

VARIATION IN DARK-EYED JUNCO (*JUNCO HYEMALIS*) NEST MASS AND NEST SIZE
ACROSS AN ELEVATIONAL GRADIENT IN SOUTHEASTERN BRITISH COLUMBIA

By

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ABSTRACT

I explored the variation in dark-eyed junco (*Junco hyemalis*) nest mass and nest size across an elevational gradient in Revelstoke, BC. I predicted that mean monthly temperature during the breeding season would be lower at high elevation compared to low elevation. I also predicted that nest mass and external diameter would be greater at higher elevation compared to low elevation, while there would be no elevational difference in internal cup diameter or internal cup depth. Results show that high elevation temperatures were significantly colder than low elevation temperatures throughout the breeding season ($P < 0.005$) but nest mass and external diameter were not different. Nests at one of the two low elevation sites were heavier and wider externally than those at both the single high elevation site and the second low elevation site ($P < 0.005$), suggesting that factors other than temperature may influence nest construction. When comparing nest mass and dimensions in Revelstoke with nests elsewhere in North America, I found no apparent trends in mass, external diameter, internal diameter or internal cup depth, suggesting that as a ground nesting species, dark-eyed juncos may modify nest construction in relation to temperature gradients less than has been observed in other species. An unexpected eight tree nests were discovered at high elevation during the 2014 field season but not during the 2013 field season, indicating that dark-eyed juncos can inter- and intra-seasonally alter their nesting behavior depending on site conditions. Further research on nest composition and placement with relation to a broader suite of environmental factors may provide better models on the drivers of nest construction along elevational and environmental gradients.

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INTRODUCTION

Questions pertaining to nest construction have been of increasing interest in avian life history research. This is due in part to the growing recognition that nest building is much more costly in energy and time than once thought, relative to the total energetic requirements of reproduction (Hansell 2000, Mainwaring *et al.* 2014). Nests must provide sufficiently strong structure to support the incubating female and her young (Heenan and Seymour 2011), thermal capacity to keep eggs and nestlings within the temperature range required for survival (Hansell 2000), and concealment from predators (Drummond and Leonard 2010, Mainwaring *et al.* 2014). Few studies have attempted to calculate the energetic costs of nest building through analyzing the bird's size, metabolic rate, average flight to and from building materials, material collection and work building the nest (Hansell 2000, Withers 1977). Larger, heavier nests presumably require more materials, more flight time, and more time building; therefore, larger nests should require more energy and time to build for individuals of given size and metabolic rate.

Birds breeding across elevational gradients face a variety of elevation-dependent challenges for survival and reproduction, such as: colder temperatures, greater exposure, high winds and snow cover (Billings 1989, Martin 2001). Studies show that high elevation birds make tradeoffs in order to persist at high elevation. For example, the breeding seasons of high elevation birds are often shortened, restricting the amount of breeding attempts available to an individual (reviewed in Boyle *et al.* 2015). Yet, nest failure due to predation and nest parasitism are often lower, and adult and juvenile survival are often higher at high elevation (reviewed in Boyle *et al.* 2015, Sasvári and Hegyi 2011). Building thicker nests promotes energy conservation in the incubating adult, eggs and nestlings at cold ambient temperatures (Heenan and Seymour 2011, Perez *et al.* 2008). In North America, yellow warblers (*Dendroica petechia*), American robins (*Turdus migratorius*) and common redpolls (*Acanthis flammea*) construct heavier, thicker-walled and externally wider nests at higher versus lower latitudes (Briskie *et al.* 1995, Crossman *et al.* 2011, Rohwer and Law 2010). Yellow warbler nests in particular were 19.2% wider and had 54% thicker walls in northern Manitoba than in southern Manitoba (Briskie *et al.* 1995). In

Britain, the nest cups of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) increased in mass with an increase in latitude (Mainwaring *et al.* 2012). Throughout the eastern United States and Canada, Northern oriole (*Icterus galbula*) nests in the north tended to be larger than nests in the south, although it is unclear whether this difference was caused by differences in body size between races, clutch size or environmental gradients (Schaefer 1976). In these studies, increasing latitude correlated with cooling ambient temperatures; therefore, heavier and larger nests are interpreted as an adaptation to colder temperatures (Crossman *et al.* 2011, Rohwer and Law 2010). Furthermore, nests are often found to decrease in mass throughout a breeding season, contributing to the theory that birds build smaller, lighter nests as a response to warming ambient temperatures (Britt and Deeming 2011, Deeming *et al.* 2012).

Few studies have explored variation in nest mass and dimensions across an elevational gradient where a species breeds continuously. Kern and van Riper (1984) studied the nests of Common amakihi (*Hemignathus virens virens*) on the Island of Hawaii, finding that nest placement and material composition varied with environmental conditions but mass did not. Bears (2002) described the differences in nest composition between low (1000 meters above sea level; masl) and high (2000 masl) elevation nests of a continuously breeding dark-eyed junco (*Junco hyemalis*) population near Jasper, Alberta. High elevation nests contained more animal fur, an insulation material used in the nest cup lining, than low nests. The mean mass of low nests was 9 grams while high nests were 10.5 grams (Bears 2002). Kern (1984) found that the nests of Mountain White-crowned sparrows (*Zonotrichia leucophrys oriantha*) from sub-alpine California and Colorado were externally larger and had thicker walls than those of Nuttall's White-crowned sparrows (*Zonotrichia leucophrys leucophrys*) on the California coast. Thicker walls resulted from an enlargement of the external diameter of nests while the internal cup diameter remained constant.

Building upon observations of birds building larger, heavier nests in response to cooler ambient temperatures, I explored the variation in dark-eyed junco nest mass and dimensions between high and low elevation. The dark-eyed junco breeds continuously across a wide elevation gradient – from sea level to alpine tree line – across its western North American range (Nolan *et*

al. 2002). In British Columbia, the species has been the focus of recent studies on avian life history tradeoffs (Bears *et al.* 2003, 2008, 2009). First, I predict that the high elevation study site will have cooler ambient temperature throughout the breeding season (May-July) than the low elevation sites. For a given time of season, I predict that the average mass of nests will be heavier and average external diameter will be wider at high elevation and there will be no elevational difference in internal cup depth or diameter; this would result in thicker nest walls at high elevation. I also predict that mass and external diameter of nests at all sites will decrease throughout the breeding season as average ambient temperature during the nest building stage increases. Furthering our knowledge on the drivers of avian nest construction across elevational gradients is important to better our understanding of avian life histories and selective pressures acting on populations now and in the future.

METHODS

STUDY AREA

This study was conducted from late April to mid-August 2014 at three sites just outside of Revelstoke, BC (50°59'55"N, 118°11'43"W: figures 1 and 2). Two low-elevation study sites were located north (Alfalfa; 51°03'21"N, 118°12'11"W) and south (RMR; 50°57'21"N, 118°09'36"W) of Revelstoke, between 400-700 masl. A high elevation site was located between 1900 to ~2340 masl on the south-west facing slope of Mt. MacKenzie (Mt. Mac; 50°57'46"N, 118°06'08"W). All sites had human modified forest cover and relatively frequent presence of human activity. RMR and Mt. Mac are the lower and upper limits of a downhill ski resort and have large tracts of cleared forest, as well as the presence of roads and occasional vehicular and foot traffic throughout the summer season. Alfalfa is located near the Revelstoke Hydroelectric Dam and is close to vehicular traffic on the access road to the dam, a dirt bike track adjacent to the site and other human activity. Alfalfa is relatively open and patchy in forest cover whereas RMR contains large openings intermixed with higher canopy cover from mixed deciduous-coniferous forest. Forest cover at Mt. Mac is also relatively open as it is a sub-alpine ecosystem (figure 2). Vegetation at Alfalfa and RMR is characteristic of the Interior Cedar-Hemlock Biogeoclimatic Ecosystem Classification (BEC) zone, dominated by interior Douglas-fir (*Pseudotsuga menziesii*),

Lodgepole pine (*Pinus contorta*), black cottonwood (*Populus trichocarpa*), trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*) and mountain alder (*Alnus crispa*). Vegetation at Mt. Mac is characteristic of the Engelmann spruce-sub-alpine fir BEC zone, dominated by Engelmann spruce (*Picea engelmannii*) and sub-alpine fir (*Abies lasiocarpa*).

STUDY SPECIES

The dark-eyed junco (*Junco hyemalis*) is a small (16-22g) songbird that breeds throughout the Pacific Northwest from sea level to sub-alpine tree line (Nolan *et al.* 2002). Around Revelstoke, juncos breed from the Columbia River valley bottom to mountain peaks, nesting in open-cup ground nests constructed of dry grass, twigs, moss, lichen, leaves and animal fur (Baicich and Harrison 1997, personal observation). Females build nests with males occasionally gathering and depositing materials at the nest site (Baicich and Harrison 1997, Nolan *et al.* 2002). Pairs will continue to build new nests and initiate subsequent broods if their first or second nests fail. Pairs that are successful will re-nest and initiate a second, and sometimes third brood once fledglings are independent. Very few pairs re-use previously built nests (Nolan *et al.* 2002, Baicich and Harrison 1997). At low elevation, dark-eyed juncos began nest-building around the end of April/beginning of May and bred until the end of July. At high elevation, they began nest-building around the end of May and bred until the end of July (personal observation).

NEST COLLECTION & MEASUREMENT

Nests were collected between May and August 2014, as soon as possible once young fledged or the nest failed, but generally within two weeks of one of these events. Nest searching commenced at the end of April at Alfalfa and RMR, when most of the ground was bare and there were only small patches of snow left in some open areas. Nest searching began at the end of May at Mt. Mac while the site remained covered in snow for the following 3-4 weeks, with rocky outcrops and vegetation patches open for ground nesting becoming larger by the day. To find nests, females (and sometimes males) were observed collecting nesting materials and depositing them at the nest and/or nest building. Once incubation commenced, further nests were found by following females during their off-bouts until they returned to their nests. Occasionally, nests were accidentally found by flushing females from them.

After fledge or fail, nest dimension measurements were taken with a ruler to the nearest half millimeter while the nest remained in the ground. External width was taken by averaging the widest and narrowest diameters that nesting material stretched to from looking at the nest from directly overhead. Internal diameter was taken with the same approach but inside the top rim of the cup opening. Internal cup depth was taken from the bottom of the nest cup to the top rim of the nest from eye level. Nests were carefully removed with all materials obviously placed by the birds intact (i.e. nests on slopes often had relatively large masses of lichen buildup on the downslope before the main grassy structure began, which we included as part of the nest). Soil or fallen vegetation was carefully removed before placing the nests in plastic Ziploc bags. Nest weights were taken a few days after removal and drying, before nests were placed in a freezer to prevent decay. Mass was re-taken in December when the nests were removed from the freezer and set out to further dry in a warm, dry room on paper towels. We used the second, dry mass value for analysis.

WEATHER DATA

Mean monthly temperature (MMT) was compiled for the three sites for the months during which dark-eyed juncos were breeding: May, June and July. Weather data for Alfalfa came from BC Hydro's nearby weather station at the Revelstoke Hydroelectric Dam. Data for RMR came from Environment Canada's weather station at the Revelstoke Airport. Data for Mt. Mac came from Revelstoke Mountain Resort's weather station at the top of The Stoke chairlift (figure 1). I used the mean temperature from each of the 24 hours in each day of each month to determine MMT.

CLUTCH INITIATION DATE

For all nests we calculated clutch initiation date (CID). If nests were found before or on the first day of egg laying, we monitored for CID. For nests that were found during incubation, we back dated CID based on knowledge of the average length of the incubation stage and the clutch size. Juncos lay one egg per day and incubate an average of 12-13 days beginning on the day the second-to-last (penultimate) egg is laid (Baicich and Harrison 1997). If hatch date was known, we counted back 13 days to determine the day the penultimate egg was laid, then

counted back another 2-3 days, depending on clutch size, to determine CID (i.e. if clutch size was 3 count back 1 more day from the penultimate egg, if clutch size was 4 count back 2 days from the penultimate egg, etc.). If nests were found during the nestling stage, we estimated chick age by comparing growth and fledge with nearby known clutches, back-dating hatch date from this age then back-dating as explained for incubation.

ANALYSIS

I used a linear regression to test for a relationship between mean temperature (MMT; dependent variable) and month (independent variable) during the breeding season, using elevation (high, low) as a categorical predictor. I did the same analysis between MMT and month, using site (Alfalfa, RMR, Mt. Mac) as a categorical predictor. Temperature data for all three sites showed a normal distribution and equal variance. Data for nest mass and dimensions (external diameter, internal cup diameter and internal cup depth) were also normally distributed and had equal variance. I used clutch initiation date (CID) as a measure of time of season for each nest. I used linear regressions to individually test for a relationship between the four nest measurements (mass, external diameter, internal cup diameter and internal cup depth; dependent variable) and CID (independent variable), using elevation (high, low) as a categorical predictor. I did the same analysis for each of the four dimensions, using site (Alfalfa, RMR, Mt. Mac) as a categorical predictor. An alpha of 0.05 ($\alpha=0.05$) and Minitab 17 Statistical Software (Version 17; State college, Pennsylvania) was used for all analyses.

RESULTS

VARIATION BY ELEVATION

The variation in mean monthly temperature (MMT) was 80.27% explained by elevation and month ($R^2=80.27\%$). Low elevation MMT was significantly warmer than high elevation MMT ($P<0.005$, $t=25.33$). Across both elevations, MMT significantly increased each month ($P<0.005$).

The variation in nest mass was 13.47% explained by elevation and CID ($R^2=13.47\%$). Low and high elevation nests were not significantly different in mass ($P=0.99$, $t=0.10$). Nest mass tended

to decrease throughout the breeding season, but this trend was not significant ($P=0.155$, $t=-1.45$).

Only 2.47% of the variation in nest external diameter was explained by elevation and CID ($R^2=2.47\%$). Low and high elevation nests were not significantly different in external diameter ($P=0.66$, $t=0.44$). External diameter tended to increase with CID but this trend was not significant ($P=0.42$, $t=0.82$).

The variation in internal diameter was 4.89% explained by elevation and CID ($R^2=4.89\%$). There was no significant difference in internal diameter between nests at high and low elevation ($P=0.84$, $t=0.21$). Internal diameter did not significantly change with CID ($P=0.54$, $t=-0.62$).

The variation in internal depth was only 5.01% explained by CID and elevation ($R^2=5.01\%$). Low and high elevation nests were not significantly different in internal depth ($P=0.24$, $t=-1.20$). Internal cup depth did not significantly change with CID ($P=0.25$, $t=-1.17$).

VARIATION BY SITE

The variation in mean monthly temperature (MMT) was 81.85% explained by site and month ($R^2=81.85\%$). MMT throughout the breeding season significantly increased from Mt. Mac to Alfalfa to RMR ($P<0.005$). Average monthly temperatures increased with breeding season across all sites ($P<0.005$).

The variation in nest mass was 17.12% explained by site and CID ($R^2=17.12\%$). Overall, RMR nests were the heaviest, followed by Mt. Mac then Alfalfa but nest mass was not significantly different by site ($P=0.49$). Nest mass tended to decrease with increasing CID but this trend was not significant ($P=0.38$, $t=0.90$).

The variation in external diameter is 29.86% explained by site and CID ($R^2=29.86\%$). Nests were significantly different in external diameter by site ($P=0.008$). RMR nests had significantly larger external diameter than Alfalfa ($P<0.005$, $t=3.37$) while nests at Mt. Mac did not have significantly larger diameter than Alfalfa ($P=0.59$, $t=0.54$). External diameter significantly increased with CID ($P=0.032$, $t=2.25$).

The variation in internal diameter was 12.10% explained by site and CID ($R^2=12.10\%$). The site with the largest average internal diameter was RMR, followed by Mt. Mac followed by Alfalfa, but this trend is not significant ($P=0.31$). There was no significant trend in internal diameter throughout the season ($P=0.98$, $t=-0.05$).

The variation in internal cup depth was 17.58% explained by site and CID ($R^2= 17.58\%$). Cup depth is highest at RMR, followed by Mt. Mac then Alfalfa, but this trend was not significant ($P=0.07$). There was no significant trend in cup depth throughout the season ($P=0.80$, $t=-0.26$).

VARIATION IN NEST SITE AT HIGH ELEVATION

Between May-August 2014, I observed eight dark-eyed junco nests in trees approximately 3-8 meters above ground at the Mt. Mac site only. There were likely more tree nests within the perimeter of our study site as we observed junco pairs feeding fledglings very early in the season when snow cover would have been very high during the incubation and nestling periods. Dark-eyed juncos were not observed nesting in trees during the same time period in 2013 (Jennifer Greenwood, personal communication). Only two tree nests were retrieved; therefore their measurements were not used in statistical analyses. The two tree nests were 51.4g and 19.4g and both had a 120mm external diameter; therefore, they were heavier and externally larger than ground nests at Mt. Mac (table 2).

DISCUSSION

The data supported our hypothesis that mean monthly temperature (MMT) throughout the breeding season (May-July) would be significantly cooler at high elevation relative to low elevation sites. I also found that not only did Mt. Mac significantly differ from Alfalfa and RMR in MMT, but the two low elevation sites (Alfalfa and RMR) also significantly differed from each other in MMT (figure 3). The data did not support our hypotheses that high elevation nests would be heavier and larger in external diameter throughout the breeding season; therefore, high and low elevation birds were building similar nests at significantly different ambient temperatures. Neither internal cup diameter nor depth differed between elevations or

throughout the season, which was expected as many open cup nesting birds build nest cups to fit their body size and clutch, rather than environmental conditions (Hansell 2000).

When analyzing differences between the three sites, variation in nest mass was still not significant but Alfalfa nests were closer in mass to Mt. Mac nests than RMR nests. Furthermore, RMR nests were significantly wider (externally) than both the RMR and Alfalfa nests, while the internal diameter and depth remained the same (table 1). External diameter appeared to significantly increase throughout the breeding season, while internal diameter and depth did not change. These observations indicate that RMR nests had thicker walls than Alfalfa and Mt. Mac nests, and that nest walls became thicker throughout the season – an unexpected correlation with warming temperatures. Varying wall thickness with constant nest mass suggests that there may be differences in nest wall density between sites and throughout the season. Skowron and Kern (1980) found that among eleven North American song bird species, denser, less porous nests were better insulators while less dense, more porous nests were poorer insulators. If RMR nests do have less dense walls, and there is a decrease in nest wall density throughout the breeding season, it could be a response to warmer temperatures. Alternatively, Rohwer and Law (2010) found that thicker, more porous nests were better insulators than thinner, denser nests.

Heenan and Seymour (2011) suggest that the dimensions of the outer nest cup are dominantly driven by need for structural support, rather than thermal requirements; therefore it is also possible that the larger size of nests at RMR were driven by microhabitat characteristics (i.e. substrate), rather than ambient temperature. Mt. Mac and Alfalfa did appear to be more similar in vegetation composition, as Alfalfa had relatively open canopy with high grass and moss cover, similar to the sub-alpine landscape at Mt. Mac. There were not obvious differences in building materials of nests between sites, but as birds are generally limited to local materials when building nests, there may have been differences in availability between the two sites that resulted in different nest mass and size (Baicich and Harrison 1997). An additional consideration is the effect of predation on nest characteristics, as optimizing nest concealment through size and placement may decrease the risk of predation to the parent and

nestlings (Smith *et al.* 2007, Drummond and Leonard 2010). Anecdotal observations suggest that compared to RMR, nests at Alfalfa experienced relatively high nest predation during the 2014 field season, which could have contributed to selection for smaller nests. A more in-depth analysis of the effects of nest site microhabitat, available building materials and predation risk between high and low elevation as well as among individual sites may contribute to a better model of the drivers of nest morphology.

To see whether trends in nest mass and dimensions found in other species were found in dark-eyed juncos, I compared measurements observed in Revelstoke with similar data from available literature. I did not find any trends in mean nest mass across an elevational gradient in Jasper, Alberta, nor did I find any trends in nest mass, external diameter, internal cup diameter or internal cup depth between four locations in North America (Revelstoke, Arizona, Ontario and Virginia; figures 4a-d); however, the sample size is limited. Bears (2002) found that in Jasper, Alberta, high elevation nests had a higher mean mass than low elevation nests, contradicting my measurements in Revelstoke (figure 4a). Jasper is located at higher latitude than Revelstoke (above 52 degrees N); therefore presumably has cooler temperatures year-round, yet the average nest masses appear to be lower than those found in Revelstoke. Nests of Carolina junco (*J.h. carolinensis*) in Arizona (reviewed in Nolan *et al.* 2002) and slate-coloured junco (*J.h. hyemalis*) in Ontario (Peck and James 1987) were very similar in external diameter to nests found in Revelstoke, despite Arizona being much farther south, and warmer year-round than Ontario and Revelstoke (figure 4b). Mean internal diameter of nests found in Arizona and Virginia (Nolan *et al.* 2002) is equivalent to those in Revelstoke, while nests in Ontario appear to be slightly larger internally (figure 4c). Mean internal cup depth of nests found in Arizona, Virginia and Ontario is equivalent to that of nests found at RMR and Mt. Mac in Revelstoke, while the nests at Alfalfa appear to be ~7-8mm shallower, yet this difference is not significant compared to RMR and Mt. Mac (figure 4d). We did not control for the amount of time nests were incubated by females, nor whether they held chicks, which can affect the dimensions of the nest, mainly the internal cup width and depth (personal observation, Rohwer and Law 2010, Calder 1973).

I considered the possibility that mean body mass of the incubating females might explain some of the slight variation in nest internal diameter and depth by comparing mean body mass of female dark-eyed juncos nearest to Arizona, Ontario, Revelstoke and Virginia (estimates for Arizona, Ontario and Virginia taken from Nolan *et al.* 2002) for these two dimensions. Female dark-eyed junco body mass was found to be highest in Virginia, followed by Arizona, Ontario then Revelstoke but only ranged from 19.8g to 18.6g. Differences in body mass do not appear to explain any of the variation in internal nest cup diameter and depth between locations, where the largest and smallest birds have the most similar internal diameter and depth measurements (figure 4c and d). Rohwer and Law (2010) found no difference in the internal cup depth or diameter when comparing Yellow warbler nests between southern Ontario and northern Manitoba.

There are climatic gradients besides temperature that may affect nest morphology such as precipitation, wind and humidity (Crossman *et al.* 2011, Kern and van Riper 1984, Rohwer and Law 2010). Rohwer and Law (2010) found that nests located in a warmer, wetter climate were smaller, less porous and retained less water than those located at a cooler drier climate. Alternatively, Kern and van Riper (1984) found that nests located in a warmer, wetter climate in Hawaii were more porous and were able to dry faster than less porous nests in a cooler, drier environment. Both Rohwer and Law (2010) and Kern and van Riper (1984) found that nests at cooler, drier environments had thicker lining than those at warmer, wetter environments, which either had thinner lining or lacked lining at all. Bears (2002) made similar observations in Jasper, where higher elevation dark-eyed junco nests contained more layers of insulative materials (i.e. hair, lichen, moss) than low elevation nests which were more homogeneous in composition. The thickness and materials of nest cup linings can correlate with changes in climatic conditions while the external nest cup remains unchanged (Mainwaring *et al.* 2012).

In addition to nests having more lining materials, Bears (2002) also found that high elevation nests were placed in more buffered microclimates, often up to 70 cm underground. Kern and van Riper (1984) observed that nests at relatively higher (drier and cooler) elevations were placed near canopy edges, presumably where they would benefit from increased solar radiation

while nests at lower elevation (warmer and wetter) were higher in the canopy but closer to tree centers. Multiple species have also been found to use nearby objects (i.e. shrubs, grass tufts, rocks, mounds) as breaks from sun and wind depending on the time of day and/or season (Austin 1974, Finch 1983, Hartman and Oring 2003). Orienting nest openings (direction of exit on ground nests) towards or away from wind and/or sun may also help to moderate nest temperatures. For example, Austin 1974 found that cactus wrens (*Campylorhynchus brunneicapillus*) built nests oriented away from prevailing winds in the early season and towards prevailing winds in the late season, presumably to initially limit and later promote convective cooling. Horned larks (*Eremophila alpestris*) in California dominantly built nests north of objects which were more shaded than nests built elsewhere during the hottest parts of the day; however, shaded nests were not significantly cooler (Hartman and Oring 2003). It is likely that the prevailing winds at the different sites are of different intensity, as we generally observed higher winds at Mt. Mac and Alfalfa. Due to the proximity of the three sites, they likely all receive similar precipitation patterns, however Mt. Mac may receive snow in May, June, and even the occasional event in July, depending on the elevation.

Of four species that Crossman *et al.* (2011) studied, three built nests that were heavier, had thicker walls and wider internal and external diameters in northern Manitoba than they did in southern Ontario, but the Savannah sparrow (*Passerculus sandwichensis*), the only ground nesting species of the group, showed no significant differences in nest mass or dimensions (Crossman *et al.* 2011). Ground nesting individuals have been shown to have smaller nests than those nesting above ground (Kern 1984), presumably because they are more sheltered and experience less convective cooling and/or benefit from insulative properties of soil and vegetation (Kern 1984). The two tree nests measured in this study were larger and heavier than nests found on the ground at any of the three sites. Ground nesting species may experience less severe wind and temperature extremes (Hadley 1969) and therefore display less variation in nest morphology across these gradients than nests above ground.

There are many nest morphology and nest site characteristics that may contribute to mediating nest temperature across elevational and environmental gradients such as: nest wall density and

porosity, type of nest material, presence and thickness of nest cup lining, position with regards to micro-topography and vegetation and orientation of the nest opening. Obtaining information on these, as well as climatic variables (i.e. wind, precipitation, humidity) other than ambient temperature at high and low elevation, and among the three sites in Revelstoke may lead to better models describing the drivers of nest construction and microclimate mediation across elevation. I conclude that dark-eyed junco nests did not significantly differ in mass, external diameter, internal diameter or internal cup depth at high versus low elevation, and that they only significantly differed in external diameter, and therefore nest wall thickness, between individual sites. The lack of trends found in nest mass and external diameter across North America, when compared to values observed in Revelstoke, further suggests that environmental gradients may not play as large of a role in nest mass and size as has been observed in other species.

TABLES & FIGURES

TABLE 1. SUMMARY OF DARK-EYED JUNCO (*JUNCO HYEMALIS*) NEST MASS, EXTERNAL DIAMETER, INTERNAL DIAMETER AND INTERNAL CUP DEPTH FOR NESTS FOUND AT MT. MAC, RMR AND ALFALFA SITES NEAR REVELSTOKE, BC, CANADA. COLUMN “N (MASS)” CORRESPONDS ONLY TO MASS MEASUREMENTS WHILE “N (DIMENSIONS)” CORRESPONDS TO THE EXTERNAL DIAMETER, INTERNAL DIAMETER AND INTERNAL CUP DEPTH MEASUREMENTS.

Site	n (mass)	mass (g)	n (dimensions)	external diameter (mm)	internal diameter (mm)	internal depth (mm)
Mt. Mac	19	11.9 ± 4.4	17	114.0 ± 12.2	63.1 ± 5.1	40.4 ± 5.4
RMR	14	15.8 ± 5.0	13	119.0 ± 12.8	67.8 ± 9.0	42.4 ± 9.8
Alfalfa	9	11.5 ± 3.0	8	95.9 ± 18.5	59.6 ± 6.1	32.6 ± 5.6
P-value	-	0.491	-	0.008	0.312	0.065

TABLE 2. SUMMARY OF DARK-EYED JUNCO (*JUNCO HYEMALIS*) NEST MASS, EXTERNAL DIAMETER, INTERNAL DIAMETER AND INTERNAL CUP DEPTH FOR NESTS FOUND ON THE GROUND AND IN TREES AT MT. MAC SITE NEAR REVELSTOKE, BC, CANADA.

Location (High Elevation)	n	mass (g)	external diameter (mm)	internal diameter (mm)	internal depth (mm)
Ground	19	11.9 ± 4.4	114.0 ± 12.2	63.1 ± 5.1	40.4 ± 5.4
Tree	2	51.4, 19.4	120.0, 120.0	72.0, 77.5	30.0, 40.0

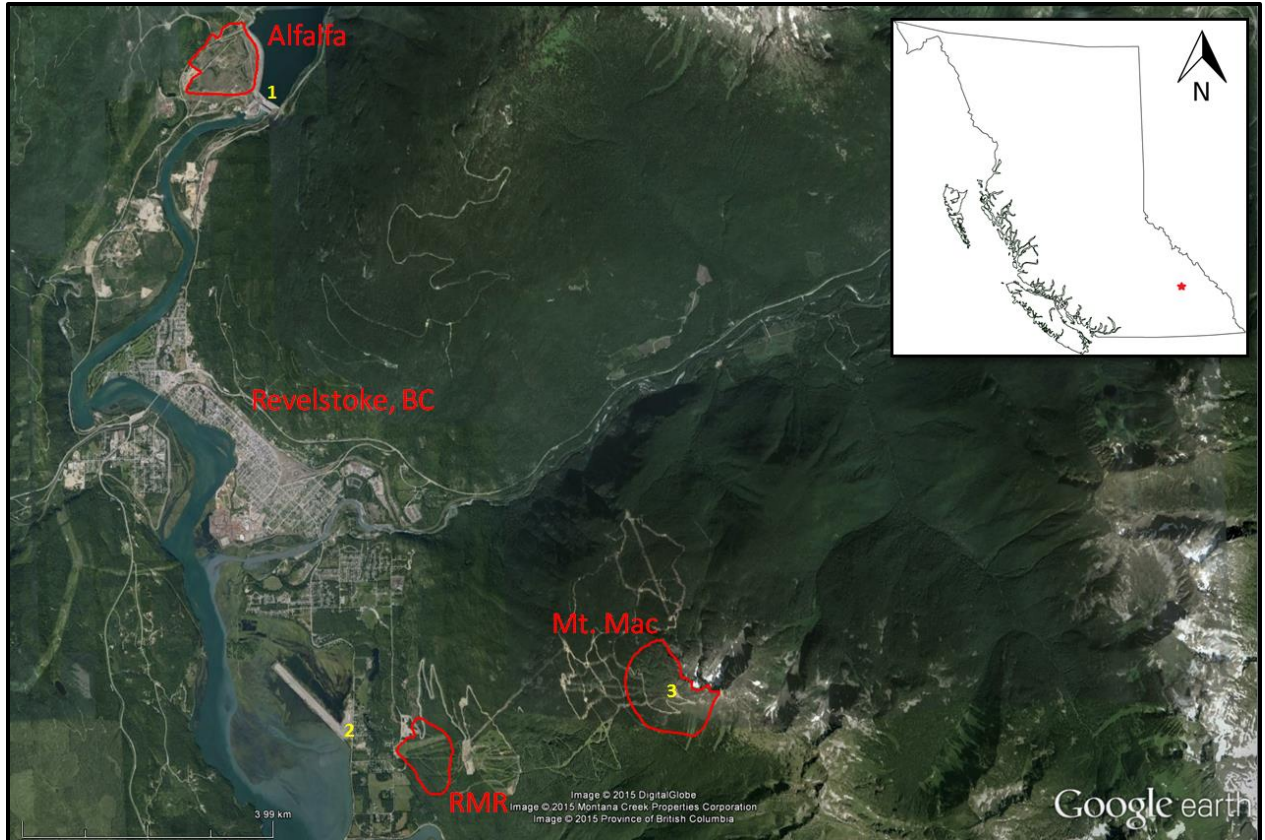


FIGURE 1. TWO LOW ELEVATION (400-700MASL; ALFALFA, RMR) AND ONE HIGH ELEVATION (1900-2340MASL; MT. MAC) STUDY SITES LOCATED NEAR REVELSTOKE, BC, CANADA (GOOGLE EARTH 2015) WHERE RED SITE PERIMETERS ARE APPROXIMATE. YELLOW NUMBERS MARK APPROXIMATE LOCATIONS OF WEATHER STATIONS USED FOR ALFALFA (1; REVELSTOKE HYDROELECTRIC DAM, BC HYDRO), RMR (2; REVELSTOKE AIRPORT, ENVIRONMENT CANADA) AND MT. MAC (3; STOKE CHAIRLIFT, REVELSTOKE MOUNTAIN RESORT). INLAY MAP MARKS APPROXIMATE LOCATION OF REVELSTOKE IN BRITISH COLUMBIA (ORIGINAL IMAGE FROM WWW.WORLDTLAS.COM).



FIGURE 2. APPROXIMATE PERIMETER OF TWO LOW ELEVATION (ALFALFA, RMR) AND ONE HIGH ELEVATION (MT. MAC) STUDY SITES NEAR REVELSTOKE, BC, CANADA (GOOGLE EARTH 2015).

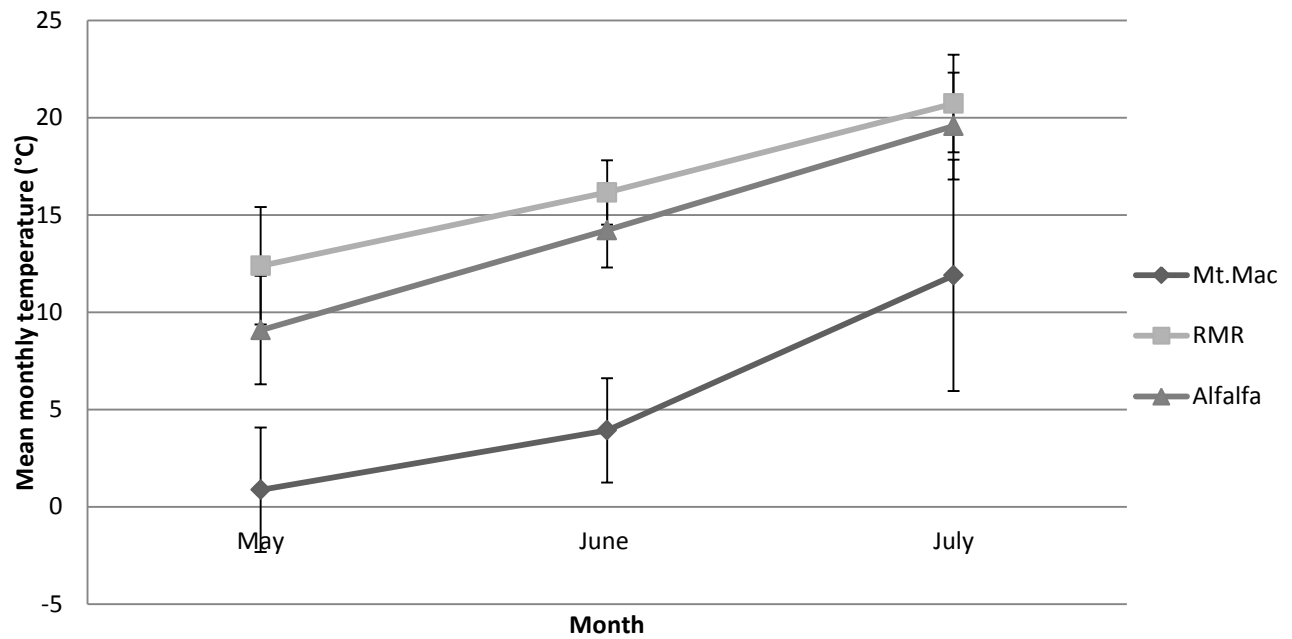


FIGURE 3. MEAN MONTHLY TEMPERATURE (°C) FOR MT. MAC, RMR AND ALFALFA STUDY SITES DURING MAY, JUNE AND JULY NEAR REVELSTOKE, BC. ERROR BARS REPRESENT STANDARD DEVIATION.

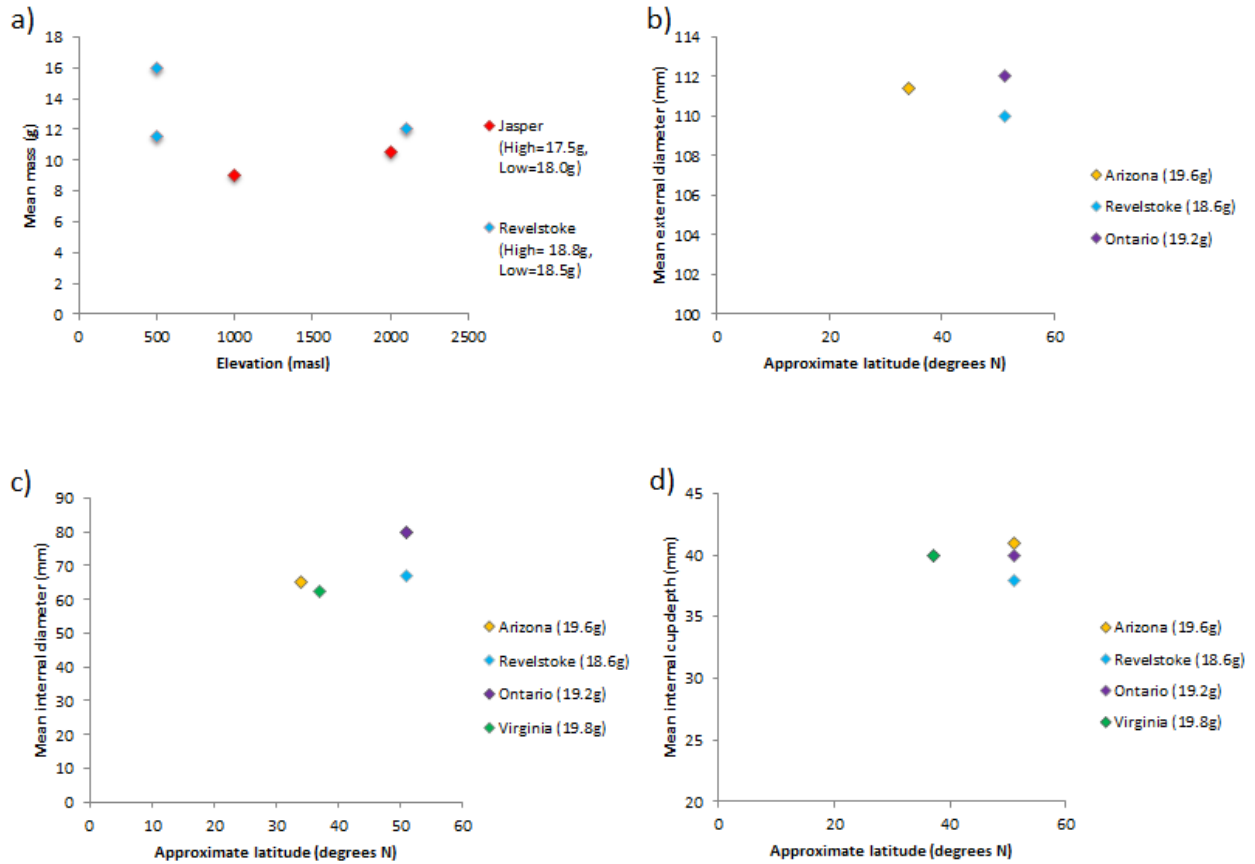


FIGURE 4. A) MEAN NEST MASS VS. ELEVATION IN REVELSTOKE, BRITISH COLUMBIA (PERSONAL OBSERVATION) AND JASPER, ALBERTA (BEARS 2002); **B)** MEAN EXTERNAL DIAMETER VS. APPROXIMATE LATITUDE IN ARIZONA (NOLAN *ET AL.* 2002), REVELSTOKE AND ONTARIO (PECK AND JAMES 1987); **C)** MEAN INTERNAL DIAMETER VS. APPROXIMATE LATITUDE IN ARIZONA (NOLAN *ET AL.* 2002), REVELSTOKE, ONTARIO AND VIRGINIA (NOLAN *ET AL.* 2002); **D)** MEAN INTERNAL CUP DEPTH VS. APPROXIMATE LATITUDE IN ARIZONA, REVELSTOKE, ONTARIO AND VIRGINIA. AVERAGE MASS OF DARK-EYED JUNCO POPULATIONS AT EACH LOCATION FOR INTERNAL CUP DEPTH AND DIAMETER ARE GIVEN IN PARENTHESES (PERSONAL OBSERVATION, BEARS 2002, NOLAN *ET AL.* 2002).

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APPENDICES

APPENDIX 1

THE GEOGRAPHIC RANGE AND HABITAT TYPES OF THE DARK-EYED JUNCO ACROSS NORTH AMERICA

Joanna K. Lee

Review paper in partial fulfilment of Cons 498 Thesis (3 credits)

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Figure 1. Approximate breeding ranges of five groups and two sub-species of dark-eyed junco (*Junco hyemalis*): slate-coloured junco (*J.h. hyemalis*; SCJU), Oregon junco (*J.h. oreganus*; ORJU), pink-sided junco (*J.h. mearnsi*; PSJU), grey-headed junco (*J.h. caniceps*; GHJU), red-backed junco (*J.h. dorsalis*; RBJU), white-winged junco (*J.h. aikenii*; WWJU) and Guadalupe junco (*J.h. insularis*; GUJU). Figure adapted from Mila *et al.* 2007.

Figure 2. Approximate elevation range vs. mean latitude of dark-eyed junco (*Junco hyemalis*) breeding ranges described in literature. There is uncertainty in the latitude and elevation of breeding ranges and most values are estimates.

INTRODUCTION

The dark-eyed junco (*Junco hyemalis*) is a well-known sparrow species that breeds and winters across a wide range of North American landscapes from Alaska to Mexico (Nolan *et al.* 2002). As a forest generalist, dark-eyed juncos nest in many habitat types from the Boreal Forest to urban campuses and residential gardens (Rogers *et al.* 1993, Liebgold *et al.* 2013). Overwintering habitat is equally as diverse, with some individuals remaining their near breeding grounds year-round and others migrating hundreds of kilometers south to warmer climates (Ketterson and Nolan 1976, Nolan *et al.* 2002). Today, all juncos with dark eyes are regarded as one species, with all fifteen sub-species belonging to one of five groups: slate-coloured, Oregon, white winged, grey-headed and Guadalupe (Mila *et al.* 2007, Nolan *et al.* 2002; table 1). Hybridization between groups is likely where range perimeters overlap, making precise identification difficult in some areas (Nolan *et al.* 2002). Many existing studies identify juncos to sub-species, while others only verify to species or group – leaving the reader to deduce sub-species from location, if possible. By reviewing existing literature pertaining to dark-eyed junco groups and/or sub-species over the last century, this paper aims to draw out specific landscape features that juncos are, or are not, associated with across their wide range.

SLATE-COLOURED JUNCO

The slate-coloured junco (*J.h. hyemalis*) breeds from Alaska throughout the Canadian Boreal Forest to the Maritime Provinces and south to New York and Pennsylvania (Nolan *et al.* 2002, Rogers *et al.* 1993; figure 1). Canadian populations breed in a wide variety of habitats, but are most commonly associated with young sapling and/or black spruce forest and muskeg in the Boreal Forest. Slate-coloured juncos are less common in mature forest where canopy closure is high, limiting understory vegetation, and are absent from bogs and marshes (Kessler and Kogut 1985, Kirk *et al.* 1996). In sub-alpine habitats of the White Mountains, New Hampshire, slate-coloured juncos nest on exposed banks, rocky outcrops and within dense shrub clumps between 750-1450 metres above sea level (masl) where conifers are small, short and patchily distributed (Sabo 1980). A fire disturbance in Minnesota reduced tree cover by about 50%,

increasing understory shrub and herb cover the following year, allowing slate-coloured juncos to establish territories that were not previously observed (Apfelbaum and Haney 1981).

Overwintering slate-coloured juncos migrate south across the continental Eastern United States to the Gulf coast, where they are the only dark-eyed junco group found in large numbers (Ketterson and Nolan 1976, Nolan *et al.* 2002). Fretwell (1969) found overwintering slate-coloured junco flocks were most abundant in open weed fields and scarce in mature coniferous and deciduous woods. Much of the overwintering information for slate-coloured juncos comes from a long-term study based near Bloomington, Indiana. Females are found to migrate farther than males, and young migrate farther than mature (Ketterson and Nolan 1976). The difference in migratory patterns based on age and/or sex within a species is called differential migration. Ketterson and Nolan (1976) and Rabenold and Rabenold (1985) describe three hypotheses for why differential migration may occur in slate-coloured juncos: (1) due to differences in body mass and fasting ability, male juncos are better suited to handle periods of snow cover better than females, and can therefore remain in more northern areas throughout the winter; (2) males that arrive on breeding grounds as early as possible are at a competitive advantage to reproduce, and therefore remain closer to breeding grounds; and (3) males outcompete females for limited food resources during the winter, forcing females to migrate farther for resources.

Carolina junco (*J. h. carolinensis*) is a sub-species of dark-eyed junco, within the slate-coloured group. They both breed and overwinter in the southern Appalachian Mountains from Georgia to west Virginia (Liebgold *et al.* 2013, Rabenold and Rabenold 1985). Carolina juncos have been observed nesting up to 2025 masl in mixed coniferous-deciduous forests. Rather than migrating south in the winter, most individuals migrate downslope, below 1000 masl, to warmer hardwood forests and clearings where they flock with overwintering slate-coloured juncos. Differential migration in elevation has also been observed in this sub-species, with a higher ratio of males remaining at high elevation throughout the winter (Liebgold *et al.* 2013, Rabenold and Rabenold 1985).

OREGON JUNCO

Oregon juncos (*J.h. oregonus*) breed from southern Alaska across British Columbia (Haida Gwaii and Vancouver Island to the Rocky Mountains) and into northern Washington and Montana (Hellmayr 1938, Nolan *et al.* 2002, Tobalske 1991; figure 1). They nest across a very wide elevational range in British Columbia, from sea level to sub-alpine tree line (>2000 masl; Bears *et al.* 2009). In the northern Canadian Rocky Mountains, Oregon juncos nest throughout the montane forest ecoregion to the upper sub-alpine zone, dominated by mixed conifer-deciduous stands below and conifer patches at higher elevation (Bears *et al.* 2003). A population breeding in Montana preferred clear-cuts (over partially logged, then uncut areas) where slash piles provide good nesting, forage and perch habitat (Tobalske 1991). In central Oregon, Reinkensmeyer *et al.* (2005) found Oregon juncos in significantly higher densities in old-growth juniper (*Juniperus* spp.) habitats compared to earlier successional stages. They have been found to nest in burned landscapes, adapting to understory vegetation removal by building nests in novel areas such as holes left by burnt tree roots and in trees (Sperry *et al.* 2012).

During the winter months, Oregon juncos migrate south to overwinter along the California coast (Hellmayr 1938) where they inhabit many types of habitats, mainly sub-alpine tree islands (Martin 2001) and open meadows or clearings in close proximity to shrub/tree cover (Davis 1973, Grinnell and Miller 1944). There is evidence of differential migration similar to, yet less pronounced than, that seen in eastern slate-coloured junco populations (Swanson 1992). This could be due to a milder coastal climate compared to the eastern continental climate, allowing more females to overwinter at more northerly latitudes. Migration to lower elevation, rather than latitude, has also been observed in Oregon junco populations in Oregon state (Swanson 1992).

California is home to three non-migratory sub species of the Oregon group: *J.h. pinosus*, *J.h. pontilis* and *J.h. townsendi*. *J.h. pinosus* reside near Jamesburg, California. The only study (to my knowledge) on this sub-species found they preferred open areas close to moderate cover and water sources (Davis 1973). *J.h. pontilis* and *J.h. townsendi* breed and overwinter in the California Sierra Mountains, respectively the Sierra Juarez range and the Sierra San Pedro

Martir (SSPM) range. Both ranges are described as montane chaparral combined with pine around 1500 masl, with the SSPM range reaching higher elevation wet conifer and aspen groves mixed with meadows (Howell 2001). Sometime around the early 1980's, a population of what is thought to be one of these mountain sub-species established at the University of California San Diego (Yeh and Price 2004). This population is confined to an area about 2.5km², is separated from the nearest populations by about 70km in the breeding season and is joined by migrant juncos over the winter. The area is characterized by urban buildings and exotic plants such as eucalyptus (*Eucalyptus* spp.), and is the only known population in the San Diego area to breed lower than 1500 masl (Yeh and Price 2004).

Once thought to be a separate species, but now considered a part of the Oregon group, The pink-sided junco (*J.h. mearnsi*) breeds just east of the Oregon junco, from southwest Saskatchewan to southern Idaho and northern Wyoming (figure 1), and overwintering from Wyoming to southern Arizona and New Mexico (Hellmayr 1938). There is little literature on this group, but similar to other dark-eyed juncos, Smith and Andersen (1982) describe pink-sided juncos nesting in sub-alpine meadows, aspen forest and spruce-fir forest above 2000 masl in northern Utah.

GREY-HEADED JUNCO

The Grey-headed junco (*J.h. caniceps*) breeds from southern Wyoming Rocky Mountains through Colorado, Utah, Nevada and Arizona to northern New Mexico (figure 1), and either migrates south towards northwest Mexico or moves to lower elevation from high mountain areas during winter (Hellmayr 1938, Franzreb 1977). The only study on grey-headed juncos (to my knowledge) was in Arizona, where they were associated mostly with Engelmann spruce (*Picea engelmannii*) in both logged and unlogged areas, followed by other spruce and fir species. They were also found to prefer shorter trees than other avian species in the area, and both foraged and nested in logged areas whereas other species mainly foraged. Similar to the Oregon junco, grey-headed juncos benefit from post-logging slash piles for nesting, foraging and perching (Franzreb 1977).

The red-backed junco (*J.h. dorsalis*) exclusively breeds in the high mountains of northern Arizona and New Mexico, and overwinters in southwest Texas and northern Mexico (Hellmayr 1938; figure 1). In the Guadalupe Mountains of Texas, red-backed juncos breed between 2100 and 2805 masl in ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) mixed forests (reviewed in Tweit 2006). At one time, they were thought to belong to the yellow-eyed junco (*Junco phaeonotus*) species but has since been distinguished as a dark-eyed junco of the grey-headed group.

WHITE-WINGED JUNCO

The white-winged junco (*J.h. aikenii*) has a small range relative to other dark-eyed junco groups, breeding in the Bear Lodge Mountains of Wyoming and Black Hills of South Dakota and into northwest Nebraska (figure 1), and overwintering in the Black Hills to southern Colorado, Kansas and New Mexico (Hellmayr 1938). Baylor *et al.* (1976) report white-winged juncos frequenting artificial feeding areas in the Black Hills, and at banding stations located at the authors' residences near the edge of mountainous foothills at 1067 masl. To my knowledge, there is not any other literature to be found specifically on this sub-species.

GUADALUPE JUNCO

The Guadalupe junco (*J.h. insularis*) is endemic to Guadalupe Island, located about 250km off the Pacific coast of Baja California (Hellmayr 1938, Howell 2001; figure 1). Guadalupe Island is only 250km², and has a stable maritime climate (Léon de la Luz *et al.* 2003). The Guadalupe junco was once one of the most abundant avian species on the island, but numbers have declined drastically since the late 1800's due to habitat grazing by introduced goats, and presumed predation by feral cats (Birdlife International 2012, Leon de la Luz 2003, Howell 2001). Mirsky (1976) reported Guadalupe juncos nesting in wild tobacco (*Nicotiana attenuata*) bushes on the northeast part of the island. A trip to the island in 1906 found that they were resident over the entire island, but more abundant in higher elevation (~800-1000 masl) cypress (*Cupressus guadalupensis guadalupensis*), pine (*Pinus radiata var. binata*) and oak (*Quercus tomentella*) forests (Thayer and Bangs 1908). A recent trip found that there are a few hundred breeding pairs remaining in about 300 acres of dwindling cypress groves (Atwell *et al.*

2015). The Guadalupe junco appears most similar to the pink-sided junco in plumage colour, but genetic testing proves that it is genetically differentiated from other dark-eyed juncos and is most closely related to the Guatamala junco (*Junco phaeonotus alticola*), a yellow-eyed junco species (Atwell *et al.* 2015). Unfortunately, they currently remain a dark-eyed junco and are therefore listed as “least concern” on the IUCN’s Red List even though records state that this isolated group is nearing extinction (Birdlife International 2012, Island Conservation 2007, Howell 2001).

CONCLUSION

Although there is limited literature on the precise breeding ranges of the five dark-eyed junco groups discussed, there appears to be a general trend of dark-eyed juncos breeding at higher elevation habitats at lower latitudes and inland (figure 2). Exceptions are the resident Oregon junco population at the University of California San Diego (~120masl) and the Guadalupe junco, whose breeding ground is limited by the elevation of Guadalupe Island (~1300 masl; figure 2). Dark-eyed juncos mainly reside in low elevation mixed coniferous-deciduous forests or montane forest-meadow landscapes with relatively open canopy and understory vegetation. The species appears to prefer well-developed understory structure to conceal themselves and their nests - understory that does not exist in mature, closed canopy forests. Nesting substrate comes in many forms: rocks, logs, slash piles, grass clumps, vegetation and roots to name a few. Dark-eyed juncos likely limit breeding to high elevation in southern and inland areas because they prefer forested areas over relatively arid conditions that exist in many southern, inland locations in North America. For example, much of low elevation Arizona is arid and desert-like, with no forest.

During the winter, when dark-eyed juncos (mostly) leave their breeding areas, they can be found throughout much of the central to southern United States and Mexico, flocking near artificial feeders in urban areas as well as in open fields, often with tree or shrub cover nearby. They are relatively unaffected by the presence of human activity and development on the landscape and are often found in urban areas. Some populations have increased in abundance after forest harvesting or fire disturbance, and will nest on huma-altered landscapes such as

roadside cut banks and ditches, forest edges, urban gardens, parks and ski runs (personal observation). Overall, dark-eyed juncos are a hardy, forest and sub-alpine generalist species able to adapt to changing landscapes over spatial and temporal gradients. However, the decline of the Guadalupe junco shows that large scale habitat loss can have negative implications for dark-eyed junco populations. It is possible that we will see changes in dark-eyed junco breeding ranges, depending on how their preferred forest types adapt to increasing atmospheric temperatures under climate change (Aitken *et al.* 2008).

An area that would benefit from further study would be the occurrences of, and drivers behind, nests built off the ground. There are some, but few, accounts of tree/shrub nests in the literature, but brief statements online hint towards more observations. Early published occurrences include juncos nesting in vegetation 8 feet above the ground (Smith 1936) and on the lower branches of a Guadalupe Island pine tree (Thayer and Bangs 1908). Sperry *et al.* (2008) found juncos nesting on braches of trees higher than 10 m off the ground after forest fire destroyed understory canopy. Oregon juncos were observed feeding nestlings in eight tree nests between 1900 and 2200 masl near Revelstoke, BC during June and July 2014, over which time other junco pairs were nesting on the ground (personal observation). Pairs observed feeding young early in the season suggests that there were more tree nests earlier in the season that were not found. Juncos were not observed nesting in trees over the same time period and study site in the previous season (Jennifer Greenwood, personal communication). In both Minnesota and Revelstoke, dark-eyed juncos were observed nesting in trees on historical breeding grounds that were likely devoid of understory vegetation due to recent wildfire and snow cover – two disturbance types that result in similar, barren landscapes for a period of time. Although these disturbances are different, their effects on vegetation are ecologically similar, and may be driving dark-eyed juncos to nest in trees. Increased research on nest building and placement would contribute to a deeper understanding of dark-eyed junco habitat preferences and behavioral plasticity.

TABLES AND FIGURES

TABLE 1. FIVE GROUPS AND FIFTEEN SUB-SPECIES OF DARK-EYED JUNCO (*JUNCO HYEMALIS*) BASED ON SYSTEMATICS DESCRIBED BY NOLAN *ET AL.* 2002. SUB-SPECIES IN BOLD ARE DISCUSSED WITHIN THIS REVIEW.

Group	Sub-species	Common name
Hyemalis	<i>J.h. hyemalis</i>	slate-coloured junco
	<i>J.h. carolinensis</i>	Carolina junco
	<i>J.h. cismontanus</i>	
Oregonus	<i>J.h. oregonus</i>	Oregon junco
	<i>J.h. mearnsi</i>	Pink-sided junco
	<i>J.h. pontilis</i>	
	<i>J.h. townsendi</i>	
	<i>J.h. shufeldti</i>	
	<i>J.h. montanus</i>	
	<i>J.h. pinosus</i>	
Caniceps	<i>J.h. caniceps</i>	grey-headed junco
	<i>J.h. dorsalis</i>	red-backed junco
Aikeni	<i>J.h. aikeni</i>	white-winged junco
Insularis	<i>J.h. insularis</i>	Guadalupe junco

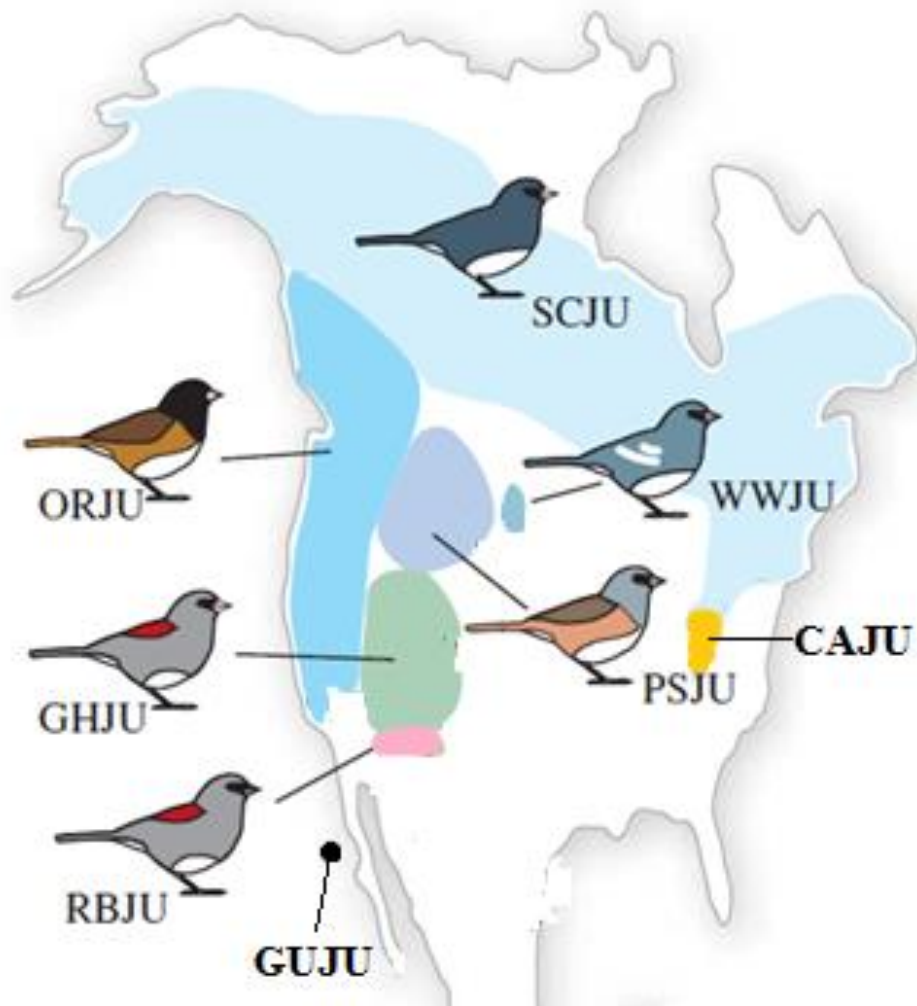


FIGURE 1. APPROXIMATE BREEDING RANGES OF FIVE GROUPS AND TWO SUB-SPECIES OF THE DARK-EYED JUNCO (*JUNCO HYEMALIS*); *J.H. HYEMALIS* (SLATE-COLOURED JUNCO; SCJU), *J.H. OREGANUS* (OREGON JUNCO; ORJU), *J.H. MEARNESI* (PINK-SIDED JUNCO; PSJU), *J.H. CANICEPS* (GREY-HEADED JUNCO; GHJU), *J.H. DORSALIS* (RED-BACKED JUNCO, RBJU), *J.H. AIKENI* (WHITE-WINGED JUNCO; WWJU) AND *J.H. INSULARIS* (GUADALUPE JUNCO; GUJU). FIGURE ADAPTED FROM MILA ET AL. 2007.

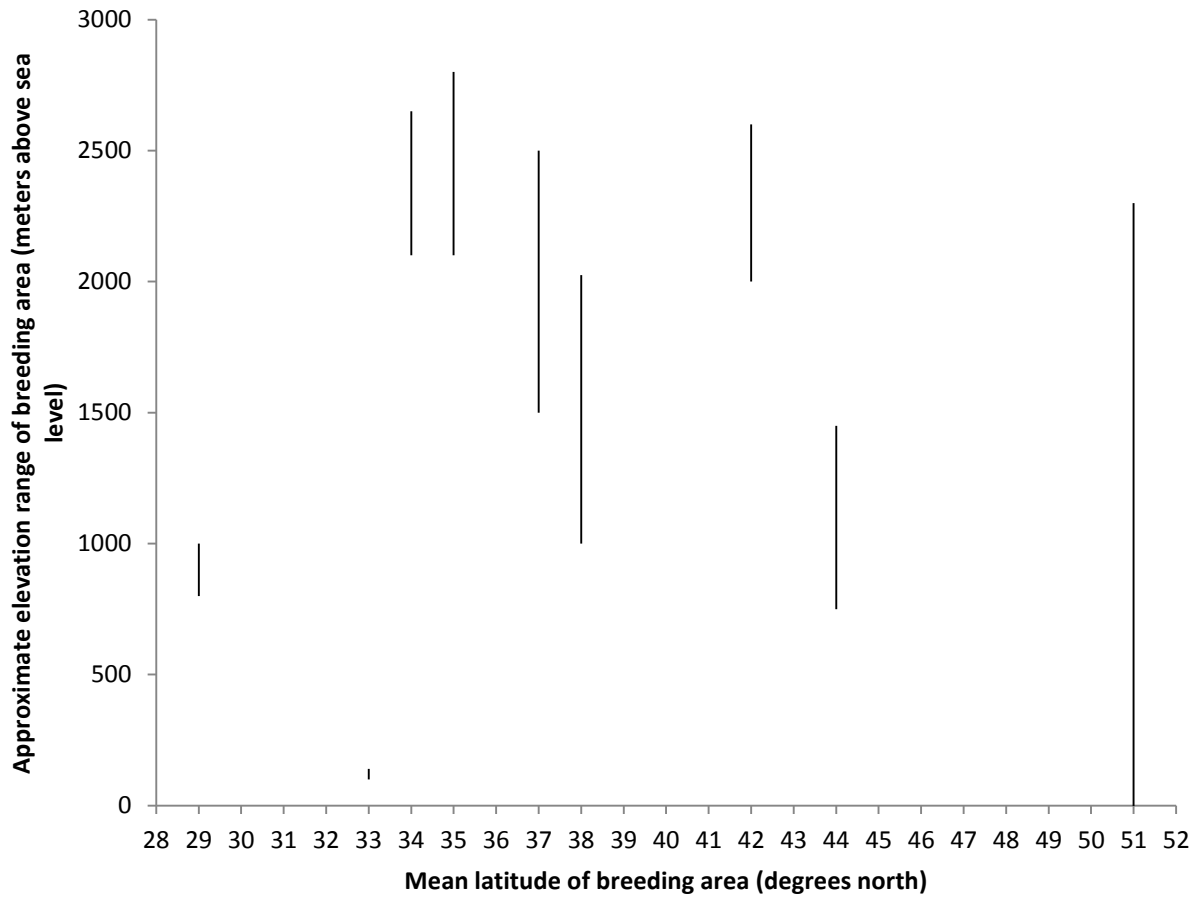


FIGURE 2. APPROXIMATE ELEVATION RANGE VS. MEAN LATITUDE OF DARK-EYED JUNCO (*JUNCO HYEMALIS*) BREEDING RANGES DESCRIBED IN LITERATURE. THERE IS UNCERTAINTY IN LATITUDE AND ELEVATION LIMITS TO BREEDING RANGES AND MOST VALUES ARE ESTIMATES.

TABLE 2. APPROXIMATE LOCATION, LATITUDE AND ELEVATION RANGE OF DARK-EYED JUNCO (*JUNCO HYEMALIS*) GROUPS AND SUB-SPECIES DESCRIBED IN THE LITERATURE. THERE IS UNCERTAINTY IN LATITUDE AND ELEVATION LIMITS TO BREEDING RANGES AND MOST VALUES ARE ESTIMATES.

Group	Sub-species	Location of reference	Approximate latitude (degrees north)	Approximate elevation range of breeding area (masl)	References
Guadalupe Oregon		Guadalupe Island San Diego	29 33	800-1000 100-140	Thayer and Bangs 1908, juncoproject.org Yeh and Price 2004
Grey-headed	Red-backed	Arizona, New Mexico	34	2100-2650	reviewed in Tweit 2006
Grey-headed	<i>J.h. pontilis, J.h. townsendi</i>	Arizona California Sierra Mountain ranges	35 37	2100-2800 1000-2500	Franzreb 1977 Howell 2001
Slate-coloured Oregon	Carolina Pink-sided	Virginia Utah	38 42	1000-2025 2000-2600	Liebgold et al. 2013, Rabenold and Rabenold 1985 Smith and Andersen 1982
Slate-coloured		New Hampshire	44	750-1450	Sabo 1980
White-winged Oregon		Wyoming, South Dakota British Columbia	44 51	Not enough information 0-2300	Bears 2007

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