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Avian strategies for living at high elevation: life-history variation and coping mechanisms in mountain habitats

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Mountain ecosystems comprise over one-quarter of the global landbase and support a diverse array of birds during breeding and post-breeding seasons (UNEP 2002, Martin 2012). While birds have been recorded flying at altitudes above Mt Everest, breeding is restricted to the habitable alpine zone with the highest breeding records in Eurasia at 6600 m for the Grandala *Grandala coelicolor*, a Muscicapidae, and at 6000 m for the Tibetan Lark *Melanocorypha maxima* and Snow Pigeon *Columba leuconota* (Potapov 2004). In North America, the highest breeding records exceed 4000 m for Rosy Finch *Leucosticte australis,* Horned Lark *Eremophila alpestris* and White-tailed Ptarmigan *Lagopus leucura*. Thus, birds survive and reproduce at elevations where it is difficult for many mammals, including humans, to survive and remain conscious.

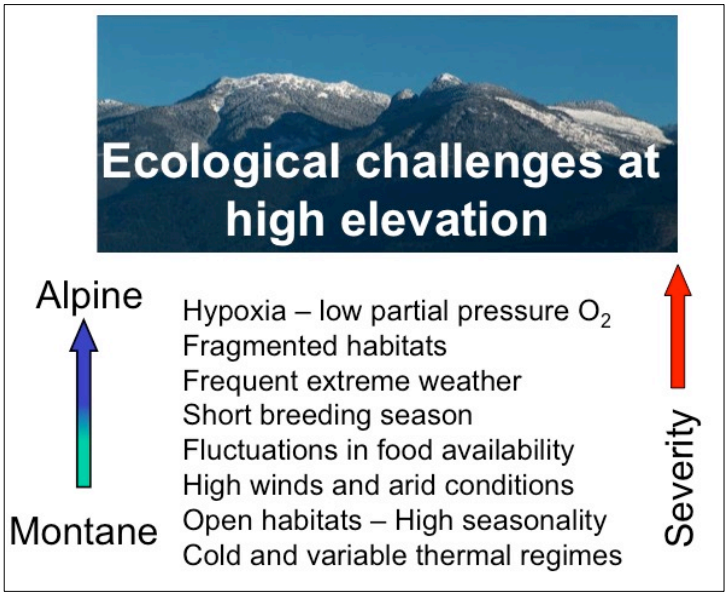

Figure 1 The environmental and ecological challenges for birds living in mountain and upland habitats generally increase in severity with increasing elevation.

Mountain ecosystems comprise 25% of the North American landbase, including alpine habitats with persistent or permanent snowfields, rocky ridges, occasional wind-shaped trees and continuous to scattered tundra vegetation, the sub-alpine zone with woody shrubs, and the upper limits of small trees, and upper montane forest consisting of open parklands and closed high-elevation forest. The energetic and ecological challenges for birds living in mountains increase with increasing altitude as key abiotic factors (temperature, solar radiation, oxygen partial pressure) influencing avian biology change with elevation (Fig. 1).

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There are no global estimates of avian biodiversity for mountain ecosystems, but continental tallies indicate that mountains pull above their weight in terms of species richness and species endemism. Although a few species are alpine specialists, the majority of birds inhabiting upland and mountain habitats in temperate zones are elevation generalists that use mountains for breeding and post-breeding periods (Fig. 2).

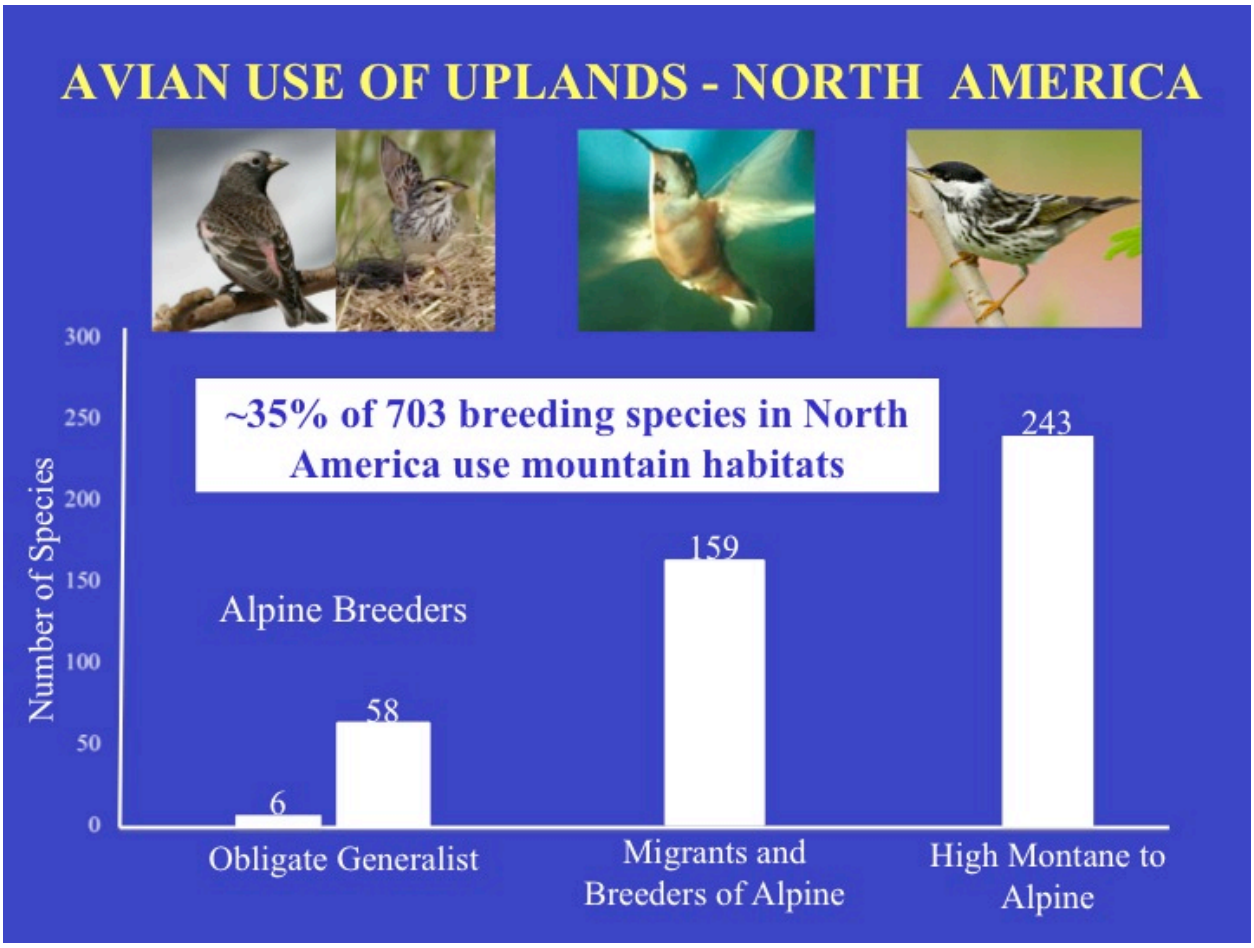

Figure 2 Avian species richness in mountain areas in North America: in North American temperate mountains, six of the 64 bird species known to breed in these environmentally challenging habitats are alpine specialists (obligate alpine breeders), and 58 species are alpine generalist breeders (breed in alpine habitats, but also in other habitats at lower elevations or high-latitude tundra environments). A total of 159 species are migrants and/or breeders in North America alpine habitats (breeding and/or migration stopover above treeline). Total species richness increases to 243 when all species using high montane forests and/or alpine or subalpine for any key life-history stage (breeding, migration, wintering) are included (Wilson and Martin 2005). This means that 35% of the 703 bird species known to breed in North America (Canada and United States, excluding Mexico and Hawaii) use high mountain habitats for one or several key life-history stages (Dick Cannings, Bird Studies Canada, personal communication for number of breeding birds in NA. http://alpine.forestry.ubc.ca/).

For a comparison with northern Europe, 19 and 55 bird species breed in upland and mountain ecosystems in the UK and Sweden, respectively (Thompson et al. 2012).

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Our research on fitness-related traits and indicators of competitiveness for White-tailed Ptarmigan and four songbird species reveal that most birds living at high elevation are well adapted for their challenging habitats, and are not young or inferior individuals that have been excluded from higher quality low-elevation habitats (Martin 2012). In common garden experiments, high-elevation Dark-eyed Juncos *Junco hyemalis* released from their environmental constraints match or outperform their low-elevation conspecifics (Bears *et al*. 2009). At high elevation, mountain songbirds have on average 57% less time to breed each season, and produce 50–60% fewer offspring annually than conspecifics at lower elevations (Martin et al. 2009, Camfield *et al*. 2010). High-elevation populations have shorter and later breeding seasons, smaller clutches, and longer developmental periods. Annual fecundity is lower at high elevations primarily because high-elevation populations produce on average one brood per season while lower elevation conspecifics can produce two or more broods annually. For three passerine species at high elevation, annual survival of adults was 15–20% higher, and there was a doubling of offspring return rates compared to low elevation. This elevated survival of adults and young may offset lower annual fecundity (op. cit.). Adult survival for white-tailed ptarmigan at high elevations was 10% higher than for low elevation populations at high latitudes (Wilson and Martin, 2011). However, for some species such as the Pacific Wren *Troglodytes pacificus*, upper montane and subalpine zones represent marginal habitats where Wrens have low fecundity and local survival (Evans-Odgen *et al*. 2012). A global meta-analysis of vital rates showed consistent reductions in fecundity with increasing elevation for temperate birds but variable survival (Boyle *et al*. 2014).

Several factors enable avian persistence in alpine regions. Birds living in these environmentally challenging habitats are able to make behavioural and physiological adjustments to avoid severe stress responses and breeding failure due to delayed breeding or storm events (Martin 2012). Some birds are able to resist hypoxia effects via high-elevation haemoglobin genotypes while others adjust their oxygen binding capacity biochemically in response to their elevation. Birds use behavioural adjustments to moderate thermal conditions. For example, on warm days female Ptarmigan with no overhead nest cover prevent their developing embryos from overheating by taking incubation recesses before or after the hottest period of the day. Adults and nestlings of most bird species breeding across elevations have larger body sizes and adjusted morphology that enable them to cope with more strenuous physical conditions and moderate their stress levels. Lower predation rates at high elevation may enable nestlings to remain in the nest longer and reach a larger size before fledging, but high elevation populations may also have slower development times due to colder ambient temperatures, so a net increase in body size or mass is not necessarily predicted.

Horned Larks are able to maintain their clutch size despite delays in onset of breeding of several weeks, thus enabling them to cope with variable alpine environments (Camfield et al. 2010). High cold tolerance of developing embryos is another enabling factor for alpine bird breeding success. Developing embryos of mountain-breeding Horned Larks and Eurasian Dotteral (*Charadrius morinellus*) are able to survive extended periods of chilling, considerably greater than is considered possible for most breeding birds. Although alpine avian embryos maintain high viability with chilling, the incubation period is prolonged and may result in higher nest predation.

Mountain habitats are interrupted landscapes that function as 'sky islands', and thus the maintenance of connectivity processes across time and space is critical. Alpine grouse populations, which exhibit low population

densities and stochastic annual fecundity and survival, have demonstrated impressive abilities to maintain viable and genetically diverse populations. The movement of alleles through fragmented landscapes is achieved by White-tailed Ptarmigan via episodic breeding dispersal movements, for which there are no apparent fecundity costs even when dispersal occurs after the onset of the breeding season (Martin et al. 2000, Fedy et al. 2008).

Mountain habitats support stable populations of several open country passerines, such as Horned Larks, that are showing rapid declines at low elevations across North America. Overall, both temperate and tropical mountains provide opportunities for seasonal altitudinal migration for a diversity of species (Wilson and Martin 2005). In western Canada, mountains serve as important autumn migration stopover habitats as some latitudinal migrant songbirds gain mass faster at high elevation than at low elevation (Evans-Odgen et al. 2013). Hence, mountains provide important refuge habitats for birds during both breeding and migration. Although most mountain habitats remain relatively free from direct human disturbance, high-elevation ecosystems are considered among the most vulnerable to global climate change impacts. Mountain habitats are experiencing globally significant increases in climate warming, extreme weather and rising tree- and shrub-lines, resulting in increasingly unreliable conditions for birds at high elevations. Mountain bird populations can cope to cope with impressively challenging abiotic conditions both in average seasonal conditions and in extreme environmental episodes. Alpine Horned Larks can adjust their incubation rhythms to deal with cold night-time regimes, but when exposed to cold day-times, hatching success declines (MacDonald et al. 2013). Also, sympatric congeneric species can have different responses to environmental conditions based on their life-history variation (slow vs fast lifestyles, Wilson and Martin 2010).

In summary, we have much to learn about the coping mechanisms and enabling factors that birds use to solve the problem of living in mountain habitats, and which abiotic and ecological factors pose the greatest challenges for them. Research priorities include investigating the pathways birds have developed to live in mountain habitats, the limits to their coping mechanisms and the costs associated with these adaptations. It is critical to determine the vulnerabilities of mountain birds to climate and other anthropogenic change to manage for their persistence in alpine and upland habitats.

Additional links

Author profile: http://profiles.forestry.ubc.ca/person/kathy-martin/;
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