

**LIFE HISTORY TRADEOFFS, INCUBATION BEHAVIOR AND
CONSERVATION OF HORNED LARKS (*Eremophila alpestris*)**

by

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ABSTRACT

Nearly 30 percent of the earth's terrestrial surface is mountainous and despite representing a large proportion of the planet's protected areas, the ecology of vertebrates in high elevation areas have received little attention from researchers and managers. As human land use expands and low elevation habitat continues to be disproportionately developed, high elevation habitat may provide important areas of refuge for an increasing number of alpine generalist species. I studied two subspecies of horned larks (*Eremophila alpestris articola* and *E. a. strigata*) that breed at high elevation and latitude in British Columbia, Canada and at low elevation and latitude in Washington, USA, respectively. I addressed the general question of how the life history of alpine breeding songbirds might differ from their low elevation conspecifics and I showed that life history variation can be found even among closely related groups. Overall, my results were consistent with other comparative demographic studies which suggest that alpine vertebrate populations tend to show survivor life history strategies when compared to their low elevation counterparts. In addition, population growth rates were stable for *E. a. articola* suggesting that this subspecies is well adapted to the challenges of breeding in an alpine environment. *E. a. strigata*, however, is declining rapidly and the remaining breeding habitats in Washington do not support stable populations. I used demographic models to show that within reasonable ranges for each vital rate (fecundity, adult and juvenile survival), management actions that target a single rate independently are unlikely to result in a stable or recovering population. However, if all vital rates are increased simultaneously it may be possible for streaked horned lark populations to stabilize or grow and management actions that target multiple vital rates should be prioritized.

Finally, to further investigate how *E. a. articola* have adapted to their harsh alpine environment I examined how they modify their incubation behavior in response to changes in ambient temperatures which were generally well outside the range of temperatures that are optimal for normal embryonic development. I found that females spent less total time on the nest as ambient temperature increased to 12-13 degrees C. Ambient temperature had less influence on the total time a female spent incubating above 12-13 degrees C. Females adjusted the amount of time spent incubating by varying the frequency rather than the duration of recesses and even at very low ambient temperatures they appeared to shift their investment toward the survival of their eggs by increasing the total time spent on the nest instead of taking longer or more frequent foraging bouts.

Although it is often assumed that alpine areas represent relatively unproductive environments, the results of my thesis indicate that high elevation areas may in fact be productive breeding habitat for some songbirds and point to the potential of alpine areas to serve as refuge for alpine generalist songbird species as low elevation habitat disappears. Future studies that examine a range of species from alpine specialists to alpine tolerant species will help us to predict with more generality which groups of songbirds are more or less able to survive and reproduce at high elevations.

TABLE OF CONTENTS

ABSTRACT.....	ii
TABLE OF CONTENTS.....	iv
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
LIST OF PHOTOS.....	x
ACKNOWLEDGEMENTS.....	xi
DEDICATION.....	xiii
CO-AUTHORSHIP STATEMENT.....	xiv
CHAPTER 1: GENERAL INTRODUCTION AND THESIS OVERVIEW.....	1
Thesis Objectives.....	4
Study Species.....	4
Study Area.....	6
Thesis Overview.....	7
References.....	14
CHAPTER 2: LIFE HISTORY TRADEOFFS IN TWO SUBSPECIES OF HORNED LARK ACROSS A LATITUDINAL AND ELEVATIONAL GRADIENT.....	18
Introduction.....	18
Methods.....	22
Study site and study species.....	22
Data collection.....	22
Demographic rates of horned larks.....	24
Data Analysis.....	27
Results.....	29
Discussion.....	33
Acknowledgements.....	46

References.....	47
CHAPTER 3: EVALUATING MANAGEMENT SCENARIOS FOR THE ENDANGERED STREAKED HORNED LARK: INSIGHTS FROM DEMOGRAPHIC MODELS.....	
Introduction.....	55
Methods.....	58
Study site and study species.....	58
Data collection.....	59
Estimation of vital rates.....	60
Simulating changes in population growth.....	61
Results.....	63
Discussion.....	65
Management implications.....	71
Acknowledgements.....	81
References.....	82
CHAPTER 4: THE INFLUENCE OF AMBIENT TEMPERATURE ON SONGBIRD INCUBATION BEHAVIOR IN AN ALPINE ENVIRONMENT	
Introduction.....	89
Methods.....	93
Study site and study species.....	93
Data collection.....	93
Data analysis.....	94
Results.....	97
Ambient temperature and total minutes on the nest.....	98
Ambient temperature and recess frequency.....	98
Ambient temperature and recess duration.....	99
Ambient temperature and on-bout duration.....	99
Discussion.....	100
Acknowledgements.....	117
References.....	118

CHAPTER 5: CONCLUSIONS.....	124
References.....	130
APPENDIX 1.....	134
APPENDIX 2.....	135

LIST OF TABLES

Table 2.1. Demographic rates of <i>E. a. articola</i> (2003-2006) and <i>E. a. strigata</i> (2002-2005); dates are Julian dates with day 1=January 1, data are means \pm SE or proportions (with <i>n</i> in parentheses). Where they were possible, a priori predictions are given. Statistically significant outcomes after Bonferroni correction are in bold.....	39
Table 2.2. Model rankings from program MARK (White and Burnham 1999) to estimate apparent survival (ϕ) and re-sighting probabilities (<i>p</i>) for <i>E. a. articola</i> and <i>E. a. strigata</i> adults. Models included groups for adult males and females. The period symbol (.) means that the parameter was held constant in the model.....	42
Table 3.1. Values of vital rates for streaked horned larks in western Washington from 2002-2005 and the value needed to give a stable streaked horned lark population if only one vital rate is changed at a time and the other two are held constant. For comparison, values are given for pallid horned larks in northern British Columbia from 2003-2006. Data on current vital rates are from Chapter 2.....	73
Table 3.2. Proposed management actions and techniques for streaked horned larks and their predicted effect on fecundity, adult survival and juvenile survival (+ + indicates a large positive effect, + indicates a smaller positive effect).....	74
Table 4.1. Summary of model selection results for incubation rhythms for horned larks in alpine habitat in British Columbia in 2005 and 2006. All models include nest as a random factor and the fixed factors shown in Table 4.2	108
Table 4.2. General linear mixed model predicting the total number of minutes a female horned lark spends on the nest, the frequency recesses and recess and on-bout duration between 06:00-20:00 h. Nest was included in the model as a random effect, parameters are from the model with the most support using AIC model selection. Parameters with $ t > 1.96$ have 95% confidence intervals that do not include 0 (in bold).....	110

LIST OF FIGURES

Figure 1.1. Survey wide count data for horned larks from the North American Breeding Bird Survey showing a 50% decline in the mean number of individuals detected per survey from 1966-2007. Data are from Sauer et al. 2008.....	10
Figure 1.2. Study area for <i>E. a. articola</i> located on Hudson Bay Mountain, Smithers, British Columbia, Canada (Map prepared by Matt Tomlinson).....	11
Figure 1.3. Study areas for <i>E. a. strigata</i> located in the Puget Lowlands, Washington, USA (Map prepared by Matt Tomlinson). Field data collected by S.F. Pearson, Washington Department of Fish and Wildlife	12
Figure 2.1. Frequency distribution of estimates of lambda (λ) for two horned lark subspecies, <i>E. a. articola</i> in alpine habitat in British Columbia, Canada, 2003-2006 and <i>E. a. strigata</i> in grasslands and sandy shorelines in Washington, USA, 2002-2005. The bold line indicates $\lambda = 1$, values to the right of the line show the proportion of simulations that predicted a growing population. Forty seven percent of the simulations predicted a growing population for <i>E. a. articola</i> , while none predicted a growing population for <i>E. a. strigata</i> ...	43
Figure 2.2. Life-Stage Simulation Analysis for <i>E. a. articola</i> and <i>E. a. strigata</i> . Light grey diagonal lines are regression lines, horizontal lines are shown at $\lambda = 1$, the value at the intercept of the two lines gives the parameter value needed to support a stable population. Vertical solid and dashed lines show the estimated mean value for each vital rate and its standard errors. For <i>E. a. articola</i> the mean values fall on the intercept of the two lines indicating that the population is stable. In all cases for <i>E. a. strigata</i> the vital rate estimates fall to the left of the intercept of the two lines indicating that the population is declining. The r^2 values show the proportion of the variation in λ over all simulations that is explained by variation in each vital rate.....	44
Figure 3.1. Predicted values of lambda for streaked horned larks with successive 10 percent increases in each vital rate. Each point represents a 10 percent increase in the vital rate, only one vital rate was manipulated at a time. The solid horizontal line represents lambda=1.....	77
Figure 3.2. Predicted values of fecundity and lambda for streaked horned larks with successive 10 percent increases in breeding success (the number of fledglings produced per egg laid) and with 10 percent decreases in the reneating interval. Each point represents a 10 percent change in the rate, only one rate was manipulated at a time. The solid horizontal line represents lambda=1.....	78

Figure 3.3. Predicted values of lambda for streaked horned larks as fecundity and juvenile survival are simultaneously increased by increments of 10 percent starting with current empirical levels of 0.91 for fecundity and 0.16 for juvenile survival. X and Y axis show the value for fecundity and juvenile survival after successive increases of 10 percent. Adult survival of female streaked horned larks was held constant at its current empirical level of 0.47 (a), increased by 10 percent to 0.52 (b) and increased to the level of pallid horned larks in British Columbia (0.65; c).....79

Figure 4.1. Temperature fluctuations recorded in a single horned lark nest over the course of one day. Steep drops in temperature indicate departures of the female from the nest, steep increases in temperature indicate the return of the female to the nest..112

Figure 4.2. Ambient temperature fluctuations illustrating temperature changes of more than 30° C at ground level near a single horned lark nest on Hudson Bay Mountain, Smithers, BC. Temperatures were recorded over the course of several days during the 2005 breeding season113

Figure 4.3. Frequency of observed mean ambient temperatures between 06:00-20:00 h on Hudson Bay Mountain in British Columbia in 2005 and 2006 between ($n = 2930$, 2 hour time periods). The bold line indicates the physiological zero temperature for embryos ($\leq 26^{\circ}\text{C}$).....114

Figure 4.4. Mean ($\pm\text{SE}$) number of minutes on the nest, number of recesses and recess and on-bout duration during 2 hour time periods vs. ambient temperature for horned larks ($n = 54$ nests)115

Figure 4.5. Representative graphs showing how incubation patterns change with incubation day, date and time of day for horned larks. A Julian date of 140 represents 20-May, 190 represents 09-July, means are shown $\pm\text{SE}$ 116

LIST OF PHOTOS

Photo 1.1. Alpine tundra on Hudson Bay Mountain in Smithers, British Columbia, Canada, showing typical nesting habitat for horned larks (approximately 1,700 m above sea level). Photo taken 04 June 2006 (Photo by Alaine Camfield).....13

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DEDICATION



Martha Camfield



Carol Camfield



Vera Spooner

This dissertation is dedicated to my grandmothers (Martha “Mutt” Camfield and Vera Warbasse Spooner) and my mother (Carol Spooner Camfield) who helped pave the way for women as scientists and naturalists.

CO-AUTHORSHIP STATEMENT

Although I have followed the tradition of using the first-person throughout the dissertation, significant amounts of data used in Chapters 2 and 3 were provided by Scott F. Pearson.

Chapter 2 was co-authored with Scott F. Pearson and Kathy Martin. I was responsible for collecting the data at the study site in British Columbia, data analysis, manuscript writing and presentation. Scott F. Pearson collected data at the study site in Washington and assisted in manuscript preparation and revision. Kathy Martin assisted with the identification of the study site and field work in British Columbia and in manuscript preparation and revision. A version of this chapter was submitted for publication in June 2008.

Camfield, A.F., S.F. Pearson and K. Martin. *In review*. Life history tradeoffs in two subspecies of horned lark across a latitudinal and elevational gradient.

Chapter 3 was co-authored with Scott F. Pearson and Kathy Martin. I was responsible for collecting the data at the study site in British Columbia, data analysis, manuscript writing and presentation. Scott F. Pearson collected data at the study site in Washington and assisted in manuscript preparation and revision. Kathy Martin assisted with the identification of the study site and field work in British Columbia and in manuscript preparation and revision. A version of this chapter will be submitted for publication in November 2008.

Camfield, A.F., S.F. Pearson and K. Martin. Using demographic models to evaluate management scenarios for the endangered streaked horned lark.

Chapter 4 was co-authored with Kathy Martin. I was responsible for collecting the data, data analysis, manuscript writing and presentation. Kathy Martin assisted with the identification of the study site and in manuscript preparation and revision. A version of this chapter was submitted for publication September 2008.

Camfield, A.F. and K. Martin. *In review*. The influence of ambient temperature on songbird incubation behavior in an alpine environment.

CHAPTER 1: GENERAL INTRODUCTION AND THESIS OVERVIEW

Nearly 30% of the earth's terrestrial surface is mountainous and is host to a great degree of biodiversity and many locally endemic species (UNEP World Conservation Monitoring Center 2002). Globally, 32% of protected areas are in mountainous regions, in the United States more than half are at elevations higher than 2,400 meters and in British Columbia, 61% of the protected areas are located in alpine and subalpine habitat (Scott et al. 2001, Bocking 2000, UNEP World Conservation Monitoring Center 2002). Despite representing a large proportion of the planet's protected areas, the ecology of vertebrates in high elevation areas have received little attention from researchers and managers (Martin 2001).

Some wildlife species reside in high elevation habitat year-round and are found only in alpine habitat, others overwinter at low elevations but breed only in alpine areas (alpine specialists). In contrast, alpine generalists breed across a wide range of elevations. In some areas the range of alpine generalists is becoming restricted to high elevation habitat as low elevation habitat is developed or modified by humans (Martin 2001). For example, in central Europe, black grouse (*Tetrao tetrix*) were once found in a variety of high and low elevation habitats, but as a result of forestry activities and intensive agriculture they are now found only in high elevation habitat (Storch 2000). As human land use continues to expand and low elevation habitat continues to be disproportionately developed, high elevation habitat may provide important areas of refuge for an increasing number of alpine generalist species.

Native prairies and grasslands are among the most endangered ecosystems in North America (Noss et al. 1995). As a result, grassland birds are the most rapidly declining group of birds in North America (Askins 1993, Knopf 1994, Herkert et al. 1996). Some grassland bird species, such as savannah sparrows (*Passerculus sandwichensis*) and horned larks (*Eremophila alpestris*) are found across wide elevational gradients and breed in low elevation grasslands, arctic tundra and high elevation alpine tundra (Wheelwright and Rising 1993, Beason 1995). While we know that many grassland birds are declining in their low elevation habitats, little demographic data exist for songbird populations breeding at high elevations. It is therefore difficult to evaluate the long-term viability of high elevation populations and overall population trends for alpine generalist species.

Animals that live at high elevation face different challenges than their low elevation conspecifics; the growing season is shorter and environmental stochasticity increases with elevation (Martin 2001, Bears et al. 2003). Temperatures can vary up to 40°C a day and snow, hail and below freezing temperatures can occur at any time during the breeding season. Birds that live and breed at high elevations have behavioral, physiological and morphological adaptations that allow them to cope with extreme environmental conditions (Martin and Wiebe 2004, Potapov 2004). For example, songbirds in high elevation areas in the Himalayas have longer, pointed wings to allow for increased flight stability in strong winds (Landmann and Winding 1993, 1995) and some high elevation songbirds have a dampened stress response which allows them to continue breeding during inclement weather (Bears et al. 2003). Examples of behavioral adaptations include placing nests in areas with favorable microclimates or increasing

male provisioning to spread the energetic costs of brood rearing between both parents (Martin and Wiebe 2004). In lieu of abandoning a nest when confronted with an extreme weather event during breeding, a bird may shift its investment in incubation, brooding and feeding nestlings to balance the needs of its offspring with its own self-maintenance. An understanding of how breeding songbirds adjust their behaviors in response to challenging weather is important in evaluating their ability to cope with harsh alpine environments.

In order to maximize lifetime reproductive success, alpine generalist species may show varying life histories among elevations. For birds breeding at high elevation, short breeding seasons and inclement weather often translate into lower annual fecundity (Badyaev 1997, Badyaev and Ghalambor 2001, Bears 2007). For example, cardueline finches breeding at high elevations have lower annual fecundity than their low elevation counterparts. However, extended parental care and low levels of natal dispersal result in higher juvenile survival for high elevation birds and may allow the birds to compensate for reduced fecundity (Badyaev 1997). Trade-offs between survival and fecundity are often apparent among species that occupy diverse habitats and the ability of songbirds to adjust their life history strategies may be key to their ability to persist in alpine areas.

Alpine habitat may become increasingly important for the persistence of certain species, but in order to assess whether we can rely on high elevation areas as refuge habitat for alpine generalist species we need a better understanding of the ability of organisms to adapt to the challenges present in alpine environments (Martin 2001). In addition, we need to evaluate if alpine areas generally represent high quality habitat or fringe habitat that is occupied by young or inferior individuals.

THESIS OBJECTIVES

My study addresses the general questions of how the life history of alpine breeding songbirds (specifically horned larks) differs from their low elevation conspecifics. In addition, given declines in low elevation populations of horned larks I evaluate possible causes of the declines and make management recommendations for an endangered subspecies of horned lark. Finally, I examine how alpine breeding songbirds adjust their incubation behavior in order to breed successfully in a challenging alpine environment.

My thesis objectives were:

- 1) To examine life history tradeoffs between two avian subspecies living at a different elevation and latitude (Chapter 2);
- 2) To evaluate management strategies using demographic data for an endangered grassland bird (Chapter 3);
- 3) To examine how songbirds breeding at high elevations modify their incubation behavior in response to changes in ambient temperature (Chapter 4).

STUDY SPECIES

Horned larks (*Eremophila alpestris*) are medium-sized (28-40 g) ground nesting songbirds that prefer open, sparsely vegetated habitat. They are found across North America, throughout Europe, Russia and Asia and in outlying populations in Colombia and Morocco in diverse types of open habitats ranging from arctic and alpine tundra to native prairies and deserts. They are the only native member of the family Alcedidae found in North America (Beason 1995, BirdLife International 2004) and the only lark species to inhabit tundra and alpine habitats (del Hoyo et al. 2004). Their original

scientific name, *Alauda alpestris*, means “lark of the mountains.” In Eurasia they breed primarily in tundra habitat and can be found breeding as high as 5,400 meters in the Himalayas (del Hoyo et al. 2004).

Horned Larks are socially monogamous; only the female incubates, however, both males and females provision nestlings. Females are usually smaller and have duller coloration than males. They build their nests on the ground and are primarily insectivorous during the breeding season (Beason 1995). The length of the breeding season depends on location and habitat type. In southern North America they begin breeding in mid February while in northern Russia they do not begin nesting until mid June (del Hoyo et al. 2004).

There are 21 subspecies of horned lark in North America. One subspecies *E. a. alpina* breeds only in alpine habitat in the Cascade and Olympic mountains of Washington State; other subspecies may be found in diverse habitat types. I collected data on *E. a. articola* (pallid horned lark) in northern British Columbia, Canada. The current range of pallid horned larks extends from the mountains of southern British Columbia north to Alaska and the Yukon (Beason 1995). For comparative purposes, I also present data on a second subspecies (*E. a. strigata*; streaked horned larks) that were collected by S.F. Pearson in Washington, USA. Historically, streaked horned larks bred from southern British Columbia, through the Puget Trough in Washington and in the Willamette and Rogue River Valleys in Oregon (Fraser et al. 1999, Stinson 2005). However, the breeding range has contracted over time and currently streaked horned larks are found only in western Washington and Oregon (Drovetski et al. 2005). They are listed as endangered by the Species at Risk Act in Canada and the state of

Washington and in 2001 were classified as a federal candidate for listing under the Endangered Species Act in the United States.

Despite their broad geographic distribution, horned larks are declining throughout much of their range (Sauer et al. 2008). Estimates from the North American Breeding Bird Survey indicate that horned larks have declined by over 50% across North America since 1966 (Figure 1.1). The decline is largely a result of habitat loss and horned larks may increasingly rely on higher elevation habitats as their low elevation habitats are lost. Data on population trends outside North America are scarce, however, since the 1960's population declines have been noted in Scandinavia and in the Colombian Andes (Dierschke and Bairlein 2002, del Hoyo et al. 2004). Long-term studies of marked individuals are lacking for horned larks (Beason 1995), so my study and S.F. Pearson's data from Washington provide basic life history information that is unknown for this species in North America.

STUDY AREA

I studied pallid horned larks in alpine habitat on Hudson Bay Mountain near Smithers, British Columbia, Canada (52° N, 127° W; Figure 1.2, Photo 1.1) from 2003-2006. The study area was approximately 4km² and elevation ranged from 1500-1850 m above sea level. The site is within the Prince Rupert Forest Region and the biogeoclimatic zones found on the study site are: Alpine Tundra and Engelmann Spruce – Subalpine Fir (Moist Cold and Wet, Very Cold; Banner et al. 1993). The site is characterized by extremes in environmental conditions; temperatures can vary more than 30°C in a single day and snow, hail and below freezing temperatures can occur throughout the breeding season.

Data for streaked horned larks were collected by S.F. Pearson at seven sites in Washington State, USA in grass and forb dominated habitats located in south Puget Sound prairies and airports, coastal Washington dune habitats and on islands in the lower Columbia River from 2002-2005 (Pearson et al. 2008). Study sites included: Olympia Airport (46° 58' N, 122° 53'W), 13th Division Prairie on Ft. Lewis (47° 01' N, 122° 26'W), Gray Army Airfield on Ft. Lewis (47° 05' N, 122° 34'W), McChord Air Force Base (47° 08' N, 122° 28'W), Damon Point (46° 56'N, 124° 06' W), Midway Beach (46° 46'N, 124° 05' W) and Whites Island (46° 08'N, 123° 18' W; Figure 1.3). Study areas ranged in size from 0.07 to 2.49 Km² and elevation ranged from 3 to 122 m above sea level. Field techniques were similar for both subspecies and are described in individual chapters.

THESIS OVERVIEW

In Chapter 2, I examined variation in life history patterns between a horned lark subspecies (*E. a. articola*) in British Columbia, Canada, in a high elevation and latitude alpine habitat and a second subspecies (*E. a. strigata*) in Washington, USA in lower latitude and elevation grassland and sandy shoreline habitats. Given the shorter breeding season at high latitude and elevation and the larger body size of *E. a. articola* I expected that *E. a. articola* would show a “survivor” life history strategy while *E. a. strigata* would show a “high-reproductive” strategy. I found that *E. a. articola* had higher adult survival than *E. a. strigata*. However, contrary to my expectations there was also a trend toward higher fecundity for *E. a. articola*. I showed that population growth rates for *E. a. articola* were stable while *E. a. strigata* was declining rapidly. Finally, I used Life-Stage

Simulation Analysis to show that population growth rates for both subspecies were most sensitive to changes in survival. I discuss why the declining population growth rate may provide an explanation for the deviation from my expectation of higher reproduction in *E. a. strigata*.

Given the strong population declines shown in Chapter 2 for *E. a. strigata*, in Chapter 3, I used demographic models to simulate changes in three vital rates (adult survival, juvenile survival and fecundity) to examine how much they would need to be adjusted either independently or in concert to achieve a stable population for *E. a. strigata* in Washington, USA. I also evaluated which fecundity components had the greatest impact on population growth rates. I used estimates of vital rates for *E. a. articola* for comparative purposes and I found that within reasonable ranges for each vital rate, improving a single rate independently was unlikely to result in a stable or recovering population for *E. a. strigata*. Proportional increases in breeding success and decreases in the reneesting interval had similar effects on population growth rates. I then discuss management techniques that should be prioritized for *E. a. strigata* and suggest areas for future research.

Incubation is one component of the breeding cycle that may be most challenging for alpine breeding songbirds because they face extreme temperature fluctuations yet the thermal requirements of the eggs are the same as in more moderate environments (Wiebe and Martin 1997). The results of Chapter 2 suggest that *E. a. articola* is well adapted to the difficulties of breeding in an alpine environment. Therefore in Chapter 4, I focused on incubation rhythms of *E. a. articola* to evaluate how they might modify their behavior to cope with their challenging breeding environment. I examined the influence of

ambient temperatures on incubation rhythms for horned larks breeding in alpine habitat in British Columbia, Canada. I found that females spent less total time on the nest as ambient temperature increased to 12-13 °C; above 12-13 °C ambient temperature had less influence on the total time a female spent incubating. Females adjusted the amount of time spent incubating by varying the frequency rather than the duration of recesses; recess duration was not affected by ambient temperature. I then discussed possible explanations for the observed relationship and suggested that horned larks are well adapted to the breeding conditions in alpine habitat.

In Chapter 5, I summarized the main conclusions of each research chapter. I discussed the implications of the overall research programme in relation to the understanding of songbird adaptations to breeding at high elevations, the potential of high elevation areas to serve as refuge habitat and the management of an endangered subspecies of horned lark. Finally, I suggest directions for future research to further our understanding of avian adaptations to high elevation and the management of streaked horned larks.

Chapters 2, 3 and 4 were written as stand alone manuscripts.

Figure 1.1. Survey wide count data for horned larks from the North American Breeding Bird Survey showing a 50% decline in the mean number of individuals detected per survey from 1966-2007. Data are from Sauer et al. 2008.

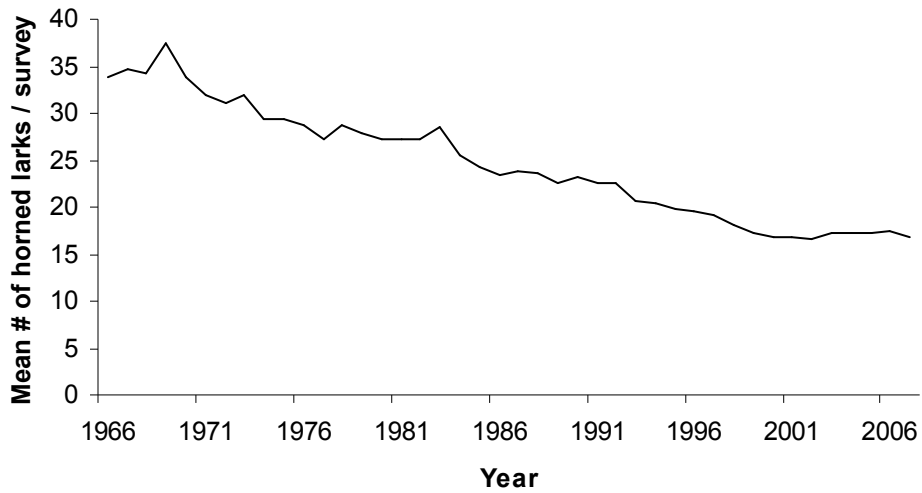


Figure 1.2. Study area for *E. a. articola* located on Hudson Bay Mountain, Smithers, British Columbia, Canada (Map prepared by Matt Tomlinson).

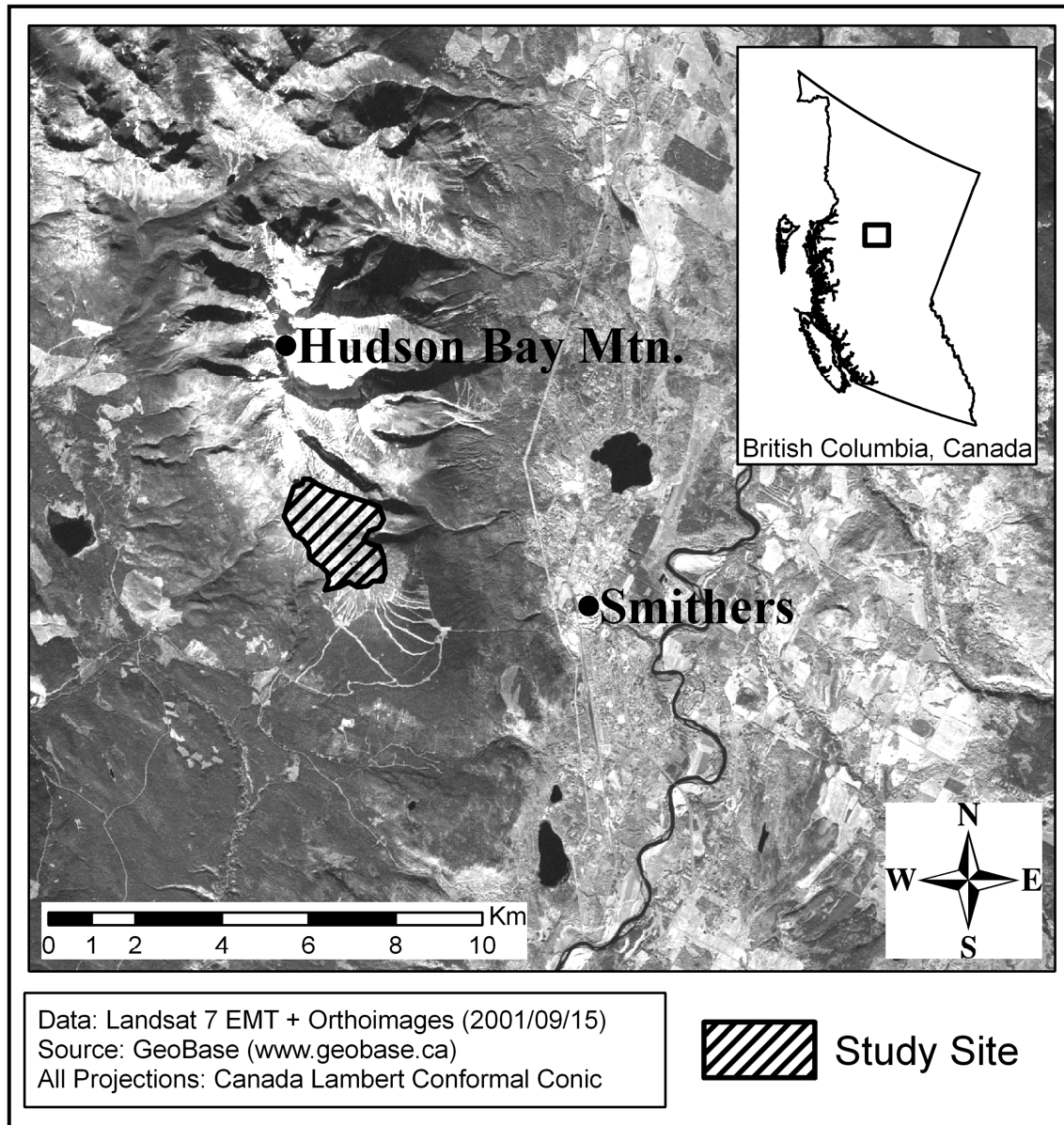


Figure 1.3. Study areas for *E. a. strigata* located in the Puget Lowlands, Washington, USA (Map prepared by Matt Tomlinson). Field data collected by S.F. Pearson, Washington Department of Fish and Wildlife.

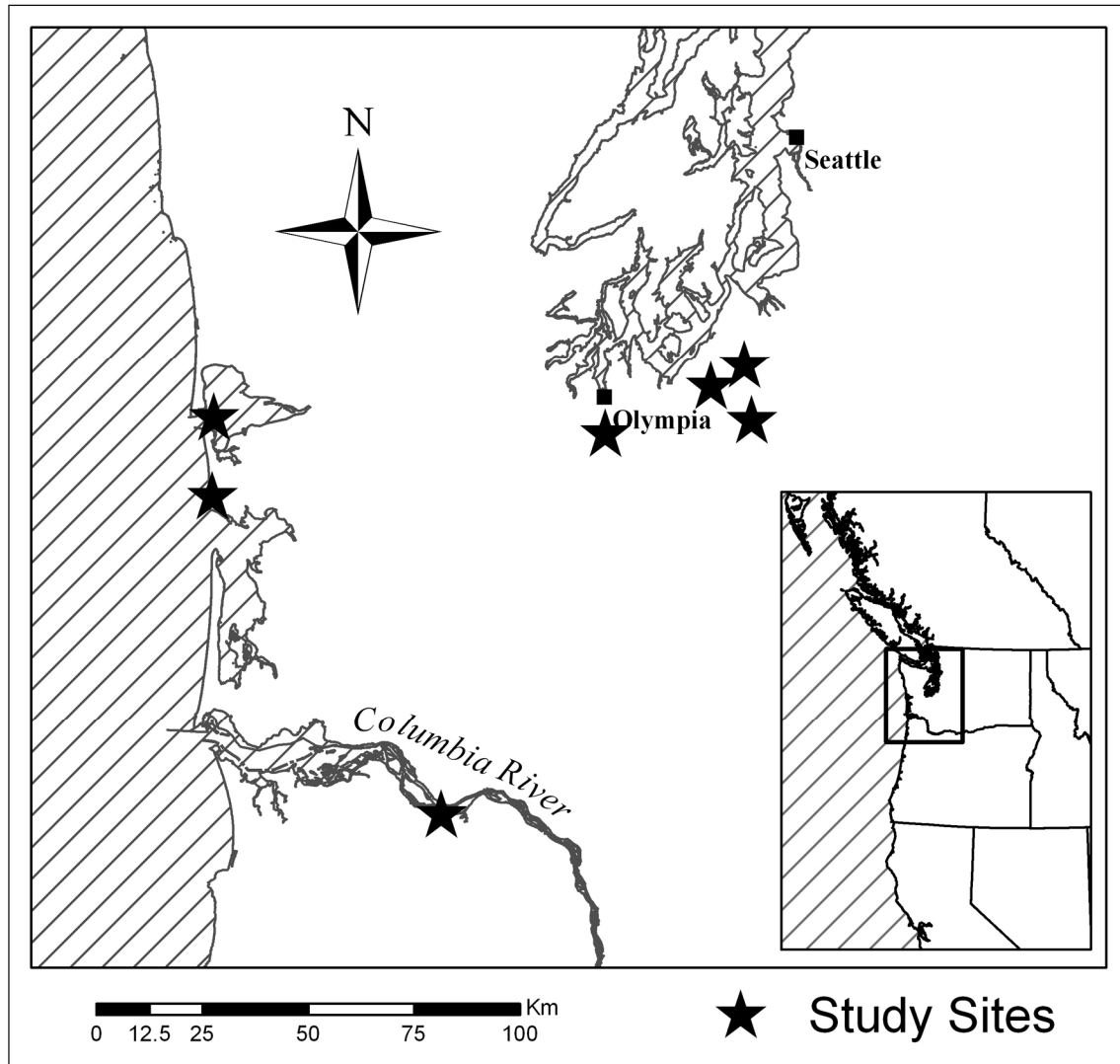


Photo 1.1. Alpine tundra on Hudson Bay Mountain in Smithers, British Columbia, Canada, showing typical nesting habitat for horned larks (approximately 1,700 m above sea level). Photo taken 04 June 2006 (Photo by Alaine Camfield).



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CHAPTER 2: LIFE HISTORY TRADEOFFS IN TWO SUBSPECIES OF HORNED LARK ACROSS A LATITUDINAL AND ELEVATIONAL GRADIENT¹

INTRODUCTION

Life histories vary greatly among species occupying different environments with most iteroparous species falling along a continuum from “high-reproductive” species (high fecundity and low survival) to “survivor” species (low fecundity and high survival; Saether et al. 1996, Saether and Bakke 2000). It is generally assumed that the variation in survival and fecundity is due to tradeoffs in investment between somatic maintenance and reproduction (Stearns 1989), and that the mechanisms driving these tradeoffs can be influenced by different environmental factors such as predation, climate, food and breeding season length (Sandercock et al. 2005). These environmental characteristics can result in habitat that is either favorable for breeding or favorable for survival, and species may be categorized in relation to the quality of their habitat. Survivor species live in favorable survival habitat but poor breeding habitat, and high-reproductive species live in favorable breeding habitat, but poor survival habitat (Saether et al. 1996).

As latitude and elevation increase, breeding seasons are shorter, mean temperatures lower and the proportion of birds raising multiple broods decreases (Sanz 1998, Martin and Wiebe 2004). For songbirds that have multiple broods, differences in breeding season length can have dramatic effects on fecundity (Grzybowski and Pease 2005) and therefore may influence where a species falls along the life history continuum.

¹ A version of this chapter has been submitted for publication. Camfield, A.F., S.F. Pearson and K. Martin. *In review*. Life history tradeoffs in two subspecies of horned lark across a latitudinal and elevational gradient.

For example, dark-eyed juncos (*Junco hyemalis*) breeding across elevational gradients show a more than two-fold difference in the number of hatchlings produced each year (Bears 2007). This difference may be attributable to differences in the length of the breeding season with high elevation birds experiencing a shorter season. Overall, individuals that live at high elevations have lower reproductive rates but higher survival than those at low elevations (Bears 2007).

In addition to differences in demographic parameters, differences in body size are also found among species at different elevations and latitudes, with body size increasing as latitude and elevation increases (Landmann and Winding 1995, Blackburn and Gaston 1996, Ashton et al. 2000, Ashton 2002, Bears et al. 2008). The general trend, known as Bergmann's rule was originally explained by the need for decreased surface area to mass ratio as a way to conserve heat in cool climates (Mayr 1956). Although this explanation has been challenged (e.g. see Cushman et al. 1993, Cotgreave and Stockley 1994, Mousseau 1997), the general pattern often prevails. Differences in body size can correlate with differences in fecundity and survival; large-bodied species generally have higher survival and lower fecundity than small-bodied species (Western and Ssemakula 1982, Saether 1988, 1989).

Many comparative life history studies have focused on one or a few easily measured traits such as clutch size and the result is a limited or misleading understanding of life history evolution. Examining alternative explanations for variation in life histories and the correlations among multiple life history traits may aid in the continued development of life history theory (Ricklefs 2000, Martin 2004, Sandercock et al. 2005). Most commonly, interspecific comparative studies are conducted to investigate the

mechanisms underlying the reproduction-survival continuum (e.g., Reznick et al. 1990, Badyaev and Ghalambor 2001, Bielby et al. 2007). However, populations of the same species living in different environments can also show variation along the continuum. Recent studies have focused on life history variation within single species (Gillis et al. 2005, Ozgul et al. 2006, Bears 2007, Wilson 2008), thus controlling for confounding influences of phylogenetic relationships among the species being studied (Martin 1995, Cardillo 2002, Sandercock and Jaramillo 2002).

I investigate variation in life history patterns between two closely related subspecies of horned larks (Drovetski et al. 2005), one nesting in alpine habitat at higher latitude and elevation in British Columbia, Canada *Eremophila alpestris articola* (pallid horned lark), and the other in grasslands and sandy shorelines at lower latitude and elevation in the Puget lowlands, coast and lower Columbia River of Washington, USA (*E. a. strigata*, streaked horned lark). The range of *E. a. articola* extends from the mountains of British Columbia north to Alaska and the Yukon (Beason 1995). *Eremophila alpestris strigata* is found in western Washington and Oregon (Drovetski et al. 2005). Ecological factors that differ between the habitats of the two populations allow for specific predictions about the potential trade-offs between vital rates and the life history strategies employed by each subspecies.

I predicted that *E. a. articola* at high elevation and latitude in British Columbia would exhibit a survivor life history due to the relatively short breeding season as a result of persistent spring snow cover and early onset of fall. I predicted that *E. a. strigata* at lower elevation and latitude in Washington would exhibit a high-reproductive life history where the potential breeding season is fairly long due to the maritime coastal climate and

lack of persistent snow. Specifically, I predicted annual fecundity would be lower in *E. a. articola* than *E. a. strigata* because opportunities for multiple broods are likely limited by the relatively short breeding season and I expected adult survival of *E. a. articola* to be higher than *E. a. strigata* to compensate for the seasonal reproductive deficits. The high latitude and elevation *E. a. articola* are larger in body size than *E. a. strigata* (Beason 1995) and I predicted that the differences in body size would result in higher survival for *E. a. articola* and higher fecundity for *E. a. strigata*.

Given that vital rates and life history strategies are correlated, the impact of changes in survival or fecundity on population growth should depend in part on the life history strategy of the species. For example, a reduction in the survival of a species that has low fecundity and high survival should be more detrimental to population growth than a reduction in the survival of a high reproducing, short lived species (Heppell et al. 2000). In birds and mammals, numerous examples show that the population growth rates of survivor species tend to be most sensitive to changes in survival and the population growth rates of high-reproductive species tend to be most sensitive to changes in fecundity (Saether et al. 1996, Heppell et al. 2000, Oli and Dobson 2003). To further explore differences in the life history strategies of two horned lark subspecies, I calculated population growth rates and evaluated which demographic variables contributed most to changes in population growth for the two subspecies using Life-Stage Simulation Analysis (Wisdom and Mills 1997, Wisdom et al. 2000). I expected survival to contribute more to the variability in population growth for *E. a. articola* and fecundity to contribute more to the variability in population growth for *E. a. strigata*.

METHODS

Study site and study species

I present data collected for two subspecies of horned larks at eight sites between 2002 and 2006. I studied *E. a. articola* (pallid horned lark) at a single site in alpine habitat on Hudson Bay Mountain near Smithers, British Columbia, Canada (52° N, 127° W) from 2003-2006. The study area was approximately 4 km² and elevation ranged from 1500-1850 m above sea level. S.F. Pearson collected data for *E. a. strigata* (streaked horned lark) on seven sites in Washington State, USA in grass and forb dominated low elevation habitats located in south Puget Sound prairies and airports, coastal Washington dune habitats and on islands in the lower Columbia River from 2002-2005. Study sites included: Olympia Airport (46° 58' N, 122° 53'W), 13th Division Prairie on Ft. Lewis (47° 01' N, 122° 26'W), Gray Army Airfield on Ft. Lewis (47° 05' N, 122° 34'W), McChord Air Force Base (47° 08' N, 122° 28'W), Damon Point (46° 56'N, 124° 06' W), Midway Beach (46° 46'N, 124° 05' W) and Whites Island (46° 08'N, 123° 18' W). Study areas ranged in size from 0.07 to 2.49 Km² and elevation ranged from 3 to 122 m above sea level.

Data collection

Field techniques were similar for both *E. a. articola* and *E. a. strigata*. Throughout the breeding season (early May to early August in British Columbia, April to mid-August in Washington), I searched for nests on horned lark territories. Nests were located by observing adults leaving or approaching nests with and without nesting materials or carrying food, by flushing incubating or brooding adults and by searching appropriate

habitat. Nests were found during nest building, incubation and nestling stage. The status of each nest (presence of parents, eggs, nestlings) was recorded approximately every 3-5 days, more frequently near the expected hatch and fledging dates. For *E. a. articola* the study site was visited daily, for *E. a. strigata* study sites were visited approximately three times/week. For both subspecies, territories continued to be monitored after nests failed in order to locate renests and allow for the estimation of renesting intervals.

Adult birds were captured using mist nets or bow traps; morphological measurements were taken (wing chord, tarsus and weight) and they were individually color marked. Nestlings were banded in the nest between days 7-9 post-hatching or occasionally shortly after fledging. The proportion of adult banded birds on each study site increased as the study progressed and ranged from approximately 20-80% for *E. a. articola* and 10-40% for *E. a. strigata*. Approximately 70% of the nestlings of both subspecies were banded each year. Complete surveys of the study areas were conducted each year to determine which individuals returned. For *E. a. articola*, the entire study area was systematically surveyed to identify returned birds (by 2-3 people daily for approximately 10 days) as male larks were establishing breeding territories early in the breeding season. After breeding was initiated and territories were established, individual identities were verified and accessible breeding territories on the edges of the study site were visited to identify any individuals that might have been missed during the initial surveys. For *E. a. strigata*, study sites were surveyed weekly between 01 April and mid-August. Surveyors walked transects and mapped territories. When a bird was encountered surveyors recorded whether or not each bird was banded and recorded the band combination. Resighting probabilities of *E. a. articola* and *E. a. strigata* were high

and were similar for both subspecies indicating that the ability to detect returned birds was not biased toward one subspecies.

Demographic rates of horned larks

I measured 10 demographic variables and estimated 4 population parameters for each subspecies:

1) Clutch initiation date is the date the first egg in a clutch was laid and, unless observed directly, was calculated by backdating from known dates (hatching dates, estimated age of nestlings, or fledging dates). I used the following time intervals to calculate clutch initiation dates: egg laying = 1 egg laid per day (thus, the number of eggs in a clutch = the length of the egg laying stage), incubation = 12 days, nestling = 9 days (Beason 1995). These time intervals were nearly identical to those measured during this study for both subspecies.

2) Breeding season length (B) is the interval between the first and last known clutch initiation date within one year.

3) Clutch size (C) was calculated from nests that were observed with the same clutch size more than once (at least one day apart) during incubation.

4) Proportion hatched is the proportion of eggs laid that hatched and includes nests that hatched at least one egg with a known clutch size.

5) Proportion fledged is the proportion of nestlings that successfully left the nest and was calculated by subtracting the number of nestlings that disappeared or dead nestlings that remained in the nest after the others had fledged and dividing by the number of eggs that hatched.

- 6) Fledglings per egg laid (S) is the proportion of eggs laid that produced a fledgling.
- 7) Nest survival is calculated using the Mayfield (1975) estimator and is the probability that a nest fledged at least one nestling. Nests were counted as successful if adults were seen with fledglings, or if the nest was found empty with no signs of depredation on or after the expected fledging date. Nests with signs of depredation (see below) were counted as unsuccessful.
- 8) Proportion nests depredated is the proportion of the total nests found that were destroyed by a predator. Signs of depredation included damaged eggs, blood and/or feathers in or near the nest and nests found empty during incubation or during the nestling period when nestlings were too young to have fledged (< 8 days post hatching).
- 9) Replacement nest interval (r_f) is the number of days between nest failure and the next clutch initiated by the same female.
- 10) Multiple brood interval (r_s) is the number of days between the successful fledging of a nest and the initiation of an additional brood. For parameters 9 and 10, only nests with banded adults or on territories that were consistently monitored were included in the calculation.
- 11) Annual fecundity (F) is the number of female fledglings per female per year and was estimated using the technique of Ricklefs and Bloom (1977; Appendix 1) with the following variables: Length of the breeding season (B) calculated using the proportion of active nests during each month of the breeding season to correct for the fact that breeding effort is not constant across all months; clutch size (C); fledglings per egg laid (S); daily nest mortality rate (m); probability that at least one nestling fledges (p_s);

probability that a nest fails (p_f); multiple brood interval (r_s); replacement nest interval (r_f). To estimate the number of female fledglings per female, annual fecundity was divided by two. There is no evidence that the secondary sex ratio differs from theoretical expectations of 1:1 (Fisher 1930) and therefore I assume an equal sex ratio at fledging.

12) Apparent adult survival (ϕ_a) is the probability that an adult bird survived and returned to the study site the following year. Apparent survival rates based on resighting data were estimated and corrected for resighting probability using mark-recapture analyses.

13) Apparent juvenile survival (ϕ_j) is the probability that a bird banded as a nestling and that successfully fledged returns to the study site the following year. Apparent survival rates based on resighting data were estimated and corrected for resighting probability using mark-recapture analyses. Because *E. a. strigata* were studied over multiple sites, the apparent survival estimates included juveniles that dispersed from their natal site to one of the other study sites. Estimates of *E. a. articola* juvenile survival are from a single site and hence are likely to be underestimates when compared to *E. a. strigata*. To allow for direct comparisons I also provide *E. a. strigata* apparent juvenile survival estimates including only individuals that returned to their natal sites. A similar correction was not made for adult apparent survival since there were no cases of adult dispersal among the study sites.

14) Population growth rate (λ) was estimated using the equation: $\lambda = F\phi_j + \phi_a$, where F is the number of female fledglings produced per female per year, ϕ_j is apparent juvenile survival and ϕ_a is apparent adult female survival (Pulliam 1988). With the exception of the estimate of juvenile survival for *E. a. strigata* I assumed a closed

population. For *E. a. strigata* I used the juvenile survival estimate including juvenile dispersal between sites to give the most realistic estimate of population growth.

Data analysis

I used the Program MARK Version 3.1 (White and Burnham 1999) to estimate apparent survival rates (ϕ) corrected for the probability of resighting (p ; the probability the bird was seen given that it was alive) from live encounter data using the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965). The median \hat{c} approach (Cooch and White 2006) was used in Program MARK to assess goodness-of-fit of the global models ($\phi_{t*s} p_{t*s}$) with two groups for males and females (s) and time dependence (t) for apparent survival and probability of encounter for adults and time dependence (t) only for juveniles. Goodness-of-fit tests indicated that there was insufficient data to fit a time dependent model ($\hat{c} > 3$) therefore I evaluated 3 models for adult survival and probability of resighting including differences for sex (s) and without sex ($.$). Information-theoretic procedures using AIC_c (Burnham and Anderson 2002) were used for model selection. I was only able to evaluate the simplest model without time dependence or sex for juvenile survival and probability of resighting. When modeling juvenile survival in cases where juveniles are not resighted in the first year, estimates of survival in the second and third years are needed in order to determine survival and probability of resighting for the first year. During the second and third years, survival of juveniles that returned should be equal to that of adults, therefore, in order to estimate survival and resighting probability in the second and third years I used the estimate generated for adult survival and resighting probability.

I used a Monte Carlo simulation approach of 10 000 replicates to generate standard deviations for the estimates of λ . I modeled apparent survival of adult females and juveniles using random draws from beta distributions using estimates of variation for each vital rate. The beta distribution constrains the random variables between 0 and 1 and is therefore appropriate for modeling survival probabilities which must remain within these values (Morris and Doak 2002). To model fecundity, I used a stretched beta distribution which is a rescaled beta distribution that reflects a biologically realistic range for the simulated vital rate (Morris and Doak 2002). After each iteration the randomly drawn parameter estimates were used to calculate λ .

Finally I used Life-Stage Simulation Analysis (Wisdom and Mills 1997, Wisdom et al. 2000) to assess the effect of changes in F , ϕ_j , and ϕ_a on λ . Using the randomly drawn sets of parameters I performed linear regressions with λ as the dependent variable and the three vital rates as the independent variables. I used the coefficient of determination (r^2 value) to estimate the proportion of the variation in λ that was explained by simulated variation in each vital rate. Vital rates with the highest r^2 value have the greatest potential to influence λ .

A consistent effort was made to survey sites in Washington for replacement nests and multiple broods, however, because a conservative approach was used when determining pairs to include in the estimates of renesting intervals (see above), the sample sizes for *E. a. strigata* replacement nest and multiple brood intervals were small. Also, the sampling regime across multiple sites in Washington may have made it more likely that replacement nests were not detected. To account for the possibility that the estimates of replacement nest and multiple brood intervals were low I re-estimated

fecundity for *E. a. strigata* using the estimates from *E. a. articola* and using the minimum observed replacement nest interval for *E. a. strigata*. I also re-estimated lambda and re-ran the Life-Stage Simulation Analysis using both fecundity estimates.

I used the program R (R Development Core Team 2006) to perform Monte Carlo simulations and regressions, χ^2 statistics in Program Contrast (Sauer and Williams 1989) to compare adult and juvenile apparent survival rates and SPSS version 10.1 (SPSS Inc. 1999) to perform z-tests to compare nest survival and depredation, and to perform t-tests and Mann-Whitney U-tests for all other pairwise comparisons. Overall significance was designated at $\alpha=0.05$. To reduce the possibility of type I errors I conducted Bonferroni corrections ($\alpha=0.05/k$) for each of the four categories in Table 2.1 (Rice 1989). After Bonferroni corrections, for breeding season $\alpha=0.025$, for morphology $\alpha=0.008$, for fecundity $\alpha=0.006$ and for survival $\alpha=0.01$. However, because Bonferroni corrections are highly conservative I include the calculated p-values for each test to allow readers to evaluate for themselves which contrasts are biologically meaningful (as per Cabin and Mitchell 2000). Means are reported \pm SE except where noted.

RESULTS

During the course of this study I monitored 188 *E. a. articola* nests and S.F. Pearson monitored 257 *E. a. strigata* nests. I banded 117 *E. a. articola* adults and 175 juveniles, and S.F. Pearson banded 58 *E. a. strigata* adults and 80 juveniles. Nest depredation was the dominant cause of nest failure for both subspecies and all study sites.

Breeding season length was significantly longer in Washington than British Columbia (Table 2.1). The mean initiation date for first clutches was 16 days later for *E.*

a. articola than *E. a. strigata* and the length of the breeding season in British Columbia was less than half as long as in Washington (38.5 and 94 days respectively). Male and female *E. a. articola* in British Columbia were larger than *E. a. strigata* in Washington. *E. a. articola* had significantly longer tarsi, wing chord and weighed more than *E. a. strigata* (Table 2.1).

Clutch size was 0.56 eggs larger for *E. a. articola* than *E. a. strigata*, with no correlation between date of first egg and clutch size for either population (*E. a. articola*: $r_{s78} = 0.09$, $p=0.45$, *E. a. strigata*: $r_{s135} = 0.06$, $p=0.49$, Spearman's rank correlation), and no difference between clutch size for initial and replacement clutches (*E. a. articola*: initial 3.53 ± 0.08 vs. replacement 3.77 ± 0.16 , $Z_{55,22} = -1.45$, $p=0.15$, *E. a. strigata*: initial 3.05 ± 0.06 vs. replacement 2.75 ± 0.25 , $Z_{135,8} = -1.30$, $p=0.19$, Mann-Whitney U-test). Although the breeding season was much longer in Washington, the replacement nest and multiple brood intervals for *E. a. strigata* were almost four times longer than *E. a. articola* (Table 2.1). The extremely long re-nesting intervals for *E. a. strigata* combined with smaller clutch size, lower hatchability of eggs, lower fledging success and high clutch depredation rates resulted in 12% more fledglings per egg laid by *E. a. articola* (0.35) than *E. a. strigata* (0.23) and thus higher annual fecundity in *E. a. articola* (1.75 female fledglings/female/year) than in *E. a. strigata* (0.91, Table 2.1). Although the differences in the number of fledglings per egg laid and annual fecundity were not statistically significant after Bonferroni correction, the trend was toward higher fecundity for *E. a. articola* for all the components of fecundity I measured (with the exception of breeding season length).

Apparent survival rates for adults and juveniles were calculated using a reduced model with survival and probability of encounter held constant (ϕ, p). This was the most parsimonious model for adult survival (Table 2.2). Since models that included groups for males and females had less support than the reduced model for both subspecies, I present data for apparent adult survival both with males and females pooled and with each sex separately (Table 2.2). Median \hat{c} estimates showed no lack of fit of the global models. Overall, apparent adult survival was significantly higher for *E. a. articola* ($\phi_{adult}=0.69$; 95% CI 0.59, 0.77) than *E. a. strigata* ($\phi_{adult}=0.51$; 95% CI 0.40, 0.62; Table 2.1). After Bonferroni correction the trend toward higher apparent juvenile survival for *E. a. articola* ($\phi_{juvenile}=0.20$; 95% CI 0.12, 0.33) was not significantly different from *E. a. strigata* ($\phi_{juvenile}=0.074$; 95% CI 0.03, 0.15; Table 2.1). The probability of encounter was 1 for all adult horned larks across all years. The probabilities of encounter for *E. a. articola* and *E. a. strigata* juveniles were 0.79 ± 0.18 and 0.83 ± 0.15 respectively. The proportion of banded nestlings that returned to the study sites (without correcting for resighting probability) were 15% for *E. a. articola* and 14% for *E. a. strigata*.

To compare apparent juvenile survival between the two subspecies, I used only *E. a. strigata* juveniles that had returned to their natal sites. This is a more valid pairwise comparison than using the apparent survival estimate that includes recruitment across sites for *E. a. strigata* juveniles because I did not have the ability to detect local dispersal for *E. a. articola* given that I followed only one site in British Columbia. When dispersed *E. a. strigata* juveniles were added, apparent survival was 0.16 ± 0.04 ($n=88$; 95% CI 0.09, 0.27) and there was no difference in apparent juvenile survival between *E. a. articola* and *E. a. strigata* ($\chi^2=0.39$, $p=0.53$). To calculate λ and for the Life-Stage

Simulation Analysis I used the estimate for *E. a. strigata* apparent juvenile survival including juveniles that had dispersed because I wanted the results to reflect as closely as possible the true value of population growth for the *E. a. strigata* subspecies.

The simulated estimates of population growth rates predicted a stable population for *E. a. articola* ($\lambda = 1.00 \pm 0.12$ SD; Figure 2.1 A.) and a decreasing population for *E. a. strigata* ($\lambda = 0.61 \pm 0.10$ SD; Figure 2.1 B.). For *E. a. articola*, 47% of the simulations predicted $\lambda > 1$ while none of the simulations predicted $\lambda > 1$ for *E. a. strigata*. The Life-Stage Simulation Analysis revealed that for *E. a. articola*, juvenile survivorship accounted for the majority of the variation in λ ($r^2 = 0.56$) followed by adult survivorship ($r^2 = 0.29$) and annual fecundity ($r^2 = 0.14$; Figure 2.2 A.). Counter to my predictions, adult survival explained the highest proportion of the variation in λ for *E. a. strigata* ($r^2 = 0.75$) followed by juvenile survival ($r^2 = 0.17$) and annual fecundity ($r^2 = 0.08$; Figure 2.2 B.).

When fecundity for *E. a. strigata* was re-estimated using the replacement nest and multiple brood intervals for *E. a. articola* (5.97 and 6 days) and using the minimum observed replacement nest interval for *E. a. strigata* (10 days), fecundity increased to 1.67 ± 0.32 female fledglings/female/year and 1.38 ± 0.26 female fledglings/female/year, respectively. Estimates of λ increased to 0.74 ± 0.12 and 0.69 ± 0.11 . Re-running the Life-Stage Simulation Analysis did not change the order of importance of each vital rate in explaining variation in λ . For adult survival $r^2 = 0.46$ and 0.55 , for juvenile survival $r^2 = 0.37$ and 0.30 and for fecundity $r^2 = 0.16$ and 0.13 , respectively.

DISCUSSION

Variation in physical and environmental factors such as body size, food availability, predation and climate have all been invoked to explain patterns of life history differences among species (Lack 1966, Saether 1989, Martin 1995, Sandercock et al. 2005). The detailed demographic data for two subspecies of horned larks demonstrates that life history variation can be found even among closely related groups. Consistent with my predictions, I found that the larger, high latitude and elevation subspecies *E. a. articola* showed significantly higher apparent adult survival and a trend toward higher apparent juvenile survival than the low latitude and elevation subspecies *E. a. strigata*. However, counter to my predictions I found a trend toward higher annual fecundity for *E. a. articola* than for *E. a. strigata*. The results of the Life-Stage Simulation Analysis for *E. a. articola* matched my predictions in that juvenile and adult survival explained the majority (85%) of the variation in population growth. However, counter to my predictions, adult and juvenile survival, not fecundity, explained almost all (92%) of the variation in population growth for *E. a. strigata*. Even when the replacement nest and multiple brood intervals for *E. a. articola* and the minimum observed replacement nest interval for *E. a. strigata* were used to re-estimate fecundity for *E. a. strigata*, there was no change in either the trend toward higher fecundity in *E. a. articola* or in the order of importance of each vital rate in explaining variation in lambda for *E. a. strigata*.

Although the breeding season was more than twice as long for *E. a. strigata* in Washington, *E. a. articola* in British Columbia produced almost twice as many fledglings per year. Season length, renesting frequency and the production of multiple broods can have large influences on annual fecundity and may explain as much variation in annual

fecundity as nest success (DeCecco et al. 2000, Underwood and Roth 2002). Horned larks feed primarily on insects during the breeding season (Beason 1995). In the summer, large numbers of insects are carried on winds from lower elevations and deposited on snowfields in alpine habitats where they are easily captured by foraging birds (Crawford and Edwards 1986, Antor 1995). This abundant food source, combined with longer day length and therefore more time for foraging at higher latitudes may provide *E. a. articola* with the extra energy needed to allow for short renesting intervals. While the sample size was admittedly low, *E. a. strigata* appeared to have renesting and interbrood intervals that were more than three times longer than *E. a. articola* and the minimum observed renesting interval for *E. a. articola* was 3 days while the minimum observed renesting interval for *E. a. strigata* was 10 days. In effect the potential benefits of the longer breeding season for *E. a. strigata* may have been cancelled by the prolonged renesting intervals. Larger clutch size, higher nest survival and short interbrood intervals may allow *E. a. articola* to compensate for the short breeding season.

The estimates of apparent survival were in the direction predicted with higher apparent adult survival in *E. a. articola* than in *E. a. strigata*. The estimates of apparent juvenile survival in *E. a. articola* were high (20%) and are likely underestimates since I was not able to detect dispersal to other sites. Overwinter juvenile horned lark survival for a single year in shortgrass prairie in north-central Colorado was 4.4% (Boyd 1976) and median juvenile survival rates for migratory and non-migratory passerines typically range from 2.6 to 10.5% (Weatherhead and Forbes 1994). Badyaev and Ghalambor (2001) found songbirds that live at high elevation have lower fecundity than low elevation birds, but invest more in parental care and hence their young have higher

survival rates. It is possible that I observed a similar tradeoff between offspring number and offspring quality and that *E. a. articola* invest more in their offspring than *E. a.*

strigata resulting in a trend toward higher juvenile survival in *E. a. articola*.

Alternatively, it is possible that juvenile *E. a. articola* in British Columbia had stronger natal philopatry than *E. a. strigata* in Washington. Unfortunately, I do not have the data to distinguish between the two possibilities.

The estimates of lambda for the two subspecies provide an explanation for the deviations from my expectation of higher reproduction in *E. a. strigata*. *E. a. strigata* is a federal candidate for listing under the Endangered Species Act in the United States and is listed as endangered in Canada by the Species at Risk Act (Species at Risk Act Public Registry 2007). Overall numbers of *E. a. strigata* are known to be declining and there has been considerable habitat loss, but it is unclear whether declines are due to range contraction resulting from habitat loss, or due to an inability of existing habitat to support populations. My measures of lambda suggest that *E. a. strigata* in existing habitat is declining rapidly (40% per year). While habitat loss undoubtedly contributes to the declining numbers (estimates suggest that 97% of the Puget Prairies have been lost), the two factors appear to be acting in concert. It is possible that historically the habitat used by *E. a. strigata* may have been poor for survival, but favorable for breeding and that the population trends measured here mirror a shift that has rendered *E. a. strigata* habitat poor for both survival and for breeding.

In order to estimate lambda I assumed that the populations are closed. However, it is likely that there is immigration into the populations so the estimates of lambda may be underestimates. However, the estimate of apparent juvenile survival used to calculate

lambda for *E. a. strigata* does include juvenile dispersal among the 7 sites and adult dispersal is likely uncommon. Over four years there were no instances of adult dispersal among the study sites even though 21 sites were monitored for returns in Oregon and Washington but birds were only banded on 7 sites in Washington. In Washington, lark habitat and lark nesting only occur at discrete sites of appropriate habitat in a region dominated by conifer forests and nearly all known breeding sites were monitored for banding returns. While there are no data on range-wide population trends for *E. a. strigata*, transect counts and data from territory mapping indicate rapid declines in their numbers (S.F. Pearson *unpublished data*). Therefore the estimates of lambda, while possibly underestimated, reflect actual population declines for *E. a. strigata*.

Genetic analyses suggest that *E. a. strigata* in Washington have gone through a bottleneck and as a result have high levels of inbreeding and low levels of genetic diversity (Drovetski et al. 2005). Inbreeding in birds can result in reduced hatching success (Bensch et al. 1994, Briskie and Mackintosh 2004, Spottiswoode and Moller 2004). In this study hatchability was 9% lower in *E. a. strigata* than *E. a. articola*. If the reduction in hatching success was related to inbreeding depression it is possible that historically *E. a. strigata* had a higher hatching rate. In addition, increased anthropogenic disturbance near *E. a. strigata* habitat compared to *E. a. articola* in British Columbia may have led to elevated rates of nest depredation and may be the result of increased predator numbers commonly associated with developed areas (i.e. domestic cat (*Felis domesticus*), northern raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*) and American crow (*Corvus brachyrhynchos*; Marzluff et al. 2001). The cumulative effects of inbreeding and anthropogenic disturbance may be responsible for reducing annual fecundity in *E. a.*

strigata to the point where it is almost half that of *E. a. articola* and may not reflect historically divergent life histories between the two groups. To further illustrate this point, using the estimates of apparent juvenile and adult survival and assuming immigration rates are low, in order for lambda to be stable for *E. a. strigata*, females would need to produce 3.31 female fledglings/female/year. If this estimate approximates historic levels of fecundity for *E. a. strigata* then I would see differences in fecundity between the two subspecies in the direction predicted by life history theory.

The declining population growth rate for *E. a. strigata* also helps to explain the results of the Life-Stage Simulation Analysis. The estimates of vital rates for *E. a. strigata* suggest that their fecundity is depressed such that the importance of adult survivorship may be elevated relative to its historical importance. A similar result was found for Mariana crows (*Corvus kubaryi*) on Guam (Beissinger et al. 2006). Nest predation by introduced brown tree snakes (*Boiga irregularis*) led to severely reduced fecundity in the crows and elasticity analyses showed a tremendous importance of adult survival. Because the model was based on fecundity values which were depressed by the snakes, the importance of adult survival was exaggerated (Beissinger et al. 2006). Meats (1971) also showed that in declining populations changes in survival have the greatest impact on lambda.

Overall, my study is consistent with other comparative demographic studies which suggest that alpine vertebrate populations tend to show survivor life history strategies (Dobson 1992, Sandercock et al. 2005, Bears 2007). Although the estimates of fecundity were in the opposite direction predicted, *E. a. strigata* is declining and it is likely that the fecundity of *E. a. strigata* is depressed. The results of this study

underscore the importance of including estimates of λ when comparing the life histories of two or more groups. If a population is either declining or increasing rapidly as a result of modified habitat then its current demographic rates may not reflect their long term mean values. Thus it would be easy to place the group in the incorrect position along the life history continuum. This example using two horned lark subspecies illustrates the need to measure λ along with other vital rates when examining life history tradeoffs especially if species are experiencing rapid environmental change to which they may not have had time to adapt.

Table 2.1. Demographic rates of *E. a. articola* (2003-2006) and *E. a. strigata* (2002-2005); dates are Julian dates with day 1=January

1, data are means \pm SE or proportions (with *n* in parentheses). Where they were possible, a priori predictions are given. Statistically significant outcomes after Bonferroni correction are in bold.

	<i>E. a. articola</i>	<i>E. a. strigata</i>	Statistic	P	Predicted	Outcome
<u>A. Breeding Season</u>						
Clutch initiation date	151 \pm 0.61 (129)	135 \pm 1.25 (143)	$Z_{143,129} = -9.54$	< 0.0001	BC>WA	BC>WA
Season length (days)	38.5 \pm 1.26 (4)	94.0 \pm 10.53(4)	$Z_{4,4} = -2.32$	0.02	BC<WA	BC<WA
<u>B. Morphology</u>						
Wing chord (mm; female)	101.58 \pm 0.29 (43)	89.75 \pm 0.52 (20)	$t_{61} = -21.24$	< 0.0001	BC>WA	BC>WA
Tarsus (mm; female)	21.81 \pm 0.14 (44)	20.63 \pm 0.19 (18)	$t_{60} = -4.83$	< 0.0001	BC>WA	BC>WA
Weight (g; female)	34.01 \pm 0.34 (44)	26.92 \pm 0.47 (14)	$t_{56} = -10.70$	< 0.0001	BC>WA	BC>WA
Wing chord (mm; male)	108.85 \pm 0.38 (47)	97.45 \pm 0.36 (31)	$t_{76} = -20.67$	< 0.0001	BC>WA	BC>WA
Tarsus (mm; male)	22.71 \pm 0.13 (47)	21.18 \pm 0.43 (31)	$t_{76} = -4.05$	< 0.0001	BC>WA	BC>WA
Weight (g; male)	35.14 \pm 0.40 (47)	28.56 \pm 0.28 (27)	$t_{72} = -11.63$	< 0.0001	BC>WA	BC>WA

	<i>E. a. articola</i>	<i>E. a. strigata</i>	Statistic	P	Predicted	Outcome
<u>C. Fecundity</u>						
Clutch size (<i>C</i>)	3.61±0.07 (93)	3.05±0.06 (135)	$Z_{93,135} = -5.51$	< 0.0001		BC>WA
Proportion hatched	0.92±0.02 (65)	0.83±0.03 (61)	$Z_{65,61} = -2.37$	0.02		BC>WA
Proportion fledged	0.91±0.03 (39)	0.87±0.03 (38)	$Z_{39,38} = -1.11$	0.27		BC>WA
Fledglings per egg	0.35±0.04 (91)	0.23±0.04 (123)	$Z_{123,91} = -2.12$	0.03		BC>WA
Nest survival	0.35 (188)	0.23 (257)	$z = 2.78$	0.005		BC>WA
Proportion nests depredated	0.35 (188)	0.45 (249)	$z = 2.11$	0.03		BC<WA
Replacement nest interval (r_f)	5.97±0.84 (38)	22.25±4.25 (8)	$t_{44} = 3.76$	< 0.001		BC<WA
Multiple brood interval (r_s)	6.00±0.91 (8)	22 (1)				BC<WA
Annual fecundity	1.75±0.24 (4)	0.91±0.17 (4)	$t_6 = -2.82$	0.03	BC<WA	BC>WA

	<i>E. a. articola</i>	<i>E. a. strigata</i>	Statistic	P	Predicted	Outcome
<u>D. Apparent Survival</u>						
Adult (φ_a)	0.69±0.04 (117)	0.51±0.06 (58)	$\chi^2=6.23$	0.01	BC>WA	BC>WA
Male	0.72±0.06 (65)	0.55±0.08 (32)	$\chi^2=2.89$	0.09		BC>WA
Female	0.65±0.07 (52)	0.47±0.08 (26)	$\chi^2=2.87$	0.09		BC>WA
Juvenile without dispersal (φ_j)	0.20±0.05 (175)	0.074±0.03 (80)	$\chi^2=4.67$	0.03	BC>WA	BC>WA
Juvenile with dispersal	n/a	0.16±0.04 (88)	n/a	n/a		

Table 2.2. Model rankings from program MARK (White and Burnham 1999) to estimate apparent survival (ϕ) and re-sighting probabilities (p) for *E. a. articola* and *E. a. strigata* adults. Models included groups for adult males and females. The period symbol (.) means that the parameter was held constant in the model.

Model	AICc	Δ AICc	AICc Weights	Parameters	Deviance
<u>A. <i>E. a. articola</i> adults</u>					
$\{\phi (.)p(.)\}$	139.41	0	0.63	2	9.47
$\{\phi (\text{sex.})p(.)\}$	141.0	1.57	0.28	3	8.92
$\{\phi (\text{sex.})p(\text{sex.})\}$	143.14	3.73	0.09	4	8.93
<u>B. <i>E. a. strigata</i> adults</u>					
$\{\phi (.)p(.)\}$	106.70	0	0.64	2	11.47
$\{\phi (\text{sex.})p(.)\}$	108.39	1.69	0.27	3	10.99
$\{\phi (\text{sex.})p(\text{sex.})\}$	110.63	3.93	0.09	4	10.99

Figure 2.1. Frequency distribution of estimates of lambda (λ) for two horned lark subspecies, *E. a. articola* in alpine habitat in British Columbia, Canada, 2003-2006 and *E. a. strigata* in grasslands and sandy shorelines in Washington, USA, 2002-2005. The bold line indicates $\lambda = 1$, values to the right of the line show the proportion of simulations that predicted a growing population. Forty seven percent of the simulations predicted a growing population for *E. a. articola*, while none predicted a growing population for *E. a. strigata*.

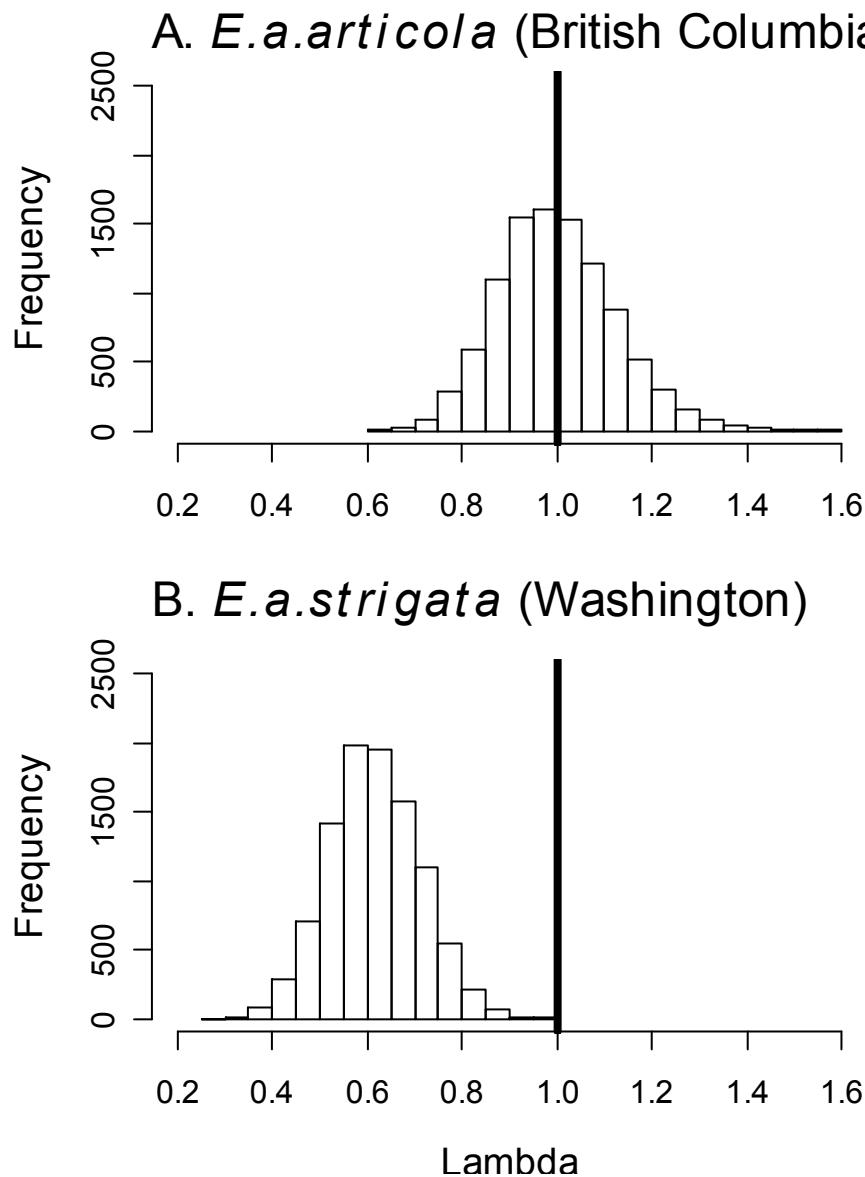
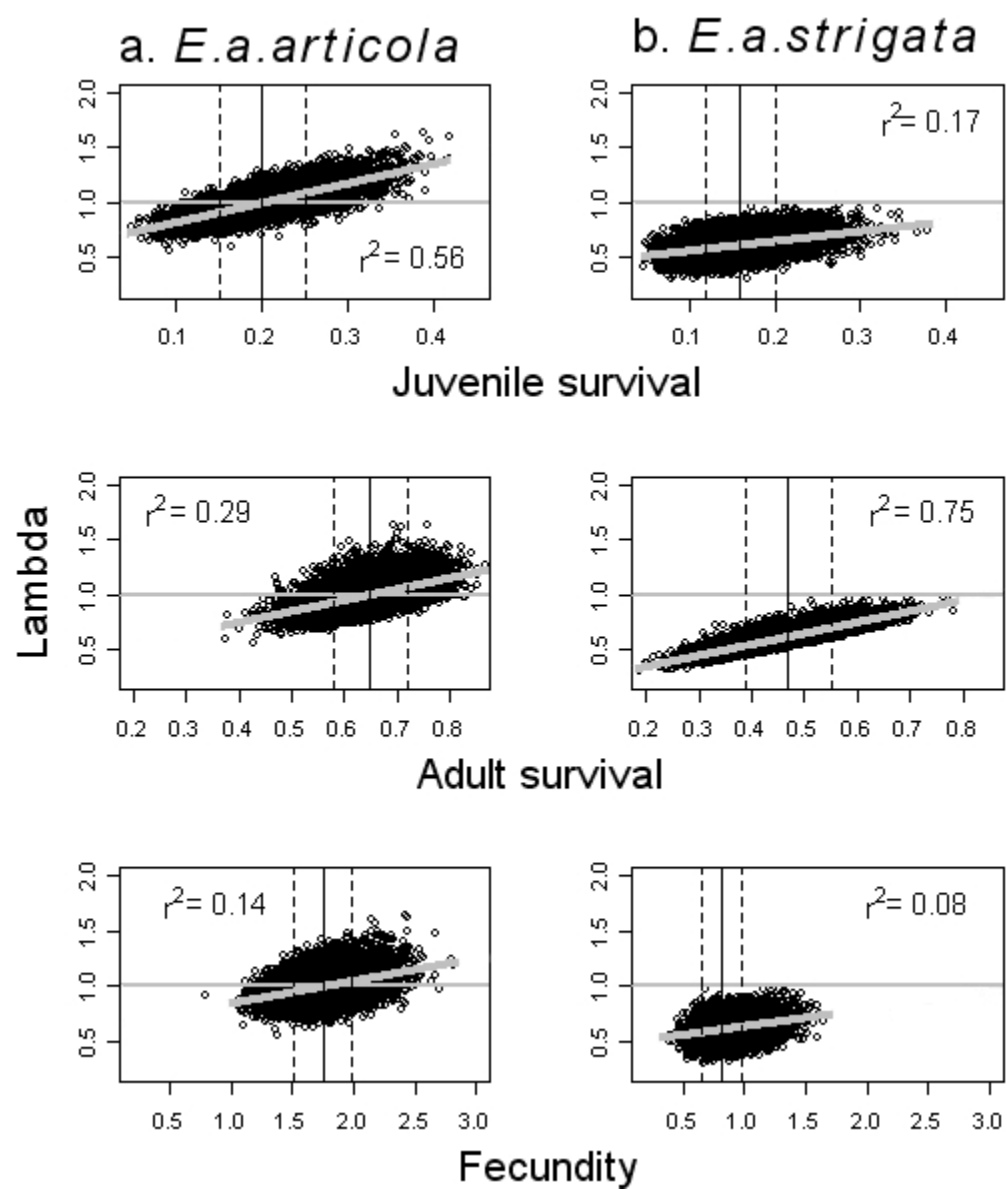


Figure 2.2. Life-Stage Simulation Analysis for *E. a. articola* and *E. a. strigata*. Light grey diagonal lines are regression lines, horizontal lines are shown at $\lambda = 1$, the value at the intercept of the two lines gives the parameter value needed to support a stable population. Vertical solid and dashed lines show the estimated mean value for each vital rate and its standard errors. For *E. a. articola* the mean values fall on the intercept of the two lines indicating that the population is stable. In all cases for *E. a. strigata* the vital rate estimates fall to the left of the intercept of the two lines indicating that the population is declining. The r^2 values show the proportion of the variation in λ over all simulations that is explained by variation in each vital rate.



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CHAPTER 3: EVALUATING MANAGEMENT SCENARIOS FOR THE ENDANGERED STREAKED HORNED LARK: INSIGHTS FROM DEMOGRAPHIC MODELS²

INTRODUCTION

As a result of the loss of agricultural grasslands and native prairies, grassland birds are the most rapidly declining group of birds in North America (Askins 1993, Knopf 1994, Herkert et al. 1996). The streaked horned lark (*Eremophila alpestris strigata*) is a ground nesting grassland bird that prefers sparsely vegetated open habitat (Beason 1995, Rogers 2000, Stinson 2005). The streaked horned lark is listed as endangered by the state of Washington and was classified as a federal candidate for listing under the Endangered Species Act in the United States in 2001. There are no known individuals remaining in Canada and they were listed as endangered by the Species at Risk Act in Canada in 2002 (Canadian Species at Risk Act 2002, c.29). Historically, streaked horned larks bred from southern British Columbia, through the Puget trough in Washington and in the Willamette and Rogue River Valleys in Oregon (Fraser et al. 1999, Rogers 2000, Stinson 2005). However, the breeding range has contracted over time with local extirpation from former breeding sites across the range (Rogers 2000, Beauchesne and Cooper 2003, Stinson 2005). More than 90 percent of the original grasslands have been lost in the south Puget Sound (Crawford and Hall, 1997, Stinson 2005). Major threats to remaining streaked horned lark habitat include development, dredging activities, intensification of

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agriculture, and the incursion of trees, shrubs and non-native invasive species (such as Scotch broom (*Cytisus scoparius*); Stinson 2005).

Given limited resources for the management of declining species, it is helpful to evaluate the potential impacts of different management options on populations of interest in order to determine where efforts may be best directed to decrease or reverse population declines. The cost of field experiments and potential risk to sensitive species often prohibits direct tests of the effects of alternative management techniques (Heppell et al. 1994). Demographic modeling has become a common tool to evaluate alternative management actions for declining populations where experimentation may not be possible (Mills et al. 1999). Techniques such as sensitivity analysis (de Kroon et al. 1986, de Kroon et al. 2000, Caswell 2001) and Life-Stage Simulation Analysis (Wisdom and Mills 1997, Wisdom et al. 2000) are often used to target vital rates for management. These techniques differ in their approach; however, both are used to evaluate the relative importance of various vital rates on population growth rates (λ) and the results can be used to inform management decisions and direct conservation efforts. For example, conservation of loggerhead turtles (*Caretta caretta*) was initially focused on improving hatching success of eggs. However, sensitivity analysis indicated that efforts to reduce by-catch of juveniles in trawl nets would have a greater influence on λ and led to the widespread use of turtle excluder devices on nets (Crouse et al. 1987).

Although demographic modeling can provide important insights for managers, caution is warranted in interpreting the results of such analyses and using the results to select among various management options. For example, some vital rates may show less plasticity in response to management actions, and efforts may be better directed toward

vital rates with less influence on λ but with potential for greater change (Caswell 2000, Norris and McCulloch 2003). In addition, predictions of λ in response to changes in vital rates can be inaccurate if they do not use a simulation approach or otherwise take into account the range of variation of the vital rates (Mills et al. 1999).

Estimates indicate that there may be fewer than 1000 streaked horned larks remaining (Pearson and Altman 2005). Genetic data show that the streaked horned lark is unique, isolated, and has little genetic diversity (Drovetski et al. 2005). In addition, existing populations appear to be declining rapidly (Chapter 2). A Life-Stage Simulation Analysis for streaked horned larks in Washington showed that variation in adult survival explained 75% of the variation in λ , followed by juvenile survival and fecundity (17 and 8% respectively, Chapter 2), suggesting that improvements in adult survival have the greatest potential to influence λ .

There are a number of management actions that may be taken to improve streaked horned lark survival and reproduction including: 1. habitat manipulations such as fire or herbicide treatments to control trees, shrubs and non-native perennial grasses to maintain or create suitable breeding and overwintering habitat and increase food resources, 2. supplemental feeding, 3. adding nest exclosures to protect nests from predators, 4. targeted control of known predators, 5. reduction of human-related disturbance, 6. conducting land management outside of peak breeding times, 7. reducing the number of airstrikes at breeding sites near airports. Some of these techniques have been used successfully for other species (e.g. nest exclosures have been successful in improving snowy plover (*Charadrius alexandrinus*) nesting success; U.S. Fish and Wildlife Service 2007), however, there is a need to evaluate the potential for the management actions

listed above to improve streaked horned lark population growth and to prioritize the available options.

In this chapter I simulated changes in three vital rates (fecundity, adult survival and juvenile survival) to examine how much they would need to be adjusted either independently or in concert to achieve a stable or increasing lark population ($\lambda \geq 1$). In addition, I evaluate which fecundity component (the number of fledglings per egg laid, or reneating interval) has the greatest impact on λ . Elasticity analyses do not indicate which factors are causing population declines or which vital rates are low compared to a healthy population (Hiraldo et al. 1996, Beissinger and Westphal 1998), therefore I compare the vital rates of streaked horned larks to those of a stable population ($\lambda = 1$) of pallid horned larks (*E. a. articola*) in British Columbia (Chapter 2). Finally, based on the results of the simulations I suggest which management options should be prioritized in order to facilitate streaked horned lark recovery.

METHODS

Study site and study species

Data were collected by S.F. Pearson for *E. a. strigata* (streaked horned lark) at seven sites in Washington State, USA in grass and forb dominated habitats located in south Puget Sound prairies and airports, coastal Washington dune habitats and on islands in the lower Columbia River from 2002-2005. Study sites included: Olympia Airport (46° 58' N, 122° 53' W), 13th Division Prairie on Ft. Lewis (47° 01' N, 122° 26' W), Gray Army Airfield on Ft. Lewis (47° 05' N, 122° 34' W), McChord Air Force Base (47° 08' N, 122° 28' W), Damon Point (46° 56' N, 124° 06' W), Midway Beach (46° 46' N, 124° 05' W) and

Whites Island (46° 08'N, 123° 18' W). Study areas ranged in size from 0.07 to 2.49 km², were between 1.8 and 145 km apart and elevation ranged from 3 to 122 m above sea level.

To compare vital rates of streaked horned larks to a stable horned lark population, I also present data collected for *E. a. articola* (pallid horned lark) from 2003-2006 at a single site in alpine habitat on Hudson Bay Mountain near Smithers, British Columbia, Canada (52° N, 127° W; Chapter 2). The study area was approximately 4km² and elevation ranged from 1500 to 1850 m above sea level.

Data collection

Field techniques were similar for both streaked and pallid horned larks with the breeding season extending from April to mid-August in Washington, early May to early August in British Columbia. Nests were found during nest building, incubation and nestling stages and were located by observing adults leaving or approaching nests with and without nesting materials or carrying food, by flushing incubating or brooding adults and by searching appropriate habitat. The status of each nest (presence of parents, eggs, nestlings) was recorded every 3-5 days, more frequently near the expected hatch and fledging dates.

Adult birds were captured using mist nets or bow traps, were individually color marked and morphological measurements were taken (wing chord, tarsus and weight). Complete surveys of the study areas were conducted each year to determine which birds returned (for additional details on monitoring see Chapter 2). Nestlings were banded in the nest between days 7-9 post-hatching or occasionally shortly after fledging.

Estimation of vital rates

I calculated annual fecundity (F) using the technique of Ricklefs and Bloom (1977; Appendix 1) with the following variables: Length of the breeding season calculated using the proportion of active nests during each month of the breeding season to correct for the fact that breeding effort was not constant across all ($B = 94.0 \pm 10.53$, $n=4$ years); clutch size ($C = 3.05 \pm 0.06$, $n=135$ nests); breeding success ($S = 0.23 \pm 0.04$, $n=123$ nests); daily nest mortality rate ($m = 0.058 \pm 0.003$, $n = 257$ nests); probability that at least one nestling fledges ($p_s = 0.24 \pm 0.02$, $n=257$ nests); probability that a nest fails ($p_f = 0.76 \pm 0.02$, $n=257$ nests); multiple brood interval ($r_s = 22$, $n=1$ nest); replacement nest interval ($r_f = 22.25 \pm 4.25$, $n=8$ nests). Estimates of each variable are from Chapter 2, and details on how each variable was estimated can be found within. To calculate the number of female fledglings per female, annual fecundity was divided by two, assuming an equal sex ratio at fledging.

I used the Program MARK Version 3.1 (White and Burnham 1999) to estimate apparent adult and juvenile survival rates (ϕ) corrected for the probability of resighting (p ; the probability the bird was seen given that it was alive) from live encounter data using the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965). For details see Chapter 2.

Population growth rate (λ) was estimated previously (Chapter 2) using the equation: $\lambda = F\phi_j + \phi_a$, where F is the number of female fledglings produced per female per year, ϕ_j is apparent juvenile survival and ϕ_a is apparent adult female survival (Pulliam 1988). To estimate λ I assumed a closed population. I used a Monte Carlo simulation approach of 10 000 replicates to generate standard deviations for estimates of λ . The

simulation approach used in these analyses allowed me to incorporate the variability of the vital rates into the estimates of λ . I modeled apparent survival of adult females and juveniles using random draws from beta distributions using the estimates of variation for each vital rate. The beta distribution constrains the random variables between 0 and 1 and is therefore appropriate for modeling survival probabilities which must remain within these values (Morris and Doak 2002). A stretched beta distribution was used to model fecundity. The stretched beta distribution is a rescaled beta distribution that reflects a biologically realistic range for the simulated vital rate (Morris and Doak 2002). After each iteration the randomly drawn parameter estimates were used to calculate λ .

A consistent effort was made to survey sites for replacement nests and multiple broods, however, because a conservative approach was used when determining pairs to include in the estimates of renesting intervals (Chapter 2), the sample sizes for replacement nest and multiple brood intervals were small. Also, the sampling regime across multiple sites may have made it more likely that replacement nests were not detected. To account for the possibility that the estimates of replacement nest and multiple brood intervals were low I re-estimated fecundity using the estimates from *E. a. articola* (5.97 and 6.00 days, respectively) and using the minimum observed replacement nest interval for streaked horned larks (10 days; Chapter 2).

Simulating changes in population growth

For each of the three vital rates (adult female survival, juvenile survival and fecundity), I determined the value needed to give a stable population ($\lambda=1$) by changing one rate at a time while holding the other vital rates constant. I compared these values to the estimates

of current streaked horned lark vital rates and to estimates from a stable population of horned larks in British Columbia (Chapter 2). To evaluate the relative influence of each vital rate independently on λ I increased each vital rate independently by 10 percent (proportionally) in each iteration and repeated this process until each rate was increased by 100 percent (or doubled). After each 10 percent increase I re-ran the simulation described above to generate a new estimate of λ . I chose to run each simulation after a 10 percent change because smaller increments were not necessary to show overall patterns.

Potential management activities for streaked horned larks may influence fecundity by increasing the number of fledglings produced per egg laid (hereafter called breeding success) which can be done by decreasing nest failure or increasing hatching and fledging success, or by decreasing renesting intervals. I used the technique described above to examine how increases in breeding success or decreases in renesting intervals affected λ . To accomplish this, I re-calculated annual fecundity after each 10 percent increase in either breeding success or decrease in renesting interval and then used this new fecundity estimate in the Monte Carlo simulation of λ . This process was repeated, manipulating one variable at a time until it was increased by 100 percent.

To examine how much fecundity and juvenile survival would need to increase in concert to achieve $\lambda \geq 1$, I re-ran the simulations described above, but allowed the two rates to vary simultaneously. I evaluated every possible combination of 10 percent increase for the two rates (i.e., fecundity increased by 10 percent, juvenile survival increased by 20 percent, fecundity increased by 10 percent, juvenile survival increased by 30 percent, etc.). This process was repeated three times, once using the current empirical value for adult female survival, a second time with adult female survival raised by 10

percent and a third time with adult female survival raised to the level measured for pallid horned larks in British Columbia.

All analyses were performed using the program R (R Development Core Team 2006). Estimates of apparent survival and fecundity are reported as means \pm SE, estimates of λ are reported as means \pm SD.

RESULTS

The vital rate estimates (female survival = 0.47, juvenile survival = 0.16 and fecundity = 0.91; Table 3.1) derived over four years and over a significant portion of the streaked horned lark breeding range indicate that the population is rapidly declining ($\lambda=0.61\pm0.1$ SD). When I increased each vital rate independently while holding the other two constant, it was necessary to increase female survival, juvenile survival and fecundity to 0.85, 0.58 or 3.31 respectively in order to achieve $\lambda=1$. Vital rates from a stable pallid horned lark population on Hudson Bay Mountain in Smithers, BC ($\lambda=1.0\pm0.12$ SD) were 0.65 for adult survival, 0.20 for juvenile survival and 1.75 for fecundity (Chapter 2; Table 3.1). Increasing adult survival eventually leads to $\lambda\geq1$ when adult survival is raised to 0.85 (an 80 percent increase). Increasing either fecundity or juvenile survival by 100 percent (to double current values) did not raise λ above one (Figure 3.1).

Increasing breeding success and reducing renesting intervals have similar impacts on λ (Figure 3.2). The stable pallid horned lark population had a mean renesting interval of 6 days and mean breeding success of 0.35 (Chapter 2). For streaked horned larks to reach the same levels as pallid horned larks, breeding success would need to be increased

by 50 percent (from 0.23 fledglings/egg laid to 0.35) and renesting intervals would need to be reduced by 70 percent (from 22 to 6 days) from current values.

When both fecundity and juvenile survival were manipulated simultaneously to investigate their combined influence, λ approached one only when juvenile survival and fecundity were each increased by more than 80 percent (Figure 3.3 a). When adult survival was increased by 10 percent (0.47 to 0.52), λ approached one only when juvenile survival and fecundity were increased by over 60 percent (Figure 3.3 b). When adult survival was raised to the level measured for pallid horned larks (0.65), λ approached one when juvenile survival and fecundity were each increased by over 50 percent (Figure 3.3c).

When fecundity was re-estimated using the replacement nest and multiple brood intervals for *E. a. articola* and using the minimum observed replacement nest interval for streaked horned larks, fecundity increased to 1.67 ± 0.32 female fledglings/female/year and 1.38 ± 0.26 female fledglings/female/year, respectively. Estimates of λ increased to 0.74 ± 0.12 and 0.69 ± 0.11 (Chapter 2). Using these estimates, if fecundity is increased independently while holding the other vital rates constant, fecundity would need to be increased by 98 and 140 percent, respectively in order to achieve $\lambda=1$. When the initial estimate of 1.67 ± 0.32 was used for fecundity and both fecundity and juvenile survival were manipulated simultaneously, λ approached one when each rate was increased by 45 percent. Using 1.38 ± 0.26 as the initial fecundity estimate, λ approached one when each rate was increased by 55 percent.

DISCUSSION

When evaluating available management strategies for the streaked horned lark, it is clear that techniques that target multiple vital rates or techniques used in combination to target multiple vital rates should be prioritized. In the models, increasing either juvenile survival or fecundity independently by 100 percent did not lead to $\lambda \geq 1$. Even if renesting intervals for *E. a. articola* are used to estimate fecundity for streaked horned larks, fecundity still needs to increase by 98% to lead to $\lambda = 1$. Targeting adult survival, the vital rate that had the most influence on λ (Chapter 2), will lead to a stable streaked horned lark population only if it is increased by 80 percent (from 0.47 to 0.85). However, if all vital rates are increased simultaneously it may be possible for streaked horned lark populations to stabilize or grow.

Survival is one of the most difficult and time consuming vital rates to measure and may be difficult to influence through management (Porneluzi and Faaborg 1999, Anders and Marshall 2005, Knutson et al. 2006). However, given that proportional increases in adult survival have the greatest potential to increase λ for streaked horned larks, such efforts are warranted. Horned larks are the most commonly reported species involved in bird aircraft collisions in the United States (BASH 2006) and they nest at four airports in Washington and one in Oregon. Therefore efforts to reduce the number of collisions by improving nesting habitat away from active runways and taxiways would improve adult survival. Additional management actions that target adult survival include increasing food supply through habitat manipulations or food supplementation, controlling predators and reducing human-caused disturbances (Table 3.2). Adult streaked horned larks in Washington show strong breeding site fidelity (Pearson et al.

2008), consequently it is also critical to preserve habitat that currently supports breeding pairs.

Apparent survival of adult songbirds is often lowest during the migration and overwinter period (Powell et al. 2000, Sillett and Holmes 2002). Some streaked horned larks that breed in Washington overwinter in the Willamette Valley of Oregon (Pearson et al. 2005), however, there is little information about the type of habitat they select and the causes of mortality during the nonbreeding season. Given the importance of adult survival for population growth rates of streaked horned larks, management actions focused on improving nonbreeding habitat and overwinter adult survival and studies of overwinter habitat use and mortality are needed.

Of the three vital rates I examined, fecundity, rather than adult survival may have the greatest potential for improvement through management activities (Table 3.2). Although streaked horned lark population growth is highly sensitive to changes in adult survival, focusing on the most sensitive vital rate may not be the best strategy and efforts directed toward improving fecundity could be more effective. Similar results were found for the lesser kestrel (*Falco naumanni*) where demographic models showed that population growth was most sensitive to changes in adult survival. There was limited scope to increase adult survival rates, however, management could dramatically improve birth rates and thus the long-term viability of the population (Hiraldo et al. 1996). In this study, annual fecundity for streaked horned larks in Washington was half that of pallid horned larks in British Columbia (0.91 female fledglings/year compared to 1.75) suggesting that there is scope for improvements in fecundity. For streaked horned larks, management that targets either breeding success (number of fledglings/egg laid) or

renesting intervals will have similar impacts on annual fecundity. While renesting intervals for other horned larks typically range from 2 to 6 days (Beason 1995), streaked horned larks in Washington had renesting intervals of 22.25 ± 4.25 days and the minimum observed renesting interval was 10 days. Supplemental feeding can reduce renesting intervals in songbirds (Zanette et al. 2006), and may be an easy and cost effective way to increase annual fecundity for streaked horned larks. Caution is advised, however, as supplemental food may also attract potential nest predators (Schoech et al. 2008) so feeding stations would need to be designed to minimize the risk of attracting predators. In addition, there is a physiological limit to the speed at which females can reneest after a clutch fails. Therefore if the estimates of renesting intervals presented here are overestimates and the interval is actually closer to that recorded for *E. a. articola*, there is less scope for management to reduce the renesting interval.

In order to improve breeding success, management needs to address the hatchability of eggs, the proportion of nestlings that fledge in successful nests and/or total nest failure. Efforts are currently underway to evaluate the cause of reduced hatchability of streaked horned lark eggs and to determine if reduced hatching success is the result of contaminants in the eggs or a byproduct of inbreeding. The majority of nest mortality is caused by predators, although human activities that prevent females from returning to their nests for extended periods of time may lead to nest abandonment (Pearson et al. 2005, 2008). Supplemental feeding or habitat manipulations to improve food supply may help increase fledging success and, if successful, predator control and the use of nest exclosures will increase breeding success by reducing nest depredation. Nest loss can also be reduced through management of the timing of agricultural activities such as

scheduling mowing between peak nesting periods and by reducing other sources of human related failure (including construction projects and recreational activities near nests) through education and by excluding humans from nesting areas (Table 3.2).

Along the coast, habitat requirements for streaked horned larks in Washington overlap with snowy plovers. Removal of non-native and invasive beach grasses (*Ammophila spp.*) to create unvegetated and sparsely vegetated dune and beach habitat has resulted in use by both plovers and larks. Nest exclosures have been successfully used for snowy plovers and initial attempts to use these on streaked horned larks have met with some success (S.F. Pearson *personal observation*). Collaborating with snowy plover management efforts may reduce the expense and hasten recovery efforts for streaked horned larks.

Mortality rates for most songbirds are highest during the first few weeks after fledging (Anders et al. 1997, Kershner et al. 2004, Suedkamp Wells et al. 2007) and this is likely to be the case for juvenile horned larks. Newly fledged larks are unable to fly and can be easily captured by predators in their open habitats with limited escape cover. Although juvenile streaked horned lark survival is relatively high (≥ 0.16 in the first year) compared to other songbirds (Weatherhead and Forbes 1994), efforts directed toward increasing survival immediately post-fledging could potentially have large impacts on juvenile survival. Management actions to improve post-fledging survival include increasing food supply through habitat manipulations or supplemental feeding and predator control (Table 3.2).

Estimates of apparent survival rates are minimum estimates of survival because they do not make a distinction between permanent emigration and mortality (Lebreton et

al. 1992). The estimate of juvenile survival for streaked horned larks includes birds that dispersed throughout the study region. When estimates of juvenile survival are restricted to those individuals that returned to their natal sites, apparent juvenile survival drops to 0.07 (Chapter 2) suggesting that there is a lot of movement of juveniles among sites. In this study, the ability to detect dispersal events is unusually high because extensive surveys were conducted and streaked horned larks breed in distinct locations in a matrix of unsuitable habitat in western Washington. If not all dispersal events were detected the estimate of juvenile survival may be slightly underestimated. In contrast to juvenile dispersal, adult dispersal appears to be less common as there were no instances of adult dispersal between study sites (Pearson et al. 2008).

The simulations of streaked horned lark population dynamics assume that the population is closed. It is likely, however, that there is immigration into the population so the estimates of λ may be low. It is often difficult to estimate emigration/immigration and therefore many models do not incorporate estimates of dispersal (Beissinger and Westphal 1998). It is not uncommon for predictions of λ based on estimates of vital rates to be lower than predictions of population growth from count data. In a study of acorn woodpeckers (*Melanerpes formicivorus*), λ was less than one when calculated using birth and death rates, however, the population size at the study site did not decline over the 10 year study (Stacey and Taper 1992). The authors suggested that immigration of birds from other areas allowed the study population to persist over time. Similarly, Fletcher et al. (2006) suggested that population dynamics of grassland birds function at large spatial scales and called for additional investigation of immigration and dispersal when they

showed that estimates of λ for dickcissels (*Spiza americana*) and bobolinks (*Dolichonyx oryzivorus*) appeared to be low when compared to count data.

While there are no data on range-wide population trends for streaked horned larks, territory mapping data from four sites in the Puget lowlands indicate that the average number of territories per site have decreased from 19.3 in 2004 to 10.5 in 2007 (a total decrease of 45% from 77 territories in 2004 to 42 in 2007; S.F. Pearson *unpublished data*). Although the rate of decline observed by mapping territories is smaller than that predicted from the models, both indicate significant population declines. If the renesting interval for streaked horned larks is actually lower than the estimate from this study, annual fecundity may be higher than the 0.91 female fledglings/female/year presented here. Slightly higher fecundity combined with low levels of immigration into the population could explain the difference between the population decline predicted by my model and that estimated by territory mapping. Given difficulties in accurately estimating λ , it is often recommended that rather than comparing absolute changes in the outcomes of different management actions using demographic models it is more useful to look at the relative effects of changing each vital rate (Beissinger and Westphal 1998, Beissinger et al. 2006). Even if the estimate of λ is an underestimate, the results of management efforts focused on each vital rate should qualitatively if not quantitatively follow the trends discussed above.

The Willamette Valley of Oregon is the only portion of the breeding range for streaked horned larks that is not included in this study. It is possible that individuals from the Willamette Valley population immigrate to Washington and augment the population there. However, this rescue effect may be small given the low reproductive

success reported for *E. a. strigata* in the Willamette Valley (14%, n=13 nests; Altman 1999, 27%, n=16 nests in 2007; R. Moore *personal communication*). Estimates of immigration rates are needed to determine where source populations are located and to ensure that these populations are maintained. It is also possible that breeding sites with lower productivity are overrepresented in the data set or that the early years of the study represent particularly poor years for streaked horned lark breeding and/or survival. However, the vital rates for streaked horned larks reported here come from sites representing nearly all habitat types currently used by streaked horned larks (except agricultural fields in the Willamette Valley) and represent populations spanning over half of the geographic range of the subspecies.

Surprisingly few studies have collected detailed demographic data for horned larks despite their ubiquitous presence across the continent. Horned larks in North America are declining through much of their range (Sauer et al. 2004); the baseline data presented here and subsequent efforts to manage streaked horned larks will provide valuable information for management of horned larks and other grassland songbirds across North America.

Management Implications

The most immediate action managers can take is to preserve existing habitat and maintain or improve vegetation structure within existing habitat patches to ensure they remain suitable or are improved for breeding horned larks. However, if preserved or restored habitats do not support stable populations, as appears to be the case for streaked horned larks in Washington, management must also focus on improving demographic rates.

Management actions that target multiple vital rates should be prioritized. Efforts to reduce the number of predators or predation rates in breeding areas will improve adult survival, juvenile survival and fecundity and should be a management priority. The use of nest exclosures similar to those used for snowy plovers will protect nests from predators and may also protect incubating females and/or adults while they are feeding nestlings. Finally, scheduling land management and other human activities outside peak nesting periods is a relatively simple and inexpensive way to reduce accidental nest loss. For example, mowing regimes at airport breeding sites in Washington (Olympia Airport and Gray Army Airfield) have already been adjusted to reduce the potential for destroying nests. Given high values for juvenile survival, and assuming that density dependent effects would be weak due to small population sizes, improvements in fecundity could have large cascading effects on population growth rates.

Table 3.1. Values of vital rates for streaked horned larks in western Washington from 2002-2005 and the value needed to give a stable streaked horned lark population if only one vital rate is changed at a time and the other two are held constant. For comparison, values are given for pallid horned larks in northern British Columbia from 2003-2006.

Data on current vital rates are from Chapter 2.

Vital rate	Streaked horned lark		Pallid horned lark	
	Current	Value to achieve stable population		
Adult female survival	0.47±0.08 (<i>n</i> =26)		0.85	0.65±0.07 (<i>n</i> =52)
Juvenile survival	0.16±0.04 (<i>n</i> =88)		0.58	0.20±0.05 (<i>n</i> =175)
Fecundity	0.91±0.17 (<i>n</i> =4)		3.31	1.75±0.24 (<i>n</i> =4)

Table 3.2. Proposed management actions and techniques for streaked horned larks and their predicted effect on fecundity, adult survival and juvenile survival (+ + indicates a large positive effect, + indicates a smaller positive effect). ¹

Management action	Technique	Season or habitat	Fecundity		Effect on		Cautions
					Adult survival	Juvenile survival	
1. Habitat manipulations:	Fire or herbicide treatments to control trees, shrubs and non-native perennial grasses	Breeding/ wintering	+ +		Unclear	Unclear	Should be conducted in non-breeding season to avoid breeding disruption
a) focused on vegetation structure							
b) focused on food resources	Planting, vegetation control	Breeding/ wintering	+		+ (if food limiting)	+ (if food limiting)	Larks select sparsely vegetated habitat, planting should not increase vegetation density
2. Supplemental feeding	Provide food	Breeding/ wintering	+		+ (if food limiting)	+ (if food limiting)	Might provide food to predators and result in increased predation risk

Management action	Technique	Season or habitat	Effect on			Cautions
			Fecundity	Adult survival	Juvenile survival	
3. Nest exclosures	Mini-exclosures similar to those used for snowy plovers	Breeding	++	Unclear	Unclear	Might cause nest abandonment; predators may key in on exclosures and prey on adults
4. Predator control	Targeted control of known predators	Breeding	++	+	+	
5. Reduce human- related disturbance	Exclude from nesting areas, education	Breeding	+	Unclear	Unclear	
6. Timing of land management	Conduct mowing agricultural management (i.e. mowing) outside of peak breeding times	Breeding	+	Unclear	Unclear	

Management action	Technique	Season or habitat	Effect on		Cautions
			Fecundity	Adult survival	Juvenile survival
7. Reduce number of airstrikes	Improve nesting habitat away from active runways and taxiways	Breeding/ wintering	No change if habitat is suitable	+	+
					Could result in relocation of larks from productive sites to less suitable sites resulting in a net negative effect on lambda

¹ Assuming suitable habitat (with appropriate site conditions and size) within the species range.

Figure 3.1. Predicted values of lambda for streaked horned larks with successive 10 percent increases in each vital rate. Each point represents a 10 percent increase in the vital rate, only one vital rate was manipulated at a time. The solid horizontal line represents $\lambda=1$.

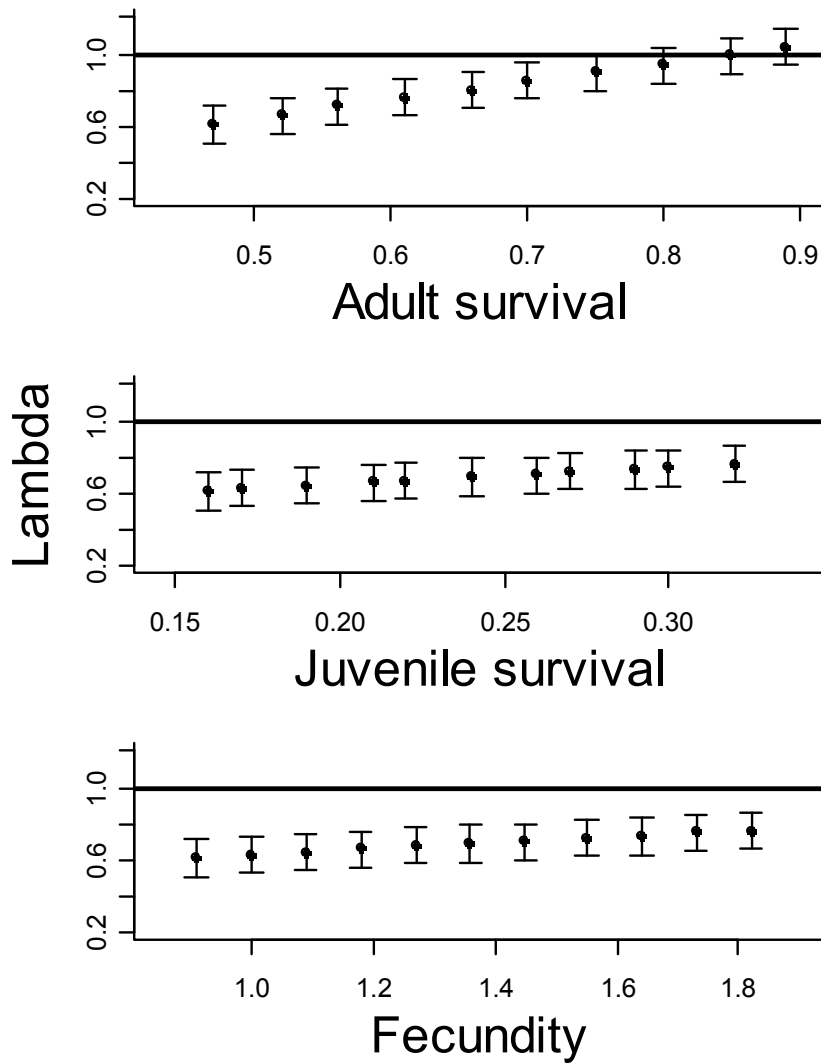


Figure 3.2. Predicted values of fecundity and lambda for streaked horned larks with successive 10 percent increases in breeding success (the number of fledglings produced per egg laid) and with 10 percent decreases in the renesting interval. Each point represents a 10 percent change in the rate, only one rate was manipulated at a time. The solid horizontal line represents $\lambda=1$.

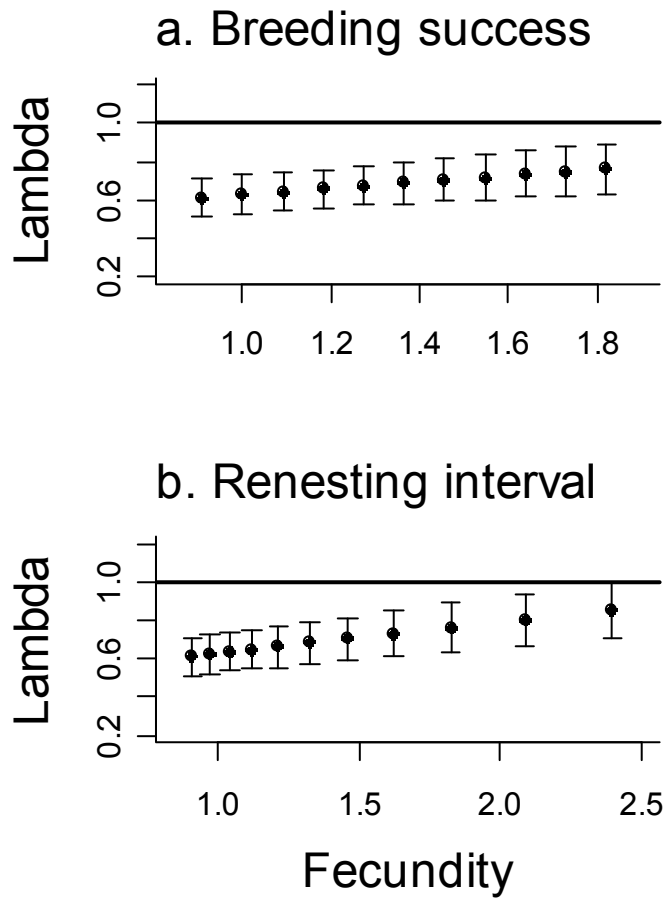
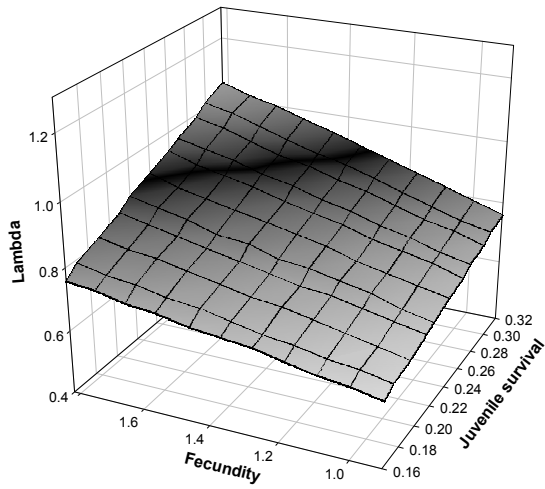
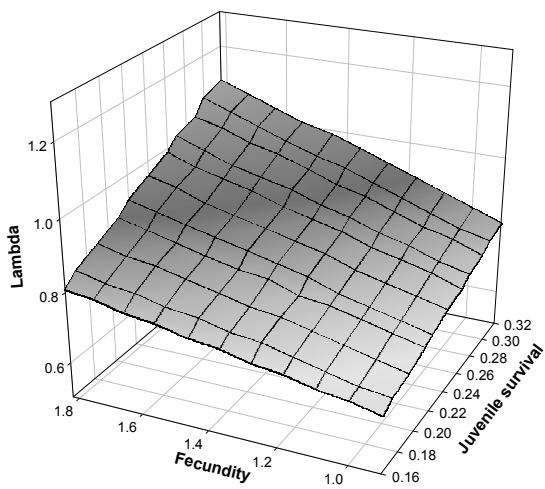


Figure 3.3. Predicted values of lambda for streaked horned larks as fecundity and juvenile survival are simultaneously increased by increments of 10 percent starting with current empirical levels of 0.91 for fecundity and 0.16 for juvenile survival. X and Y axis show the value for fecundity and juvenile survival after successive increases of 10 percent. Adult survival of female streaked horned larks was held constant at its current empirical level of 0.47 (a), increased by 10 percent to 0.52 (b) and increased to the level of pallid horned larks in British Columbia (0.65; c).

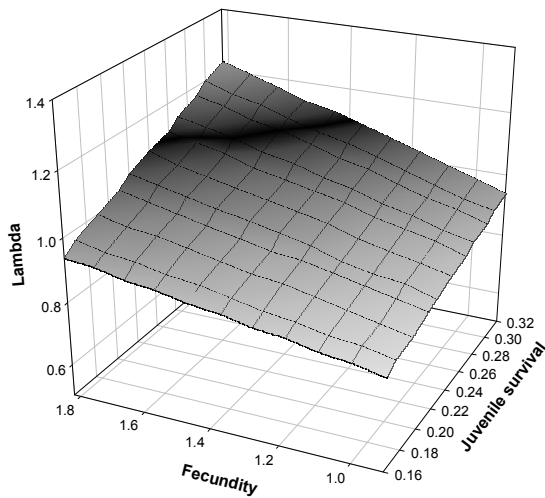
a. Adult survival (0.47)



b. Adult survival (0.52)



c. Adult survival (0.65)



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CHAPTER 4: THE INFLUENCE OF AMBIENT TEMPERATURE ON SONGBIRD INCUBATION BEHAVIOR IN AN ALPINE ENVIRONMENT³

INTRODUCTION

Incubation is an energetically costly activity for birds and requires the incubating parent to tradeoff between their need to forage to meet their own energetic requirements and the thermal needs of the eggs (Webb 1987, Williams 1996, Thomson et al. 1998, Visser and Lessells 2001). For optimal embryo development, egg temperatures must be maintained between 36-38 °C (Drent 1975, Webb 1987), and in most environments, fluctuations in ambient temperatures make incubation necessary to prevent cooling or overheating of the eggs. Temperature deviations outside the optimal range can reduce the hatchability of eggs and/or extend the incubation period (Webb 1987, Strausberger 1998, Reid et al. 2000, Black and Burggren 2004). Incubation may be particularly challenging for birds breeding at high elevations where they face extreme temperature fluctuations yet the thermal requirements of the eggs are the same as in more moderate environments (Wiebe and Martin 1997, Martin and Wiebe 2004).

In order to maximize fitness, individuals must adjust their behavior in response to fluctuating environmental conditions. When ambient temperatures reach high or low extremes, both the metabolic rates of adult birds and the need for cooling or warming the eggs increase. However, the total time available for foraging and incubating remains the same and an incubating parent must therefore shift its investment either toward self-maintenance or the survival of the eggs or compromise both (Drent 1975, Biebach 1981,

³ A version of this chapter has been submitted for publication. Camfield, A.F. and K. Martin. *In review*. The influence of ambient temperature on horned lark incubation behavior in an alpine environment.

Vleck 1981a, Haftorn and Reinertsen 1985, Black and Burggren 2004). At some point individuals may be forced to abandon a reproductive attempt if further investment in incubation would result in the immediate death of the adult. For example, breeding songbirds may enter an “emergency life history stage” and abandon their nests in response to prolonged periods of severe weather (Wingfield 2003). If an incubating parent favors its own survival and future reproduction over the current reproductive attempt at extreme temperatures it will change its behavior by decreasing the total amount of time spent incubating and increasing the amount of time spent foraging. Alternatively, the parent can change its behavior to favor the current reproductive attempt by increasing the total time spent on the nest and decreasing the amount of time foraging.

Life history theory predicts that when faced with a tradeoff between survival and reproduction, longer lived individuals with more opportunities to breed should be less willing to invest in current reproduction than shorter lived species with fewer breeding opportunities (Charlesworth 1980, Stearns 1992, Saether et al. 1996, Ghalambor and Martin 2000). There are also tradeoffs between current and future reproduction within a single breeding season where increased investment in one breeding attempt may preclude additional breeding attempts later in the season. In an environment where there is ample time to renest if the first nest fails, the benefit of maintaining a nest in unfavorable conditions may not outweigh the cost of forgoing additional breeding attempts later in the season. At high elevations the breeding season for songbirds is short (Chapter 2) and there are few opportunities to renest after a clutch fails. Therefore alpine breeding songbirds may compensate for short breeding seasons with few opportunities for multiple

broods by increasing their relative investment in each brood (Badyaev and Ghalambor 2001).

If an incubating parent increases its total time on the nest at temperature extremes it can do so by either reducing the duration of recesses, taking fewer recesses or both. However, there will be a threshold in recess length below which the energy gained from foraging will not outweigh the cost of rewarming the eggs (Conway and Martin 2000a). Conversely, if the parent decreases its time on the nest it can either increase recess duration, take more frequent recesses or both. There are tradeoffs between recess frequency and duration. Taking more frequent recesses results in higher levels of activity at the nest which may increase the risk of attracting predators to the nest (Conway and Martin 2000b, Ghalambor and Martin 2000; 2002). However, the risk to the embryo increases the longer the eggs are exposed to temperatures outside the range of temperatures that are optimal for development. Finally, because the rate of egg cooling slows as egg temperature approaches ambient temperature, taking less frequent but longer recesses minimizes the total energy required by the parent to rewarm the eggs after a recess (Drent 1975).

The relationship between ambient temperature and avian incubation patterns is often ambiguous with observational studies reporting positive, negative and no correlation between nest attentiveness, recess duration, on-bout duration and ambient temperature (e.g. see Vleck 1981b, Zerba and Morton 1983, Lombardo et al. 1995). While most studies have looked for linear relationships between ambient temperature, incubation constancy, recess duration and on-bout duration, Conway and Martin (2000a) suggested that the relationship should not be linear, but should vary across wide ranges of

temperatures. They showed that for orange-crowned warblers (*Vermivora celata*) recess and on-bout durations were positively correlated with ambient temperatures between 9-26°C and negatively correlated with ambient temperatures <9 °C and >26 °C. However, the correlations between ambient temperature and incubation patterns varies among species and additional studies are needed to improve our general understanding of the relationship (Conway and Martin 2000a).

In this chapter I examined both linear and non-linear relationships between ambient temperature and the total time spent incubating in horned larks (*Eremophila alpestris*) breeding in alpine habitat in British Columbia in order to determine if incubating females adjusted their incubation rhythms as ambient temperature varied. To explore how horned larks adjusted the total time spent on the nest I examined the relationships between ambient temperature and the frequency of recesses, recess duration and on-bout duration. My study site was an ideal location to investigate correlations between incubation rhythms and ambient temperature given that temperatures varied more than 30 °C in a single day and below zero temperatures occurred throughout the breeding season. In addition, the tradeoff between time spent on the nest vs. time spent foraging is particularly important for birds such as horned larks that have unassisted single sex incubation and depend on exogenous resources throughout the incubation period (Williams 1991, Beason 1995). Breeding season length for horned larks at my site was less than half that at lower elevation and latitude (Chapter 2) and the opportunity to renest after nest failures was therefore restricted. Given limited breeding opportunities each year for horned larks at my site, I expected that at low ambient temperatures females would change their incubation behavior by increasing the total time spent on the nest.

METHODS

Study site and study species

Horned larks are medium-sized (28-40 g) ground nesting songbirds that prefer open habitat. They are widely distributed and can be found in diverse habitats ranging from arctic and alpine tundra to native prairies and deserts. Both parents participate in feeding nestlings, however, only females incubate (Beason 1995). I studied horned larks in alpine tundra on Hudson Bay Mountain near Smithers, British Columbia, Canada (52° N, 127° W), 1500-1850m above sea level, from 2005-2006.

Data collection

Throughout the breeding season (early May to early August), I searched for nests on horned lark territories. Nests were located by observing females leaving or approaching nests with and without nesting materials, by flushing incubating females and by searching appropriate habitat. I recorded incubation rhythms by inserting the temperature probe of a data logger (HOBO Pro Series, #H08-031-08, Onset Computer Co., Pocasset, MA, USA) through the nest lining until about 0.5 cm of the probe was visible in the nest cup. The data logger took a temperature reading inside the nest every 30 s, 24 hr/day for the duration of incubation. In addition, the data loggers recorded ambient temperature within 2 m of the nest every 30 s, 24 hr/day. Because horned larks are ground nesting songbirds I measured ambient temperature at ground level as this most closely approximates the temperatures experienced at the nest. The data loggers were placed in areas with similar aspect and protection from the wind as the nest. The temperature probes did not touch the eggs, so I was not measuring the exact temperature of the eggs during incubation.

However, using the fluctuations in temperatures recorded by the data loggers I was able to determine with high accuracy when a female left or returned to a nest. I conducted behavioral observations at selected nests to verify that the temperature fluctuations recorded by the data loggers coincided with the recesses and on-bouts of the incubating females. If nests were located after the clutch was complete, I calculated initiation date by backdating from the time of hatch. I used the following time intervals to calculate clutch initiation date: egg laying = 1 egg laid per day (thus, the number of eggs in a clutch = the length of the egg laying stage), incubation = 12 days (mean incubation period for known nests was 12.3 ± 0.5 days, range 12-13, $n = 23$). If the nest was found with a complete clutch and failed before hatching, initiation date could not be calculated and the nest was excluded from the analysis. Adult birds were banded and territories monitored regularly so I was able to determine if the nest was an initial nest or a re-nest.

Data analysis

I used the program Rhythm (1.0; Cooper and Mills 2005) to select incubation recesses from the temperature recordings. I considered an observation to be a recess if the temperature inside the nest dropped by more than 3 degrees and the decline in temperature lasted more than 3 minutes. I then used the program Raven Pro (1.3) to visually inspect the time series and manually select any recesses that had not been selected by Rhythm (for example, a sharp drop in temperature that lasted slightly less than 3 minutes). Figure 4.1 shows temperature fluctuations within a single horned lark nest over the course of a day. Once I knew the time of initiation and the duration of each recess I was able to calculate the time of initiation and the length of on-bouts. For seven

daily time periods (06:00-07:59 h, 08:00-09:59 h, 10:00-11:59 h , 12:00-13:59 h, 14:00-15:59 h, 16:00-17:59 h and 18:00-19:59 h) I calculated the total number of minutes the female was on the nest, the number of recesses and the mean length of recesses and on-bouts for each time period.

To evaluate the influence of ambient temperature on incubation rhythms I used general mixed effect models using a maximum likelihood method of parameter estimation in the statistical package R (nlme; R Version 2.4.0; R Development Core Team 2006). Mixed effects models allowed me to account for the repeated sampling of individuals over time (Pinheiro and Bates 2000). I modeled four response variables: 1. total minutes on the nest/2 hour period, 2. recess frequency/2 hour period, 3. mean recess duration, 4. mean on-bout duration. Ambient temperature was modeled as a fixed effect and nest was a random factor. I also fit models which allowed the slope of the random factor to vary and thus allowed me to assess if the relationship between the four response variables and ambient temperature varied by nest. To control for the fact that incubation patterns for many songbirds vary with clutch size, date, stage in the incubation cycle, time of day, vegetation cover around the nest, nest orientation and the aspect of the slope where the nest is built (Smith 1989, Wiebe and Martin 1998, Conway and Martin 2000a, Joyce et al. 2001, Wheelwright and Beagley 2005, Zimmerling and Ankney 2005), I added these variables as fixed effects. I also included year (2005, 2006) and nesting attempt (first nest or renest) as fixed effects. Data for recess and on-bout durations were not normally distributed so were log transformed prior to analysis, percent cover was arcsine transformed and aspect and orientation were assigned categories in relation to their deviation from north (i.e. N=1, E=2, S=3 and W=4). Three of the response

variables (total minutes on the nest, recess frequency and mean on-bout duration) showed quadratic relationships with time of day so an additional parameter (time of day²) was added to the models for these three variables. Four of the 48 females included in this study were monitored in both 2005 and 2006 and two females were monitored twice in 2006 (first nest and renest); data for each nest were included as independent observations after analysis showed that there was no difference in the results when the replicated females were excluded.

Visual inspection of the data suggested that the relationship between ambient temperature and the four response variables varied among three temperature zones (with a linear relationship <12°C, no relationship between 12-25°C and a linear relationship >25°C). Following the methods of Conway and Martin (2000a) I divided ambient temperature into the three zones and added an ambient temperature*temperature zone interaction to the models. However, I consistently found no difference in slope between the two highest temperature zones, suggesting that a quadratic model for temperature would be a better fit for the data. Therefore, I tested four different models for each response variable. The full model included variation in both the slope and the intercept for the random factor nest, a quadratic term for temperature, and the additional fixed factors listed above. I then tested models with and without variation in slope for the random factor and with and without the quadratic term for temperature. Information-theoretic procedures using AIC (Burnham and Anderson 2002) were used for model selection and model assumptions were examined following the analysis. I calculated the proportion of the total variance in the four response variables explained in the most

supported models as $r^2 = 1 - \sigma^2 / \sigma_o^2$ (σ^2 is the variance of the residuals for the model and σ_o^2 is the total variance in the response variable; Xu 2003). Means are presented \pm SE.

RESULTS

I collected data on incubation rhythms for horned larks at 15 nests in 2005 and 39 nests in 2006 for a total of 478 nest days. The median number of days monitored per nest was 8 days (range 1.5-12.3 days). Throughout the study, ambient temperatures at nest sites varied from -5.5 to 39.8 °C, occasionally varying by more than 30 °C in a single day (Figure 4.2). Mean ambient daytime temperatures were higher in 2006 than in 2005 (15.37 ± 0.21 vs. 11.21 ± 0.20 °C). During the daytime, mean temperatures were highest between 14:00-16:00 h and lowest between 06:00-08:00 h. During approximately 50% of the incubation periods mean temperature was 12 °C or lower, higher temperatures (≥ 26 °C) were observed during about 11% of the incubation periods (Figure 4.3).

On average, females spent 68% of their time or a total of 81.5 ± 0.3 min/2 hour period ($n = 2930$ observation periods, $n = 54$ nests) on the nest between 06:00-20:00 h. During the day females left the nest an average of 4.9 ± 0.04 times/2 hour period ($n = 2930$ observation periods, $n = 54$ nests). Mean recess duration was 8.6 ± 0.1 min ($n = 2865$ observation periods, $n = 54$ nests) and mean on-bout duration was 23.4 ± 0.8 min ($n = 2864$ observation periods, $n = 54$ nests). The majority of the females began night time incubation between 20:00-23:00 h depending on the time of year and remained on the nest during the night. Overnight incubation period was calculated using the longest incubation period that occurred between 20:00-06:00 h. Average overnight incubation period lasted 7.0 ± 0.1 hr (range 3-19 hr, $n = 457$ nights) and females spent an average of

93% of their time or a total of 111.8 ± 0.3 min/2 hour period ($n = 2159$ observation periods, $n = 54$ nests) on the nest between 20:00-06:00 h.

Ambient temperature and total minutes on the nest

The best model to predict the total number of minutes a female spent on the nest included a quadratic term for temperature and allowed both the slope and intercept to vary for the random factor nest (Table 4.1). This model had an Akaike weight of 1, indicating it received the strongest support from the data. For this model $r^2 = 0.25$. Parameter values for ambient temperature were negative for the linear term and positive for the quadratic term and predict a pattern of an initial decrease in the total time a female spent incubating as ambient temperatures increased and a slight increase in the total time spent incubating at ambient temperatures above 12-13 °C (Table 4.2; Figure 4.4 A). The total minutes females spent incubating varied with the time of day with the least time spent on the nest in the middle of the day (Table 4.2; Figure 4.5 B).

Ambient temperature and recess frequency

The best model to predict how frequently a female left the nest included a quadratic term for temperature and allowed both the slope and intercept to vary for the random factor nest (Table 4.1). This model had an Akaike weight of 1, indicating it received the strongest support from the data. For this model $r^2 = 0.39$. Parameter values for ambient temperature were positive for the linear term and negative for the quadratic term and predict a pattern of an initial increase in recess frequency as ambient temperatures increased and a slight decrease in recess frequency at ambient temperatures above 12-13

°C (Figure 4.4 B). In addition, there was a significant influence of year, date, incubation day and time of day on recess frequency (Table 4.2). Females increased the number of recesses as incubation day increased (from 3.2 ± 0.19 recesses/2hr; $n = 122$ on incubation day 2 to 5.9 ± 0.16 recesses/2hr; $n = 162$ on incubation day 12), took more recesses in the middle of the day and later in the season (Figure 4.5 C) and took fewer recesses in 2006 than in 2005 (4.6 ± 0.04 recesses/2hr; $n = 2049$ vs. 5.5 ± 0.08 ; $n = 896$).

Ambient temperature and recess duration

Ambient temperature was not a significant factor in predicting recess duration (Table 4.2, Figure 4.4 D). The Akaike weights suggest that there was little difference in the models with and without a quadratic term for temperature (Table 4.1). There was a significant influence of year and incubation day on recess duration, but the other fixed factors were not significant (Table 4.2). Females took longer recesses in 2006 than in 2005 (8.9 ± 0.2 min; $n = 896$ vs. 7.2 ± 0.2 ; $n = 2049$) and recess duration decreased as incubation day increased (from 13.3 ± 0.96 min; $n = 122$ on incubation day 2 to 7.4 ± 0.44 min; $n = 162$ on incubation day 12). For this model $r^2 = 0.34$.

Ambient temperature and on-bout duration

The best model to predict on-bout duration had an Akaike weight of 1 and included a quadratic term for temperature and allowed both the slope and intercept to vary for the random effect of nest (Table 4.1). For this model $r^2 = 0.31$. Parameter values for ambient temperature were negative for the linear term and positive for the quadratic term and predict a pattern of an initial decrease in on-bout duration as ambient temperatures

increased and a slight increase in on-bout duration at ambient temperatures above 12-13 °C (Figure 4.4 C). Date, incubation day and time of day were also important in determining on-bout duration. On-bout duration decreased as incubation day increased (from 33.7 ± 4.2 min; $n = 122$ on incubation day 2 to 16.0 ± 1.4 min, $n = 162$ on incubation day 12) and was shorter in the middle of the day and later in the season (Table 4.2, Figure 4.5 A).

In summary, I found non-linear relationships between ambient temperature and incubation patterns. Female horned larks spent less time on the nest as ambient temperature increased up to 12-13 °C. At ambient temperatures above 12-13 °C, there was a slight increase the total time females spent on the nest. Rather than modify the amount of time they spent off the nest during each recess, females adjusted the total amount of time spent on the nest by increasing the frequency of recesses as temperature increased. The time of day, year, date and incubation day influenced incubation patterns in horned larks with the general pattern of decreased time on the nest mid-day and later in the season and incubation period. Finally, nest site characteristics (percent cover, orientation and aspect) did not have a significant influence on incubation patterns (Table 4.2).

DISCUSSION

At low ambient temperatures when both the metabolic rate of adults and the need for cooling or warming of the eggs were elevated, incubating horned larks appeared to shift their investment toward the survival of their eggs by increasing the total time spent on the nest instead of taking longer or more frequent foraging bouts. Even in the early morning

(06:00-07:59 h), when temperatures were low and females may have been energy deficient after a 7 to 8 hour overnight incubation bout, they were still able to spend 74% of their time on the nest. In order to increase the total time spent on the nest at low temperatures, females reduced the number of recesses rather than modify recess duration. Finally, I found general support for the model proposed by Conway and Martin (2000a) which predicts a non-linear influence of ambient temperature on incubation patterns. Below 12-13 °C there were strong relationships between ambient temperature and the total time spent on the nest, the frequency of recesses and on-bout duration, at temperatures above 12-13 °C there was a lesser influence of temperature on incubation rhythms.

Because incubation and foraging are mutually exclusive activities, incubating females must maximize the energy gained from foraging during recesses while minimizing the risk of the eggs chilling in addition to minimizing the cost of rewarming the eggs upon returning to the nest (Jones 1989). Optimal recess duration depends on the foraging efficiency of the female and the rate of cooling of the eggs. I did not find a relationship between ambient temperature and recess duration in horned larks; instead of reducing recess duration, females increased the time on the nest by reducing the number of recesses. Reid et al. (1999) found a similar tradeoff between recess duration and frequency in starlings (*Sturnus vulgaris*) where females on experimentally warmed nests increased the total time spent incubating by reducing the number of recesses they took, but recess duration remained constant. Given that increased activity at the nest may result in increased predation risk (Conway and Martin 2000b, Ghalambor and Martin 2000; 2002), it is not surprising that in order to modify the time spent on the nest females

reduced the number of trips they took instead of adjusting recess length. Also, reducing recess length at extreme temperatures would result in a net loss of energy for the female if the energy gained on a short foraging bout did not outweigh the cost of rewarming the eggs. In order to reduce the number of recesses and increase the total time spent on the nest, females may have relied on endogenous energy reserves and sacrificed their body condition in favor of their eggs (Conway and Martin 2000a). Alternatively, if females do not always spend 100 percent of their non-incubating time foraging, they may have compensated by increasing the amount of time spent foraging during incubation recesses.

I did find a relationship between on-bout duration and ambient temperature, with longer on-bouts at low temperatures. When ambient temperatures are such that the incubating bird must either risk the eggs cooling or sacrifice their own body condition, the parents should spend more time off the nest when the risk to the eggs is minimized (Reid et al. 1999). At moderate temperatures the eggs cool or warm slowly and the danger of embryo temperature dropping below 36 °C or exceeding 38 °C (the temperature range for optimal embryo development; Drent 1975, Webb 1987) declines. Many studies have shown increases in on-bout duration at low temperatures (e.g. see Haftorn and Ytreberg 1988, Mallory and Weatherhead 1993, Lombardo et al. 1995, Norment 1995) and this is what would be predicted if foraging time is limited and parents are behaving in such a way as to maximize foraging bout duration when the risk of cooling the eggs is minimized (Reid et al. 1999). In addition, since rewarming eggs is costly (Drent 1975) females can minimize the cost of rewarming the eggs by spending less time on the nest at moderate temperatures when fluctuations in egg temperature are reduced.

During this study 89% of the 2 hour time periods had mean ambient temperatures below the physiological zero temperature for embryos ($\leq 26^{\circ}\text{C}$, the temperature below which embryo development is suspended; Lundy 1969, Figure 4.3) and none of the periods had temperatures above the upper lethal temperature for embryos ($\geq 40.5^{\circ}\text{C}$, the temperature above which causes embryo death; Lundy 1969). Given the infrequent occurrence of extremely high ambient temperatures but the persistent cool temperatures, developing eggs in nests in alpine habitat may face a higher risk of hypothermia than hyperthermia. In order to cope with low temperatures, alpine breeding songbirds can employ a range of behavioral strategies in addition to modifying incubation patterns. Birds breeding in alpine habitat often line their nests with feathers, fur or plant materials to help protect eggs from the cold (Martin 2001, Martin and Wiebe 2004). This behavior is commonly observed in horned larks at my site (Camfield, A.F. *unpublished data*). In addition, the males of some species such as American pipits (*Anthus rubescens*) feed females during the incubation period allowing the females to remain on the nest for longer durations while incubating (Verbeek and Hendricks 1994). However, male incubation feeding has not been observed in horned larks (Beason 1995).

In the models several fixed factors other than ambient temperature were important in predicting incubation rhythms. As incubation progressed, mean recess and on-bout duration decreased and the frequency of recesses increased, however, the total time spent on the nest did not change. A similar result was found for alpine white-tailed ptarmigan (*Lagopus leucura*) where the total time spent incubating did not change through the incubation cycle, but females increased recess frequency and decreased recess duration as incubation progressed (Wiebe and Martin 1997). Later in the incubation cycle,

fluctuations in temperature may be more harmful to the eggs (Webb 1987), so it is possible that females control egg temperatures more precisely as incubation progresses (Wiebe and Martin 1997). The body condition of incubating birds often declines through the incubation period (Williams 1996) and therefore changes in incubation rhythms as incubation progresses may also reflect the changing energetic needs of the parents. Year, time of day and date were also important variables in several of the models. Female body condition and food availability likely vary between years and throughout the breeding season and could be responsible for the observed patterns.

Microhabitat selection can have important thermoregulatory consequences for birds and many species select nest sites that moderate exposure to environmental variation (Nelson and Martin 1999, Rauter and Reyer 2000, Burton 2007). After the influence of temperature was controlled for, nest site characteristics (percent overhead cover, aspect or nest orientation) were not important in the models. However, this does not necessarily indicate that nest site characteristics do not influence incubation patterns per say. If nest site characteristics affect nest temperature, their influence on incubation patterns would not be evident after controlling for temperature. In addition, there was little variation among individuals in the three nest site variables included in the model; 91% of the nests were on a northwest slope, 80% were oriented toward the southeast and 79% of the nests had between 45-60% overhead cover. The low levels of variation presumably represent optimal patterns of nest site selection and could also explain why nest site characteristics were not significant in the models.

At ambient temperatures within the thermal neutral zone, metabolic rates for incubating birds are equal to resting metabolic rates, however, at lower ambient

temperatures incubation metabolic rates can be 19-50% higher than resting metabolic rates (Williams 1996). The cost of rewarming eggs also increases as ambient temperature declines (Biebach 1986). Therefore, it is likely that in alpine environments with large daily fluctuations in temperatures birds are faced with increased energetic requirements during incubation compared to birds in other environments (Zerba and Morton 1983, Martin 2001, Martin and Wiebe 2004). Even though energy demands were likely higher for birds at my site as a result of persistent low temperatures, the total amount of time female horned larks spent on the nest during the day (68%) was similar to that reported for other passerine species in more moderate environments. For example, on Kent Island in New Brunswick where temperatures on a typical sunny day ranged only about 7 °C (from about 11-17 °C), savannah sparrows (*Passerculus sandwichensis*) spent 64% of their time incubating during the day in the early season and 60% of their time incubating later in the season (Wheelwright and Beagley 2005). Similarly, black-throated blue warblers (*Dendroica caerulescens*) in New Hampshire spent 64% of the day incubating (Joyce et al. 2001).

Songbirds that breed at high elevations typically have fewer broods each year than their low elevation counterparts (Badyaev 1997, Badyaev and Ghalambor 2001, Bears 2007). Horned larks may be able to maintain similar levels of nest attentiveness as songbirds in less challenging environments because they have fewer nesting attempts and are therefore able to invest more energy in each attempt. In addition, horned larks feed primarily on insects during the breeding season and there is high food abundance in the alpine (Beason 1995, Martin 2001). In the summer, large numbers of insects are carried on winds from lower elevations and deposited on snowfields in alpine habitats where

they are easily captured by foraging birds (Crawford and Edwards 1986, Antor 1995). Improved foraging efficiency may also allow horned larks in alpine habitat to maintain high levels of incubation constancy even though they face increased energetic demands. Similarly, the peak periods of flowering and insect emergence occur in late July to early September in alpine areas (Korner 1999) and may allow female horned larks to recoup their body condition after the young fledge.

For all four response variables, the models with the most support allowed the slope of the random factor nest to vary. This result indicates that there is considerable variation in how individual females respond to variation in ambient temperature and could reflect differences in individual body condition, territory quality and/or predation risk (Drent 1975, Conway and Martin 2000a,b). Of the models I evaluated, the top models explained only 25-39% of the variation in incubation patterns. Incubation patterns are clearly affected by variables in addition to those evaluated here and further research should be conducted to determine how individual body condition, territory quality and predation risk influence horned lark incubation patterns.

Overall, my results are consistent with the hypothesis that songbirds breeding at high elevation compensate for shorter breeding seasons and reduced renesting opportunities by increasing parental investment (Chapter 2, Badyaev and Ghalambor 2001). In response to thermally demanding conditions, it appears that female horned larks in alpine habitat modify their behavior so as to favor the survival of their eggs and to minimize the cost of rewarming eggs. It is also possible that foraging efficiency, metabolic rates and/or reliance on energy reserves differ for alpine breeding songbirds and allow them to maintain high levels of nest attentivity in thermally challenging

environments. Future investigation in these areas will help elucidate how females incubating in alpine environments cope with extreme variations in temperature. The ability of horned larks to maintain high levels of nest attentiveness when environmental conditions are challenging suggests that they are well adapted to the degree of environmental variation they experience in alpine habitats.

Table 4.1. Summary of model selection results for incubation rhythms for horned larks in alpine habitat in British Columbia in 2005 and 2006. All models include nest as a random factor and the fixed factors shown in Table 4.2.

	-2LogL	K	<i>n</i>	AIC	Δ AIC	w_i
1. Total minutes on nest						
Temperature ² , variation in slope	24424.50	19	2930	24300.51	0	1
Temperature ² , no variation in slope	24443.04	18	2930	24360.49	59.98	0
Temperature, no variation in slope	24426.90	17	2930	24460.89	160.38	0
Temperature, variation in slope	24326.88	18	2930	24364.89	64.38	0
2. Recess frequency						
Temperature ² , variation in slope	12107.36	19	2930	12147.35	0	1
Temperature ² , no variation in slope	12260.68	18	2930	12296.67	149.32	0
Temperature, no variation in slope	12444.18	17	2930	12478.18	330.83	0
Temperature, variation in slope	12218.08	18	2930	12256.08	108.73	0
3. Recess duration						
Temperature ² , variation in slope	-1442.95	19	2864	-1404.95	0	0.54
Temperature ² , no variation in slope	-1339.14	18	2864	-1305.14	99.817	0
Temperature, no variation in slope	-1332.80	17	2864	-1300.8	104.15	0
Temperature, variation in slope	-1440.63	18	2864	-1404.63	0.32	0.46

	-2LogL	K	<i>n</i>	AIC	ΔAIC	<i>w_i</i>
4. On-bout duration						
Temperature ² , variation in slope	549.97	18	2865	589.97	0	1
Temperature ² , no variation in slope	640.54	17	2865	676.54	86.57	0
Temperature, no variation in slope	766.27	16	2865	800.26	210.30	0
Temperature, variation in slope	663.21	17	2865	819.12	229.15	0

Table 4.2. General linear mixed model predicting the total number of minutes a female horned lark spends on the nest, the frequency of recesses and recess and on-bout duration between 06:00-20:00 h. Nest was included in the model as a random effect, parameters are from the model with the most support using AIC model selection. Parameters with $|t| > 1.96$ have 95% confidence intervals that do not include 0 (in bold).

Parameter	1. Total minutes on nest		2. Recess frequency		3. Recess Duration		4. On-bout duration	
	Estimate±SE	t-value	Estimate±SE	t-value	Estimate±SE	t-value	Estimate±SE	t-value
Intercept	121.19±20.74	5.84	-7.60±2.78	-2.73	1.51±0.28	5.39	2.78±0.32	8.71
Temperature	-1.30±0.16	-8.25	0.22±0.02	10.11	-0.003±0.002	-1.49	-0.02±0.003	-8.50
Temperature ²	0.03±0.003	8.52	-0.005±0.0005	-10.73	0.00007±0.00005	1.52	0.0006±0.00007	8.86
Clutch size	1.72±1.37	1.26	-0.09±0.19	-0.48	-0.03±0.02	-1.33	0.03±0.02	1.18
Year	-1.85± 2.01	-0.92	-0.73±0.27	-2.69	0.10±0.03	3.54	0.03±0.03	1.01
Renest	0.55±2.63	0.21	0.02±0.36	-0.06	0.03±0.04	0.75	0.01±0.04	0.26
Date	-0.01±0.12	-0.07	0.04±0.02	2.39	-0.002±0.002	-1.37	-0.005±0.002	-2.55
Incubation day	-0.21±0.15	-1.36	0.19±0.02	9.20	-0.02±0.002	-8.26	-0.02±0.002	-7.46
Time of day	-12.59±1.38	-9.11	1.32±0.17	7.66	0.002±0.001	1.05	-0.25±0.02	-10.24

1. Total minutes on nest			2. Recess frequency			3. Recess Duration			4. On-bout duration		
Parameter	Estimate±SE	t-value	Estimate±SE	t-value		Estimate±SE	t-value		Estimate±SE	t-value	
Time of day ²	0.90±0.09	9.48	-0.10±0.01	-8.39		-	-		0.02±0.002	11.50	
Percent cover	-1.68±10.45	-0.16	-0.20±1.41	-0.14		0.08±0.14	0.58		0.14±0.16	0.87	
Aspect1 ^a	3.18±6.23	0.51	0.37±0.85	0.44		-0.002±0.08	-0.02		-0.005±0.09	-0.05	
Aspect2 ^a	16.66±10.26	1.62	0.64±1.31	0.49		-0.25±0.15	-1.72		-0.009±0.15	-0.06	
Aspect3 ^a	0.88±3.90	0.23	-0.25±0.54	-0.48		0.01±0.05	0.19		0.04±0.06	0.73	
Orientation1 ^a	7.63±7.70	0.99	0.56±0.98	0.57		-0.19±0.11	-1.75		-0.02±0.12	-0.16	
Orientation2 ^a	9.10±7.80	1.17	0.53±0.99	0.54		-0.19±0.11	-1.68		-0.008±0.12	-0.06	

^a Aspect and orientation were assigned categories in relation to their deviation from north (i.e. N=1, E=2, S=3 and W=4). For aspect, category 4 was used as the reference group so does not appear in the model output. Category 4 was also used as the reference group for orientation. For nest orientation there were no observations of nests in category 3 therefore only two categories are shown.

Figure 4.1. Temperature fluctuations recorded in a single horned lark nest over the course of one day. Steep drops in temperature indicate departures of the female from the nest, steep increases in temperature indicate the return of the female to the nest.

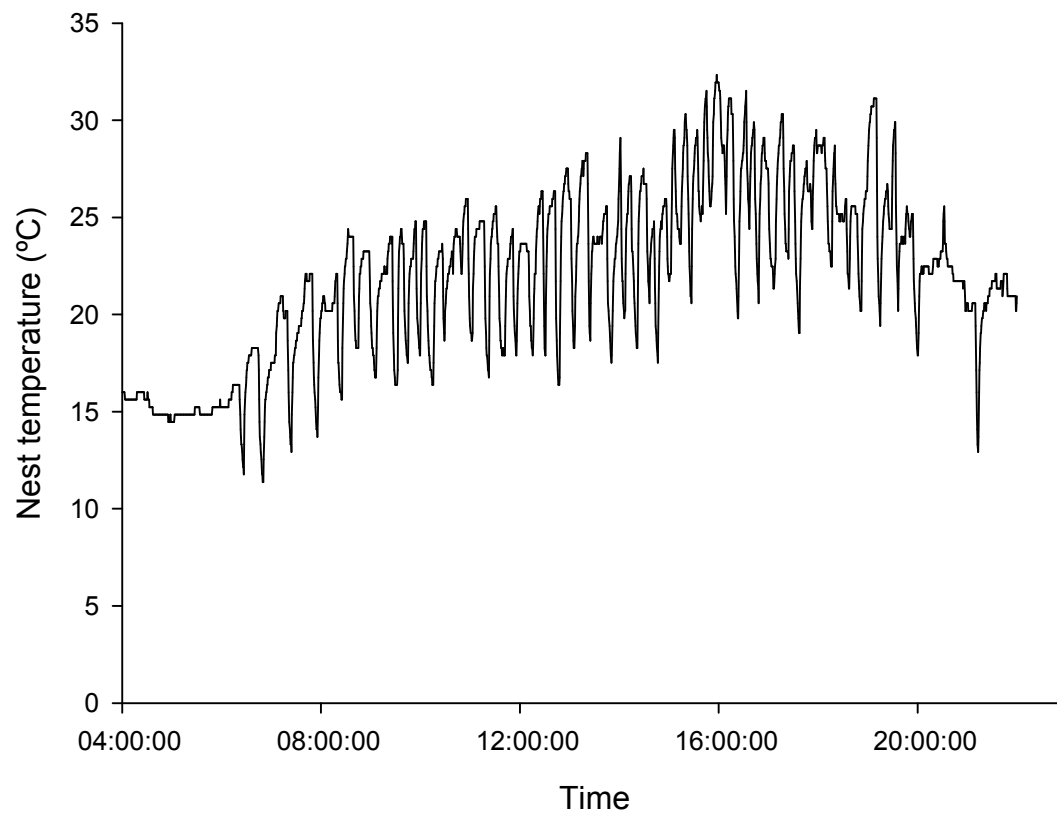


Figure 4.2. Ambient temperature fluctuations illustrating temperature changes of more than 30° C at ground level near a single horned lark nest on Hudson Bay Mountain, Smithers, BC. Temperatures were recorded over the course of several days during the 2005 breeding season.

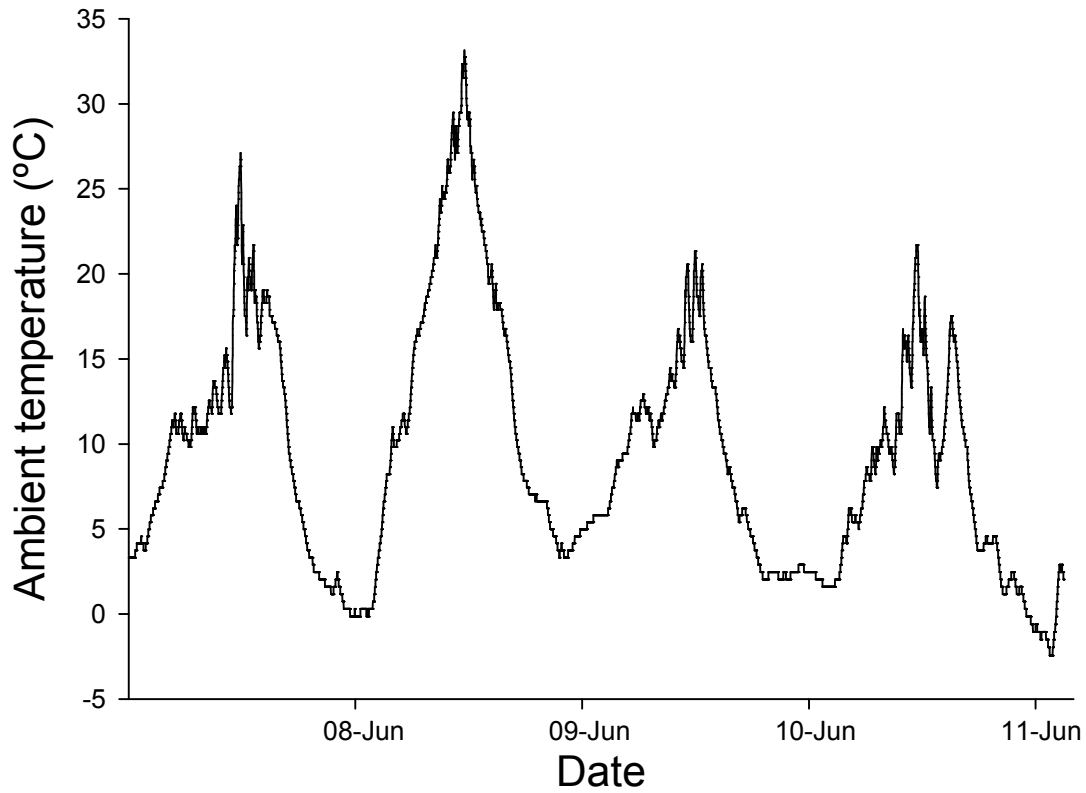


Figure 4.3. Frequency of observed mean ambient temperatures between 06:00-20:00 h on Hudson Bay Mountain in British Columbia in 2005 and 2006 between ($n = 2930$, 2 hour time periods). The bold line indicates the physiological zero temperature for embryos ($\leq 26^\circ\text{C}$).

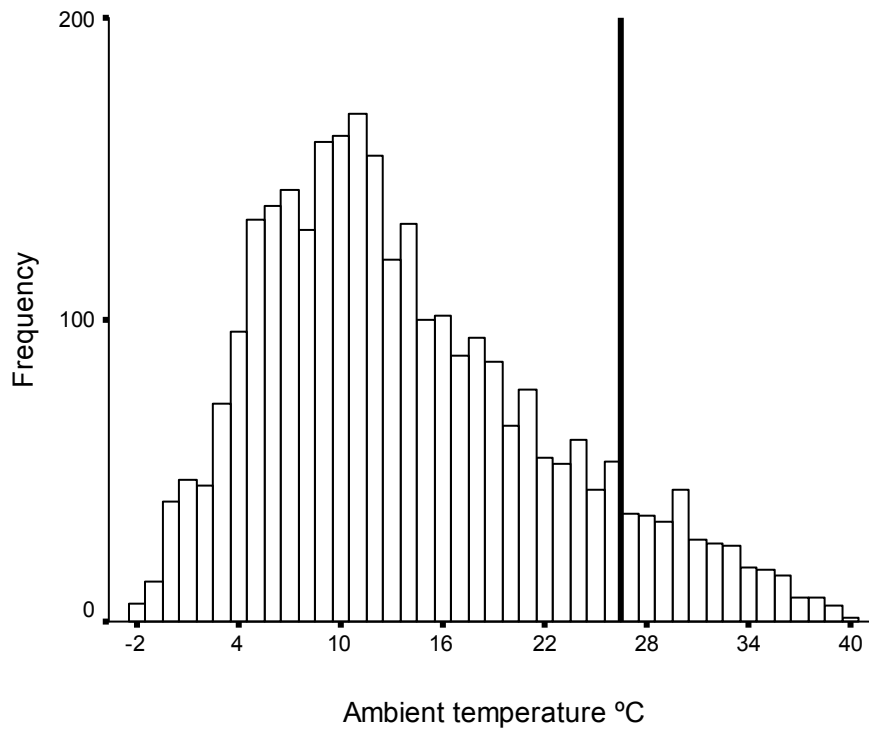


Figure 4.4. Mean (\pm SE) number of minutes on the nest, number of recesses and recess and on-bout duration during 2 hour time periods vs. ambient temperature for horned larks ($n = 54$ nests).

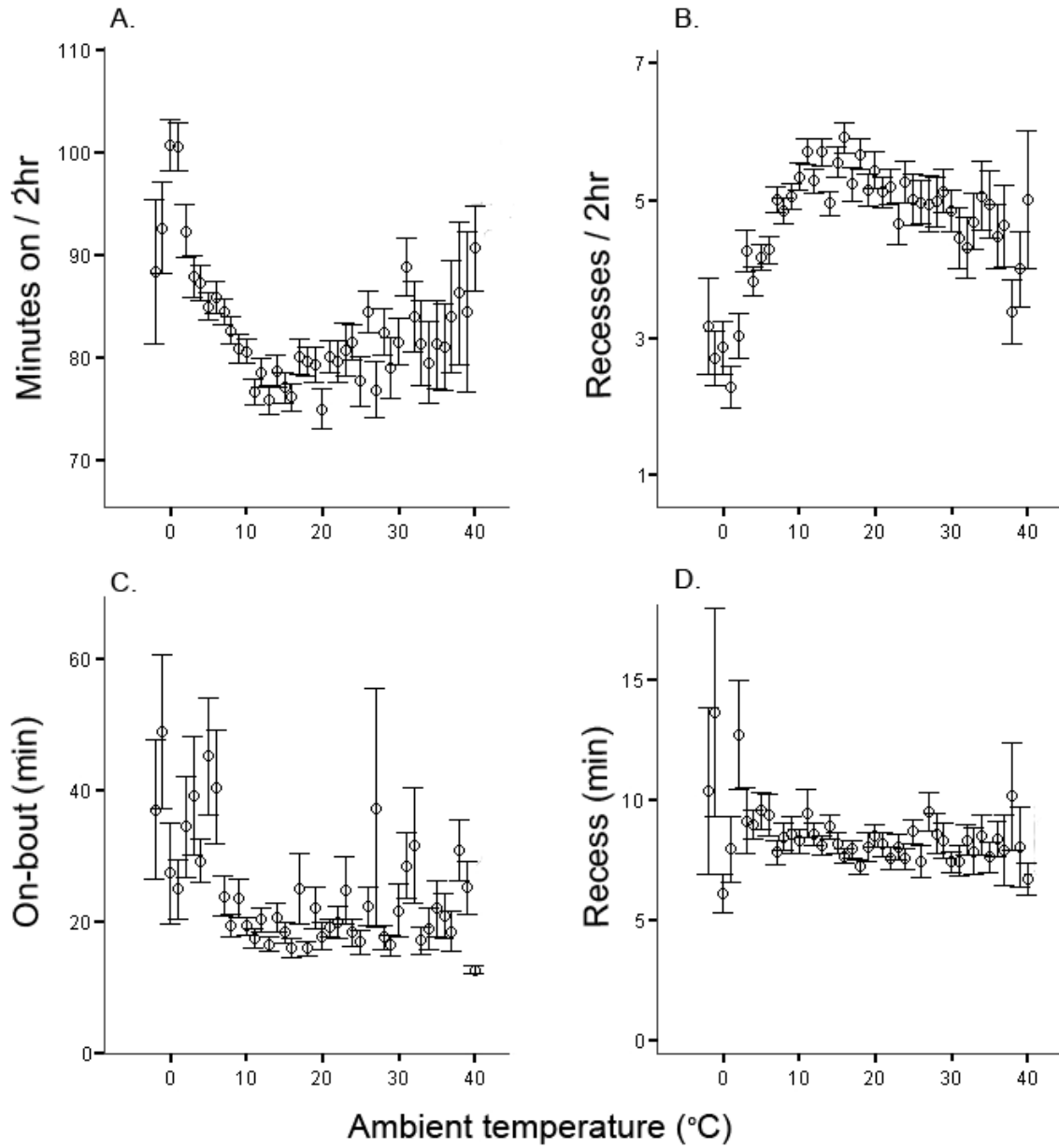
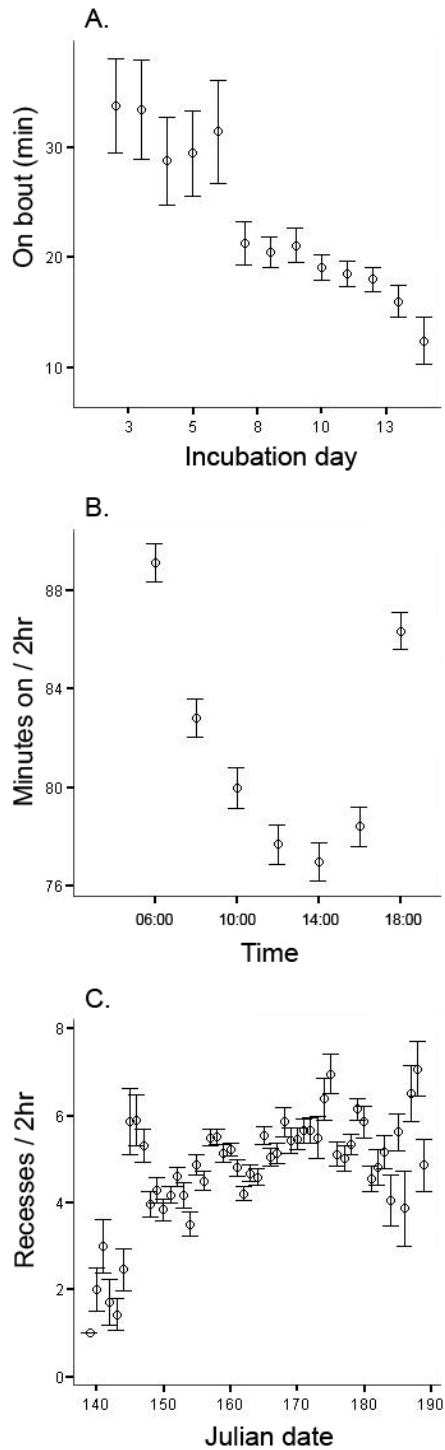


Figure 4.5. Representative graphs showing how incubation patterns change with incubation day, date and time of day for horned larks. A Julian date of 140 represents 20-May, 190 represents 09-July, means are shown \pm SE.



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CHAPTER 5: CONCLUSIONS

Horned larks breeding on Hudson Bay Mountain in British Columbia appear to be well adapted their high elevation habitat. Population growth rates are stable even in the absence of immigration, they have the ability to renest quickly after losing a clutch (Chapter 2) and although energy demands for incubating females were likely elevated for birds at my site, they were able to maintain high levels of attentiveness (Chapter 4). Overall, my results are consistent with the hypothesis that songbirds breeding at high elevation compensate for shorter breeding seasons and reduced annual fecundity by increasing parental investment (Badyaev 1997, Badyaev and Ghalambor 2001). The estimates of apparent juvenile survival for horned larks on Hudson Bay Mountain were more than twice that typically observed for migratory passerines (Weatherhead and Forbes 1994) and may be the result of high levels of parental investment. In addition, the trend toward a high survivor life history for high elevation horned larks may be more related to truncated breeding seasons and limited renesting opportunities rather than an inability to successfully fledge a brood.

My results point to the potential of alpine habitat to serve as areas of refuge for alpine generalist songbird species as low elevation habitat disappears. However, more work needs to be done to determine the generality of these results before they are broadly applied across passerine species. Data for savannah sparrows (*Passerculus sandwichensis*) breeding in the same habitat as horned larks on Hudson Bay Mountain indicate that this alpine generalist species can also successfully fledge broods in a high elevation habitat. In addition, while fecundity for savannah sparrows is restricted by

breeding season length, adult and juvenile survival rates appear to be quite high and may compensate for reduced annual fecundity (Martin 2008). While data from Hudson Bay Mountain support the results of several other studies which suggest that alpine habitat is not occupied by young or low-quality individuals forced to breed at high elevations (Kollinsky and Landmann 1996, Bears 2007), conflicting evidence has been found for other species. For example, high elevation habitat appears to be peripheral habitat occupied by yearling male Townsend's warblers (*Dendroica townsendi*; Rohwer 2004) and winter wrens (*Troglodytes troglodytes*; L. Evans-Ogden, *personal communication*). It is likely that alpine generalist songbirds fall along a continuum whereby some species are more able to cope with alpine conditions than others (Martin 2001). Future studies that examine a range of species from alpine specialists to alpine tolerant species will help us to predict with more generality which groups of songbirds are more or less able to survive and reproduce at high elevations.

Even though alpine areas may be able to provide important refuge habitat for songbirds if low elevation habitat is destroyed, we can not ignore the preservation of low elevation grasslands and the species that inhabit them. When they exist, management opportunities for low elevation grassland birds should be pursued. As is the case for streaked horned larks, low elevation populations may represent genetically distinct groups (Drovetski et al. 2005). A goal of conservation biology is often to maintain the evolutionary potential of a species and in order to do so the genetic variability present across populations must be preserved (Moritz 1994, Crandall et al. 2000). In this thesis I outlined numerous potential management strategies for streaked horned larks in Washington (Chapter 3). While there does not appear to be a simple solution to improve

population growth rates for this endangered subspecies, recovery may be possible using a combination of management techniques. Of the three vital rates I examined, fecundity has the greatest potential for improvement through management activities. Because juvenile survival appears to be relatively high for this subspecies (Chapter 2 and 3), improvements in fecundity might have large cascading effects on population growth rates in the absence of strong density dependence. Given the importance of adult survival on population growth rates for streaked horned larks (Chapter 2 and 3) and the fact that little is known about the factors influencing survival during the non-breeding season, future research should include efforts to track individual survival and habitat use during the overwinter period.

Alpine areas are generally regarded as pristine environments; however, development, resource extraction and recreation pose increasing threats to these sensitive ecosystems (Martin 2001). In fact, the recent approval of an expansion of the Ski and Ride Smithers resort on Hudson Bay Mountain has the potential to severely reduce the quality of this area for breeding songbirds. New lift lines are being cut in the sub-alpine forest and a lift has been proposed that would cross the tundra (Ski & Ride Smithers Ski Area Master Plan 2008). Construction of new ski lifts could have significant impacts on the tundra vegetation which is slow to recover from disturbance (Svoboda and Henry 1987) and could potentially reduce the quality of nesting habitat for songbirds. While the ski season does not overlap with the alpine songbird breeding season, there are plans to turn the area into a four season resort (Ski & Ride Smithers Ski Area Master Plan 2008). The area is currently used by a small numbers of hikers in the summer; however, large influxes of recreationists resulting from the new development could substantially reduce

songbird breeding productivity. As the number of visitors to alpine areas increases so does the number of generalist nest predators (Smith et al. 1997). In addition, songbirds often interpret human presence as a predation risk and may abandon eggs or young after being disturbed by humans (Frid and Dill 2002). Many hikers are accompanied by dogs which chase wildlife, flush incubating birds and destroy nests (Camfield, A.F., *personal observation*) and light traffic by hikers with dogs has reduced the breeding success of songbirds with territories near trails (Clason 2007). Also, hikers often either intentionally or unintentionally leave the hiking trail and may trample vegetation and disturb wildlife. All of these disturbances are likely to increase with the development of a four season resort. There are strategies that can be implemented to reduce impacts, such as enforcing an on-leash policy for dogs, clearly marking designated trails and providing interpretive signs to educate recreationists (Camfield 2008). Alpine areas are known for their ruggedness and beauty and should be enjoyed by recreational users, but steps must be taken to mitigate the harm that our presence may inflict.

The predicted impacts of climate change are also important to consider when evaluating the potential for alpine habitats to serve as refuge habitat. As the climate changes, environmental stochasticity and the frequency of extreme conditions are predicted to increase (Diaz and Bradley 1997, Giorgi and Hewitson 2001) and the capacity of songbirds to respond to environmental variability may be reached. Increases in environmental stochasticity and a greater frequency of extreme conditions often lead to reductions in population growth rates and increased risk of extinction (May 1974, Lande 1993, Boyce et al. 2006, Wilson 2008). The results presented in Chapter 4 suggest that horned larks are able to handle the current levels of temperature fluctuations during the

incubation period. However, at even greater temperature extremes their limits may be reached and their ability to reproduce may be challenged. In addition, advances in treeline are occurring as temperatures warm and are likely to result in loss of alpine tundra habitat and increased fragmentation in alpine areas (Wardle and Coleman 1992, Kullman 2001). Climate modeling suggests that alpine tundra in British Columbia may be reduced by up to 60% by 2025 (Hamann and Wong 2006).

Not all the impacts of climate change will be negative for alpine songbirds. Warmer spring temperatures could lead to earlier melting of the snowpack and extended breeding seasons. However, if shifts in the timing of breeding do not coincide with phenological shifts in the timing of peak insect abundance or plant flowering, earlier breeding may lead to reductions in reproductive output (Visser et al. 1998, Visser et al. 2006). Furthermore, gains in reproductive output as a result of increases in breeding season length may be reversed by nest failure caused by increases in extreme weather events during the breeding season (Martin and Wiebe 2006).

Although it is often assumed that alpine areas represent relatively unproductive habitat, the results of my thesis indicate that high elevation areas may in fact be quite productive breeding habitat for some songbirds. While there are numerous grassland songbirds that are able to breed across elevational gradients, there are also many species found only at low elevations. Future studies that simultaneously examine several species in the same high elevation habitat will allow us to assess how strategies differ among species and will allow us to evaluate what makes some species better able to cope with alpine conditions. This type of study will allow us to generate predictions about which species are able to tolerate high elevation habitats (e.g., dark-eyed juncos and horned

larks) and which are not (e.g., Townsend's warblers and winter wrens). Finally, the perception of high elevation habitat as pristine and untouched may be misplaced, so as climate change progresses we must continue to assess the ability of these areas to support healthy songbird populations.

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APPENDIX 1

Annual production of fledglings per pair (P) was calculated following the technique described in: Ricklefs, R. E., and G. Bloom. 1977. Components of avian breeding productivity. *Auk* 94:86-96.

$$P = F * B$$

$$F = \text{young fledged/pair/day} = C * S * I$$

$$B = \text{length of the breeding season (days)}$$

$$B = 30 \exp(-\sum p_i \log_e p_i)$$

$$p_i = \text{proportion of clutches laid by a population during month } i$$

$$C = \text{clutch size}$$

$$S = \text{breeding success (fledglings per egg laid)}$$

$$I = \text{rate of nest initiation (clutches/pair/day)} = \frac{m}{p_f + m(p_s r_s + p_f r_f)}$$

m = nest mortality rate (proportion of nests failing per day), p_s = probability that a nest successfully fledges at least one young, p_f = probability that a nest fails before fledging ($p_f = 1 - p_s$), r_s = delay before a new clutch is laid after successful fledging, r_f = delay before a new clutch is laid after nest failure.

$$p_s = e^{-mT}$$

$$T = \text{length of the nest cycle from clutch initiation to fledging (days)}$$

APPENDIX 2

Animal Care Certificate issued by the University of British Columbia



THE UNIVERSITY OF BRITISH COLUMBIA

ANIMAL CARE CERTIFICATE

Application Number: A03-0095

Investigator or Course Director: Kathy M. Martin

Department: Forest Sciences

Animals:

Birds - Other 900

Start Date: April 1, 2001

Approval Date: March 10, 2006

Funding Sources:

Funding Agency: Natural Science Engineering Research Council
Funding Title: Climate variability monitoring for northern alpine bird research

Funding Agency: UBC Grants from Federal Departments
Funding Title: Effects of extreme environmental variation on the behaviour and breeding biology of alpine horned larks and savannah sparrows

Funding Agency: UBC VPR Research Development Fund
Funding Title: Support for an NSERC - International Polar Year award entitled "Climate forcing of alpine tundra ecosystems"

Funding Agency: Natural Science Engineering Research Council
Funding Title: Ecology of alpine and forest birds

Funding Agency: Environment Canada
Funding Title: Alpine and Forest landbird ecology and conservation research

Funding Agency: Dean of Forestry
Funding Title: Support for an NSERC - International Polar Year award entitled Climate forcing of alpine tundra ecosystems in southwest Yukon: a Canadian contribution to the International Polar Year

Funding Agency:	Environment Canada
Funding Title:	The Importance of High Versus Low Elevation Stopover Sites: Using Physiology to Quantify Habitat Quality
Funding Agency:	UBC Grants from Federal Departments
Funding Title:	Effects of extreme environmental variation on the behaviour and breeding biology of alpine horned larks and savannah sparrows
Funding Agency:	Natural Science Engineering Research Council
Funding Title:	Climate forcing of alpine tundra ecosystems in southwest Yukon: A Canadian contribution to the International Polar Year
Funding Agency:	Natural Science Engineering Research Council
Funding Title:	Ecology of Alpine and Forest Birds - Alpine Songbirds
Unfunded title:	n/a

The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual review is required by the CCAC and some granting agencies.

A copy of this certificate must be displayed in your animal facility.

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