. Second, we miss the opportunity to learn a lot about the selective pressures that result in migration by ignoring comparatively tractable systems. Third, an incomplete understanding of avian movement interferes with our ability to protect species. This review first describes major patterns and the prevalence of altitudinal migration in birds globally, briefly outlines explanations and evidence for altitudinal migrations, then explores the patterns and prevalence of altitudinal migration within the North American avifauna via a systematic survey.

### The What, Where, and How of Altitudinal Migration

Unlike obligate, latitudinal migrations, altitudinal migrations typically (1) involve short distances, (2) are controlled facultatively, and often (3) consist of partially migratory populations. These attributes make biological sense; ecological gradients change quickly over short distances with elevational change (Körner 2007), meaning that birds may not need to move as far as do latitudinal migrants to experience similar fitness payoffs from migration (e.g., escaping unfavorable climatic conditions, exploiting food resources in areas with different phenological patterns). Lower movement costs likely reduces selection for morphological and physiological adaptations required to complete those movements. Thus, the expression of migration can be more flexible, varying among individuals (e.g., Gillis et al. 2008) or within individuals under different circumstances during their lifetimes (Norbu et al. 2013).

Altitudinal migrant birds live in all major mountain ranges of the Earth (Figure 1). Asia may be home to the greatest number of altitudinal migrants in the world where, purportedly, up to 65% of high-elevation–breeding species in the Himalayas engage in such movements. Altitudinal migrants are distributed throughout the avian tree of life with representatives in orders as morphologically and ecologically distinct as the Charadriiformes (Ferrari et al. 2008) and Psittaciformes (Chassot and Monge-Arias 2012). Altitudinal migrants also represent a broad range of foraging guilds. Neotropical nectarivores and frugivores are well-known altitudinal migrants (Stiles 1980, Strewe 2006), but nectarivores elsewhere (Grant and Grant 1967), insectivores (Nocedal 1994), carnivores (Bildstein 2004), piscivores (Mackas et al. 2010), granivores (Horvath and Sullivan 1988, Borras et al. 2010), and birds of other dietary guilds (e.g., Martínez del Rio et al. 2009) also migrate altitudinally. They range in body size from under a few grams to several kilograms (Boyle 2011). Altitudinal migrants live in forests, deserts, shrublands, and terrestrial aquatic environments. They dwell at all levels from the ground (e.g., Dark-eyed Juncos; Rabenold and Rabenold 1985) up to the canopy (e.g., Great Green Macaws; Chassot and Monge-Arias 2012), are flocking (e.g., Mountain Quail; Brennan et al. 1987) or solitary (e.g., Andean Condors; Sick 1993), and represent diverse mating systems.

Although species differ in the elevations they occupy, many migrants breed at higher elevations than where they spend their nonbreeding season in both tropical and temperate regions (Dixon and Gilbert 1964, Ramos-Olmos 1983, Norment and Green 2004, Powell and Bjork 2004). Many exceptions do occur, however. For example, the endangered Nēnē or Hawaiian Goose (*Branta sandvicensis*)



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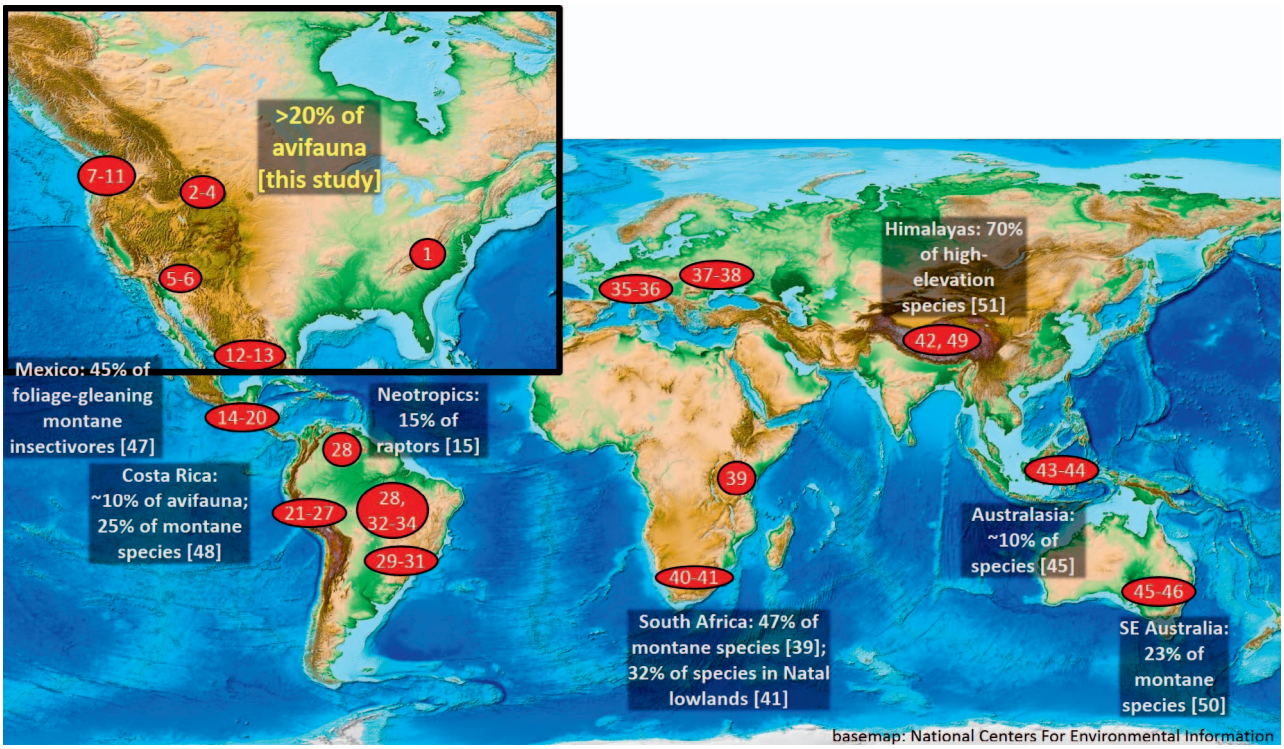



**FIGURE 1.** Altitudinal bird migration around the world. Numbers in red ovals correspond to references listed below documenting altitudinal migration in most major mountain ranges globally. Tallies of community- or guild-level prevalence of altitudinal migration (reported in dark boxes) provide a comparison to the results of this study in North America (inset). [1] Rabenold and Rabenold 1985; [2–4] Cade and Hoffman 1993, Connelly 1988, Dixon and Gilbert 1964; [5, 6] Dunning and Bowers 1984, Horvath and Sullivan 1988; [7–11] Garwood et al. 2009, Gillis et al. 2008, Grinnell and Miller 1944, Laymon 1989, Lorenz and Sullivan 2009; [12, 13] Des Granges 1979, Solórzano et al. 2000; [14–20] Boyle 2011, Chassot and Monge-Arias 2012, Chaves-Campos 2004, Chaves-Campos et al. 2003, Fraser et al. 2008, Loiselle and Blake 1991, Stiles 1980; [21–27] Newsome et al. 2015, Tinoco et al. 2009, Strewe and Navarro 2003, Hobson et al. 2003, Hilty 1997, Hughes 1980, 1984; [28] Beebe 1947; [29–31] Galetti 2001, Bencke and Kindel 1999, Areta and Bodrati 2010; [28, 32–34] Beebe 1947, Bildstein 2004, Alves 2007, Capllonch 2007; [35, 36] Borras et al. 2010, Klemp 2003; [37, 38] Brambilla and Rubolini 2009, De La Hera et al. 2014; [39] Burgess and Mlingwa 2000; [40, 41] Brown 2006, Johnson and Maclean 1994; [42] Lu et al. 2010; [43, 44] Kimura et al. 2001, Ryan 2012; [45, 46] Dingle 2004, 2008; [47] Nocedal 1994; [48] Stiles and Skutch 1989; [32] Bildstein 2004; [39] Burgess and Mlingwa 2000; [41] Johnson and Maclean 1994; [49] Barve et al. 2016; [45] Dingle 2004; [50] Tidemann et al. 1988; [51] Dixit et al. 2016.

breeds and molts at low elevations, migrating to high elevations during the nonbreeding season (Hess et al. 2012). A few species apparently make both uphill and downhill movements post-breeding; in the New England region of New South Wales, Australia, Eastern Spinebills (*Acanthorhynchus tenuirostris*) migrate uphill in winter (Ford and Pursey 1982), whereas farther south in the same mountain range, this species migrates to lower elevations in winter (Tidemann et al. 1988). In partially migratory populations, the elevation where nonmigrant individuals reside year-round can be at either the upper or lower end of the elevational gradient. In species where nonmigrants spend the nonbreeding season at high elevation, the migrants and residents generally breed together but spend the nonbreeding season apart (e.g., Resplendant Quetzals; Solórzano et al. 2000). In contrast, where nonmigrants spend the nonbreeding season at low elevations, then migrants and residents breed separately, meaning that the potential for assortative mating is strong (e.g., American Dippers; Middleton et al. 2006).

We know little regarding how birds make altitudinal migratory movements. Mountain Quail apparently traverse >2,000 m elevational gradients primarily on foot (Gutiérrez and Delehanty 1999). Whether small songbirds make altitudinal migrations in nocturnal flights as do many of their long-distance counterparts is unknown. Likewise, for most species, we do not know whether migrations occur in a single directed flight or many short flights. In Central American Three-wattled Bellbirds (*Procnias tricaunculata*), radio-tagged birds typically departed their high-elevation, Pacific-slope breeding areas in a single sustained flight to the Caribbean lowlands. A few months later, they recrossed the Continental Divide in multiple flights to the Pacific lowlands before returning to



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high-elevation breeding areas (Powell and Bjork 2004). Satellite-tagged Nēnē exhibit considerable inter-individual flexibility in the duration and distance of migratory journeys, with some individuals making nonstop flights while others make multiple stopovers (Leopold and Hess 2014). In some tropical passerines, it seems likely that migratory flights can be fast and directed given the rapid increase in capture rates of altitudinal migrants following storm events (Ramos-Olmos 1983, Boyle et al. 2010). In this way, some altitudinal migrations parallel the unpredictable, short-term elevational movements of birds escaping from inclement weather (Hahn et al. 2004, O'Neill and Parker 1978); a key distinction is that, once in the lowlands, tropical altitudinal migrants remain for the rest of the nonbreeding season.

## Why Do Birds Migrate Altitudinally?

The causes of altitudinal migration have only been studied in a few systems and species. Soon after altitudinal migration was described for tropical birds (Beebe 1947, Slud 1964), the idea that such movements were driven by spatial and temporal variation in food resources gained traction (Stiles 1980, 1988; Wheelwright 1983). This hypothesis made strong intuitive sense, especially given broad species-level associations between short-distance intra-tropical migration and dependence on nectar or fruit (Levey and Stiles 1992). Several studies tested predictions of this hypothesis to explain community-level (Loiselle and Blake 1991) and species-level patterns of abundance and movement (e.g., Rosselli 1994, Chaves-Campos 2004). Frequently, while part of the annual movement cycle was consistent with birds seeking elevations with high food abundance, the timing and direction of return movements did not match food-based predictions. For example, Bare-necked Umbrellabirds (*Cephalopterus glabricollis*) bred in locations and seasons of high food abundance, but migrated downhill to elevations having lower food availability (Chaves-Campos et al. 2003). Species-pairs of frugivorous migrants and nonmigrants revealed that neither dietary specialization nor competitive asymmetries could explain differences in migration, but even within genera, migrants consumed more fruit relative to arthropod prey (Boyle et al. 2011a). This finding suggested that energetic constraints driven by dependence on nutritionally dilute foods may underlie migratory tendency in some tropical species.

Evidence exists for alternative processes driving altitudinal migration including predation risk (Fretwell 1980, Greenberg 1980) and climatic constraints (Cox 1985). For instance, differences in nest predation risk could potentially explain the movements of birds between middle and high elevations (Boyle 2008a). However, in many species, the temporal and spatial patterns predicted by multiple ecological processes overlap (Ornelas and Arizmendi 1995). Climatic constraints have received relatively little attention in tropical regions despite Skutch (1969: 85) writing, "The Bellbird's wanderings appear to be caused partly by changes in weather. . .." However, Nocedal (1994) conjectured that in western Mexico, interannual variation in migratory propensity may well reflect individual differences in climatic tolerances and interannual variation in weather.

A mechanistic link between dietary guild, climate, and migration exists; dependence on low-protein, low-fat, dilute foods means that frugivores and nectarivores must forage frequently. Intense rain storms or cooler weather that increase thermogenic costs will affect small birds most acutely as they have narrow energetic safety margins and require high food intake rates. Storms can potentially limit the number of foraging hours to such an extent that such birds with high metabolic rates risk starvation, not because there is not enough food, but because the climate constrains their ability to forage (Boyle 2008b). Evidence in support of this hypothesis comes from Costa Rican White-ruffed Manakins (*Corapipo altera*); heavy rainfall is perceived by birds as a stressor and leads to increased fuel storage and dependence on stored energy for survival (Boyle et al. 2010). Additionally, in a diverse set of species, more altitudinal migrants reach the lowlands in years with wetter wet seasons (Boyle 2011). Thus, it seems likely that, at least in some tropical systems, the relationship between diet and migratory strategy are not driven by simple food availability, but via interactions with climate and energetics to shape individual and species-level migratory behavior.

In temperate North America, interest in altitudinal migration dates back farther than in tropical systems (e.g., Presnall 1935, Grinnell and Miller 1944, Dixon and Gilbert 1964). Climate has always made intuitive sense in explaining why birds might "escape" from temperate high elevations during winter. However, for most dietary guilds, seasons of climatic harshness coincide with food scarcity, and few authors have attempted to determine whether direct physiological challenges imposed by weather or insufficient food is more important in shaping movement. Carolina Dark-eyed Juncos engage in female-biased downhill migration away from high-elevation breeding areas (Rabenold and Rabenold 1985), as would be predicted by the *dominance*, *body-size*, and *arrival time* hypotheses proposed to explain differential and partial latitudinal migration (Ketterson and Nolan 1983). Interannual variation in the identity and abundance of high-elevation residents implicates climate in mediating some costs of residency and that, likely, competition for scarce winter food explains why many individuals depart breeding grounds. In other well-studied temperate systems, competition also appears to be important in shaping migratory strategies. American Dippers breed at both high and low elevations in southwestern Canada and winter together



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along low-elevation rivers. Snow and ice restricts access to food during winter at high elevations. Because fecundity is lower in migrants, and survival is only a little higher, the benefits of breeding at high elevation are less clear (Green et al. 2015) and, possibly, altitudinal migration in this system is driven by intraspecific competition for food-rich low-elevation territories. In contrast, Yellow-eyed Juncos (*Junco phaeonotus*) breeding at high elevations of Southern Arizona's sky islands appear to be limited in their ability to remain at high elevations year-round due to direct and indirect energetic consequences of cold temperatures and snow limiting foraging opportunities during winter (Lundblad 2014).

Generalization regarding the causes of altitudinal migration within major biogeographic regions or among them is extremely difficult due to the few species that have been the subject of detailed investigations. Given the diversity of patterns exhibited by altitudinal migrants, multiple ecological processes almost certainly shape this behavior. One important emergent conclusion is that altitudinal migrations are often facultative, at least within the Americas. Thus, the fitness costs and benefits of alternate strategies can be interpreted in the context of current ecological drivers, making them excellent systems in which to understand the evolutionary pressures that have shaped less labile movement strategies.

## ALTITUDINAL MIGRATION: A GAP IN NORTH AMERICAN ORNITHOLOGY?

Perhaps because they represent less spectacular feats of navigation and endurance, altitudinal migration is understudied in North American ornithology. In a recent search of the ISI Web of Knowledge database, the number of articles (all years, all journals) returned for "altitudinal migration" or "elevational migration" in combination with "bird" resulted in only 45 studies. Recent volumes (Jan 2011–Aug 2016) of *The Auk: Ornithological Advances* and *The Condor: Ornithological Applications* tell a similar story. A search on the word "migration" within abstracts resulted in 80 and 82 articles, respectively. Forty (*Auk*) and 45 (*Condor*) of those studies focused on topics relating to annual, return movements of birds, and all focused on long-distance latitudinal migration. This bias is reflected in pedagogical materials; in a commonly used 750-page ornithology textbook, altitudinal migration was mentioned in only 2 sentences that referred to tropical frugivores and nectarivores wandering unpredictably in search of food resources (Gill 2007).

Why do we know so little about altitudinal and other short-distance migrations of North American birds? One possibility is that there are few of them in our avifauna. Therefore, focusing on such movements lacks local relevance. An alternative is that understanding such movements does not advance fundamental understanding of animal movement generally, and therefore the topic has been ignored for a reason. A third hypothesis is that we have overlooked these movements due to artifacts of the cultural history of ornithology in North America—because of geography or random chance, research traditions have taken the discipline elsewhere. I reviewed the prevalence and patterns of altitudinal migration in North American birds, then used those results to frame an evaluation of these 3 hypotheses.

### A Systematic Survey

I systematically assessed the prevalence of altitudinal migration in the landbirds breeding in North America north of the Mexico border (i.e. Canada and the USA) and Hawaii. I used the *Birds of North America* (Rodewald 2015) as it represents the most comprehensive set of life histories available for this avifauna presented in a common format. I accessed this source and tabulated data during the summer and fall of 2014. I included all 607 extant, native landbirds breeding in this region, excluding the orders Pelecaniformes, Procellariformes, Gaviiformes, Podicipediformes, Phaethontiformes, Suliformes, and the families Stercorariidae and Alcidae as these groups are almost exclusively aquatic with limited opportunities for altitudinal movements. Nomenclature and species concepts follow the *American Ornithologists' Union Check-list* and supplements (American Ornithologists' Union 1998, Chesser et al. 2013).

I read the Introduction, Migration, Distribution, and Habitat sections for each species. I tabulated information for all species for which any populations were mentioned migrating altitudinally, referencing original sources. Use of the word "migration" varied among authors of life history accounts. Accordingly, I included species referenced as undertaking "elevational movements," "downhill dispersal," or other similar terms when they referred to seasonal movements between breeding and nonbreeding areas. I coded the strength of evidence qualitatively. I considered evidence to be "strong" when accounts reported results of movement-focused studies or if reports from multiple populations reported altitudinal migration with no ambiguity in the language describing altitudinal movements. I considered the strength of evidence to be "intermediate" when references consisted of more anecdotal information, but different authors working in different populations reported such movements and authors did not use ambiguous wording. I considered the evidence to be "weak" if movement descriptions were accompanied by words denoting uncertainty (e.g., "In montane areas, Pileated Woodpeckers *may* move to lower elevations in winter (Burleigh 1972; Simpson and Pratt 1992)"). I coded each putative altitudinal migrant species as completely or partially migratory, and if partially migrant, whether that



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variation occurred among or within populations. For partially migratory populations, I coded individuals as either breeding or wintering together. I noted species that included latitudinal migrant populations, and whether any population overwinters within the continental USA and Canada. I coded species for geographic overlap in breeding and wintering range and, where present, whether that overlap occurred within the continental USA and Canada.

I classified species into one of eight broad geographic distributions: "western" and "eastern" for species whose ranges primarily lie west or east of the 100th meridian, "widespread" for species occurring commonly in both eastern and western regions, "northern" for species occurring wholly or primarily in boreal or more northerly regions, "southwestern" for species only occurring in North America in deserts or sky islands of the Southwest or extreme southern Texas, "Hawaii" for species not found elsewhere in North America, and "other" for species not easily classifiable into any of these categories. I excluded extinct or introduced birds in the summaries below, but read and tabulated data for such species' accounts when they were available. Although there were few missing species accounts, life histories varied in the date of initial publication and subsequent revision, and it is possible that new studies may have been published since tabulation. Given constraints of study design and the relative paucity of studies on altitudinal migration in North America, the estimates presented below should be viewed as extremely conservative minima.

## RESULTS

Of 607 native, extant breeding landbirds covered in the *Birds of North America* series, accounts for 163 species (26.8%) reported altitudinal migration in at least one population somewhere in their range (Table 1). Of those, 10 species only occur in Hawaii; altitudinal migrants represent 28.6% of the 32 extant landbird species restricted to Hawaii. Ninety-eight (64.1%) of the 153 continental altitudinal migrants belong to species that also engage in latitudinal migrations. The majority (111 species; 72.5%) of continental altitudinal migrants were partially migratory at the population level (87 species), the individual level (51 species), or both (27 species). In species where migratory behavior varies among individuals, 70.1% of species breed together and spend the nonbreeding season at different elevations (e.g., Lesser Goldfinch, *Spinus psaltria*). Likewise, 75.2% of continental partial migrants breed at higher elevations than where they winter.

One hundred and sixteen continental species undertake altitudinal migrations within the USA or Canada (75.8% of continental altitudinal migrants or 20.2% of all continental species in the dataset). This represents 30.3% of the 383 continental landbirds that overwinter within the USA and Canada. Evidence for altitudinal migration was strong for 45 species, intermediate for 45 species, and weak for 26 species. One hundred and twelve (36.3%) of the 309 species with overlapping North American breeding and wintering distributions migrate altitudinally. The West was home to half (58) of the species that engage in altitudinal migrations within North America. An additional 40 altitudinal migrant species were distributed on both sides of the 100th meridian. Thirteen of the 68 southwestern species (19.1%) contained references documenting altitudinal migration within the region. Only one species coded as eastern (Northern Bobwhite, *Colinus virginianus*; Rosene 1969) was noted undertaking seasonal altitudinal migrations.

Within orders and families, the prevalence of altitudinal migration varied considerably (Table 2). Only 5 orders contained no altitudinal migrants, and these all are represented in North America by $\leq$6 breeding species. In 6 orders, and 8 families within Passeriformes, $>$25% of species migrate altitudinally somewhere within their range (Table 2).

Several species displayed complex movement patterns that challenged categorization. For instance, Black Rosy-Finches (*Leucosticte atrata*) generally winter at lower elevations, but can make multiple uphill and downhill movements at any time of year, responding to short-term weather events (King and Wales 1964, Hendricks and Swenson 1983, Johnson 2002). In Arizona, Phainopeplas (*Phainopepla nitens*) breed in low-elevation Sonoran deserts in February–April, then move upslope, breeding again in oak–sycamore canyons in May–July, then move even higher during August–September (Swarth 1904, Crouch 1943, Walsberg 1977). In October, Phainopeplas migrate back down to the lowest elevations for the remainder of the nonbreeding season, and where they can be quite mobile (Chu and Walsberg 1999). Uphill post-breeding movements to higher elevations, followed by downhill movements to wintering areas below the breeding elevation, was described for several species including Greater Sage-Grouse (Schroeder et al. 1999), Prairie Falcon (Steenhof 2013), Anna's Hummingbird (Clark and Russell 2012), Clark's Nutcracker (Tomback 1998), and Orange-crowned Warbler (Gilbert et al. 2010). Individuals and populations of many other species included in Table 1 combine both latitudinal and altitudinal movements, a pattern common to altitudinal migrant bats (McGuire and Boyle 2013). For example, Golden-crowned Kinglets exhibit "downslope altitudinal migration in winter in western mountains" (Swanson et al. 2012). However, what is not clear is the extent to which high-elevation breeders also shift south like their boreal-breeding conspecifics.

Species accounts for some extinct species referenced altitudinal migration including the Hawaiian 'Ö'ö (*Moho*



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**TABLE 1.** All 163 extant species described as making altitudinal migrations or whose life history accounts suggested they make regular movements along elevational gradients anywhere within their range. See text for basis of categorical assignment of the strength of evidence (weak, intermediate, strong) and region (eastern, western, widespread, northern, southwest, Hawaii, other). Additionally, I coded each species based on whether or not descriptions of altitudinal migrations pertained to movements made within North America (i.e. continental USA and Canada; "Alt mig in NA?"), whether or not the species was partially migratory and, if so, whether the variation in migratory behavior partitioned at individual and/or population levels ("Partially migratory?"), whether altitudinal migrations involved downward movements from higher elevation breeding areas or vice versa ("Breeds high?"), and whether (in partially migratory populations) migrants and residents breed at the same elevations ("Breeds together?"). Original sources for migration descriptions referenced in the *Birds of North America* accounts are listed by number below the table.

| Family | Scientific name | Common name | Evidence | Alt mig in NA? | Region | Partial migrant? | Breeds high? | Breeds together? | References |
|---|---|---|---|---|---|---|---|---|---|
| Anatidae | | | | | | | | | |
| | *Branta sandvicensis* | Hawaiian Goose | strong | | Hawaii | individ | | x | [1–7] |
| | *Cygnus buccinator* | Trumpeter Swan | intermediate | x | widespread | both | x | x | [8] |
| | *Anas wyvilliana* | Hawaiian Duck | weak | | Hawaii | individ | x | x | [9] |
| | *Anas cyanoptera* | Cinnamon Teal | weak | | western | | | | [10] |
| | *Histrionicus histrionicus* | Harlequin Duck | intermediate | x | widespread | individ | x | x | [11, 12] |
| | *Bucephala albeola* | Bufflehead | strong | x | widespread | | x | | [13] |
| | *Bucephala islandica* | Barrow's Goldeneye | strong | x | widespread | | x | | [14] |
| | *Lophodytes cucullatus* | Hooded Merganser | weak | x | widespread | | x | | [14] |
| | *Mergus merganser* | Common Merganser | weak | x | widespread | | x | | [15, 16] |
| | *Oxyura jamaicensis* | Ruddy Duck | intermediate | x | widespread | | x | | [17] |
| Odontophoridae | | | | | | | | | |
| | *Oreortyx pictus* | Mountain Quail | strong | x | western | | x | | [18–24] |
| | *Callipepla californica* | California Quail | weak | x | western | individ | x | | [8] |
| | *Callipepla gambelii* | Gambel's Quail | weak | x | western | individ | x | | [25, 26] |
| | *Colinus virginianus* | Northern Bobwhite | intermediate | x | eastern | pop | x | | [27] |
| Phasianidae | | | | | | | | | |
| | *Centrocercus urophasianus* | Greater Sage-Grouse | strong | x | western | both | | x | [28–35] |
| | *Falcipennis canadensis* | Spruce Grouse | strong | x | widespread | individ | | | [36–38] |
| | *Lagopus lagopus* | Willow Ptarmigan | strong | x | northern | both | x | x | [39–42] |
| | *Lagopus leucura* | White-tailed Ptarmigan | strong | x | western | both | x | x | [36, 43–47] |
| | *Dendragapus obscurus* | Dusky Grouse | strong | x | western | both | | x | [48, 49] |
| | *Dendragapus fuliginosus* | Sooty Grouse | strong | x | western | both | | x | [48, 49] |
| | *Tympanuchus phasianellus* | Sharp-tailed Grouse | intermediate | x | western | both | | x | [50–52] |
| Cathartidae | | | | | | | | | |
| | *Coragyps atratus* | Black Vulture | weak | x | widespread | both | x | x | [53, 54] |
| Accipitridae | | | | | | | | | |
| | *Accipiter gentilis* | Northern Goshawk | weak | x | widespread | | | | [8] |
| | *Buteo lineatus* | Red-shouldered Hawk | intermediate | x | widespread | | x | | [55] |
| | *Buteo albonotatus* | Zone-tailed Hawk | intermediate | | western | both | x | x | [56] |
| Falconidae | | | | | | | | | |
| | *Falco mexicanus* | Prairie Falcon | strong | x | western | both | | x | [57] |
| Rallidae | | | | | | | | | |
| | *Gallinula galeata* | Common Gallinule | intermediate | x | widespread | pop | x | | [58] |
| | *Fulica americana* | American Coot | intermediate | x | widespread | pop | x | | [59, 60] |
| Scolopacidae | | | | | | | | | |
| | *Calidris virgata* | Surfbird | strong | x | northern | | x | | [8] |
| | *Calidris ptilocnemis* | Rock Sandpiper | strong | x | northern | pop | x | | [8] |



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**TABLE 1.** Continued.

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|---|---|---|---|---|---|---|---|---|---|
| Laridae | | | | | | | | | |
| | *Pagophila eburnea* | Ivory Gull | strong | | northern | pop | x | | [61, 62] |
| | *Larus californicus* | California Gull | strong | x | western | pop | x | | [8, 63] |
| Columbidae | | | | | | | | | |
| | *Patagioenas leucocephala* | White-crowned Pigeon | strong | | other | both | | x | [64] |
| | *Patagioenas fasciata* | Band-tailed Pigeon | weak | x | western | both | x | x | [8] |
| | *Columbina passerina* | Common Ground-Dove | weak | | other | both | x | x | [8] |
| Strigidae | | | | | | | | | |
| | *Megascops trichopsis* | Whiskered Screech-Owl | weak | x | southwest | individ | x | | [8] |
| | *Glaucidium gnoma* | Northern Pygmy-Owl | strong | x | western | | x | | [65–70] |
| | *Strix occidentalis* | Spotted Owl | strong | x | western | both | x | x | [71–76] |
| | *Strix nebulosa* | Great Gray Owl | intermediate | x | widespread | pop | x | | [77–79] |
| | *Aegolius acadicus* | Northern Saw-whet Owl | strong | x | widespread | pop | x | | [80–82] |
| Caprimulgidae | | | | | | | | | |
| | *Phalaenoptilus nuttallii* | Common Poorwill | intermediate | x | western | both | x | | [83] |
| | *Antrostomus ridgwayi* | Buff-collared Nightjar | weak | | southwest | pop | x | | [56] |
| | *Antrostomus arizonae* | Mexican Whip-poor-will | weak | | southwest | pop | x | | [84] |
| Apodidae | | | | | | | | | |
| | *Aeronautes saxatalis* | White-throated Swift | intermediate | x | western | | x | | [17, 82, 84–86] |
| Trochilidae | | | | | | | | | |
| | *Lampornis clemenciae* | Blue-throated Hummingbird | intermediate | | southwest | pop | x | | [87] |
| | *Eugenes fulgens* | Magnificent Hummingbird | strong | | southwest | | x | | [88–91] |
| | *Calothorax lucifer* | Lucifer Hummingbird | weak | | southwest | | | | [92, 93] |
| | *Archilochus alexandri* | Black-chinned Hummingbird | weak | x | western | individ | | x | [8] |
| | *Calypte anna* | Anna's Hummingbird | strong | x | western | both | | x | [94–99] |
| | *Calypte costae* | Costa's Hummingbird | weak | | western | pop | | | [100–102] |
| | *Selasphorus rufus* | Rufous Hummingbird | intermediate | | western | | | | |
| Picidae | | | | | | | | | |
| | *Melanerpes lewis* | Lewis's Woodpecker | intermediate | x | western | | | | [17, 103–106] |
| | *Melanerpes uropygialis* | Gila Woodpecker | intermediate | x | southwest | both | | x | [107, 108] |
| | *Sphyrapicus thyroideus* | Williamson's Sapsucker | intermediate | x | western | pop | x | | [108, 109] |
| | *Sphyrapicus nuchalis* | Red-naped Sapsucker | intermediate | x | western | both | | | [109] |
| | *Sphyrapicus ruber* | Red-breasted Sapsucker | strong | x | western | | x | | [70, 110, 111] |
| | *Picoides nuttallii* | Nuttall's Woodpecker | intermediate | x | western | individ | | x | [17] |
| | *Picoides villosus* | Hairy Woodpecker | intermediate | x | widespread | individ | x | x | [17, 70] |
| | *Picoides arizonae* | Arizona Woodpecker | intermediate | x | southwest | individ | x | x | [86, 108] |
| | *Picoides albolarvatus* | White-headed Woodpecker | weak | x | western | | x | | [112, 113] |
| | *Colaptes auratus* | Northern Flicker | intermediate | x | widespread | | x | | [17, 114, 115] |
| | *Dryocopus pileatus* | Pileated Woodpecker | weak | x | widespread | individ | x | x | [116, 117] |
| Tyrannidae | | | | | | | | | |
| | *Camptostoma imberbe* | Northern Beardless-Tyrannulet | weak | x | southwest | individ | x | x | [108] |
| | *Contopus pertinax* | Greater Pewee | strong | | southwest | pop | x | | [84, 118–122] |
| | *Empidonax difficilis* | Pacific-slope Flycatcher | weak | | western | | x | | [8] |
| | *Empidonax occidentalis* | Cordilleran Flycatcher | weak | | western | | x | | [8] |
| | *Empidonax fulvifrons* | Buff-breasted Flycatcher | intermediate | | southwest | | x | | [8] |



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|---|---|---|---|---|---|---|---|---|---|
| | *Sayornis nigricans* | Black Phoebe | intermediate | x | western | pop | | | [17, 91] |
| | *Pyrocephalus rubinus* | Vermilion Flycatcher | intermediate | x | southwest | | x | | [8] |
| | *Myiarchus tuberculifer* | Dusky-capped Flycatcher | intermediate | | western | | x | | [84] |
| Vireonidae | | | | | | | | | |
| | *Vireo plumbeus* | Plumbeous Vireo | weak | | western | | x | | [86, 123, 124] |
| | *Vireo huttoni* | Hutton's Vireo | intermediate | x | western | | x | | [94, 108, 125, 126] |
| | *Vireo gilvus* | Warbling Vireo | weak | | western | | | | [8] |
| | *Vireo altiloquus* | Black-whiskered Vireo | weak | | other | pop | | | [127] |
| Corvidae | | | | | | | | | |
| | *Perisoreus canadensis* | Gray Jay | weak | x | widespread | individ | x | x | [128–130] |
| | *Cyanocitta stelleri* | Steller's Jay | strong | x | western | pop | x | | [108, 131, 132] |
| | *Aphelocoma californica/ woodhouseii* | California/ Woodhouse's Scrub-Jay | strong | x | western | | x | | [132–136] |
| | *Nucifraga columbiana* | Clark's Nutcracker | strong | x | western | pop | | | [137–143] |
| | *Pica hudsonia* | Black-billed Magpie | intermediate | x | western | both | x | x | [8, 144] |
| | *Corvus brachyrhynchos* | American Crow | weak | x | widespread | | x | | [17, 126, 134, 145] |
| | *Corvus hawaiiensis* | Hawaiian Crow | strong | | Hawaii | | x | | [2, 146] |
| Alaudidae | | | | | | | | | |
| | *Eremophila alpestris* | Horned Lark | intermediate | x | widespread | pop | x | | [147, 148] |
| Hirundinidae | | | | | | | | | |
| | *Tachycineta thalassina* | Violet-green Swallow | strong | | western | pop | x | | [147] |
| | *Stelgidopteryx serripennis* | Northern Rough-winged Swallow | weak | | widespread | pop | | | [8] |
| Paridae | | | | | | | | | |
| | *Poecile gambeli* | Mountain Chickadee | strong | x | western | pop | x | | [149, 150] |
| | *Poecile rufescens* | Chestnut-backed Chickadee | intermediate | x | western | | | | [126, 144] |
| | *Baeolophus wollweberi* | Bridled Titmouse | intermediate | x | western | pop | x | | [108, 151, 152] |
| Aegithalidae | | | | | | | | | |
| | *Psaltriparus minimus* | Bushtit | intermediate | x | western | pop | x | | [124, 153, 154] |
| Sittidae | | | | | | | | | |
| | *Sitta canadensis* | Red-breasted Nuthatch | strong | x | widespread | pop | x | | [144, 155, 156] |
| | *Sitta carolinensis* | White-breasted Nuthatch | weak | x | widespread | individ | x | x | [82] |
| | *Sitta pygmaea* | Pygmy Nuthatch | strong | x | western | pop | x | | [123, 126, 157–166] |
| Certhiidae | | | | | | | | | |
| | *Certhia americana* | Brown Creeper | weak | x | widespread | pop | x | | [108, 144, 167] |
| Troglodytidae | | | | | | | | | |
| | *Salpinctes obsoletus* | Rock Wren | weak | x | western | pop | x | | [17, 108, 168] |
| | *Catherpes mexicanus* | Canyon Wren | weak | x | western | individ | x | x | [169] |
| | *Troglodytes aedon* | House Wren | weak | x | widespread | pop | | | [17] |
| | *Troglodytes pacificus* | Pacific Wren | strong | x | western | both | x | | [126, 144, 170] |
| Cinclidae | | | | | | | | | |
| | *Cinclus mexicanus* | American Dipper | strong | x | western | individ | x | | [171–174] |
| Regulidae | | | | | | | | | |
| | *Regulus satrapa* | Golden-crowned Kinglet | strong | x | widespread | pop | x | | [144, 175–178] |
| | *Regulus calendula* | Ruby-crowned Kinglet | intermediate | x | widespread | pop | x | | [144, 177, 178] |
| Turdidae | | | | | | | | | |
| | *Sialia mexicana* | Western Bluebird | strong | x | western | pop | x | | [102, 179–181] |



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|---|---|---|---|---|---|---|---|---|---|
| | *Sialia currucoides* | Mountain Bluebird | weak | x | western | pop | x | | [8] |
| | *Myadestes townsendi* | Townsend's Solitaire | strong | x | western | pop | x | | [8] |
| | *Catharus ustulatus* | Swainson's Thrush | weak | | widespread | | | | [182] |
| | *Catharus guttatus* | Hermit Thrush | intermediate | x | widespread | pop | x | | [179] |
| | *Turdus migratorius* | American Robin | weak | x | widespread | pop | x | | [8] |
| | *Ixoreus naevius* | Varied Thrush | weak | x | western | | x | | [8] |
| Mimidae | | | | | | | | | |
| | *Toxostoma crissale* | Crissal Thrasher | intermediate | x | southwest | pop | x | | [98, 183–188] |
| Motacillidae | | | | | | | | | |
| | *Anthus rubescens* | American Pipit | strong | x | western | pop | x | | [84, 144, 189–192] |
| Ptilogonatidae | | | | | | | | | |
| | *Phainopepla nitens* | Phainopepla | strong | x | southwest | pop | | | [98, 193–196] |
| Peucedramidae | | | | | | | | | |
| | *Peucedramus taeniatus* | Olive Warbler | intermediate | x | southwest | individ | x | | [86, 197] |
| Calcariidae | | | | | | | | | |
| | *Plectrophenax nivalis* | Snow Bunting | weak | | northern | individ | x | x | [198, 199] |
| Parulidae | | | | | | | | | |
| | *Protonotaria citrea* | Prothonotary Warbler | weak | | eastern | | | | [182, 200] |
| | *Oreothlypis celata* | Orange-crowned Warbler | intermediate | x | widespread | | | | [8] |
| | *Setophaga pitiayumi* | Tropical Parula | intermediate | | southwest | pop | x | | [84] |
| | *Setophaga caerulescens* | Black-throated Blue Warbler | weak | | eastern | individ | | x | [201] |
| | *Setophaga coronata* | Yellow-rumped Warbler | weak | x | widespread | pop | x | | [202, 203] |
| | *Setophaga graciae* | Grace's Warbler | intermediate | | southwest | pop | x | | [151, 204] |
| | *Setophaga occidentalis* | Hermit Warbler | intermediate | x | western | | | | [205] |
| | *Myioborus pictus* | Painted Redstart | intermediate | x | southwest | individ | x | | [8] |
| Emberizidae | | | | | | | | | |
| | *Pipilo chlorurus* | Green-tailed Towhee | strong | x | western | | x | | [17, 108, 176, 206, 207] |
| | *Pipilo maculatus* | Spotted Towhee | intermediate | x | western | | x | | [108, 124, 156] |
| | *Aimophila ruficeps* | Rufous-crowned Sparrow | intermediate | x | western | individ | x | x | [94, 108, 181, 208–211] |
| | *Melozone fusca* | Canyon Towhee | intermediate | x | southwest | pop | x | | [134, 206] |
| | *Melozone crissalis* | California Towhee | intermediate | x | western | | x | | [17, 212, 213] |
| | *Spizella atrogularis* | Black-chinned Sparrow | intermediate | x | southwest | both | x | x | [84, 108, 188, 214, 215] |
| | *Amphispiza bilineata* | Black-throated Sparrow | intermediate | x | western | pop | x | | [108, 156, 214] |
| | *Artemisiospiza nevadensis/belli* | Sage Sparrow | strong | x | western | | x | | [216] |
| | *Calamospiza melanocorys* | Lark Bunting | intermediate | x | other | | | | [217, 218] |
| | *Passerculus sandwichensis* | Savannah Sparrow | weak | x | widespread | pop | x | | [8] |
| | *Passerella iliaca* | Fox Sparrow | strong | x | widespread | pop | x | | [219, 220] |
| | *Melospiza melodia* | Song Sparrow | intermediate | x | widespread | pop | x | | [221–223] |
| | *Melospiza lincolnii* | Lincoln's Sparrow | weak | x | widespread | individ | | | [8] |
| | *Zonotrichia leucophrys* | White-crowned Sparrow | weak | | widespread | | | | [224] |
| | *Zonotrichia atricapilla* | Golden-crowned Sparrow | intermediate | x | western | | | | [17, 126, 225, 226] |
| | *Junco hyemalis* | Dark-eyed Junco | strong | x | widespread | both | x | x | [227] |
| | *Junco phaeonotus* | Yellow-eyed Junco | strong | x | southwest | both | x | | [228, 229] |
| Cardinalidae | | | | | | | | | |
| | *Piranga flava* | Hepatic Tanager | intermediate | | southwest | pop | x | | [90, 122, 230–232] |



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|---|---|---|---|---|---|---|---|---|---|
| | *Piranga ludoviciana* | Western Tanager | intermediate | | western | pop | | | [230, 233] |
| | *Cardinalis sinuatus* | Pyrrhuloxia | weak | x | southwest | individ | x | | [234] |
| | *Pheucticus melanocephalus* | Black-headed Grosbeak | weak | | western | pop | x | | [84, 195] |
| Icteridae | | | | | | | | | |
| | *Agelaius tricolor* | Tricolored Blackbird | strong | | western | pop | | | [235–237] |
| | *Sturnella neglecta* | Western Meadowlark | intermediate | x | western | pop | x | | [233, 238] |
| | *Euphagus cyanocephalus* | Brewer's Blackbird | strong | x | western | pop | x | | [239–241] |
| | *Molothrus bonariensis* | Shiny Cowbird | strong | | other | individ | x | | [242] |
| | *Molothrus aeneus* | Bronzed Cowbird | intermediate | | southwest | pop | x | | [233] |
| Fringillidae | | | | | | | | | |
| | *Leucosticte tephrocotis* | Gray-crowned Rosy-Finch | strong | x | western | both | x | x | [17, 126, 243] |
| | *Leucosticte atrata* | Black Rosy-Finch | strong | x | western | pop | x | | [243, 244] |
| | *Leucosticte australis* | Brown-capped Rosy-Finch | strong | x | western | pop | x | | [245–247] |
| | *Pinicola enucleator* | Pine Grosbeak | intermediate | x | widespread | individ | x | x | [17, 128, 248, 249] |
| | *Haemorhous purpureus* | Purple Finch | strong | x | widespread | pop | x | | [250–253] |
| | *Haemorhous cassinii* | Cassin's Finch | strong | x | western | both | x | x | [254–258] |
| | *Haemorhous mexicanus* | House Finch | strong | x | widespread | pop | x | | [259, 260] |
| | *Spinus pinus* | Pine Siskin | weak | | widespread | both | x | | [8] |
| | *Spinus psaltria* | Lesser Goldfinch | strong | x | western | both | x | x | [17, 98, 156, 160, 261, 262] |
| | *Spinus lawrencei* | Lawrence's Goldfinch | weak | | southwest | pop | | | [125, 263] |
| | *Coccothraustes vespertinus* | Evening Grosbeak | strong | x | widespread | pop | x | | [264–266] |
| | *Loxioides bailleui* | Palila | strong | | Hawaii | pop | x | | [267, 268] |
| | *Chlorodrepanis virens* | Hawaii Amakihi | intermediate | | Hawaii | individ | x | | [269–272] |
| | *Chlorodrepanis flavus* | Oahu Amakihi | weak | | Hawaii | individ | x | | [8] |
| | *Chlorodrepanis stejneger* | Kauai Amakihi | weak | | Hawaii | individ | | | [270] |
| | *Drepanis coccinea* | Iiwi | strong | | Hawaii | individ | | | [2, 269, 273, 274] |
| | *Palmeria dolei* | Akohekohe | intermediate | | Hawaii | individ | x | | [275] |
| | *Himatione sanguinea* | Apapane | intermediate | | Hawaii | | | | [2, 269, 273] |

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**TABLE 2.** The number and percentage of species for which there is evidence of altitudinal migration in the *Birds of North America* life history accounts (Rodewald 2015). Included are all landbird orders and the 14 families within Passeriformes represented by at least 5 species in the region.

| | altitudinal migrant species | |
|---|---|---|
| Taxon | *N* | % |
| Anseriformes | 10 | 21.7 |
| Galliformes | 11 | 57.9 |
| Ciconiiformes | 0 | 0.0 |
| Accipitriformes | 4 | 14.8 |
| Falconiformes | 1 | 14.3 |
| Gruiformes | 2 | 15.4 |
| Charadriiformes | 4 | 4.6 |
| Columbiformes | 3 | 37.5 |
| Psittaciformes | 0 | 0.0 |
| Cuculiformes | 0 | 0.0 |
| Strigiformes | 5 | 26.3 |
| Caprimulgiformes | 3 | 33.3 |
| Apodiformes | 8 | 42.1 |
| Trogoniformes | 0 | 0.0 |
| Coraciiformes | 0 | 0.0 |
| Piciformes | 11 | 52.4 |
| Passeriformes | 102 | 31.6 |
| Tyrannidae | 8 | 23.5 |
| Vireonidae | 4 | 30.8 |
| Corvidae | 7 | 38. 9 |
| Hirundinidae | 2 | 28.6 |
| Paridae | 3 | 25.0 |
| Troglodytidae | 4 | 40.0 |
| Turdidae | 7 | 43.8 |
| Mimidae | 1 | 10.0 |
| Calcariidae | 1 | 16. 7 |
| Parulidae | 8 | 16.0 |
| Emberizidae | 17 | 39.5 |
| Cardinalidae | 4 | 28.6 |
| Icteridae | 5 | 23.8 |
| Fringillidae | 18 | 52.9 |

*nobilis*), which apparently made diurnal and seasonal altitudinal movements in search of nectar. The percent of migrants in the extant Hawaiian communities is likely similar to that of historical communities; the scant data on extinct taxa indicates that probably 11 of 38 endemic landbird species were altitudinal migrants. Some nonnative species recently established in North America engage in altitudinal migrations; Chukars (*Alectoris chukar*) breeding $\geq$1800 m descend below the snow line during winter (Christensen 1954), mirroring movements in their native range (McGowan and Kirwan 2016).

Fewer than half (46.7%) of the sources referenced in descriptions of altitudinal migration came from peer-reviewed journals. Of 275 references cited in Table 1, 44.2% were books or lengthy monographs (bird atlases, distributional monographs, annotated checklists, or other similar literature). Reports and theses comprised 9.1% of the references. The median publication date was 1980, 25% of



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references dated from 1954 or earlier, and the oldest dated from 1876 (Henshaw 1876).

## DISCUSSION

What does this review tell us about altitudinal bird migration generally, and in North America specifically? On a global scale, altitudinal bird migration appears to be common (Figure 1). The summaries of information compiled by North America's leading ornithologists paint a surprising picture: altitudinal migration is similarly common in North America. At a minimum, 26.8% of our landbird species migrate altitudinally somewhere within their range, 20.2% do so within the USA and Canada, representing 30.3% of the species that spend the winter within the continent. Many of these species combine altitudinal and latitudinal movements in the same or different parts of their range. The complexities of migration behaviors exhibited by the North American avifauna is grossly simplified by such coarse tallies. Furthermore, estimates will certainly increase as more research is devoted to short-distance movements. Nevertheless, we can rule out the first hypothesis for why this behavior has been ignored—North America is *not* a global anomaly in having few altitudinal migrants.

The second hypothesis is also largely incorrect; understanding altitudinal migration does advance our fundamental understanding of animal movement generally. Most research questions relating to migration are equally as applicable to altitudinal migrants as latitudinal, long-distance migrants. Examples of core questions in migration research that are well suited to tackling in altitudinal migrant systems include documentation of movement patterns and migratory connectivity via new tracking methods, molt-migration (e.g., Fraser et al. 2010), the consequences of migration for community ecology, changes in migration timing and patterns under changing climates, and studies of how migration constrains and is affected by life-history trade-offs. For each of these topics, it matters little whether birds are migrating to sites 10,000s of kilometers away or only over a few 100s of meters in elevation.

There are certainly some topics in migration research unsuited to altitudinal migration systems. For instance, one cannot study the physiological adaptations that permit sustained, energetically costly flight for long, uninterrupted bouts in a short-distance migrant (Watanabe 2016). Likewise, understanding how trans-equatorial migrants correctly respond to and integrate both austral and northern day-length cues by necessity must involve migrants traversing large latitudinal gradients. However, for plenty of questions, selecting an altitudinal migrant would be preferable. The phenotypic flexibility we typically see in altitudinal migrants and other short-distance migrants makes addressing fundamental questions more tractable. Evolutionary ecologists can exploit intraspecific behavioral variation to understand how endogenous and exogenous factors interact to influence costs and benefits of migration vs. residency—something that is impossible in obligate long-distance migrants.

The third hypothesis is highly plausible; we probably know so little about these birds' movements due to chance artifacts of ornithological history. While apparently the topic was interesting to naturalists a century ago, publications on this topic are dated. The reason may be related to the geographic distribution of altitudinal migration, which is necessarily constrained by the location of mountains. In the above tallies, half the altitudinal migrants were "western" species, and although 35% more were widespread, often only western populations of those species migrated altitudinally. The historic and current densities of researchers, cities, and centers of higher learning are roughly the inverse of topographical complexity on this continent. To this day, only 33% of ornithologists belonging to the American Ornithological Society live and work in states west of the 100th meridian where the most of the species making these movements live (data courtesy S. W. Gillihan; May 2016). Consequently, it is highly likely that such movements have flown under the radar of the ornithological community because they do not occur in most ornithologists' back yards.

### Why Study Altitudinal Migration?

There are at least 4 main reasons to fill this gap in knowledge.

**(1) Embrace the messy.** No avifauna, including that of North America, consists of species falling neatly into tidy migrant and resident categories (e.g., Seifert et al. 2016), or even the arbitrary "long-distance" and "short-distance" migrant groups—terms that mean different things to different authors (e.g., short-distance = 10s of km (Nilsson et al. 2008), or up to 1,000 km (Kondo and Omland 2007)). Furthermore, other movement categorizations including irruptions and nomadism belie the vast variation found in both latitudinal (e.g., Strong et al. 2015) and altitudinal movements (e.g., White-headed Woodpecker, *Leuconotopicus albolarvatus*; Richards 1924). Embracing the sometimes messy, facultative, partial migration behaviors brings opportunities to understand the causes of many potential movement responses arising from environmental selective pressures and constraints. In a recent example, Himalayan altitudinal migrants provided the opportunity to contrast physiological adaptations to high elevations in year-round residents compared to more mobile species that must be phenotypically flexible to cope with changing atmospheric conditions over their annual cycle (Barve et al. 2016). Additionally, the study of "messy" movements can lead to results that challenge dogma arising from study of a biased



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sample of movement behaviors. An example of this is the molt-migration of many Western songbirds, a pattern important to the understanding of interspecific differences in behavior, evolution, and conservation that has only been described and appreciated in the past few decades (Rohwer and Manning 1990, Leu and Thompson 2002).

A second argument is that studies of "messy" migrations are necessary to fully understand classic obligate migrations. For example, Ramenofsky et al. (2012) highlighted the paucity of studies describing the physiological regulation of facultative migrations, and explained how all migrations are likely governed by combinations of mechanisms. The hypothalamic–pituitary–gonad axis (HPG) is the primary pathway controlling the timing and physiological preparation for obligate migrations, while the hypothalamic–pituitary–adrenal axis (HPA) is probably involved in cueing facultative migrations. However, both types of migrations likely are controlled by both the HPG and HPA to different degrees and/or under different circumstances. As geolocator data is making increasingly obvious (e.g., Stutchbury et al. 2016), obligate migrants frequently engage in nonbreeding movements that do not fit neatly into the paradigm of tidy flights between breeding ranges and wintering ranges via discrete, short-term stopover sites (Newton 2012). A better understanding of the control of more flexible migration systems would inform how and why obligate migrants move in the way they do during these facultative phases of their migratory cycle.

**(2) Variation is the fodder of evolution.** Many hypotheses have been proposed for how long-distance, obligate migration arises in birds (Alerstam and Enckell 1979, Cox 1985, Lundberg 1988, Holmgren and Lundberg 1993). All share a common feature: individuals vary in their movement behavior, and selection acts on that variation. Altitudinal migration and other short-distance facultative migrations have been proposed to be precursors of long-distance migration in Neotropical lineages (Levey and Stiles 1992). Understanding the selective costs and benefits in obligate long-distance migrants requires that we adopt a comparative approach and make inferences regarding the migratory behavior of ancestral species (e.g., Outlaw and Voelker 2006). However, we know that migration is extremely labile; European Starlings (*Sturnus vulgaris*) in North America have altered their migratory propensity since being introduced to the continent in 1890 (Bitton and Graham 2015), and House Finches (*Haemorhous mexicanus*) transported to eastern North America have "evolved" migratory behavior over the past 8 decades (Able and Belthoff 1998). Thus, inferences regarding the selective pressures that have tipped fitness cost–benefit trade-offs toward migrating may be obscured by saturation of gains and losses in phylogenetic contexts. By studying altitudinal migrants and other partial, "messy" migrations, we can study ecological selective pressures in the here and now. In effect, such systems permit us to conduct empirical tests of hypotheses regarding the evolution of migration as it is happening.

**(3) Efficiency.** We live in an age of competitive job markets (Marshall et al. 2009) and scarce funding (https://debblog.nsfbio.com/category/deb-numbers/), factors that favor high research efficiency per unit time and dollar. Studying migration over large spatial scales frequently involves costly travel and technology. If such studies take place in wintering areas, they can also involve environmentally costly air travel and time-intensive acquisition of foreign research permits. In altitudinal migration systems, we can usually test the same hypotheses with fewer logistical challenges at the expense of fewer grant dollars relative to comparable studies with latitudinal migrants (e.g., Boyle 2008a vs. McKinnon et al. 2010). Such considerations are particularly relevant to graduate student research where careful choice of study system can permit full annual cycle field-based migration studies, even while completing academic requirements (e.g., Morrissey 1997, Lundblad 2014).

It is possible that the shorter-distance, facultative movements have been bypassed because overlapping summer and winter ranges make broad movement patterns harder to pin down. New tracking technologies are overcoming many of these logistical constraints as ever-smaller tracking devices come on the market, increasing the volume, precision, and accuracy of spatial data. Additionally, altitudinal gradients typically vary in isotopic signatures over short distances (Hobson 2005). By judicious choice of tissue sampling, detecting individual differences in altitudinal migration using isotopes is now possible in birds of any size at relatively low cost (Hobson et al. 2003, Boyle et al. 2011b).

**(4) Save the birds.** Just as we cannot understand the causes of population declines or implement effective conservation for long-distance migrants if we do not know where they go, we cannot ensure the future of the rest of our avifauna if we are ignorant of their movements. Declines in migratory birds are not limited to long-distance latitudinal migrants. In some cases, critically endangered birds undergo seasonal altitudinal migrations; understanding where, when, and how they move may prove crucial to protecting their future (Guevara et al. 2015). To date, no comparison exists of population trends of altitudinal migrants relative to nonmigrants or long-distance migrants. However, we do know that montane species are subject to unique challenges as climates change (La Sorte and Jetz 2010), and that the biology of montane birds is not as well understood as lowland species (Boyle and Martin 2015). Explicitly designing studies to allow detection and documentation of the patterns and prevalence of altitudinal



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migration at community or population levels should be a priority in future ornithological studies.

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