

**HOW AND WHY A SMALL SONGBIRD, THE OREGON JUNCO
(*Juncus hyemalis oregonus*), BREEDS OVER A STEEP ELEVATION
GRADIENT: SHIFTING LIFE-HISTORIES, ADAPTATIONS, AND
COSTS AND BENEFITS WITH ELEVATION**

by

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ABSTRACT

I used a comparative approach to examine phenotypic plasticity in morphology and life-history traits of a songbird, the Oregon Junco (*Juncus hyemalis oregonus*), at the lowest (1, 000 m asl; 4 sites) and highest (2, 000 m asl; 4 sites) elevational extremes of its breeding range in Jasper National Park, Alberta, Canada. Further, I tested if juncos differ in stress levels and sensitivity to stressors ("adrenocortical sensitivity") among elevations by measuring baseline corticosterone concentration, and increases in corticosterone 30 and 60 minutes after exposure to a standardized stressor. The extremes of the elevation range used encompassed very different environmental conditions, with high elevations experiencing colder temperatures, more precipitation, delayed snowmelt and frequent snow and hail storms throughout the summer. Biotic communities also changed considerably with elevation, with high elevation habitats having lower plant productivity, and hosting different animal communities. These abiotic and biotic variables were expected to cause measurable differences in selected morphological, life history and endocrinological traits in juncos among elevations.

High and low elevation males and females did not differ in wing length, beak size, tarsus length, body mass, and intrafurcular fat. However, high elevation males had longer central retrix feathers, which could enhance balance and stabilization in windy conditions. Intrafurcular fat levels in females at high elevations also decreased seasonally. Nests at higher elevations were constructed with greater amounts of insulative materials and placed in better-buffered microclimates. High elevation habitats supported lower junco densities. Juncos at high elevations produced fewer broods per season compared to low elevation juncos. In addition, the number of fledglings per brood surviving to 20-30 days of age was lower at high compared to low elevations. Adults and offspring returned at similar rates to their sites of capture at low and high elevation sites between years. Overall, high elevation birds had a lower seasonal fecundity. Despite this seasonal deficit in reproduction, juncos at high elevations were not more likely to belong to an inferior competitive class (younger, smaller or later arrivers). Thus, the wide spread in elevation occupied by this bird is not caused by dominants excluding subordinates

from optimal habitat, but by a trade-off in costs and benefits among elevations. Lower fecundity at high elevations may have been partially compensated by low levels of infection by the blood parasites *Haemoproteus*, *Leucoctozoon* and *Trypanosoma spp*, in adults and fledglings. Also, fledglings at high elevations were heavier and had more intrafurcular fat prior to fall migration. These 3 factors could increase adult and fledgling survival.

Baseline corticosterone concentration in juncos did not differ among elevations. Stress-induced corticosterone increases in juncos did not differ markedly among elevations during the initial stages of the stress reaction, but the degree of increase was slightly greater between 30 and 60 minutes post-capture at low elevations. Females had a lower adrenocortical response to stress than males, and breeding individuals had a lower response to stress than non-breeders. The influence of gender and breeding stage may be explained by a previously established interaction between testosterone and indirect up-regulation of corticosterone in juncos.

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CHAPTER 1: GENERAL INTRODUCTION

With increasing elevation, several physical variables change markedly: precipitation, wind, and solar radiation increase while mean temperature, oxygen concentration, and growing season length decrease. High elevations experience regular hailstorms, wind, snow deposition, and freezing temperatures, often extending through the summer (Appendices I-III; Martin 2001). Biotic communities also change considerably with elevation (Appendix V), with high elevation habitats having lower plant productivity, and generally hosting a lower faunal diversity (Kikkawa and Williams 1971; Martin 2001). These qualities make high elevation habitats very different from their low elevation counterparts. Consequently, species that span wide elevation ranges display a host of traits to cope with their local environments (*e.g.*, Dunmire 1960; Zammuto and Millar 1985a,b; Grant and Dunham 1990; Badyaev 1997). Further, the costs and benefits (*e.g.*, relative predation risk, interspecific competition, parasite exposure, offspring production, survival, *etc.*) may shift considerably with elevation (Martin 2001).

Many species have evolved as 'elevational specialists', residing within relatively narrow elevation bands encompassing conditions within their range of tolerance (*e.g.*, Scheid and Hashim 1997). Some, however, are able to live and breed over wide elevation gradients that encompass very different conditions among extremes. Comparative studies of mammals (*e.g.*, Dunmire 1960; Zammuto and Millar 1985a,b), and reptiles (*e.g.*, Grant and Dunham 1990; Mathies and Andrews 1995) have elucidated traits that can differ among elevations due to phenotypic plasticity. However, only a handful of studies on birds (*e.g.*, Hamann *et al.* 1989; Landmann and Winding 1993; Kollinsky and Landmann 1996; Widmer 1999) have compared single species among elevations. Most comparative studies of birds breeding along elevation gradients have been interspecific, and thus are confounded by phylogeny (Bjorklund 1994; Landmann and Winding 1995a; Badyaev 1997; Pearson and Rohwer 1998; Blackburn and Ruggiero 2001). While interspecific comparisons can reveal many genetically based differences among elevations, variation among locations could be relics from evolutionary events that occurred in conditions irrespective of present day variables (*e.g.*, Fjeldsa 1992). Thus,

understanding phenotypic variation with elevation is particularly important, as it can give insight into how animals interpret and adapt to their current environment.

Adaptations to environmental constraints can occur through modifying a number of traits. Landmann and Winding (1995a,b) found that high elevation songbirds above the treeline in Nepal were larger than their low elevation counterparts. A positive relationship between body mass and elevation was also present in endemic Andean birds, while the mass of non-endemic species was positively correlated with mid-point of species' elevational distributions (Blackburn and Ruggiero 2001). On the other hand, Widmer (1999) found no relationship between body mass or tarsus length with breeding elevations in a single species, the garden warbler (*Sylvia borin*), over a 1000 m elevation range in Europe. In the Himalayas, high elevation songbirds have longer, more pointed wings for flight in strong winds. Chats and Finches at the highest elevations have square ended or shallow forked tails for flight stability in wind, and strong limbs with small feet for ground foraging (Landmann and Winding 1993, 1995a, b). Claw length (*e.g.*, Landmann and Winding 1995a), beak size (*e.g.*, Price 1991), fat (*e.g.*, Martin *et al.* 1993), intraspecific variation in plumage (*e.g.*, Graves 1985), and other allometric relationships (*e.g.*, Bjorklund 1994) can also vary with elevation. High elevation birds may also exhibit behavioural differences, such as placing nests within more benign microclimates (Verbeek 1967; Medin 1987; Böhn and Landmann 1995; Landmann and Winding 1995b; Martin 2001), and they also adapt physiologically to environmental conditions (*e.g.*, Clemens 1988; Carey 1980; Scheid and Hashim 1997).

A wide elevational distribution of a single species of bird could be the result of a number of causes. First, if a certain portion of the elevation range is less desirable, less competitive and subordinate individuals may be forced to breed within these habitats due to intraspecific competition in the more desirable portions. In such a situation, a disproportionately higher number of less competitive classes (younger, smaller, later arriving individuals; Cristol *et al.* 1990; Grasso *et al.* 1996) would be expected to live at the less desirable elevation. To date, there has been little support for this hypothesis in songbirds (Kollinsky and Landmann 1996; Widmer 1999). Alternatively, a wide elevation range could be maintained by species experiencing different costs and benefits at various locations across their elevation range, and individuals may adhere to different lifetime reproductive strategies in order to maximize the benefits of their local

habitats. For instance, birds generally have fewer offspring per season at higher elevations (*e.g.*, Krementz and Handford 1984; Badyaev 1997), due to an attenuated favorable season for reproduction and lower clutch sizes per brood. Birds suffering from lower seasonal reproduction may be compensated by alternate advantages, such as a lower exposure to parasites and diseases (Stabler *et al.* 1974; Braun *et al.* 1993), or the production of hardier offspring, which can increase survival (Leary *et al.* 1999; Oddie 2000).

Two dominant questions are at the forefront of comparative research on birds breeding among elevations: 1) How do individuals acclimatize to the various conditions that change with elevation?, and 2) What drives the distribution of individuals across an elevation gradient? In this thesis I address these two questions for one subspecies of bird, the Oregon Junco (*Junco hyemalis oregonus*), breeding across a steep elevation gradient in Jasper National Park, AB, Canada. Juncos are distributed continuously along this gradient, and therefore gene flow is facilitated. Consequently, phenotypic plasticity, resulting from direct physiological responses to environmental factors (Via and Lande 1985; Stearns 1989), is expected to dominate over genotypic selection (Endler 1977) as the mode of adaptation.

The Oregon Junco is suitable for exploring trends in phenotypic plasticity, as well as costs and benefits associated with different breeding elevations. It has one of the widest elevational distributions in North America, and can breed over the continuum of conditions from sea level to the subalpine-alpine treeline. Within Jasper National Park, the junco breeds from the montane valley (1,000 m asl) to the subalpine-alpine treeline (1,900-2,100 m asl). While this is only a subsection of the total range over which the junco can breed (as the lowest elevation in the park does not drop below 1,000 m asl), this gradient differs considerably among extremes. Upper elevations are ~5 °C colder, and receive more precipitation in the form of rain, hail, and snow as compared to lower elevations during the May-August breeding season (Appendix I, II, III). Snowmelt at the upper elevation portion of this gradient is also delayed by 1-1.5 months; it melts by the end of April at low elevations while it can remain until mid June at upper elevations.

In **Chapter 2**, I investigate some morphological, reproductive, and behavioural traits that may allow Oregon Juncos to adapt to, and breed within, such different environmental conditions at the extremes of their elevation range in Jasper. Further, I examine costs and benefits of breeding among locations. Specifically, I test whether less competitive individuals are forced into

an elevationally 'inferior' extreme, or if there is evidence of shifting costs and benefits across elevations.

In **Chapter 3**, I explore elevational adaptation via a differential sensitivity of the adrenocortical response to stress, a previously unexplored phenomenon in birds that span wide elevation ranges. With reference to ideas of Wingfield (1995a,b) I test the prediction that high elevation birds will have a decreased adrenocortical sensitivity to stress in high relative to low elevation habitat. A sensitive adrenocortical response to a stressor normally provides a cue for the behavioural or physiological abandonment of a reproductive attempt until conditions improve. However, because high elevations have a short breeding season that is frequently interrupted by storms, a sensitive response to stress could cause reproductive loss, leaving insufficient time for re-nesting. The same sensitivity to stress in low elevation birds could cause occasional nest abandonment, but re-nesting might be possible afterwards due to a longer breeding season. Thus, down regulation of adrenocortical sensitivity could be advantageous to high elevation birds.

Understanding how species adapt to shifting conditions with elevation, and the forces that drive this geographic spread, is fundamental in our understanding of selective constraints and adaptations of mountain species. Further, information on species-elevation relationships may aid in predicting the effects of low elevation development, and future climate change (Storch 2000; Luckman 1998; Martin 2001), both of which threaten to displace and/or confine individuals to the upper elevational segments of their former ranges (Storch 2000). The better we can assess how species adapt naturally to environmental ecoclines, the better we will be able to predict how they will react to human-induced changes to their habitat.

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CHAPTER 2: VARIATION IN MORPHOLOGY AND LIFE HISTORY TRAITS OF OREGON JUNCOS (*Juncus hyemalis oregonus*) ACROSS AN ELEVATION GRADIENT

Abstract

I use a comparative approach to examine phenotypic plasticity in morphology and life-history traits of a songbird, the Oregon Junco, at the lowest (1,000 m asl) and highest (2,000 m asl) elevational extremes of its breeding range in Jasper National Park, Alberta, Canada. I address two general questions: 1) How does a small songbird accomplish the task of breeding across this steep 1000 m gradient? 2) What costs and benefits can be identified for breeding at either elevational extreme? High and low elevation males and females did not differ in wing length, beak size measures, tarsus length, body mass and intrafurcular fat. However, high elevation males had longer central rectrix feathers, which could enhance balance and stabilization in high wind conditions. Intrafurcular fat in females also decreased throughout the summer at high elevations. Nests at higher elevations were constructed with greater amounts of insulative materials and placed in better-buffered microclimates. High elevation juncos had lower densities and fewer broods per season compared to low elevation juncos. Further, the number of fledglings per brood was lower at high compared to low elevations. Adults and offspring returned at similar rates to their sites of capture at low and high elevation sites between years, suggesting that high elevation birds have a lower lifetime reproductive success. The lower seasonal fecundity at high elevations may have been partially compensated by low levels of infection by the blood parasites *Haemoproteus*, *Leucoctozoon* and *Trypanosoma* spp. in adults and fledglings. Also, fledglings at high elevations were larger and had more intrafurcular fat prior to fall migration.

Introduction

Over a compressed spatial scale, several environmental variables change dramatically with increasing elevation. Precipitation, wind, and solar radiation increase while mean temperature, oxygen concentration, plant productivity, and growing season length decrease (Thompson and Whitfield 1993; Martin 2001). High elevations also

experience hail, wind, snow deposition, and freezing temperatures, often through the summer months (Martin 2001; Appendix I-III). These qualities make high elevation habitats very different from their low elevation counterparts. As a result, reproductive, life history, morphological, and behavioural traits in animals that breed over wide elevation gradients can vary greatly with changing environmental constraints (reviewed in Chapter 1).

Comparative studies of mammals (*e.g.*, Dunmire 1960; Zammuto and Millar 1985a,b), and reptiles (*e.g.*, Grant and Dunham 1990; Mathies and Andrews 1995) have revealed multiple traits that vary among elevations. However, few studies on birds (*e.g.*, Hamann *et al.* 1989; Landmann and Winding 1993; Kollinsky and Landmann 1996; Widmer 1999) have investigated the ways in which a single species varies among elevations. Most comparative studies of birds breeding between elevations have been interspecific, and thus confounded by phylogeny (Bjorklund 1994; Landmann and Winding 1995a,b; Badyaev 1997; Pearson and Rohwer 1998; Blackburn and Ruggiero 2001). While interspecific comparisons can reveal genetically based differences among elevations, differences could be relics from an evolutionary event that occurred in conditions irrespective of present day variables (*e.g.*, Fjeldsa 1992). Understanding how phenotypes vary with elevation can give insight into how animals interpret and adapt to their current environment.

Studying phenotypic plasticity in birds along wide elevation gradients may also aid conservationists in predicting the outcome of habitat changes. For instance, human development has focused disproportionately in lower elevations and may be restricting populations of mountain species to the upper segments of their former ranges, or pushing them above their natural range, causing reproductive failures or extirpations (*e.g.*, Storch 2000). In addition, climate change is impacting mountain environments (Luckman 1998), and threatening to cause an upward shift in animal communities and/or to alter the timing of life history events. In order to predict the outcomes of these influences, one must understand how traits vary with elevation, as well as the relative costs and benefits of breeding within different portions of the elevation range of a species.

Objectives

My general aim in this chapter is to increase current understanding of how and why some songbirds can breed over wide elevation gradients. I use a comparative approach to examine differences in phenotypes, as well as shifting costs and benefits in the Oregon junco breeding in the lowest (1,000 m asl; 'low' hereafter) and highest (2,000 m asl; 'high' hereafter) portion of its elevation range in Jasper National Park, Alberta, Canada. From May- August of 2000 and 2001, mean temperatures at high elevation sites were approximately 5 °C cooler than low elevation sites, received 13 % more humidity, and experienced 17 more snowstorms (Appendices I, II). Along this 1000 m gradient, juncos breed continuously from one extreme to the other. Therefore, gene flow is facilitated and phenotypic plasticity, a direct physiological response to environmental factors (Via and Lande 1985; Stearns 1989), is expected to dominate as the mode of adaptation. I compare some morphological, reproductive and behavioural traits in juncos, as well as fledgling traits and parasite prevalence at the lower and upper extremes of its elevation range in the mountains of Jasper National Park, in order to address two general questions: 1) How does a small songbird accomplish the task of breeding across this steep 1000 m gradient? 2) What costs and benefits can be identified for breeding at either elevational extreme? More specifically, I test the following predictions (see chapter 1 for background and rationale): 1) juncos at high elevations will display reproductive, morphological, and behavioural adaptations, primarily aimed at dealing with colder temperatures, more frequent storms, and a shorter breeding season, 2) high elevation juncos will suffer from a lower seasonal fecundity due to a shorter favourable season for reproduction, 3) high elevation individuals will be inferior competitors, forced to breed in high elevations due to competitive exclusion in the low elevation habitat (or), 4) there are advantages present over the lifetime of an individual at high elevations that could compensate for a seasonal reproductive deficit.

Methods

Study sites

Juncos were captured and monitored at eight 50 - 70 ha study sites in Jasper National Park (52°53', 118°3'), Alberta, from 01 May to 20 August in 2000, and from 15 April and 20 August in 2001. Four sites were located at the lowest elevation within the

Park (1000 – 1020 m asl), separated by 5-10 km at the following locations: L1 (52° 62', 118°6' 1020m), L2 (52°59', 118°4' 1020m), L3 (52°54', 118°2' 1027m), and L4 (52°53', 118°3', 1014m). Four sites were at the highest elevation that juncos breed within the park (1950-2100 m asl), and were separated by > 18 km at the following locations: Columbian Icefields (H1) (53°30', 117°30', 2000-2070 m), Marmot Basin (H2) (52°48', 118°6', 1950-2114 m), Edith Cavell (H3) (53°40', 118°3', 1900-1920 m), and Pyramid Mountain (H4) (52°53', 118°7', 1900-2050 m). All high elevation sites had south or southeast aspects. Low elevation sites were in the montane forest ecoregion, dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). High elevation sites were in the upper subalpine zone, dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), lodgepole pine, whitebark pine (*Pinus albicaulis*) and white spruce.

Capture Techniques and Measurements (2000, 2001)

Birds were captured between 700 and 1200 hrs using Japanese mist nets baited with painted model male juncos. Nets were monitored constantly. Juncos were lured towards the net by playing the taped song of a conspecific. Temperature and relative humidity (%) records were taken between the 7th and 21st day of every month using Hobo Pro © data loggers placed on tree trunks 1 m above ground level. Additional weather data were obtained from Environment Canada weather stations in the northern Rockies of Alberta, at similar elevations to our study sites, or from industrially operated weather stations within 2 km of our high elevation study sites (Columbian Icefields and Marmot Basin) (Appendix I, II, III).

After capture, birds were weighed (to ± 0.1 g) and scored on a 0-5 nominal scale (leanest-fattest) for intrafurcular fat accumulation (Rogers and Smith 1993). Birds were sexed and aged as SY (second year) and ASY (after second year) breeders using methods of Pyle *et al.* (1987). Brood patch development in females, and cloacal protuberance in males were noted during capture. Morphological measurements were taken, including: tarsus length, wing length, rectrix length, beak length, beak width, and beak depth using measurement techniques suggested by Pyle *et al.* (1987). Birds with extremely worn feathers were noted, but not used in feather length measurements. Each bird was given a

numbered aluminum Fish and Wildlife Service band, and a color band combination conveying sex, age, and site information. Eighty hours of recapture effort in 2001, distributed evenly around sites, was used in order to estimate the degree to which adults and fledglings returned to their sites of capture between years.

Census Techniques and Monitoring (Summer of 2000, 2001)

During 2000 and 2001, phenology was monitored by estimating the age of fledglings seen with adults (Pyle *et al.* 1987) and back dating to estimate the date of egg-laying, or by back dating from the age of hatchlings found in the nest to the date of egg-laying. In some cases, the precise date of egg-laying was known because a nest was found when laying had just begun. Family counts were conducted in order to estimate the number of fledglings produced per brood. When a pair was seen with fledglings, an observer watched the family for at least 15 minutes, until all fledglings were counted and their age was estimated (Pyle *et al.* 1987). In order to decrease any bias in the estimates of mortality, families were revisited, and only those counted between 20 – 30 d of age were used for comparisons between elevations. We identified families by the bands on adults and their fledglings, combined with location and mapping information. If there was any uncertainty, the record for the family not used. New families were searched for weekly. Fledglings from approximately 60 % of families were captured by setting up mist nets across observed flight paths. Fledglings were weighed, and colour banded for future brood identification. To increase the sample size obtained during fledgling counts, counts were made in areas extending up to 30 ha outside the normal study plot boundaries.

During the summer of 2001, two low elevation (L1 and L3) and two high elevation (H1 and H2) sites, 50 and 70 ha in size, respectively, were systematically monitored using spot mapping (Kendeigh 1944; Pyle *et al.* 1987). We estimated the maximum number of breeding pairs per site during the entire summer. For 82% percent of families found, we banded at least one member of the pair in May – early June for identification throughout the breeding season. The four census plots were used to estimate the densities of breeding females. In addition, the number of successful broods produced, and the extent of brood overlap could be estimated by observing known pairs with fledglings throughout the breeding season. During spot mapping, other bird species were also recorded (Appendix V).

Nest Finding (Summer of 2000, 2001)

Individuals that were nest building or provisioning nestlings were observed and followed to nests. This method was unsuccessful at high elevation sites where the nesting period was attenuated, and where parents provided few behavioural clues about nesting activity. Approximately 1/3 of nests found in high elevation habitats were from using an infrared temperature scope (on temporary loan from Parks Canada). Using this scope, I looked for hot spots in the ground in known pair territories between 2400 – 0300 hrs at high elevation sites. Once a nest was found, the date of egg-laying was determined, and eggs or hatchlings were counted and weighed. Latex gloves were worn in order to prevent the transfer of human scent. Nests were revisited every 3 days to monitor their outcomes. After the nesting period, nest site measurements were taken following Pyle *et al.* (1987), and all nests were collected for analysis of building materials. Vegetation in nests was identified (to genus level when possible), dried, and weighed in the lab. Hairs found in nests were identified to the species level, using methods described by (Pierre *et al.* 2000), and Pasitchniak-Arts and Messier (1995).

Blood Collection and Parasite Identification (Summer of 2001)

Blood samples were taken from each bird caught between 01 May and 30 August, 2001, by puncturing the alar vein with a needle and collecting ca. 40 µl of blood in a heparinized microhematocrit tube. Because blood parasites may show a diurnal periodicity (Gore *et al.* 1982), the birds selected for parasite identification were all caught at approximately the same time each day (700-1200 hrs). Blood was blown out of microhematocrit tubes into centrifuge tubes. Within 10 hours of collection, 5 µl of blood was used to produce 3 microscope slides per bird using the methods of Harrison and Harrison (1986) and Bennett and Fallis (1970). The slides were fixed in 100% methanol immediately. In the laboratory, blood smears were stained with Geimsa stain for 30 minutes, and rinsed with distilled water followed by acetone under a fumehood (Deviche *et al.* 2001). Smears were examined under 400 x magnification, and 50 fields of view per slide were classified as negative or positive for various parasites. Parasites were identified to genus level by examination under high power (1000 x magnification) with oil immersion, using various keys (Pierce 1981, Bennet and Pierce 1988, Burrey-Caines

and Bennett 1992, Bennet *et al.* 1994), and by direct comparisons with photos of blood parasite photos from juncos captured in Alaska (Supplied by Pierre Deviche).

Results

*Before pooling data from various sites to compare among elevations, ANOVA's were performed to ensure that sites within an elevational treatment did not differ significantly (*i.e.* belonged to a homogeneous group).

Morphology, mass, fat and age class comparisons

No significant differences in mass, fat, or any other morphological features measured were found among females breeding at either elevation (Table 2.1, $P > .21$, $df=2$; Mann-Whitney U). Similarly, males did not differ in most traits examined among elevations (Table 2.1, $P > .06$, $df=2$; Independent Samples T-test), with one exception: high elevation males had statistically longer retrain feathers (Table 2.1, $P < .01$, $df=2$; Independent Samples T-test), but the effect size was small (approximately 2 % of the trait). Following the cautions of Green (2001), comparisons were made without scaling to a standard body size measurement. However, if allometric adjustments by tarsus length were made, the same results emerged. The age class proportions of ASY to SY juncos were virtually identical among elevations (Table 2.2, $P = .98$, $df = 2$; G test). Fat scores were negatively correlated with date in high elevation females (Fig. 2.1, $P = .02$, $r = -.59$; Spearman's rank), but male fat score did not change seasonally at either elevation, nor did female fat score change at low elevations ($P > .59$; Pearson's r). Body mass ($P > .07$; Pearson's r) did not change seasonally at either elevation in both sexes and age groups. Finally, there was no differential wear of feathers, which could cause retrain or wing length to change seasonally ($P > .12$; Pearson's r).

Density, re-nesting, and interannual site return

Mean densities were approximately 3 times higher at low ($0.90 \text{ ♀/ha} \pm 0.01$) than at high elevations ($.29 \text{ ♀/ha} \pm .15$). During recapture efforts, similar numbers of returning adults were observed at high and low elevation sites. Twenty % (12/60) and 23 % (14/60) of adult males banded in 2000 were recaptured in 2001 from low and high elevation sites, respectively. One female (of 5 banded in 2000) was recaptured from high elevation sites, and none ($n=4$) were recaptured from low elevation sites. Twenty five percent (20/80) of fledglings banded at low elevations in 2000 were recaptured in 2001. Two of 10

fledglings banded in 2000 were re-captured in 2001 at high elevation sites. All fledglings recaptured at either elevation were caught in their respective natal habitats.

Table 2.1 Morphological measures (mm), mass (g), and intrafurcular fat score (1-5 nominal scale) from male and female Oregon Juncos breeding at Low (1000 m asl) versus High (2000 m asl) elevations. P- values are from independent sample t-tests for morphology and mass measurements for males, and from Mann-Whitney U-tests for females. P-values for fat scores are from Chi-squared tests.

<i>Males (N= 83, 83)</i>	<i>Low Mean \pm SE</i>	<i>High Mean \pm SE</i>	<i>Significance (2-tailed P)</i>
Retrix	65.78 \pm .58	67.96 \pm .58	.01
Wing	76.92 \pm .26	77.15 \pm .25	.52
Tarsus	20.45 \pm .10	20.18 \pm .11	.06
Beak Length	7.91 \pm .004	7.96 \pm .005	.46
Beak Width	5.90 \pm .003	5.87 \pm .003	.33
Beak Depth	5.34 \pm .003	5.44 \pm .005	.86
Mass	18.59 \pm .11	18.39 \pm .10	.20
Fat	1.99 \pm .12	1.81 \pm .11	.28
<i>Females (N=11, 12)</i>	<i>Low Mean \pm SE</i>	<i>High Mean \pm SE</i>	<i>Significance(2-tailed P)</i>
Retrix	63.94 \pm 1.84	66.71 \pm 1.27	.24
Wing	72.70 \pm .40	74.22 \pm .93	.16
Tarsus	19.74 \pm .18	19.80 \pm .25	.21
Beak Length	8.01 \pm .12	7.59 \pm .11	.24
Beak Width	5.68 \pm .007	5.59 \pm .004	.65
Beak Depth	5.27 \pm .004	5.20 \pm .007	.21
Mass	18.03 \pm .22	17.51 \pm .57	.41
Fat	2.50 \pm .48	2.10 \pm .29	.61

Table 2.2 Counts (number) of SY and ASY age Oregon Juncos captured at low (1000 m asl; N= 94) and high (2000 m asl; N= 95) elevations. No significant difference was present among elevations (P = .98, G test).

<i>Age Category</i>	<i>Low (N = 94)</i>	<i>High (N= 95)</i>
ASY	84	83
SY	10	12

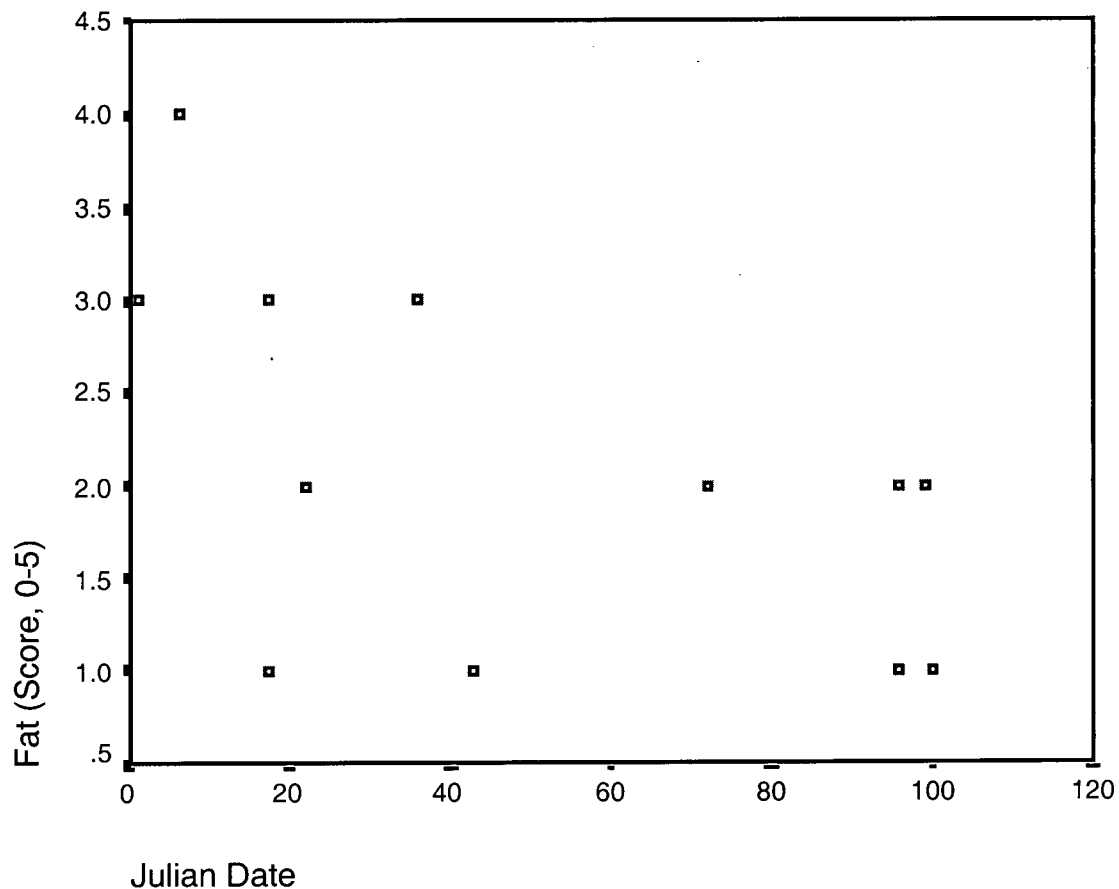


Figure 2.1. Negative relationship between date (number of days after May 1) and fat score in female Juncos breeding at high elevations ($r = -.59$, $N = 12$, $P = .02$).

Phenology and fledgling production/provisioning at high and low elevations (2000, 2001)

Egg-laying was highly asynchronous at low elevations, occurring between April 17 – August 5 (Fig. 2.2). In contrast, high elevation birds laid only between May 27 and June 15. From nests found with eggs, low elevation birds produced $3.7 \pm .82$ eggs per nest ($n=15$), while high elevation birds produced $3.6 \pm .89$ eggs per nest ($n=5$). Predation rates (nests depredated between laying and fledging) were 58% (7/12) at high elevations, and 38% (17/45) at low elevations. The number of fledglings produced per brood that survived to ≥ 20 days differed significantly among elevations; low elevation pairs were seen with 1.2 times more offspring (≥ 20 -30 days of age) than high elevation pairs ($P < .05$, $df = 1$, T-test). None of the 45 high elevation pairs observed in either year had >1

brood, or re-nested following an unsuccessful nesting attempt. In low elevation habitats, 44/72 (62%) of breeding pairs provided parental care to two broods, each of which had ≥ 1 fledgling that survived to 20-30 days old. One low pair had 3 successful broods. In 5 double-brooded families, and the one triple-brooded family, parents were seen provisioning more than one brood at a time. These birds concentrated on feeding the newer brood, while occasionally providing food to a member of the older brood, usually when the older fledgling intercepted food meant for a newer fledgling. In five cases at low elevations, pairs had one nest attempt that failed due to predation, but re-nested to produce a successful brood. Thirty-one low elevation pairs (30%) were observed with only one brood with ≥ 1 member surviving to ≥ 20 days of age (these individuals may have had other broods that were depredated before fledging).

The average fledgling mass was determined ($=\sum$ (masses of fledglings caught in a family) / N individuals caught from that family) for families where ≥ 2 individuals were caught. By 30-40 days of age, fledglings at high elevations (N= 11 families) were significantly (11%) larger on average than at low elevations (N=18) ($P < .05$, $df = 1$; Mann Whitney U-test). The average fat score in fledglings 30-40 days of age at low elevations was 1.7, while it was 4.2 at high elevations. None of the other morphological measures taken for adults (Table 2.1) differed in fledglings among elevations ($P > .13$; Mann Whitney U). The components of reproductive performance discussed in this section are summarized in Table 2.3.

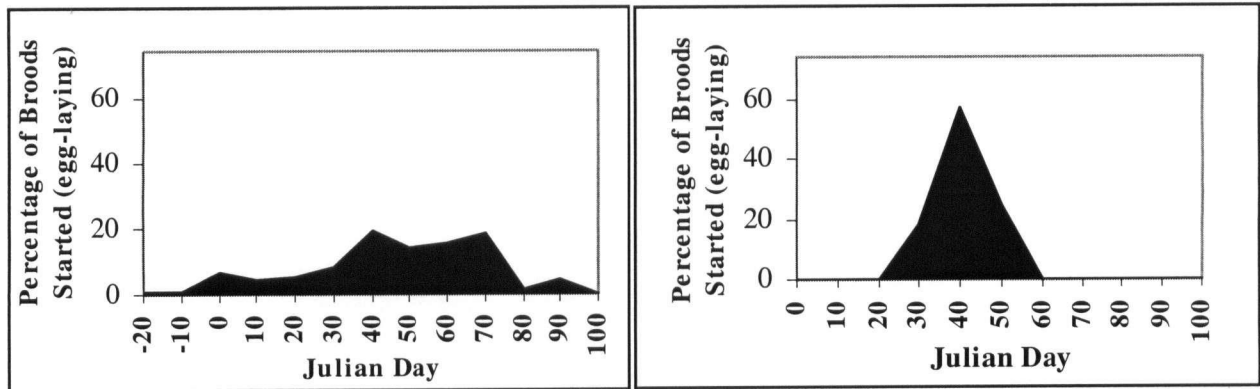


Figure 2.2. Breeding phenology for Oregon Juncos at low (1 000 m asl, left) versus high (2 000 m asl, right) elevations. Shaded area is the percentage of nests found from late April-August 30 (Julian day 0 = April 30) where eggs were laid within the corresponding Julian day (Number days after, or before, April 30). $N_{\text{low}}=72$, $N_{\text{High}}=45$.

Table 2.3 Table of various components of reproductive success in Oregon Juncos breeding in low (1, 000 m asl) and high (2, 000 m asl) elevations.

<i>Component of Reproductive Success</i>	<i>Low Elevation</i>	<i>High Elevation</i>
Onset of laying and laying phenology	Relatively Protracted See Figure 2.2	Relatively Synchronous See Figure 2.2
Mean clutch size	3.65 (N=15)	3.58 (N=5)
% Nests depredated before fledgling	38% (17/45)	58 % (7/12)
Brood size at 20-30 days after hatching	$3.25 \pm .23$ (N=72)	$2.70 \pm .2$ (N=45)
Number of broods per pair (note: unpaired individuals not considered)	0-3 broods	0-1 Brood
Fledgling mass (g) at 30-40 days	17.75 ± 1.15 (N=18 families)	20.00 ± 0.80 (N=11 families)
Fledgling intrafurcular fat score (1-5) at 30-40 days	1.70 (N=18 families)	4.20 (N=11 families)

Nest building and site selection

Nests were placed within different microhabitats at either elevation (Appendix IV). Nine of 12 nests at high elevation sites were subterranean. Seven of these nests were built in moss holes extending > 30 cm below ground level. One nest was built 20 cm into a tunnel at the base of a 1 m deep excavation, and one was found in a natural excavation between two rocks covered in moss, 50 cm below ground level. Two high elevation nests were at the bases of small willow shrubs (*Salix sp.*), and one was at the base of a white spruce sapling. These nests were built into south or southeast aspect slopes. Low elevation nests were most commonly built underneath, and close to the centre of *Shepherdia canadensis* bushes (30/45) or beneath *Juniperus* bushes (10/45). Three low elevation nests were beneath small depressions under downed woody material, and two were in excavations in the side of steep south or southeast facing depressions.

Nests at high elevations (n=12) were constructed in a highly layered fashion (Fig. 2.3). The centre of each nest was lined with hair from one or more of four different mammal species: mule deer (*Odocoileus hemionus*), black bear (*Ursus americanus*), snowshoe hare (*Lepus americanus*), and hoary marmot (*Marmota caligata*). A second layer was present below the central cup of hair that consisted mainly of lichens, mosses, and insect cocoon material. The outside of the nest was composed of dry grasses with trace amount of hair and lichens. Low elevation nests (n=45) contained similar nesting material, but in different proportions, and were built in a more homogeneous manner. The main component of low elevation nests was dry grass. Hair from elk (*Cervus elaphus*), mule deer, white-tailed deer (*Odocoileus virginianus*), and black bear, with trace amounts of lichens and mosses was integrated within the grass matrix, though it was concentrated slightly more towards the centre. The dry mass of each component within a nest was divided by the total dry mass of the nest to produce proportions of each material. Proportions of like materials were averaged within elevations, to assess the relative proportions of materials used between elevations (Figure 2.4). Low elevation birds used a greater overall mean dry mass of grass in nests than high elevation birds. High elevation birds used a greater overall mass of hair, lichens, mosses, and other materials (Figure 2.5). The mean mass of low elevation nests (all components included) was 9 g, whereas it was 10.5 g for high elevation nests.

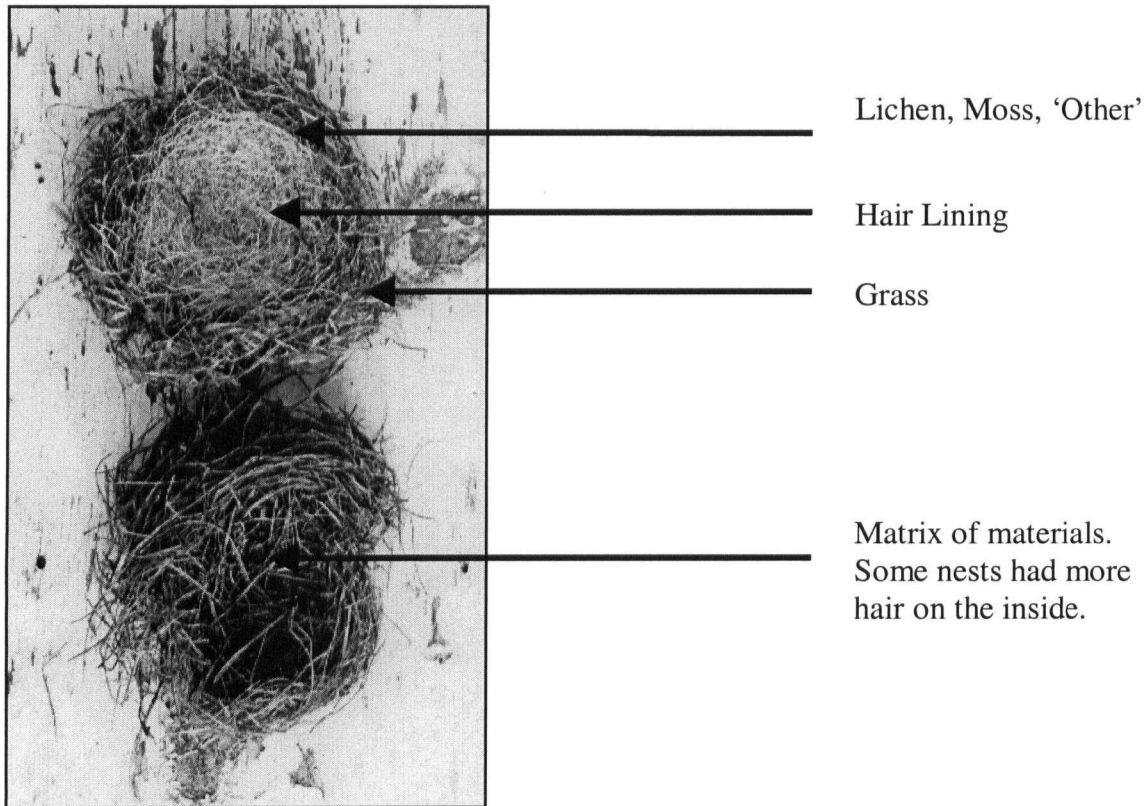


Figure 2.3. Photograph of typical low (1 000 m asl; bottom) versus high (2, 000 m asl; top) elevation junco nests. High elevation nests had distinct layers, with insulative materials placed near the centre, while low elevation nests were more homogeneous in nature. Some low elevation nests also focused hair slightly more towards the centre.

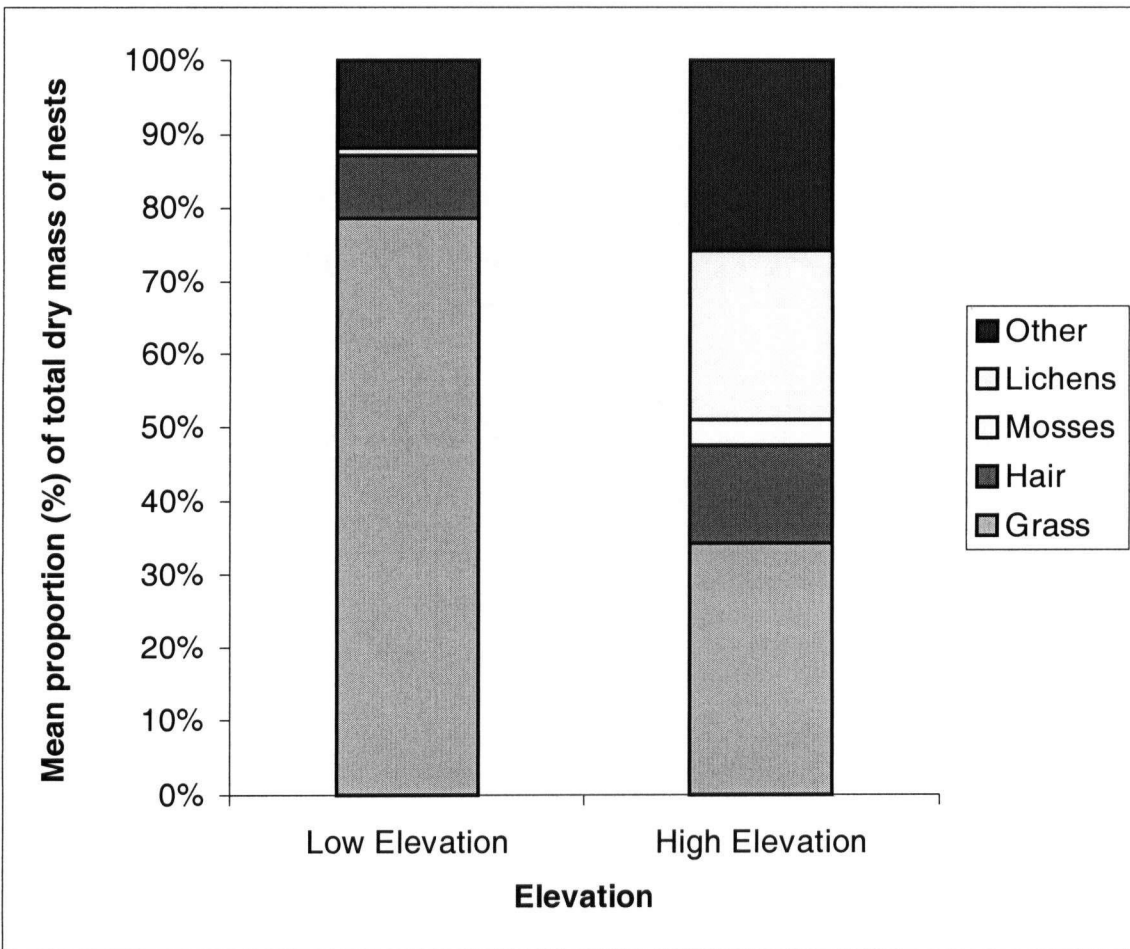


Figure 2.4 The mean proportion (percentage) of each nesting material of the total mean nest mass for low (n=45) and high (n=12) elevations. **Low Elevations (N=45):** Grass (78.6%), Hair (8.5%), Mosses (1%), Lichens (<.01), “other” (detritus, conifer needles, and twigs) (11.8%) **High Elevations (N=12):** Grass (33.9%), Hair (13%), Mosses (3.4%), Lichens (23%), Other (Bark, Twigs, detritus, conifer needles, cocoon material) (25.35%)

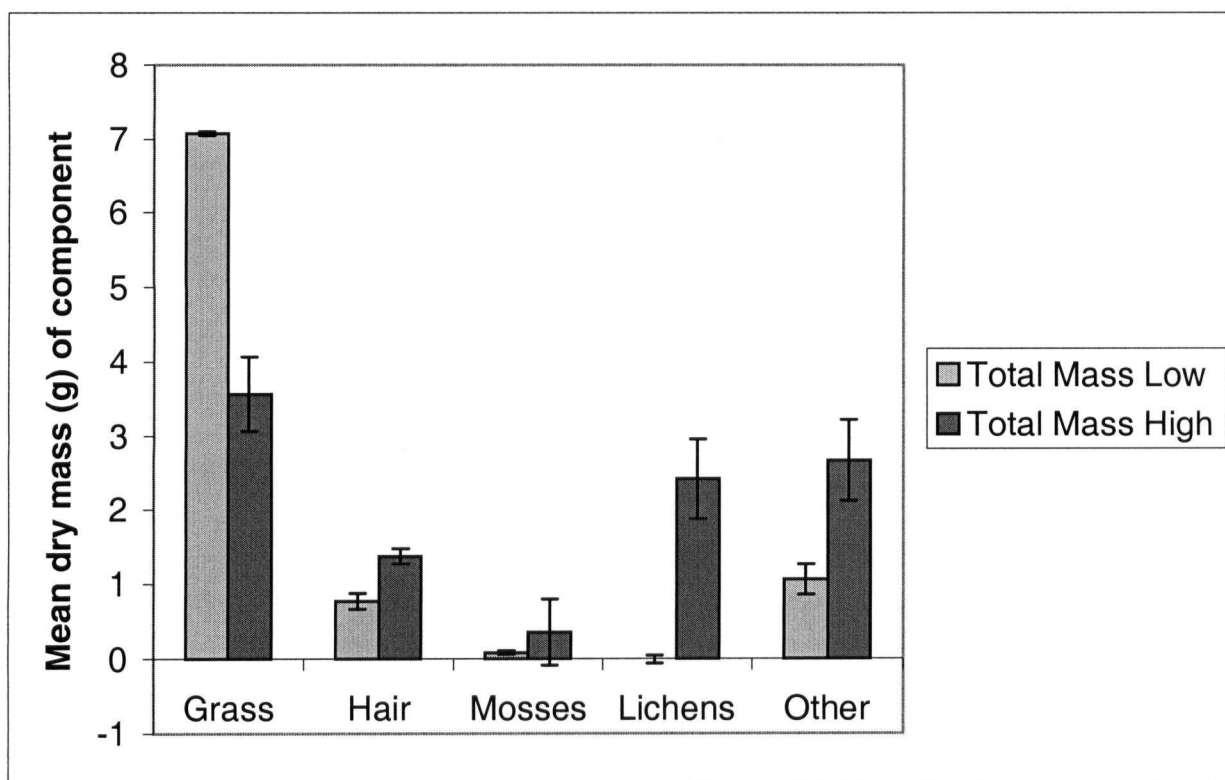


Figure 2.5 Mean dry mass (\pm SE) of components used for construction of nests at low (N = 45) versus high (N = 12) elevations. Other (low elevation) = detritus, conifer needles, twigs. Other (high elevation) = detritus, bark, twigs, conifer needles, cocoon material).

Blood parasites

Thirty-two high and 32 low elevation adult male birds caught across all 8 sites were used in this analysis. At each site, one bird was caught between the 1st -5th of each month (May – Aug), and another between the 11th -15th of each month. In addition 12 fledglings were caught at high elevations (in August) and 12 were caught at low elevations (in August). Three parasite genera were found in the blood of juncos: *Haemoproteus*, *Leucocytozoon*, and *Trypanosoma*. The most prevalent blood parasite at either elevation was *Haemoproteus*, followed by *Leucocytozoon*, and *Trypanosoma* (Table 2.4). A significantly higher proportion of low elevation birds 66% (21/32) compared to high elevation birds 28% (9/32) were infected by at least one of these parasites (Table 2.4, $P=0.002$, Fisher's Exact Test). A higher percentage of low elevation birds (34% (11/32) versus 19% (6/32) at high elevations) were infected with *Haemoproteus spp.*, but the difference was not significant (Table 2.4, $P=0.08$, Fisher's

Exact Test). Similarly, more low elevation birds (25% (8/32) versus 9% (3/32) were infected with *Leucocytozoon spp.*, again with a near significant difference (Table 2.4, $P=.07$, Fisher's Exact Test). Of these individuals, 53 % (10/19) of low elevation birds and 44 % (4/9) of high elevation birds had both *Haemoproteus* and *Leucocytozoon* parasites present in their blood. Two cases (4%) of infection with *Trypanosoma spp.* were found in low elevation birds, and none at high elevations. Thirty-four % (11/32) low elevation and 72 % (23/32) high elevation birds were not infected with any parasites. There was no relationship with date of capture and infection at low elevations ($P=.23$, $r=.33$; Pearson's r). However, at high elevations, a low proportion of individuals (2/16, 12.5%) caught between 01 May and 15 June were infected *Leucocytozoon* &/or *Haemoproteus sp.*, but between 15 June and 30 August, a significantly higher proportion (7/16, 44%) were infected ($P=.05$, Fisher's Exact Test). In samples from low elevations not used in this analysis, 2 further cases of *Plasmodium sp.* were noted. More fledglings were infected with *Leucocytozoon* at low elevations as compared to at high elevations (17% (2/12) vs 8.3 % (1/12), but the difference was not significant ($P=.39$, Fisher's Exact Test). No other blood parasites were observed in fledglings (Table 2.4).

Table 2.4 Summary of data on presence and absence of blood parasites in Oregon Juncos from low (1, 000 m asl) and high (2, 000 m asl) elevations.

Adults (ASY)	Infection/Parasite	Low (N=32)	High (N=32)
	<i>Infected</i>	21	9
	<i>Haemoproteus</i> present	*11	*6
	<i>Leucocytozoon</i> present	*8	*3
	<i>Trypanosoma</i> present	2	0
	<i>Haemoproteus</i> + <i>Leucocytozoon</i> present	10 (of 19 individuals marked with *)	4 (of 9 individuals marked with *)
	No Parasites	11	23
Fledglings	Parasite	Low (N=12)	High (N=12)
	<i>Leucocytozoon</i> present	2	1

Discussion

Of the morphological traits measured, the only difference among elevations was a longer central retrix feather length in high elevation males. Landmann and Winding (1993) also observed longer and differently shaped retrix tail feathers in high elevation bird species. Retrix feathers are used for steering and balancing, and longer feathers may stabilize birds in windy conditions at high elevations. It is unclear as to why females did not display this difference, but a larger sample size may be required to detect a statistical difference. While I did not detect differential wear of retrix feathers in males versus females, it is also possible that males experience more wear at low elevations compared to females if they move over greater distances, or spend more time foraging on rocky substrata. Female fat scores were also negatively correlated with Julian date at high elevations, whereas they were not at low elevations. Birds can alter their body mass and energy stores inversely to the amount of food available in their environment (Elkman and Hake 1990; Bednekoff *et al.* 1994; Bednekoff and Krebs 1995; Witter and Swaddle 1997). Thus, the reduction of fat may be due to an increase in food availability at high elevations during this period, and a decreased need for reserves.

High elevation nests were built in a way that suggests that juncos modify both construction and placement in order to minimize heat loss in cooler and windier environments. The subterranean placement of many nests at high elevations suggests that birds are utilizing buffered microclimates near and below the ground surface (Geiger 1965; Thompson and Whitfield 1993). Similarly, selection of nest sites in buffered microclimates at high elevations has been observed in other birds as well (Verbeek 1967; Medin 1987; Böhn and Landmann 1995). Juncos also constructed nests using a greater proportion of insulative materials, such as hair and lichens, and layered them such that insulative materials were focused in the centre of the nest nearest the heat source provided by the female. Both high and low elevation nest sites described here differ from those described by Eaton (1968) for this species in Ohio.

High elevation juncos delayed egg-laying relative to low elevation juncos, likely due to the later date of snowmelt and a need to co-ordinate hatching with productivity peaks in insects (Thompson and Whitfield 1993; Martin 2001). As a result of the delayed start and earlier finish to the breeding season, high elevation juncos only had time for a

single brood per season. Three other studies have also found fewer broods per season at high elevations (Krementz and Handford 1984; Hamann *et al.* 1989; Badyaev 1997). Further, significantly fewer fledglings were produced per brood at higher elevations. Other intra- and inter- specific studies on songbirds have found that clutch size may remain constant (*e.g.*, Hamann *et al.* 1989), or decrease (*e.g.*, Krementz and Handford 1984; Badyaev 1997) with increasing elevation. Due to the low number of high elevation nests found, the difference I observed could have been due to a lower clutch size, higher rates of predation, or to greater fledgling mortality. From the small sample of nests found at high elevations, however, clutch size did not differ between elevations. It is also possible that differential survival after 20-30 days may have occurred that I was unable to detect in this study. Also, if high elevation fledglings were less detectable, it may have been more difficult to observe all offspring over the equivalent observation period. Nest predation was also frequent at high elevations, but the sample size was low. Examining nest predation rates across elevations may be worth further study.

High elevation sites also had lower densities of breeding females. This pattern is likely due to a more patchy &/or scant distribution of resources over the landscape (Martin 2001). While decreasing density is expected with increasing elevation due to decreasing productivity, this is not always found. Densities of garden warblers (*Sylvia borin*) did not decrease with increasing elevation, and densities of alpine chats remained high with increasing elevation in the Himalayas (Landmann and Winding 1993). Further, Kollinsky and Landmann (1996) found that the density of male Black Redstarts (*Phoenicurus ochruros*) increased with elevation. These studies may, however, have been confounded by selection of non-random study plots in optimal habitat at high elevations so that mean density at that elevation was overestimated. The long movements by singing males that I observed at high sites, and more recaptures of the same male at more distant sites at high elevations, suggests that high elevation males also had larger territories, or that their habitat is unsaturated.

High elevation birds produced fewer offspring per brood of 20 – 30 days of age. They were also unable to produce a second brood, and appeared to return between years to the same sites. Thus, if there were no trade-offs that equalized the reproductive success of high versus low elevation juncos, high elevation habitats could be of inferior quality,

occupied by less competitive classes. In this system, however, I did not find a disproportionate number of birds in inferior competitive classes (smaller, younger, later arrivers; Cristol *et al.* 1990; Grasso *et al.* 1996). Kollinsky and Landmann (1996) also found no support for the idea that younger male black redstarts were forced to settle at higher elevations. Likewise, Widmer (1996, 1999) found no difference in the competitive status of garden warblers at the extremes of a 1000 m gradient in Europe. Therefore, it seems unlikely that high elevation birds are inferior competitors forced to breed at high elevations. I was only able to determine that birds arrived within the same 2-day window in the summer of 2001. If differences in arrival time as small as $\frac{1}{2}$ to 1 day influence the ability of juncos to obtain good habitat, then arrival time could still be a factor in this system. Arrival time has been shown to be significantly later at higher elevations for adult male Hermit thrushes and Townsend's warblers (Pearson and Rohwer 1998). I conclude that it is unlikely that differences in competitive abilities are associated with differences in breeding elevation. I now explore whether low elevation and high elevation birds have different reproductive strategies to aid in equalizing the lifetime reproductive success of high and low elevation birds.

The inter-annual return of birds to their site of initial capture observed at both elevations provides the first clue in support of different reproductive strategies. Natal philopatry and site fidelity of birds at high elevations were also high in other studies (Kollinsky and Landmann 1996, Widmer 1999). Returning to the same sites allows an animal to accrue local benefits. An improvement in adult and juvenile survival might balance the seasonal reproductive deficit at high elevations. I found two factors that may facilitate this improvement. High elevation adult males and fledglings had lower infection rates with blood parasites. If relief from parasites enables adults to survive longer and breed for more years, then this could aid in equalizing the lifetime reproductive success of high and low elevation birds. Blood parasites can decrease survivorship in fish directly by increasing susceptibility to predation (Vaughn and Coble 1975). In addition, there may be a trade-off between reproductive effort and the efficiency of the immune response. Parasites loads may increase during the reproductive period, as they did here at high elevations, when breeding adults spend considerable time provisioning their young and in nest and territory defence, or when breeding effort is increased experimentally (Ots and

Horak 1996, Norris *et al.* 1994, Weatherhead and Bennet 1991, 92, Rintmaki *et al.* 1999). A simpler reason for the differential susceptibility to the parasites here may be the timing of the emergence of the vectors carrying the parasites.

The two most common parasite species in this study, *Haemoproteus* and *Leucocytozoon* (family Plasmodiidae), are protozoan parasites of birds. These parasites are transmitted by a variety of biting flies that serve as vectors. Transmission of the parasite occurs when sporozoites in the salivary glands of insects enter the blood of birds when insects bite. *Haemoproteus* is primarily transmitted by insects in the families Ceratopogonidae (no-see-ums, sandflies) or Hippoboscidae (louse flies), while *Leucocytozoon* is primarily transmitted by Simuliids (black flies) (Ritchie *et al.* 1994; Roskopf and Woerpel 1996; Rintmaki 1999). The parasite *Trypanosoma* (likely *avium*), which was rare in our study, is also transmitted by members of the family Simuliidae. The principle effects of *Leucocytozoon* infection are an intravascular hemolytic anemia, weight loss, and sometimes death. *Haemoproteus* and *Trypanosoma* in birds are generally believed to be less pathogenic (Ritchie *et al.* 1994). Finally, two low elevation samples (not analysed as part of the subsample selected) contained *Plasmodium spp.*, which is transmitted by mosquitos. Although I did not sample for the presence of any of the vectors that carry these diseases, almost all insects emerged later at higher elevations, perhaps preventing exposure to the parasites for much of the season. Further, high elevation birds were at a lower density, and therefore transmission between birds may have been less likely.

High elevation fledglings were significantly larger than low elevation fledglings, and had greater intrafurcular fat reserves. This could have been the result of a timed emergence of young with insect emergence, which appeared to correspond at our sites (personal observation). Heavier young with larger fat reserves could potentially survive better (Leary *et al.* 1999; Oddie 2000), especially during their fall migration. Although young at low elevations were lighter and had less fat, they did not appear to have fault bars in their flight feathers, an indicator of nutritional stress during development (Pyle *et al.* 1987).

***How low elevation anthropogenic development and habitat loss may affect songbirds:
A thought experiment***

Given the information gathered here, what can be predicted about the effects of low elevation anthropogenic development (*e.g.*, agriculture, housing, etc.) on species like the junco? If the lower portions of the elevation range of juncos were developed to the point at which they could no longer breed in the area, a number of consequences would be expected. Reproductive output would become restricted to high elevations, habitat that, on a roughly cone-shaped mountain, has a smaller surface area over an equivalent vertical subsection. In other words, with increasing elevation, there is the problem of decreasing habitat. I have also shown that high elevations supported a lower density of individuals than low elevations. Thus, with increasing elevation, there are decreasing numbers of individuals per unit area. Further, my data also shows that high elevation birds produce fewer offspring per season. Even if populations are growing at identical rates (*e.g.* 20%), the lower absolute population numbers at high elevations will affect population size in the future, regardless of population growth rate (*e.g.*, 20% of 100 birds at low elevations versus 20 % of 20 birds at high elevations will always render relatively fewer individuals in the latter). Further, if low elevation breeders were displaced upwards by habitat loss, an increased density would result at high elevations, and we would expect to see greater resource competition. This would be especially true if other low elevation species (Appendix V) also moved to higher elevations. Similar sentiments about the importance of maintaining low elevation habitat have been expressed in studies where species diversity and numbers decreased as a function of increasing elevation (Terborgh 1977; Patterson *et al.* 1998; Goerck 1999). Disproportionate habitat loss is already occurring at low elevations, confining and pushing animals into higher elevations (Storch 2000; Martin 2001). Thus, maintaining reserves that span a range of elevations is an increasingly important conservation goal.

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CHAPTER 3: ADRENOCORTICAL SENSITIVITY IN OREGON JUNCOS (*Juncus hyemalis oregonus*) BREEDING IN LOW AND HIGH ELEVATION HABITAT

Abstract

I tested whether Oregon Juncos differed in stress levels and sensitivity to stressors across a steep elevation gradient. I compared baseline corticosterone concentration ([cort]), and increases in circulating [cort] 30 and 60 minutes after exposure to a standardized stressor in juncos breeding in low (1, 000 m asl) versus high (2, 000 m asl) elevation habitat within Jasper National Park, Alberta, Canada. In addition, I explain causes of variation within elevational treatments, and possible ecological influences on [cort]. Baseline [cort] in juncos did not differ between elevations. Stress-induced [cort] in juncos did not differ markedly among elevations during the initial stages of the stress reaction between elevations, but the degree of increase was slightly greater between 30 and 60 minutes post-capture at low elevations, but only approached statistical significance when other sources of variation were accounted for. Females had a lower adrenocortical response to stress than males, and breeding individuals had a lower response to stress than non-breeders. The influence of gender and breeding stage may correspond to an interaction between testosterone and [cort].

Introduction

A variety of physiological, social, and environmental stressors can provide proximate signals for adaptive changes, and for the orchestration of life history events. The frequent observation of similar baseline levels of stress hormones in animals residing in very different environments suggests that when individuals reach their physiological limits, behavioral modification may protect against a chronically stressed state. Further, variation in the sensitivity of animals to stressful cues suggests that sensory modification occurs according to the demands of particular reproductive strategies and environments (Crews and Moore 1986; Greenberg and Wingfield 1987; Boonstra *et al.* 1998, 2001). The sensitivity of physiological responses to stressful cues can vary between individuals because of differences in the immediate internal and external environments (*e.g.*, Wingfield 1994; Wingfield *et al.* 1995a; Astheimer *et al.* 1995). Once individual variation is accounted for, however, trends in sensitivity to stressful stimuli often still emerge at the population level (*i.e.* the response mean between two populations may differ) (Wingfield *et al.* 1992; Silverin *et al.* 1997).

Stressful stimuli, such as snowstorms, activate the adrenal tissues and result in an increase in the concentration of circulating plasma corticosterone ([cort]) in birds (called the 'adrenocortical response' to stress) (*e.g.*, Rogers *et al.* 1993). Increases in [cort] can trigger strategies designed to maximize survival by curtailing the allocation of energy from non-essential functions, such as reproduction, and funneling it back into self-maintenance (reviewed in Wingfield *et al.* 1998). During the breeding season, adrenocortical responses to storms or extreme weather may cause temporary disruption of nesting, followed by re-nesting when favorable conditions resume (Wingfield *et al.* 1997, 1998). In extreme environments, such as the high Arctic and Sonoran Desert, however, the brief breeding season limits the capacity of individuals to re-nest. Birds breeding in extreme environments may down-regulate their sensitivity to acute stressors, such as storms, so that breeding can be completed during the shorter breeding season (Wingfield *et al.* 1992; Wingfield *et al.* 1995a; Silverin *et al.* 1997; but see also Wingfield *et al.* 1995b). Further work, especially on previously unexplored systems, is required to clarify ecological bases for stress-endocrine phenomena.

The influence of Mountain elevation gradients on patterns and processes of stress endocrinology in vertebrates is poorly understood. Exploring differences in sensitivity to stress in species that span wide elevation ranges is important for a number of reasons. First, steep elevation gradients encompass growing seasons of very different lengths, and are interrupted to different degrees by stressful environmental stimuli such as storms (Appendix I, II, III). Therefore, a steep elevation gradient allows one to test the breadth of the aforementioned hypothesis about stress down-regulation in environments with different breeding season lengths and storm interruptions. Second, conditions change rapidly across mountain environments. Where a species is distributed continually over a wide elevation range, gene flow is facilitated and any differences in morphologies, life histories, behaviours, *etc.*, are most likely to be phenotypic. Therefore, comparing different traits in animals among elevations will aid our understanding of how mountain species adapt to various conditions. Finally, high elevation environments are sometimes considered to be more 'stressful' than low elevation environments due to harsher weather conditions, lower productivity, and a shorter favorable season for reproduction (*e.g.*, Sabo 1980 states: "bird species begin a sharp decline at 1100-1200 m ... as the increasing environmental stress and decreasing habitat variety selectively filter bird species"). By comparative analysis, one can test whether the conditions at high elevations cause

chronic elevation of baseline [cort], a lowered sensitivity to stress, or whether behavioral, reproductive, and morphological plasticity adapt individuals to different elevational challenges so well that stress physiology is not altered.

I investigated the adrenocortical sensitivity of Oregon Juncos along an elevation gradient in the Rocky Mountains of Alberta. Juncos in this region breed from the montane valley (1,000 m asl) to the subalpine-alpine treeline (2,000 m asl). Along this gradient, temperature and precipitation differ dramatically (Appendices I,II). Snow and hail storms are frequent throughout the breeding season at 2,000 m asl, while they are much less common and usually restricted to the month of May at 1,000 m asl (Appendices II, III). Low elevation populations begin egg-laying as early as April 17, and can continue until August 5, while high elevation populations lay eggs from May 27- June 15 (Chapter 2). Low elevation birds commonly raise two broods during the breeding season (62 % of females, Chapter I). However, high elevation birds can only produce a single brood due to the shorter favorable season for reproduction (Chapter 1). Thus, low elevation populations have time to abort nesting activities in poor conditions and to re-nest when conditions improve, subsequently protecting themselves from performing costly parental duties under prolonged stressful conditions. However, high elevation populations do not have this option, and thus their cost/benefit ratio shifts considerably. If high elevation birds get physiological cues to halt breeding, they will likely not reproduce in that year. Yet, weather data from Jasper from May-August 2000, 2001 (Table 1) indicate that high elevation birds will receive stressful cues at several points during their short breeding season. Long-term weather data at various sites at 1800-2000 m in the northern Rocky Mountains of Alberta confirm this trend (Appendix III). A high sensitivity to stressors, therefore, could interfere with the ability of high elevation birds to reproduce at all. Hence, I test the hypothesis that birds at 2,000 m asl down-regulate their adrenocortical response to stress relative to birds 1,000 m asl, due to the greater cost of high sensitivity to stress at high elevations.

Adrenocortical sensitivity to stress is likely to interact with several other factors in this system. Pair members that invest less in offspring tend to have a more exaggerated response to stress (Wingfield *et al.* 1995c; Schoech *et al.* 1998). Male and female Juncos both feed hatchlings and fledglings; males, however, do not incubate, and nest-guard less often than females (Cawthorn *et al.* 1998). Thus, males will likely have higher [cort] following exposure to

a stressor (Astheimer *et al.* 1994; Wingfield *et al.* 1995c; Silverin *et al.* 1997). In addition, males have higher levels of testosterone, a hormone known to increase both baseline and post-stress [cort] in juncos (Ketterson *et al.* 1991; Klukowski *et al.* 1997; Deviche *et al.* 2001) and other vertebrates (Boonstra *et al.* 2001). Adrenocortical sensitivity to stress can also vary at different times of the breeding season, most likely because sex hormone levels vary seasonally and interact with corticosterone secretion and bioavailability (Deviche *et al.* 2001). Therefore, I test for an influence of date of capture on baseline [cort]. The stage of breeding can also influence the corticosterone response, and the extent of sexual dimorphism in it (Romero *et al.* 1997). Thus, I also test for differences in baseline [cort], and stress-induced [cort] after exposure to a stressor in both reproducing and non-reproducing individuals. Finally, I test for correlations between baseline [cort] and body condition, age, time of day, and temperature, which also may influence the adrenocortical response (Wingfield *et al.* 1995c, 1996).

Methods

Study sites

Juncos were captured at eight sites (see Chapter 2 for locations and site descriptions) in Jasper, Alberta, between 01 May and 10 August. All male samples were collected in 2000, and half of female samples were collected in 2001. As no obvious year effect was discernable in the female samples from 2000 and 2001, data were pooled. Four low elevation sites were located within the montane valley in the Park (1,000 m asl), separated by 5-10 km. Four high elevation sites were located at the highest elevation that Juncos breed within the park (2,000 m asl), and were separated by > 18 km. No mixing of birds among sites was observed over 2 years, and adults and fledglings returned to sites of capture between years (Chapter 2).

Capture techniques, measurements, and blood sampling

Chapter 2 describes capture techniques, morphological measurements and collection of weather data.

I used the capture stress protocol (Wingfield 1997) to measure adrenocortical sensitivity to capture and handling. Adrenocortical sensitivity, as determined by increased circulating [cort] following capture and handling, can be used as an indicator of the general sensitivity of animals to other acute stressors such as storms (Astheimer *et al.* 1992; Rogers *et al.* 1993). Using capture and handling as a stressor means that all birds are stressed in a standard way, so that responses are comparable.

After capture, an initial blood sample was taken within 3 minutes by puncturing the alar vein with a needle and collecting 40 μ l of blood in a heparinized microhematocrit tube. Blood was blown out of microhematocrit tubes into centrifuge tubes and stored on ice. The first sample taken represents the baseline [cort] under prevailing conditions, as circulating levels do not rise in blood until > 3 minutes after encountering a stressor (Wingfield *et al.* 1997). Birds were then placed in a cloth holding bag and further blood samples were collected 30 and 60 minutes after capture. Blood samples were not taken from birds that were caught in cold (< -15 °C) or stormy weather (hail or extreme rain) in order to prevent mortality.

Between the first and second blood sample, birds were weighed (to \pm 0.1 g) and scored on a 0-5 nominal scale (leanest-fattest) for intrafurcular fat accumulation (Rogers and Smith 1993). Birds were sexed and aged as SY (second year) and ASY (after second year) breeders using methods of Pyle *et al.* (1987). Degree of brood patch development in females, and cloacal protuberance in males were also noted during capture. Each bird was given a numbered aluminum Fish and Wildlife Service band, and a color band combination conveying sex, age and site information.

Females captured with a brood patch, and males with full cloacal protuberance were classified as 'breeders'. 'Breeders' also included birds seen in pairs carrying food to and from a location or those still feeding newly fledged young. Females with an undeveloped brood patch and males with minimal to no cloacal protuberance were classified as 'pre-breeders'.

Corticosteroid Analysis

Tubes were centrifuged within 10 hours of sampling and plasma was collected. Plasma was stored at -20 °C and transported to the University of Washington for radioimmunoassay analysis by the author and Lynn Erckman. Corticosteroids were measured after extraction in dichloromethane (Wingfield *et al.* 1992).

Statistics

Changes in [cort] within individuals and between age groups in response to capture and handling stress were analysed using an analysis of variance for repeated measures, followed by Tukey's post-hoc tests. Kruskal-Wallis tests were used to compare male and female [cort]. Finally, an analysis of variance for repeated measures was used (using SPSS manova functions) to compare the adrenocortical response to stress among elevations and to test for interactions. Grouping variables used for the test were gender, breeding stage, and elevation to look at main

effects. The test rendered the same results when gender and breeding stage were nested by elevation. Pearson's rank correlation coefficients were used, except for fat scores, where I used Spearman's rank coefficient.

Results

Adrenocortical responses to capture stress within elevations

The trajectories of [cort] changes in male and female juncos with time after capture were similar within each elevation. Plasma [cort] increased significantly in both male and female juncos between baseline and 30- minutes post-capture at both low and high elevations (Fig. 2.1, $P < .001$ and $P < .001$ respectively; Tukey's Post Hoc tests). [Cort] in males increased only slightly between 30- and 60- minutes post-capture at high elevations, and this difference was not significant (Fig. 2.1, $P > .24$). However, there was a larger and statistically significant increase in male [cort] between 30- and 60- minutes post-capture at low elevations (Fig. 2.1, $P < .001$). Similarly, females had a non-significant increase in [cort] between 30- and 60- minutes post-capture at high elevations, but a larger and significant increase at low elevations (Fig. 2.1, $P < .05$).

Gender and age differences in the adrenocortical response to stress at either elevation

At both elevations, males had a higher [cort] than females in almost all post-capture samples (Fig. 2.1, $P < .03$, Kruskal Wallis H). The one exception was a non-significant difference in baseline [cort] among males and females at low elevations (Fig. 2.1, $H = .62$, $df = 1$, $P = .44$). Plasma [cort] did not differ between SY and ASY male juncos in any post-capture samples at either elevation [baseline: $F = 2.60$, $df = 2$, $P = .08$; 30- minute: $F = 1.22$, $df = 2$, $P = .30$; 60- minute: $F = 2.65$, $df = 2.0$, $P = .08$; ANOVA].

Breeding status and the adrenocortical response to stress

Involvement in breeding activities influenced [cort]. Since there was no interaction between elevation and breeding stage ($P > .70$), data were pooled and divided into breeders versus non-breeders of each sex. Breeding males had significantly lower baseline (Fig. 2.2, $F = 12.35$, $df = 1$, $P < .001$; ANOVA), 30-minute (Fig. 2.2, $F = 4.79$, $df = 1$, $P = .03$) and 60- minute (Fig. 2.2, $F = 4.19$, $df = 1$, $P = .045$) [cort] than pre-breeding males. Breeding females also had lower [cort] than non-breeding females, but subdivision of the small sample precluded reliable statistical testing. Finally, involvement in breeding altered the degree of sexual dimorphism in the adrenocortical response to stress. The difference between male and

female baseline, 30- and 60- min [cort] in non-breeders was 2.7 X, 1.5 X and 1.5 X, respectively, of the mean differences observed among breeders.

Other potential influences on the adrenocortical response to stress

At either elevation, baseline, 30-, and 60- minute post-capture [cort] was not closely correlated with time of capture, mass or fat score (all $P > .12$). Data used were not adjusted allometrically by a standard body size measure (tarsus length) because of cautions of Green (2001), however, when analyses were repeated with allometric adjustments, no correlations were found ($P > .15$). Temperature was not correlated with baseline or 60- minute post- capture [cort] at high or low elevations ($P > .08$). Thirty-minute post capture [cort], however, was negatively correlated with temperature at high elevations ($r = -.39$, $P = .02$). This trend was not observed in 30- minute post-capture [cort] samples from low elevations ($r = .02$, $P = .88$).

Breeding elevation and the adrenocortical response to stress

Breeding altitude had no influence on baseline ($F = .16$, $df = 1$, $P > .69$; MANOVA for repeated measures), or 30- minute post-capture [cort] ($F = .67$, $df = 1$, $P > .47$) for males and females. However, a trend was found in 60- minute post-capture for lower [cort] at high elevations ($F = 3.64$, $df = 1$, $P = .059$) in males (and $P = .057$ when temperature was included as a covariate). No significant difference was found in 60- minute post-capture [cort] in females ($F = .20$, $df = 1$, $P > .36$). No two- or three-way interactions were found between [cort] measurements and any combination of elevation, gender, or breeding stage (all $P > .17$). The statistical power for tests conducted was .76 for males and .62 for females.

High Elevation

Low elevation

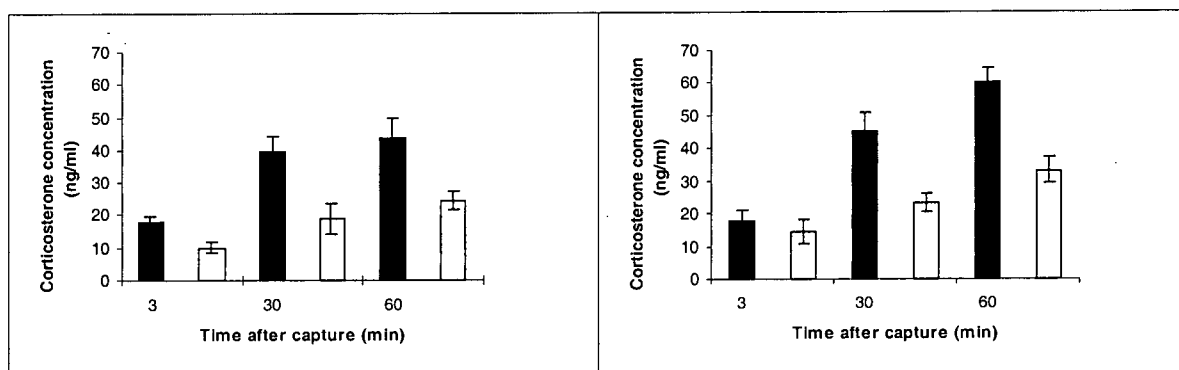


Figure 3.1 Changes in plasma [cort] (mean \pm SE) following capture and handling of male (black bars) and female (white bars) Juncos. High Elevation: N(males) = 30, N(females) = 10. Low Elevation: N(Males) = 31, N(females) = 8.

Males

Females

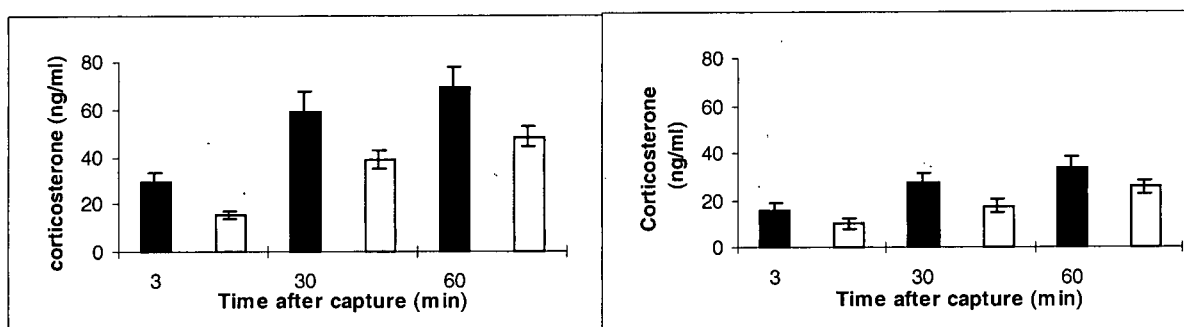


Figure 3.2. Differences in plasma [cort] (mean \pm SE) between male (left panel) and female (right panel) pre-breeding (black bars; N=11 and 6 respectively) and breeding (white bars; N=30, 12 respectively) juncos.

Discussion

Breeding elevation did not affect baseline [cort] in high and low elevation juncos, and values in the present study were similar to those reported for other passerine species (Wingfield *et al.* 1992; Romero *et al.* 1997). My data corroborate several studies that failed to find differences in baseline [cort] in conspecifics breeding in different ecological conditions (e.g. Wingfield *et al.* 1992; Astheimer *et al.* 1995; Romero *et al.* 1997). In one study, however, Wingfield *et al.* (1995b) found that males breeding in northern Japan expressed higher levels of baseline [cort] than those at a southern site. Chronic elevated baseline [cort] can cause severe problems for animals, such as immuno-incompetence, cell death in the hippocampus, reproductive failure, and the loss of muscle mass (reviewed in Wingfield *et al.* 1997). Thus, the presence of equal baseline [cort] among elevations suggests that juncos use enough “stress avoidance” adaptations (e.g., nesting in protected subterranean habitat, Chapter 2) at either elevation so that neither environment induces chronically elevated baseline [cort]. Likewise, Belovsky (1986) and Carey (1986) found that behavioral modifications allow individuals to survive once they reach their physiological limits of tolerance. Weathers (1997) also found that the principal response to temperature stress in birds is behavioral avoidance rather than to overcome it physiologically. Alternatively, poor weather may not be the primary cause of chronic stress in this system, explaining differences among studies in results. For instance, Boonstra *et al.* (1998, 2001) found that immune function and baseline cortisol levels (an equivalent mammalian stress hormone to avian ‘corticosterone’) change as predation risk fluctuates. Predation risk has not typically been explored in studies of field endocrinology in birds; perhaps it could explain some contradictory patterns in related literature.

An increase in [cort] was observed between 30- and 60- minutes, regardless of elevation or sex. The 60- minute post-capture [cort] was statistically different from the 30- minute [cort] at low elevations in both males and females, but not statistically different at high elevations. When known sources of variation were accounted for, however, only a borderline effect of breeding elevation was found at 60 minutes post-capture ($P=.059$). Thus, there is only a hint of suppression of the sensitivity of the stress response here in high elevation males, and ambiguity about the stress response in females due to a low statistical power. Increasing the power of the statistical tests conducted through higher sample sizes, especially for females, may provide more conclusive evidence for a reliable but weak adrenocortical suppression. Three studies have

found that down-regulation of the adrenocortical response to stress in certain birds occurs in short, severe breeding environments (Astheimer *et al.* 1992; Wingfield *et al.* 1992; Wingfield *et al.* 1995a; Silverin *et al.* 1997). The first two of these studies compared the stress responses among birds during the pre-breeding, winter season to that in the breeding phase in severe environments, and obtained similar results to my pre-breeder/breeder comparison (although the seasonal spread was larger). Silverin *et al.*'s (1997) study was conducted similarly to mine, as they investigated two populations of willow warblers (*Phylloscopus trochilus*) breeding at different latitudes in Sweden. Their data support the down-regulation hypothesis, as a reduced adrenocortical response to stress was found in birds breeding in northern Sweden, where conditions were more severe and the nesting season was shorter than in southern Sweden. However, a similar latitudinal comparison of bush warblers (*Cettia diphone*) breeding in Japan (Wingfield *et al.* 1995b) found that male bush warblers breeding in northern sites, which were relatively severe and had a shorter nesting season, showed a greater response to stress than those breeding in southern sites. My results show only a hint of decreased sensitivity of the adrenocortical response at high elevations, but they oppose the findings of Wingfield *et al.* (1995b).

I found three statistically significant results with regard to sex, breeding status and the adrenocortical response: 1) Females had significant reductions in baseline and stress-induced [cort] compared to males, 2) Pre-breeders of both sexes generally had a higher adrenocortical response than breeders, and 3) Sexual dimorphism of the stress response was smaller in breeders compared to non-breeders. Trends in other passerine species support the first of these findings, that females have lower baseline and stress-induced [cort] than males in general (Wingfield *et al.* 1982; Wingfield *et al.* 1995c; Astheimer *et al.* 1994; Silverin *et al.* 1997). My second finding is supported by studies showing that baseline [cort] in juncos (Deviche *et al.* 2000) and other passerines (Wingfield and Farner 1978; Silverin and Wingfield 1982) is elevated early in the breeding season. Deviche *et al.* (2001), found that [cort] in male Juncos was greater during the early compared to late breeding season, and greater in males than in females. Finally, studies on white-crowned sparrows (*Zonotrichia leucophrys gambelii*) at different stages of the breeding season also suggest that breeding stage plays a major role in the extent of sexual dimorphism in the adrenocortical response (Wingfield *et al.* 1982; Astheimer *et al.* 1994; Romero *et al.* 1997).

Differences between non-breeders and breeders, males and females, and degree of sexual dimorphism may be explained by an interaction between testosterone and corticosterone. Administration of testosterone to juncos increases baseline [cort] (Ketterson *et al.* 1991) and stress-induced [cort]. (Schoech *et al.* 1999) [cort]. Deviche *et al.* (2001) found that corticosterone binding globulins in juncos, which control the bioavailability of corticosterone, were up-regulated by testosterone, and thus that [cort] may track levels of plasma testosterone (Klukowski *et al.* 1997; Deviche *et al.* 2001). Testosterone in juncos and other songbirds is elevated during the early pre-breeding period (Deviche *et al.* 2000, 2001; Wingfield and Farner 1978; Silverin and Wingfield 1982). Further, females of this species have low or undetectable plasma testosterone levels (Deviche and Gullledge 2000). A decrease in testosterone, and hence [cort] could also explain a decreased sexual dimorphism in breeders, as testosterone decreases in males later in the season, but stays virtually undetectable in females throughout breeding (Deviche *et al.* 2001). While testosterone was not measured during my study, I have no reason to suspect that well-established seasonal and sex-linked testosterone patterns for this species would not apply to my particular system.

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CHAPTER 4: GENERAL DISCUSSION

This study has both supported and refuted previously described trends in traits that shift with breeding elevation in songbirds, while supplying much new information. My findings contribute to a more complete understanding of songbirds that live and breed over wide elevation gradients. The main findings of thesis are:

- Reproductive activities were delayed at high elevations
- Fewer broods were produced seasonally at high elevations
- Mean brood size at 20-30 d was smaller at high elevations
- Densities of breeding pairs were lower at high elevations
- Adults and fledglings returned to the same sites between years at both high and low elevations
- Neither elevation occupied by proportionally high number of young, or small ('loser' individuals)
- Longer central retrix feathers were found in high elevation males
- Intrafurcular fat decreased in females with advancing date at high elevations
- Heavier fledglings with more intrafurcular fat occurred at high elevations
- Nest placement and construction differed among elevations
- Fewer birds were infected with blood parasites at high elevations
- No difference in baseline levels of the stress hormone, corticosterone, occurred in juncos across elevations
- The later stage of the adrenocortical response to stress was slightly diminished at high, compared to low, elevations. (Within sites, lower levels of corticosterone were observed in males versus females and in breeders versus pre-breeders)

Some of my findings have been observed in prior studies. Delayed phenology of nesting is a universal trend in birds breeding over a continuum of elevations (Verbeck 1967; Beason 1995; Krementz and Handford 1984; Badyaev 1997). Also, other studies have found fewer offspring per brood are produced at high elevations (*e.g.*, Krementz and Handford 1984; Badyaev 1997). Nest construction and placement in juncos differed among elevations, as in other bird species that modify nest placement among elevations

(Böhn and Landmann 1995; Cody 1985; Landmann and Winding 1995b; Martin 2001). However, a thorough description of differences in nest construction by a single species among elevations had not been done prior to this study. I found that retri length was longer in male juncos at high elevations, similar to other studies that have noted differences in retri shapes at higher elevations in other taxa (Landmann and Winding 1993, 1995a,b). I observed a high proportion of individuals returning to their site of capture between years, supporting patterns of philopatry seen in other birds at both low and high elevations (Kollinsky and Landmann 1996; Widmer 1999). Densities of birds here were substantially lower at higher elevations, supporting three other studies (*e.g.*, Terborough 1977; Patterson *et al.* 1998; Goerck 1999), but contradicting three others (Landmann and Winding 1993; Kollinsky and Landmann 1996; Widmer 1999).

Other findings in my thesis are new to the emerging field of mountain ecology. First, this thesis challenges a long-standing conjecture that high elevation environments are inferior habitats, as they are not populated with inferior competitors. Other recent studies also refute the idea that high elevations are home to less competitive individuals (*e.g.*, Widmer 1996; Kollinsky and Landmann 1996). Therefore, the classification of high elevations as relatively “more stressful” (*e.g.*, Sabo 1980) than low elevations may be premature. I believe that the situation is more complicated than has previously acknowledged. My study suggests that individuals at either elevational extreme may follow different lifetime reproductive strategies. As mentioned above, there was lower offspring production at high elevations. Females also experienced a decreasing fat score throughout the season at high elevations. However, adult males at high elevations probably benefited from lower levels of the blood parasites *Haemoproteus*, *Leucocytozoon*, and perhaps *Trypanosoma spp.* This supports the idea that high elevation habitats are relatively “sterile” (*e.g.*, Stabler *et al.* 1974; Braun *et al.* 1993). This study strengthens the argument greatly by providing data on low elevation birds of the same species for direct comparison. High elevation birds also produced heavier offspring with greater intrafurcular fat scores than low elevation birds. These traits can contribute to higher survival of offspring (Leary *et al.* 1999; Oddie 2000). Investigation of further costs and benefits, such as relative predation pressure on adults and nests among elevations, is warranted.

Based on the theoretical considerations outlined in chapter 3, I also explored a previously unexplored mechanism for adaptation in elevationally expansive songbirds: variation in the adrenocortical response to stress. Differences in the concentration of corticosterone following a standard stressor were mainly due to factors within sites. Most notable were higher levels of corticosterone in males versus females and in pre-breeders versus breeders. When these contributors to variation were accounted for, a small difference ($P = .06$) in the adrenocortical response to stress emerged between elevations. Low elevation birds tended to have a relatively lower increase in corticosterone between 30 and 60 minutes post-capture. This provides some support for the idea that the adrenocortical response to stress is lowered in high elevation birds. Further exploration of this idea may be worthy, but the effect size here was small compared to effect sizes in studies of birds in other extreme environments. High sample sizes and comparisons of multiple species breeding over wide elevation gradients are recommended due to the large amount of inherent variability in the stress response among individuals.

This study has produced new information on birds that breed over wide elevation gradients. However, it has also raised many questions that need to be answered in future research on similar systems. Some of these questions are listed below:

- 1) Are the trends described present in other songbirds that breed over wide elevation gradients?
- 2) Do the “benefits” noted here at high elevations translate into increased survival of adults and fledglings?
- 3) What are the environmental causes of differences in fledgling size prior to fall migration (dietary differences versus different degrees of parental care)?
- 4) Do the traits that were found to vary along the elevation gradient confer an advantage for individuals within each local environment (*i.e.*, are they adaptive)?
- 5) Are there other costs and benefits that vary with elevation (*e.g.*, gut parasites, predation risk)?
- 6) Are there differences in genetic heterozygosity in populations among elevations (see Zammuto and Millar 1985 for rationale)?

- 7) Higher sample sizes of nests from high elevations would allow for comparisons of growth rates, parental care, and nest predation measures. For the system I examined, obtaining a large sample size of nests would be difficult, but data could be accumulated over multiple years. Alternatively, a comparative study of another songbird that spans a wide elevation gradient (*e.g.*, American Robin, *Turdus americanus*), and where nests are more easily found, would be useful.

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Appendix I. Mean temperature and relative humidity (%). Measurements were taken using Hobo data loggers placed 1 m from the ground on a tree at sites between the 7th and 21st of each month.

Temperature:

Elevation & Mean <i>2000</i>	<i>May</i>	<i>June</i>	<i>July</i>	<i>Seasonal</i> <i>Mean</i>	<i>Difference</i> <i>between elevations</i>
Low Mean_{N=15}	6.99	9.05	15.00	10.34	6.12
High Mean_{N=15}	0.60	4.36	7.70	4.22	
<i>2001</i>					
Low Mean_{N=4}	9.19	10.00	15.75	11.65	4.97
High Mean_{N=4}	3.38	5.60	11.06	6.68	

Relative Humidity (%):

Elevation & Mean 2000	<i>May</i>	<i>June</i>	<i>July</i>	<i>Seasonal</i> <i>Mean</i>	<i>Difference between</i> <i>elevations</i>
Low Mean_{N=10}	66.661	87.549	80.70	78.31	12.61
High Mean_{N=10}	87.416	98.016	87.35	90.93	
<i>2001</i>					
Low Mean_{N=10}	6.20	90.00	76.77	57.66	12.67
High Mean_{N=10}	63.64	71.44	75.91	70.33	

Appendix II. Number of snowstorm and hail events in the montane valley (1, 000 m) and the subalpine treeline (2, 000 m) in May, June and July within Jasper National Park in 2000, 2001.

<i>Elevation</i>	<i>May</i> <i>2000</i>	<i>May</i> <i>2001</i>	<i>June</i> <i>2000</i>	<i>June</i> <i>2001</i>	<i>July</i> <i>2000</i>	<i>July</i> <i>2001</i>
Low elevation	2	1	0	0	0	0
High elevation	4	3	6	5	2	1

Appendix III. Long-term data series (1976-2000) summarized from all available raw data from May 1 – August 30, provided by Environment Canada from weather stations at 1800-2000 m asl elevation sites in the northern Rocky Mountains of Alberta, Canada. Low elevation data is from Environment Canada for the Jasper National Park montane valley. High elevation weather station site locations used to produce averages are listed below. (NA denotes “data not available”).

Station name	Lat	Long	Elevation	Aspect
TORRENS	54.3111	-119.682	1814.7	NE
PIGEON MNT	51.0458	-115.067	1828.8	82 O/3
COPTON	54.1821	-119.419	1859.7	82 M/3
MOCKINGBIRD HILL	51.4248	-115.071	1906.6	82 O/6
BASELINE	52.1314	-115.428	1907.5	82 B/3
BLUE HILL	51.705	-115.224	1987	82 O/11
BARRIER LAKE	51.0481	-115.079	2020.5	82 O/3
CLINE	52.178	-116.411	2049.5	83 C/1
KISKA	52.2352	-116.149	2070	83 C/1
GRAVE FLATS	52.8879	-116.991	2076	83 C/15
BALDY	52.5316	-116.125	2082.1	83 C/9
KANANASKIS	50.6127	-115.068	2128.9	summit
MNT KIDD	50.9121	-115.17	2141	82 J/14
ADAMS CREEK	53.7254	-118.567	2177.63	summit

	Mean Temp (°C)	Ave Max Temp	Ave Min Temp	Snow (mm)	Rain (mm)	Hail (mm)	Ave # Snow Storms	Ave # Hail Storms
Low Elevation	14.9 (1989- 1999)	NA	NA	17 (1963- 1982)	250 (1989- 1999)	0.1 (1963- 1981)	.13 (1989- 1999)	0.00001 (1989- 1999)
High Elevation	NA	12.67 (1976- 2000)	3.86 (1976- 2000)	42 (1976- 2000)	343 (1976- 2000)	1.7 (1976- 2000)	6 (1976- 2000)	1.34 (1976- 2000)

Appendix IV: Summary table of nest selection variables measured for high and low elevation nests (measurements used suggested and described by Pyle *et al.* 1987, Chapter 2). L= Low (N=45), H=High (N=12)

	Plant Height (cm)	Nest Depth (mm)	Excavation Depth (mm)	Excavation Diameter (mm)	Canopy (%)	Support Branch	Nest dist. to plant centre (cm)	Exc Diam.	DBH (mm)
L	86 ± 12.7	36.3± 5.5	50.1± 1.9	129.1± 4.6	18.5%	1-2	31.3± 13.4	129± 4.6	3.64± 2.7
H	25 ± 13.4	40.1± 7.0	73.8± 5.5	149.0± 11.2	38%	0	0	149.0 ± 11.2	4.55± 1.5

Appendix V. Songbird species and their abundance status (rare, moderate, or common) from 2 low elevation (1,000 m asl) and 2 high elevation (2,000 m asl) sites monitored systematically from 01 May – 20 August 2001. Further analysis if species richness and diversity at all sites was done as part of M. Bandura's undergraduate research project. Results of her analysis can be found at: http://www.geocities.com/melissa_bandura/

	Low: LHW	Low: LSN	High: HCI	High: HMA
Common	<ul style="list-style-type: none"> Red-breasted nuthatch (<i>Sitta canadensis</i>) Mountain chickadee (<i>Parus gambeli</i>) Black-capped chickadee (<i>Parus atricapillus</i>) Chipping sparrow (<i>Spizella passerina</i>) American robin (<i>Turdus migratorius</i>) Yellow-rumped warbler (<i>Dendrica coronata</i>) Ruby-crowned kinglet (<i>Regulus calendula</i>) Common raven (<i>Corvus corax</i>) American crow (<i>Corvus brachyrhynchos</i>) Song sparrow (<i>Melospiza melodia</i>) Hermit thrush (<i>Catharus guttatus</i>) Swainson's thrush (<i>Catharus ustulatus</i>) Golden-crowned kinglet (<i>Regulus satrapa</i>) Solitary vireo (<i>Vireo solitarius</i>) 	<ul style="list-style-type: none"> Chipping sparrow (<i>Spizella passerina</i>) White-throated sparrow (<i>Zonotrichia albicollis</i>) Yellow-rumped warbler (<i>Dendroica coronata</i>) American robin (<i>Turdus americanus</i>) Mountain chickadee (<i>Parus gambeli</i>) Black-capped chickadee (<i>Parus atricapillus</i>) Ruby-crowned kinglet (<i>Regulus calendula</i>) Golden-crowned kinglet (<i>Regulus satrapa</i>) Red-breasted nuthatch (<i>Sitta canadensis</i>) American crow (<i>Corvus brachyrhynchos</i>) Common raven (<i>Corvus corax</i>) 	<ul style="list-style-type: none"> Golden-crowned kinglet (<i>Regulus satrapa</i>) Ruby-crowned kinglet (<i>Regulus calendula</i>) Chipping sparrow (<i>Spizella passerina</i>) Yellow-rumped warbler (<i>Dendrica coronata</i>) Black-capped chickadee (<i>Parus gambeli</i>) American Robin (<i>Turdus migratorius</i>) Red-breasted nuthatch (<i>Sitta canadensis</i>) Clark's nutcracker (<i>Nucifraga columbiana</i>) American crow (<i>Corvus brachyrhynchos</i>) Common raven (<i>Corvus corax</i>) 	<ul style="list-style-type: none"> Ruby-crowned kinglet (<i>Regulus calendula</i>) Gray jay (<i>Perisoreus canadensis</i>) Clark's nutcracker (<i>Nucifraga columbiana</i>) Red-breasted nuthatch (<i>Sitta canadensis</i>) Yellow-rumped warbler (<i>Dendroica coronata</i>) Chipping sparrow (<i>Spizella passerina</i>) Black-capped chickadee (<i>Parus gambeli</i>) Mountain chickadee (<i>Parus gambeli</i>)

	Low: LHW	Low: LSN	High: HCI	High: HMA
Moderate	<ul style="list-style-type: none"> Gray jay (<i>Perisoreus canadensis</i>) Cedar waxwing (<i>Bombycilla cedrorum</i>) Pine siskin (<i>Carduelis pinus</i>) American Redstart (<i>Setophaga ruticilla</i>) 	<ul style="list-style-type: none"> Red-eyed vireo (<i>Vireo olivaceus</i>) Solitary vireo (<i>Vireo solitarius</i>) Hermit thrush (<i>Catharus guttatus</i>) 	<ul style="list-style-type: none"> White-crowned sparrow (<i>Zonotrichia leucophrys</i>) Hermit thrush (<i>Catharus guttatus</i>) Swainson's thrush (<i>Catharus ustulatus</i>) Winter wren (<i>Troglodytes troglodytes</i>) Pine siskin (<i>Carduelis pinus</i>) 	<ul style="list-style-type: none"> Golden-crowned kinglet (<i>Regulus satrapa</i>) Hermit thrush (<i>Catharus guttatus</i>) Varied thrush (<i>Ixoreus naevius</i>) Swainson's thrush (<i>Catharus ustulatus</i>) Wilson's warbler (<i>Wilsonia pusilla</i>) American tree sparrow (<i>Spizella arborea</i>) Pine siskin (<i>Carduelis pinus</i>)
Rare	<ul style="list-style-type: none"> Warbling vireo (<i>Vireo gilvus</i>) White-winged crossbill (<i>Loxia leucoptera</i>) Barred owl (<i>Strix varia</i>) Red-tailed hawk (<i>Buteo jamaicensis</i>) Magpie (<i>Pica pica</i>) Vesper sparrow (<i>Poocetes gramineus</i>) Wilson's warbler (<i>Wilsonia pusilla</i>) Townsend's warbler (<i>Dendroica townsendi</i>) 	<ul style="list-style-type: none"> Lincoln's sparrow (<i>Melospiza lincolni</i>) Clark's nutcracker (<i>Nucifraga columbiana</i>) Swainson's thrush (<i>Catharus ustulatus</i>) Pileated woodpecker (<i>Dryocopus pileatus</i>) Pine siskin (<i>Carduelis pinus</i>) Barred owl (<i>Strix varia</i>) Gray jay (<i>Perisoreus canadensis</i>) Common redstart (<i>Setophaga ruticilla</i>) Merlin (<i>Falco columbarius</i>) 	<ul style="list-style-type: none"> Lincoln's sparrow (<i>Melospiza lincolni</i>) Fox sparrow (<i>Passerella iliaca</i>) White throated sparrow (<i>Zonotrichia albicollis</i>) Wilson's warbler (<i>Wilsonia pusilla</i>) Townsend's warbler (<i>Dendroica townsendi</i>) Blackpoll warbler (<i>Dendroica striata</i>) Gray-crowned rosy finch (<i>Leucosticte arctoa</i>) Ovenbird (<i>Seiurus aurocapillus</i>) Three-toed woodpecker (<i>Picoides tridactylus</i>) Stellar's Jay (<i>Cynocitta stelleri</i>) 	<ul style="list-style-type: none"> Winter wren (<i>Troglodytes troglodytes</i>) Olive-sided flycatcher (<i>Contopus borealis</i>) Alder flycatcher (<i>Empidonax alnorum</i>) Lincoln's sparrow (<i>Melospiza lincolni</i>) Solitary vireo (<i>Catharus ustulatus</i>) Pine grosbeak (<i>Pinicola enucleator</i>) Blue grouse (<i>Dendragapus obscurus</i>) White-winged crossbill (<i>Loxia leucoptera</i>) Black swift (<i>Cypseloides niger</i>)