THESIS

FACTORS INFLUENCING BREEDING AVIFAUNA ABUNDANCE AND HABITAT SELECTION IN THE ALPINE ECOSYSTEM OF COLORADO

Submitted by

Shelley Laine Spear

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2017

Master's Committee:

Advisor: Cameron L. Aldridge

Susan K. Skagen
Paul F. Doherty, Jr.

ABSTRACT

FACTORS INFLUENCING BREEDING AVIFAUNA ABUNDANCE AND HABITAT SELECTION IN THE ALPINE ECOSYSTEM OF COLORADO

Species in alpine habitat occupy high elevation areas with limited scope for upslope migration, and as a result are expected to react sensitively to climate-caused habitat alteration. Changes in temperature are causing an advancement of treeline and rearrangement of habitat and species distributions. Alpine birds in particular are predicted to be impacted by climate change, especially species that breed in and are endemic to this ecosystem. In order to understand just how sensitively alpine birds will respond if their habitat structure is altered by climate change, determining the fine-scale mechanisms driving their current relationships with alpine habitat is important. In Chapter 1, I discuss some of the relationships between birds and their surrounding environment and the importance of understanding these species-habitat interactions. I introduce the alpine breeding focal species and how some of these avian species have exhibited population declines in Colorado. I also present my research objectives that aimed to understand breeding avifauna abundance in relation to fine-scale habitat features (Chapter 2), and how specific habitat characteristics drive important breeding site selection for an alpine endemic species (Chapter 3). Chapters 2 and 3 (described below) are data chapters written in a format to be submitted for journal publications.

In Chapter 2, I test how fine-scale habitat and environmental characteristics influence abundance of avian species breeding in Colorado's alpine ecosystem. I provide results on how abundance and occurrence of these breeding species were influenced by abiotic, biotic,

anthropogenic, temporal, and spatial factors in the alpine. Biotic components affected the abundance of all three of the breeding birds that we modeled using count data; American pipit (*Anthus rubescens*), horned lark (*Eremophila alpestris*), and white-crowned sparrow (*Zonotrichia leucophrys oriantha*). However, abiotic, anthropogenic, spatial and temporal factors also contributed to their abundance and occurrence. Knowing which fine-scale factors influence these alpine species' abundance the most, will allow us to prioritize conservation efforts for each particular species, and improve our ability to predict how their abundance will change if alpine habitat is altered in response to climate change.

In Chapter 3, I ask how fine-scale habitat and environmental characteristics influence nest and brood-site selection by breeding white-tailed ptarmigan (*Lagopus leucura*) in Colorado's alpine. I conducted analyses across multiple spatial scales: patch and site level, at nesting and brood-rearing sites. Forage resources and protective cover were the prominent features driving selection at these two alpine sites during both breeding periods. Specifically, nest site selection at the patch scale was more influenced by percent cover of forage forbs, rock and gravel, and shrubs and willows. However, at the site scale, we found hens selected nest sites when percentage of graminoid cover was less and elevations were lower. Hens selected brood sites at the patch scale that were in closer proximity to willows and shrubs and that had rock and gravel cover to a particular threshold. A subset of our brood data indicated brood site selection was driven by abundance of insects over vegetation components. In this chapter, I highlighted the dependence on forage quantity and protective cover across two ptarmigan breeding stages, as well as differences among scales. These findings demonstrated the importance of considering a spatial resolution with a temporal aspect (i.e., different breeding stages) in resource selection studies especially when habitat covariates are collected at fine spatial scales.

With all aspects of this research, I discuss in each chapter how conducting additional and longer-term studies on a fine-scale basis helps to not only establish further alpine breeding bird-habitat relationships in these areas, but in identifying if populations are stable, and if and when they respond to changes in habitat structure. Furthermore, in my final section, Chapter 4, I suggest analyzing these relationships across a larger extent and propose how a landscape-scale analysis can be applied to breeding bird species-habitat relationships in the future to determine at what scale these species could respond if climate change impacts their alpine habitat.

ACKNOWLEDGMENTS

I would like to first and foremost thank my advisor, Dr. Cameron Aldridge, for his guidance throughout my years at Colorado State University that culminated in this thesis. His never-ending support, advice, patience and enthusiasm propelled me to be the researcher and ecologist I am today. I thank him for always having the time to answer questions and sort through issues, but also for his endless stamina and pursuit of conducting good and sound science, which constantly kept me rooted in understanding aspects of wildlife and ecology. Cam gave me the direction I needed while allowing me to explore my own interests in ecology. I also thank the other members of my committee, Dr. Susan Skagen and Dr. Paul Doherty, Jr., who provided additional support, expertise, and insight in field and data analyzation methods.

Many other individuals, who may be unaware of their support, helped me prepare this thesis and supported me while getting through graduate school. Fellow graduate students in my lab group helped me refine and hone my thinking and better understand methods, techniques, as well as statistical software packages. Lab member and fellow researcher of tremendous support, Greg Wann, taught me so much about the alpine, and I cherish even our most windy and frigid days watching birds and collecting data in Colorado’s high country. His work ethic and knowledge of species within this unique system were a great source of inspiration and motivation. I thank my other fellow lab members who included Kristin Davis, Dave Edmunds, Katie Langin, Danny Martin, Adrian Monroe, Kevin Oh, Sara Simonson, Jennifer Timmer, Nick Van Lanen, and Shawna Zimmerman, all of whom provided endless joy throughout this whole process. I am eternally grateful to the life-long friendships established within my laboratory group. Many other colleagues and friends deserve much gratitude: Clait Braun for his expertise and endless knowledge about white-tailed ptarmigan and the alpine, Brian Cade for his statistical

guidance and constant insight, Apryle Craig for all of our wildlife adventures, Daniel "Kentucky-D" Bowker for being the best crew leader and always making sure I did not fall into mountain lakes, Jill Baron for providing ample preparation for my alpine research, and Marissa Casey and Nate Quatier who were both there in the early days of my quest to pursue my passions in this field.

Field work would have not been possible without the hard work of technicians during the 2014 and 2015 field season. Billy "Critter Tracks" Dooling and Justin Borcherding (2014), and Andy Valencia and Chris Potter (2015), worked tirelessly to collect white-tailed ptarmigan data used in this analysis. I want to especially thank our technician, Jack Bushman for diligently collecting point count and habitat selection data during 2015, without which the amount and level of data we have today would not exist. I had daily adventures in some of the harshest conditions with each of these gentlemen, all of whom made even the most treacherous days the most rewarding. I wish them nothing but luck in their future careers and hope our paths cross again, be it in the alpine or elsewhere, in the near future.

This project could not have been completed without funding and support of many organizations and individuals. This project and graduate support were largely funded by the U.S. Geological Survey (USGS) and the Fort Collins Science Center, Rocky Mountain National Park, and the Natural Resource Preservation Program supported by USGS and National Park Service. The graduate school at Colorado State University provided additional support to me through the Programs for Research and Scholarly Excellence (PRSE) Fellowship, and the Natural Resource Ecology Laboratory (NREL) at Colorado State University through the James E. Ellis Scholarship, and Graduate Teaching Assistantships in Ecosystem Science and Biology. Additionally, I extend a sincere thank you to Dr. Michael Monahan and the University of

Denver’s High Altitude Lab at Echo Lake, and Scott Esser and Rocky Mountain National Park in providing us some of the best lodging facilities throughout 2014 and 2015. These cabins became our home away from home.

Finally, I would like to thank my family for their support throughout my graduate education. Thank you to my mom, dad, and stepdad for never quelling my love of nature and wildlife growing up, and encouraging that child-like wonder that still resides in me today. Thank you to my sister, Heather for listening to my science escapades and dilemmas. Thank you to my Aunt Trisha and Uncle Craig for some of my fondest summer adventures in Arkansas. I thank my grandparents, Bob and Doris Nelson, for instilling in me a deep love of bird watching, wildlife, fishing, and how to identify flowers and plants. Their loving memories live on in me today. Most importantly, I want to thank my husband, Will Spear, who has stood by me during every step of this process. He supported me during the rough patches, and always lent an ear, shoulder of support, and joke when I needed it most. He also turned out to be quite the field technician, and I cherish our alpine adventures together. Thank you for continually believing in me when I did not believe in myself. No words can express how much your support has meant to me throughout the years. I would also like to thank our two cats, Cleopatra and Jinx, and our dog, Pepper, for bringing me joy throughout this endeavor.

TABLE OF CONTENTS

ABSTRACT ii

ACKNOWLEDGMENTS v

LIST OF TABLES x

LIST OF FIGURES xvi

CHAPTER 1: CLIMATE CHANGE AND ALPINE BREEDING BIRDS IN COLORADO 1

- INTRODUCTION 1

LITERATURE CITED 4

CHAPTER 2: HABITAT AND ENVIRONMENTAL INFLUENCES OF BREEDING AVIFAUNA SPECIES IN ALPINE REGIONS OF COLORADO 6

- SUMMARY 6
- INTRODUCTION 7
- STUDY AREAS 11
- METHODS 12
  - *Field Survey Sampling Design* 12
  - *Field Surveys* 13
- DATA ANALYSES 15
  - *Detection Probabilities* 15
  - *Count Model Development* 16
  - *Model Development* 16
  - *Predictive Performance* 18
- RESULTS 19
  - *Field Surveys* 19
  - *Detection Probabilities* 19
  - *Model Selection and Evaluation* 22
  - *Assessment of predictive performance* 26
- DISCUSSION 27
- CONCLUSIONS 37

LITERATURE CITED 39

CHAPTER 3: PATTERNS OF FINE-SCALE HABITAT SELECTION BY BREEDING WHITE-TAILED PTARMIGAN (*LAGOPUS LEUCURA)* IN COLORADO’S ALPINE 84

- SUMMARY 84

INTRODUCTION 85
STUDY AREA 90
METHODS 91
Field surveys 91
DATA ANALYSES 93
Habitat selection data 93
Vegetation data 94
Insect data 94
Statistical analyses 95
Model predictive accuracy and validation 96
RESULTS 97
Patch scale nest habitat selection 100
Site scale nest habitat selection 102
Patch scale brood habitat selection 103
DISCUSSION 105
Patch scale nest habitat selection 105
Site scale nest habitat selection 109
Patch scale brood habitat selection 111
CONCLUSIONS 114
LITERATURE CITED 116
CHAPTER 4: CONCLUSIONS 153
SUMMARY 153
RESEARCH NEEDS 155
LITERATURE CITED 157
APPENDICES 159

LIST OF TABLES

Table 2.1 – Predictions posited for first hypothesis that abiotic and biotic factors will be strong effects in defining the occurrence and abundance of five alpine breeding avian species during their breeding seasons. Predictions are based on known attributes determining breeding distribution and factors important to these five breeding alpine avifauna. (+) and (-) indicate positive and negative associations, respectively, of predicted bird species relative to specific attributes at sites within two alpine areas in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). 48

Table 2.2 – Description of predictor covariates, including predictor category and covariate type, in avian point counts conducted during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). 49

Table 2.3 - Field survey results for the five breeding avian species during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Survey results shown for each study site for the combined years include the number of point count sites with occurrences (percent), total number of detections of each species, detection distance [meters; mean (□), standard error (SE)], and total truncated detection distance (m) estimated by program DISTANCE 6.2.......... 50

Table 2.4 – Field survey results for the 5 breeding avian species during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Survey results shown for each study site separated by year include the number of point count sites with occurrences (percent), and total number of detections of each species. 51

Table 2.5 – Description of covariates used in determining detection probabilities in program DISTANCE 6.2 for the five breeding bird species: American pipit (*Anthus rubescens*), brown-capped rosy-finch (*Leucosticte australis*), horned lark (*Eremophila alpestris*), white-crowned sparrow (*Zonotrichia leucophrys oriantha*), and white-tailed ptarmigan (*Lagopus leucura*) from point count data collected during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Covariates were chosen based on literature review (see References) describing each species' habitat characteristics.......... 52

Table 2.6 - Field survey results for three of the five breeding avian species during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail

Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Survey results shown for each study site for the combined years include the number of point count sites with occurrences (percent), total number of detections of each species, and detection distance [meters; mean (□), standard error (SE)]. Count data was truncated based on total truncated detection distance estimated by program DISTANCE 6.2, and subsequently fit with generalized linear models (GLMs) for each of the 3 bird species. 55

Table 2.7 - Field survey results for the three of the five breeding avian species during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Survey results shown for each study site separated by year include the number of point count sites with occurrences (percent), and total number of detections of each species. Count data was truncated based on total truncated detection distance estimated by program DISTANCE 6.2, and subsequently fit with generalized linear models (GLMs) for each of the 3 bird species 56

Table 2.8 – Results of top univariable negative binomial generalized linear models (GLMs) conducted on all covariates within four predictor categories ranked by Bayesian Information Criteria (BIC) within each predictor category, for American pipit (*Anthus rubescens*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Models listed include an offset term for detection calculated from the mean detection probability in program DISTANCE 6.2. Results presented are from standardized data and include predictor categories, covariate model, number of parameters (k), predictor (β) estimates, 95% confidence intervals (CI), log-likelihood (LL), and BIC. We only listed covariate univariable models for parameter estimates where lower and upper confidence intervals did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of American pipit density in response to each covariate and predictor category type. 57

Table 2.9 – Results of top ten multivariable negative binomial generalized linear models (GLMs) sorted by ascending Bayesian Information Criteria (BIC), for American pipit (*Anthus rubescens*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP), to compare the estimated prediction error (p_{Err}) produced from the leave-one-out cross-validation test to further confirm model fit and verify top model predictability if applied to new a new data set. Results presented are from unstandardized data with model rank based on ascending BIC, covariate model structure, number of parameters (k), log-likelihood (LL), BIC, change in BIC value from top model (ΔBIC), and Bayesian weight (w_i). Each ranked model includes an offset term (ratio of counts to survey effort), calculated from mean detection probability in program DISTANCE 6.2. 58

Table 2.10 – Results of top multivariable negative binomial generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for American pipit (*Anthus rubescens*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in

Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed includes an offset term for detection calculated from mean detection probability in program DISTANCE 6.2, along with covariates: woody species percentage (Woody), ericaceous shrub percentage, Engelmann spruce (*Picea engelmannii*) percentage, Julian date, and year. Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of American pipit density in response to each covariate. Any IRRs not provided were due to not being relevant in this analysis. 59

Table 2.11 – Results of top univariable zero-inflated Poisson (ZIP) generalized linear models (GLMs) conducted on all covariates within four predictor categories, sorted by ascending Bayesian Information Criteria (BIC) within each predictor category, for horned lark (*Eremophila alpestris*) data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Models listed include an offset term for detection calculated from mean detection probability in program DISTANCE 6.2. Results presented are from standardized data and include predictor categories, covariate model, number of parameters (k), predictor (β) estimates, 95% confidence intervals (CI), log-likelihood (LL), and BIC. We only listed covariate univariable models for parameter estimates where lower and upper confidence intervals did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of horned lark density and abundance in response to each covariate and predictor category type. Section (A) represents the count portion (abundance) of the zero-inflated Poisson model, while section (B) represents the binomial portion (presence-absence) of the zero-inflated Poisson models. 60

Table 2.12 – Results of univariable zero-inflated Poisson (ZIP) generalized linear models (GLMs) conducted on all covariates within four predictor categories, sorted by ascending Bayesian Information Criteria (BIC) within each predictor category, for horned lark (*Eremophila alpestris*) data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Models listed include an offset term for detection calculated from mean detection probability in program DISTANCE 6.2. Results presented are from standardized data and include predictor categories, covariate model, predictor (β) estimates, number of parameters (k), log-likelihood (LL), lower and upper 95% confidence intervals (CI), and BIC. We only listed covariate univariable models to compare against our predictions to determine the response in horned lark abundance and occurrence based on our hypotheses (Table 2.1). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Section (A) represents the count portion (abundance) of the zero-inflated Poisson model, while section (B) represents the binomial portion (presence-absence) of the zero-inflated Poisson models. 61

Table 2.13 – Results of top ten multivariable zero-inflated Poisson (ZIP) generalized linear models (GLMs) sorted by ascending Bayesian Information Criteria (BIC), for horned lark (*Eremophila alpestris*)

count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP), to compare the estimated prediction error (p_{Err}) produced from the leave-one-out cross-validation test to further confirm model fit and verify top model predictability if applied to new a new data set. Results presented are from unstandardized data with model rank based on ascending BIC, covariate model structure, number of parameters (k), log-likelihood (LL), BIC, change in BIC value from top model (ΔBIC), and Bayesian weight (w_i). Each ranked model includes an offset term (ratio of counts to survey effort), calculated from mean detection probability in program DISTANCE 6.2. 62

Table 2.14 – Results of top multivariable zero-inflated Poisson (ZIP) generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for horned lark (*Eremophila alpestris*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed is results of multivariable analyses with an offset term, along with covariates: herbaceous species percentage (Herb), woody species percentage (Woody), and study site (Site). Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of horned lark density and occurrence in response to each covariate. Any IRRs not provided were due to not being relevant in this analysis. Section (A) represents the count portion (abundance) of the zero-inflated Poisson model, while section (B) represents the binomial portion (presence-absence) of the zero-inflated Poisson models. 63

Table 2.15 – Results of top univariable negative binomial generalized linear models (GLMs) conducted on all covariates within four predictor categories, sorted by ascending Bayesian Information Criteria (BIC) within each predictor category, for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Models listed include an offset term for detection calculated from mean detection probability in program DISTANCE 6.2. Results presented are from standardized data and include predictor categories, covariate model, number of parameters (k), predictor (β) estimates, 95% confidence intervals (CI), log-likelihood (LL), and BIC. We only listed covariate univariable models for parameter estimates where lower and upper confidence intervals did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of white-crowned sparrow density in response to each covariate and predictor category type. 64

Table 2.16 – Results of top ten multivariable negative binomial generalized linear models (GLMs) sorted by ascending Bayesian Information Criteria (BIC), for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP), to compare the estimated prediction error (p_{Err}) produced from the leave-one-out cross-validation test to further confirm model fit and verify top model predictability if applied to new a

new data set. Results presented are from unstandardized data with model rank based on ascending BIC, covariate model structure, number of parameters (k), log-likelihood (LL), BIC, change in BIC value from top model (ΔBIC), and Bayesian weight (w_i). Each ranked model includes an offset term (ratio of counts to survey effort), calculated from mean detection probability in program DISTANCE 6.2. 65

Table 2.17 - Results of top multivariable negative binomial generalized linear models (GLMs) based on lowest Bayesian Information Criteria (BIC), for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed includes an offset term, calculated from mean detection probability in program DISTANCE 6.2, along with covariates: distance to road (m), Engelmann spruce (*Picea engelmannii*) percentage, Julian date, and year. Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of white-crowned sparrow density in response to each covariate. Any IRRs not provided were due to not being relevant in this analysis. 66

Table 2.18 – Comparisons of our estimated density estimates, calculated in program DISTANCE 6.2, from count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP), for the five known alpine breeding avian species in Colorado's alpine, with density estimates from previous research. Results presented include estimated density {birds/hectare (ha)}, 95% confidence intervals (CI), and researched density {birds/hectare (ha)} with their associated references for each avian species. 67

Table 2.19 - Results of top multivariable negative binomial generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for American pipit (*Anthus rubescens*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed is results of multivariable analyses without an offset term, along with covariates: woody species percentage (Woody), ericaceous shrub percentage, Engelmann spruce (*Picea engelmannii*) percentage, Julian date, and year. Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. 68

Table 2.20 - Results of top multivariable zero-inflated (ZIP) generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for horned lark (*Eremophila alpestris*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed is results of multivariable analyses without an offset term and herbaceous species percentage

(Herb), woody species percentage (Woody), and study site (Site). Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Section (A) represents the count portion (abundance) of the zero-inflated Poisson model, while section (B) represents the binomial portion (presence-absence) of the zero-inflated Poisson models.. 69

Table 2.21 – Results of top multivariable negative binomial generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed are results of multivariable analyses without an offset term and demonstrates results of different covariates such as distance to road (m), percentage of Engelmann spruce (*Picea engelmannii*), rock, willow, and wind (mph), and study site (Site), compared to the top model with an offset term (Table 2.19). Comparisons depict different covariate results when an offset is (Table 2.19) and is not applied. Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. 70

LIST OF FIGURES

Figure 2.1 – Location of 57 random points for the point count sampling conducted at Mt. Evans in Clear Creek County, Colorado during June to July in 2014 and 2015. Points were randomly generated within each stratum at a distance of 300 m a part. Each stratum was based on low, medium, and high elevation and shrub cover, and defined by various colors and values in matrix scale on right. Matrix Values were estimated from stratified elevation by designating three equal bins beginning at forest edge from low (bin = 10; e.g., Mt. Evans = 2,870 – 3361 m), medium (bin = 20; e.g., Mt. Evans = 3,362 – 3,853 m), and high (bin = 30; e.g., Mt. Evans = 3,854 – 4,345 m) elevations. Land cover data was derived from all Existing Vegetation Types (EVT) found within Landfire, version LF 2010. Stratified elevation was combined with low (1), medium (2), and high (3) shrub and subshrub EVT data, resulting in final Matrix Values. Due to various restrictions, only 37 of the 57 points were accessible. 71

Figure 2.2 – Location of 54 random points for the point count sampling conducted at Trail Ridge Road located in Rocky Mountain National Park (RMNP), Colorado during June to July in 2014 and 2015. Points were randomly generated within each stratum at a distance of 300 m a part. Each stratum was based on low, medium, and high elevation and shrub cover, and defined by various colors and values in matrix scale on right. Matrix Values were estimated from stratified elevation by designating three equal bins beginning at forest edge from low (bin = 10; e.g., RMNP = 2,599 – 3,104 m), medium (bin = 20; e.g., RMNP = 3,104 – 3,610 m), and high (bin = 30; e.g., RMNP = 3,611 – 4,114 m) elevations. Land cover data was derived from all Existing Vegetation Types (EVT) found within Landfire, version LF 2010. Stratified elevation was combined with low (1), medium (2), and high (3) shrub and subshrub EVT data, resulting in final Matrix Values. Due to various restrictions, only 31 of the 54 points were accessible. 72

Figure 2.3 **-** Two alpine study sites in Colorado: (1) Mt. Evans in Clear Creek County (orange polygon) and (2) Trail Ridge Road in Rocky Mountain National Park (RMNP, purple polygon) for point count surveys conducted during June to July of 2014 and 2015, for the five breeding alpine avian species. 73

Figure 2.4 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset)] relative to woody species cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a negative relationship between pipit density and woody species cover (%). Plot includes 95% upper and lower confidence intervals (CIs), and holds other covariates in top model at their median. 74

Figure 2.5 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset)] relative to ericaceous shrub species cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a negative relationship between pipit density and ericaceous shrub species cover (%). Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median. 75

Figure 2.6 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset] relative to Engelmann spruce cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a negative relationship between pipit density and Engelmann spruce percentage (%). Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median. 76

Figure 2.7 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset] relative to Julian date, from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between pipit density and Julian date. Plot includes 95% upper and lower confidence intervals (CIs), and holds other covariates in top model at their median. Colored circles represent the breeding phenology stage of American pipit (Kingery 1998), where green indicates the Julian date range (170-188) associated with pipit courtship, orange indicates the Julian date rage (173-202) associated with the period pipits occupy nests, and blue indicates the Julian date range (171-225) when pipits are feeding their young. Considerable overlap of breeding phenolgy demonstrates why there is a lower pipit density earlier in the breeding season versus toward the end...... 77

Figure 2.8 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset] relative to year, from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a a greater pipit density in the second year (2015) compared to the

first year (2014). Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median. 78

Figure 2.9 – Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to distance to road (m), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between white-crowned sparrow density and distance to road. Plot includes 95% upper and lower confidence intervals (CIs).), and holds other covariates in top model at their median. 79

Figure 2.10 – Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to Engelmann spruce cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between white-crowned sparrow density and Engelmann spruce cover. Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median. 80

Figure 2.11 – Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to grass and herbaceous species height (cm), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between white-crowned sparrow density and grass and herbaceous species height. Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median. 81

Figure 2.12 – Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to willow species cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek

County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between white-crowned sparrow density and willow species cover. Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median. 82

Figure 2.13 - Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to wind (mph), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a negative relationship between white-crowned sparrow density and wind. Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median. 83

CHAPTER 1: CLIMATE CHANGE AND ALPINE BREEDING BIRDS IN COLORADO

INTRODUCTION

Climate change in recent decades has led to species shifts in abundance and distribution across many diverse ecosystems (McCarty 2001). However, the extent to which species have been affected by changing climate is particularly uncertain for many alpine avian species. As climate change alters habitat, mobile species with close ties to existing habitat structure are especially at risk and prone to extinction (McLaughlin et al. 2002).With the geographical and temporal irregularity of climate change, future impact to avian species is difficult to predict. Habitat characteristics have often been used to determine and predict animal abundance and species-habitat relationships (Baker 1956, Armstrong 1972, Mazerolle and Villard 1999). Understanding these relationships is necessary to fully comprehend how species not only persist and survive, but how species may adapt and evolve as habitats and ecological processes change (Rotenberry 1981).

Birds have long been used as bio-indicators to establish baseline distributions as climate change occurs and to predict future distributions as climate change continues (Böhning-Gaese and Lemoine 2004, Crick 2004). In order to determine how species may respond under anticipated warming regimes in Colorado’s high elevations, assessment of fine-scale habitat features influencing avian bird abundance and occurrence is essential for conservation and management of important habitats in these alpine regions. The complexity behind avian species’ association to their environment has often been explained by habitat structure. For instance, avian species occurrence has been shown to be linked to percent canopy tree cover, canopy height, and tree species diversity (James 1971), with avian habitat selection found to be driven by plant taxa (Rotenberry 1985). Focusing on the specific habitat features necessary to ensure the success of avian species, I examined fine-scale habitat associations of the five known alpine breeding birds in Colorado: American pipit (*Anthus rubescens*), brown-capped rosy-finch (*Leucosticte australis*), horned lark (*Eremophila alpestris*), white-crowned sparrow (*Zonotrichia leucophrys oriantha*), and white-tailed ptarmigan (*Lagopus leucura*; hereafter, ptarmigan) (Braun 1980). These five breeding species represent a diverse range of not only avifauna that reproduce in these regions, but also capture a variety of habitat requirements necessary for breeding bird species' persistence in this ecosystem. Additionally, these five birds were chosen as focal species due to their susceptibility to climate change and because some of these species have exhibited population declines in recent years. For instance, white-crowned sparrow populations have declined across Colorado from 1970 – 2010 (Sauer et al. 2014). In Colorado's north-central mountains in Rocky Mountain National Park, warm winters and variable climate have been linked to a decline in ptarmigan populations by ~30% of their peak population size (Wang et al. 2002). Furthermore, in Colorado's central mountains between 1968 and 2010, precipitation and temperature were found to be significant drivers advancing ptarmigan hatch dates by an average of 10 days (Wann 2012). Understanding resource needs for these five breeding birds will be important to determine how each species could be impacted particularly if their habitat is altered by changing climate

My research objectives were to: (1) determine and quantify the environmental and habitat factors influencing alpine breeding bird abundance and occurrence; (2) determine habitat selection of an alpine-endemic avian species to identify environmental and habitat characteristics associated with fitness; and (3) draw on results from the first two objectives to inform management agencies of how alpine avian species may be affected in the future if changes to their habitat occurs. In Chapter 2, I analyze count data collected from distance sampling, and test the relationships between various habitat and environmental variables influencing bird abundance and occurrence. In Chapter 3, I utilize a use-available design to present estimates of nest and brood site habitat selection by ptarmigan and the local-scale resources influencing these two different reproductive stages. Lastly, Chapter 4 summarizes my research findings and discusses the potential future impacts these alpine breeding species may face if climate change continues to alter these important and vulnerable habitats. As climate change is expected to continue to impact alpine ecosystems, my research provides a platform to move forward in properly managing and conserving alpine habitat and its avian species in Colorado.

LITERATURE CITED

Armstrong, D.M. 1972. Distribution of mammals in Colorado. University of Kansas, Museum of Natural History, Monograph Number 3.

Baker, R.H. 1956. Mammals of Coahuila, Mexico. University of Kansas, Museum of Natural History, Monograph 9(7): 125-335.

Böhning-Gaese, K., and N. Lemoine. 2004. Importance of climate change for the ranges, communities and conservation of birds. Advances in Ecological Research 35:211-236.

Braun, C. E. 1980. Alpine Bird Communities of Western North America: Implications for Management and Research. In Workshop Proceedings: Management of Western Forests and Grasslands for Nongame Birds (R. M. Deraff, technical coordinator). USDA Forest Service General Technical Report. INT-86. Pp. 280-291.

Crick, H. Q. P. 2004. The impact of climate change on birds. Ibis 146:48-56.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin 83:215-236.

Mazerolle, M.J., and M-A.Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: A review. Ecoscience 6(1): 117 - 124.

McCarty, J. P. 2001. Ecological Consequences of Recent Climate Change. Conservation Biology 15.

McLaughlin, J. F., J.J. Hellman, C.L. Boggs, and P.R. Ehrlich. 2002. Climate change hastens population extinctions. Proceedings of the National Academy of Sciences 99:6070-6074.

Rotenberry, J. T. 1981. Why measure bird habitat? USDA Forest Service General Technical Report, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, Pp 29-32.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? . Oecologia 67:213-217.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2014. The North American Breeding Bird Survey, Results and Analysis 1966-2012. Version 02.19.2014 USGS Patuxent Wildlife Research Center, Laurel, MD.

Wang, G., N. T. Hobbs, K. M. Giesen, H. Galbraith, D. S. Ojima, and C. E. Braun. 2002. Relationships between climate and population dynamics of white-tailed ptarmigan Lagopus leucurus in Rocky Mountain National Park, Colorado, USA Climate Research 23:81-87.

Wann, G. T. 2012. Long-term Demography of a White-tailed Ptarmigan (Lagopus leucura) Population in Colorado. Department of Ecosystem Science. Diploma Thesis, Pp 125.

CHAPTER 2: HABITAT AND ENVIRONMENTAL INFLUENCES OF BREEDING AVIFAUNA SPECIES IN ALPINE REGIONS OF COLORADO

SUMMARY

The alpine is a unique, highly diverse ecosystem shaped by topography and severe weather providing habitat for an array of species, many of which are endemic to this region. With climate change altering mountain habitats, birds are but one of several species groups that have been projected to be impacted in this biome. In light of several breeding bird species found in Colorado's alpine along with projected climate change in these regions, we lack information and knowledge of what habitat and environmental factors are influencing alpine avian populations in these areas. We assessed specific breeding bird populations and evaluated how abundance and occurrence might be influenced by abiotic, biotic, anthropogenic, temporal, or spatial factors in two alpine areas of Colorado: Mt. Evans in Clear Creek county, and Trail Ridge Road in Rocky Mountain National Park. We measured specific, fine-scale attributes of the habitat and environment via distance sampling with point counts. Point count sites were randomly selected to include variation in elevation and shrub cover, two components often determining avian distribution. We estimated the response of alpine passerine counts with generalized linear models (GLMs). American pipits (*Anthus rubescens*) were influenced by biotic and temporal predictors, horned larks (*Eremophila alpestris*) were driven by biotic predictors and spatial covariates, and white-crowned sparrows (*Zonotrichia leucophrys oriantha*) were influenced by abiotic, biotic and anthropogenic factors. Much remains to be studied to understand alpine bird populations and environmental factors contributing to patterns in these

regions. Such assessments will help to understand future effects of climate change on alpine birds especially if aspects of their habitats are altered.

INTRODUCTION

Alpine habitat is a delicate ecosystem that is cold-adapted, spatially-segregated, and naturally fragmented by the landscape. The alpine is characterized as regions high above treeline where patterns of cold climates, elevation gradients, and rugged terrain results in sparse, distinct, stunted vegetation, and a spatially heterogeneous habitat compared to other environments (Bowman and Seastedt 2001). Biological diversity, species isolation, and niche division within this system's framework provides opportunities for a variety of species to persist (Chapin and Körner 1996). Globally, alpine habitat supports roughly 4% of flora (10,000 species) and 3-4% of fauna species (Chernov 1995, Körner 1995, Walker 1995). Vertical topography allows the alpine to sustain endemic species and often with comparatively high biodiversity to other ecosystems (e.g., tropical rain forests; Chapin and Körner 1996, Essl et al. 2009, Dirnböck 2011). Alpine habitat and conditions can be severe compared to other ecosystems, with increased solar radiation, shorter growing seasons, strong winds, lower temperatures, and deep snowpack contributing to the range of species' physiological responses, biodiversity, and composition within this system (Bowman and Seastedt 2001, Greenland and Losleben 2001). In contrast to other ecosystems, terrestrial animals in alpine habitat are exposed to more extreme and irregular abiotic conditions (Martin and Wiebe 2004).

Although the alpine zone is accustomed to fluctuating and extreme conditions, it is at risk from climate change. In mountain areas, warming temperatures have exceeded the global average temperature two-fold, affecting snowpack and snow lines with predicted continuation of these trends (Brunetti et al. 2009, EEA 2010). Consequently, alpine habitat acts as a global barometer of environmental change due to the sensitivity of biota to shifts in climatic regimes and species' general tolerance to existing environmental conditions (i.e., moisture, temperature, climate) (Körner and Larcher 1988, Grabherr et al. 1995, Beniston and Fox 1996). Increased temperatures could move treelines and vegetation up in elevation, with these patterns already evident in parts of Europe (Meshinev et al. 2000, Kullman 2002, Kullman 2003, Moiseev and Shiyatov 2003) and North America (Sturm et al. 2001). Many terrestrial species depend on specific vegetation and conditions, and shifts in habitat types could produce deleterious effects for many alpine species, especially alpine-endemic avifauna. For instance, climate change could affect the synchrony of invertebrate prey availability and avian reproductive output (Visser and Both 2004). Although studies involving alpine bird species and habitat factors influencing bird populations are limited, high mountain birds are projected to be one of the most vulnerable species groups impacted by climate change (EEA 2010).

Despite the often harsh climatic conditions and other environmental constraints, alpine species are not only able to survive in this environment, but also reproduce. However, these conditions limit avian species that breed in the alpine. In the alpine areas of Colorado there are five known breeding avian species: American pipit (*Anthus rubescens*), brown-capped rosy-finch (*Leucosticte australis*), horned lark (*Eremophila alpestris*), white-crowned sparrow (*Zonotrichia leucophrys oriantha*), and the alpine-endemic white-tailed ptarmigan (*Lagopus leucura*; hereafter ptarmigan; Braun 1980). Although there are several other potential alpine breeding avifauna (e.g., prairie falcon (*Falco mexicanus*), common raven (*Corvus corax*), and various passerines (Braun 1980) along with many migrant, summer visitor and resident avian species (Bowman and Seastedt 2001), these five breeding species represent a diverse group for evaluation of the alpine bird community. A recent climate change vulnerability index in the Sierra Nevada Mountains found that two species in particular, American pipit and white-tailed ptarmigan, have been designated moderately and most vulnerable (Siegel et al. 2014).

Avian abundance and occurrence are influenced by abiotic and biotic factors, with the latter often being a more significant driver within particular species (Martin 2001b). Alpine breeding avifauna with breeding distributions also occurring at lower elevations, use similar habitat structure provided it is accessible, within and outside of the breeding seasons (Wilson and Martin 2005). Although habitat size and availability in the alpine is limited compared to lower elevations, these five breeding species are known to use specific and often similar parts of alpine habitat for survival and to successfully reproduce. For example, habitat requirements for many of these five species include minimal snow cover (Verbeek 1970, Braun et al. 1993, Johnson et al. 2000), access to cover for protection from elements and predators (DeWolfe and DeWolfe 1962), proximity to water (DeWolfe and DeWolfe 1962), availability of foraging and nesting resources (Pattie and Verbeek 1966, Johnson et al. 2000, Hoffman 2006), and rock cover (Pattie and Verbeek 1966, Braun et al. 1993).

Similar to other ecosystems, predation and competition for resources occurs in the alpine, both of which are likely to affect bird distributions and abundance. Heavy grazing of herbivores has been shown to have a negative effect on bird abundance, density, and reproductive success via restructuring suitable bird habitat and exposing nests to increased predation pressure (Fuller 2001). Alternatively, grazing at low levels may increase the accessibility of available food (e.g., insects) for birds and affect reproductive output as measured by bird egg size (Evans et al. 2005). Other factors (e.g., anthropogenic) could alter bird density and occurrence in alpine regions. Proximity to roads, for example, has been shown to reduce bird abundance, occurrence and reproductive success by limiting male’s ability to attract and maintain a female bond (Foppen and Reijnen 1994).

In this study, we examined which factors of alpine habitat in two regions of Colorado influenced the abundance and occurrence of avifauna during their breeding period. Our goal was to evaluate (1) whether abiotic, biotic, anthropogenic, temporal, or spatial factors played a more prominent role in these species’ abundance and occurrence; (2) to what extent these influences varied across species; and (3) the differences or similarities of such effects on species across two distinct study areas.

We expected abiotic and biotic factors would have the largest impacts on species distribution and abundance; however, this is likely to vary by species. Although these avian species occupy similar areas within the alpine, many have different habitat needs and partition resources differently within this system. For example, a recent study on water pipit (*Anthus spinoletta*), an European alpine conspecific of American pipit, found their density and distribution at high elevations strongly depended upon open, heterogeneous habitats that included shrubs and woodlands species, whereas density decreased with high rock cover, all interacting across an elevational gradient (Melendez and Laiolo 2014). American pipit density and occurrence at high elevations in Wyoming was found to be higher with less snow cover, lower wind speeds, and warmer temperatures (Verbeek 1970). Other species like brown-capped rosy-finch tend to be found in areas with cliffs for nesting, and in areas with retreating snowfields or minimal snow cover that expose insects and seed heads for foraging (Johnson et al. 2000). Likewise, horned larks have been found to primarily feed and nest in alpine areas of abundant grasses and exposed rock (Pattie and Verbeek 1966). Another breeding species, white-crowned sparrow, uses areas abundant in shrubs and small trees, grass, bare ground, water, and in close proximity to tall conifers in high mountain areas (DeWolfe and DeWolfe 1962). During the breeding season, white-tailed ptarmigan are found in areas of higher elevation ranges (i.e., 3,350 to 4,250-m in Colorado; (Braun et al. 1993), that include higher percentages of rocks and herbaceous species, along with less snow cover and presence of shorter willow species (i.e., <1-m) with the latter often more influential in determining ptarmigan breeding sites (Choate 1963, Braun 1971, Clarke and Johnson 1992, Schmidt 1998, Hoffman 2006). Based on these diverse habitat and environmental characteristics identified as being important to these five breeding alpine avifauna, we expected each species to respond differently to alpine resource conditions (see Table 2.1 for complete predictions). We hypothesized anthropogenic factors, specifically distance to road would negatively affect all five of these breeding alpine avian species, resulting in greater species' abundance or occurrence at further distances to roads. We also hypothesized alpine avian abundance and occurrence would vary across our two study sites. This stemmed from evident differences in resource conditions at our two study sites (e.g., elevation, willow cover). Although many studies have examined these avian species and elements separately, few have studied these components collectively within the alpine ecosystem. This is important to not only improve our understanding of the diversity within the alpine breeding avian community and its habitat requirements, but to enhance habitat management programs and ecological theory in this ecosystem.

STUDY AREAS

We measured bird abundance and occurrence at two alpine study sites in Colorado from early June to July in 2014 and 2015. The Mt. Evans (39°35'N, 105°38'W – highest point) study site (Figure 2.1), located in central Colorado, is a part of the Mt. Evans Wilderness Area within Clear Creek County, including 9.2 km^2 of alpine habitat. The Mt. Evans Scenic Byway runs 14 miles directly through this region. The Trail Ridge Road (40°25’W, 105°45’W – highest point) study site (Figure 2.2) comprises 9.11 km^2 of alpine habitat located in Rocky Mountain National Park (RMNP), with nearly 11 miles of road above treeline. Elevations of both study sites range from approximately 3,300 to 4,300 m at Mt. Evans and 3,300 to 3,800 m at RMNP. Mt. Evans and Trail Ridge Road are in relatively close proximity (e.g. ~97 km apart; Figure 2.3) to one another; thus, they both exhibit similar weather patterns with prevailing, often strong winds and high accumulations of snow lingering well into spring and summer months.

METHODS

Field Survey Sampling Design

We stratified study sites based on similar metrics for elevation and shrub cover (e.g., low, medium, and high strata for each) using ArcGIS 10.2.2 (ESRI 2014) to produce a three by three matrix of nine strata. This framework was established because mountain species’ responses are often dictated by their relationship between elevation and vegetation productivity (Brown 2001). Stratification was performed to account for differences in variation in detection, reduce bias of estimates, and improve overall precision (Buckland et al. 2001) of detection and density and abundance estimates across study areas. An inward buffer of 150 m from forest edge was applied to each study site to ensure limited detection of non-target, edge-sensitive species and to reinforce the inclusion of alpine habitat. We stratified elevation by designating three equal bins beginning at forest edge from low (bin = 10; e.g., Mt. Evans = 2,870 – 3361 m, RMNP = 2,599 – 3,104 m), medium (bin = 20; e.g., Mt. Evans = 3,362 – 3,853 m, RMNP = 3,104 – 3,610 m), and high (bin = 30; e.g., Mt. Evans = 3,854 – 4,345 m, RMNP = 3,611 – 4,114 m) elevations. We derived land cover data from all Existing Vegetation Types (EVT) found within Landfire, version LF 2010 (newest release: March 2014). EVT data provided an estimate of low, medium, and high abundance of shrubs or subshrubs which we manually assigned values for each category type (e.g., 1, 2, or 3). We attempted to place five random points within each of the nine strata for a total of 45 points at each study site, however due to the accessibility of terrain (e.g., ruggedness or restricted access) we sampled 37 points at Mt. Evans and 31 at RMNP (total n = 68). We spaced points 300 m apart to maintain independent detections, a key assumption of distance sampling (Bibby et al. 1998, Buckland et al. 2001), and because distances beyond 500 m should not be surveyed because of the difficulty to locate avian species in rugged terrain, as has been shown for male rock ptarmigan (Marty and Mossoll-Torres 2012).

Field Surveys

We used point counts to measure abundance and occurrence at both sites, which is preferred over line transects in difficult or rugged terrain (Buckland et al. 2001). Our sampling window from June to July captured the range of arrival and breeding times for our five focal species. We conducted surveys in a narrow time period (e.g., weeks) to reduce seasonal variability among species. We surveyed each count site between 0700 and 1300 hr (Mountain Standard Time). This corresponded to timing of other surveys to capture peak activity and abundance of horned lark and American pipit (Norvell and Creighton 1990). We conducted ten minute point counts separated into three intervals: 1) one minute rest period to allow birds to acclimate to observer presence; 2) 5 minutes for detection of avifauna, predators, and other species; and 3) ~ four minutes to record habitat characteristics.

We counted both avian species, as well as aerial and terrestrial predators upon detection during the second time interval at point count sites. We established a fixed radial distance of 250 m from the center of each point count for aerial (e.g., golden eagle (*Aquila chrysaetos*)), large predators (e.g., coyote (*Canis latrans*)) and other large species (e.g., Rocky Mountain Elk

(*Cervus canadensis*)) surveys due to species being highly mobile and able to cover large distances, and to eliminate double counting of individuals. We also counted other species such as American pika (*Ochotona princeps*) and yellow-bellied marmot (*Marmota flaviventris*) during this period in order to see if there were other species influencing the avian species of interest. We did not fix the radial distance for detection of passerine and white-tailed ptarmigan counted, due to these species having smaller home ranges and because the open terrain made it easier for us to detect if the same individual was moving between point count sites. However, if detections of either were beyond 500 m, they were not recorded. To increase potential ptarmigan detections, we broadcast successive male territorial white-tailed ptarmigan calls (FoxPro NX4 Non-remote Game Call; FoxPro, Inc.), for a short duration (e.g., 3 successive 5-6 sec calls, separated by 20 sec in between each call) to listen for male responses. We played the ptarmigan call toward the end of the point count survey (fourth minute, second interval) to reduce the probability of attracting predators with the call, thus increasing the bias of predator detections. We measured the radial distance to each species detected using rangefinders (Bushnell Yardage Pro Scout Laser; Bushnell, Inc.) and recorded how the species was detected (e.g., aural, visual, flying over habitat for passerine or aerial predators, or on the ground).

We conducted ocular vegetation surveys during the last time interval of the point count with a fixed radial distance of 30 m. We measured shrub and small trees including species composition and total mean height (m), percent ground cover (e.g., dead and down, herbaceous, bare and litter, grass, and snow cover), and other abiotic and biotic characteristics (Table 2.2). Abiotic and biotic features have been shown to define avian distribution and habitat use, and both were important to consider particularly in light of climate change and the resulting synergistic effects to both factors (Martin 2001b).

DATA ANALYSES

Detection Probabilities

We estimated detection probabilities using program DISTANCE 6.2 (Thomas et al. 2010) and the multiple covariate distance sampling (MCDS). We tested all key functions (e.g., half-normal and hazard-rate) and series expansions affiliated with these key functions (e.g., cosine, hermite polynomial, and simple polynomial). We removed the largest 10% of point count data in DISTANCE as suggested by Buckland et al. (2001) for model selection, but also evaluated other truncation distances and bin sizes with the final model for species with small sample sizes following Buckland et al. (2001). Upon selection of key function and best adjustment, we selected several factor covariates within each of the four predictor groups, based on the biology of each species (Marques and Buckland 2003, Marques et al. 2007). We used Bayesian Information Criteria (BIC) to evaluate the strength of each model, given our data, while emphasizing the selection of the most parsimonious model (Burnham and Anderson 2002). Another model selection approach, Aikaike's Information Criteria (AIC), would have under penalized models with more parameters compared to BIC due to the differences in their base equations with parameter terms (k) and sample size (Burnham and Anderson 2002). The final model was post-stratified by site (e.g., Mt. Evans and RMNP) and year to determine if spatial and/or temporal differences in detection probabilities were apparent. We used BIC, chi-square model-fit statistics (e.g., total chi-square values) and visual inspection of the data to guide selection and assessment of our final models.

We used the best model from DISTANCE to calculate an offset term based on the mean detection function, only when sites had no detection, and survey effort (i.e., number of visits) at each point count site (Buckland et al. 2009). The offset acted as a correction term to account for potential variation of mean counts due to differences in survey effort (Kery 2010), but allowed us to use the raw count data in generalize linear models to evaluate how bird density may be shaped by predictor variables when differences in detectability are applied (Aldridge et al. 2011).

Count Model Development

We first graphically explored frequency histograms of raw count data to identify problematic outliers (Buckland et al. 2001) and presence of zero-inflated count data (Potts and Elith 2006) to identify the most appropriate covariate and model structures. We evaluated 27 variables considered within four predictor categories: 1) abiotic factors; 2) biotic factors; 3) anthropogenic factors; and 4) spatial/temporal factors (Table 2.2). We explored raw plots of counts relative to variables to determine if quadratic terms were necessary in our model structures. If variables were correlated (Pearson's $r \geq |0.7|$; Table 2.2) within or across predictor categories, we prevented them from occurring in the same candidate model, and retained the most biologically relevant variable moving forward. Following Beers et al. (1966), we transformed our measured aspect (Θ, degrees) into continuous variables as: $x = \sin[\Theta + (90 – A_{max})] + 1$, where A_{max} was the maximum value we anchored our transformation to, and values closer to two indicated more northeastern aspects and values closer to zero were more southwest. All variables were standardized prior to fitting models by subtracting its mean from the individual value and dividing by the standard deviation.

Model Development

Observations occurring beyond the truncation distances from our final detection models were removed prior to developing count-based models. We fit generalized linear models (GLMs) to our count data, plus an offset term, using either a Poisson or negative binomial (NB) link function (Potts and Elith 2006), which have been shown to handle data with minimal counts

(Coxe et al. 2009) and are also robust to deal with stochasticity in ecological count data (Lindén and Mäntyniemi 2011). We fit NB GLMs to count data, which account for overdispersion (i.e., ($\mu < \sigma^2$) of data if present (Ver Hoef and Boveng 2007, Lindén and Mäntyniemi 2011) and analyzed overdispersion by the dispersion parameter (θ, theta). We first fit a null (intercept only) model using Poisson and NB link functions and assessed model strength and fit with a Vuong's test (Yaacob et al. 2010). We then fit multivariable models using Poisson and NB link functions with covariates representative of the biology of each avian species within our four predictor categories, followed by assessment of BIC and a Vuong's test. The presence of many zeros in our count data could require the use of a zero-inflated process to properly account for the excessive zeros (Hilbe 2011). If there was evidence of zero inflation from count distributions, we also tested zero-inflated models (i.e., zero-inflated Poisson, [ZIP], or zero-inflated negative binomial, [ZINB]), where species' counts were modeled jointly via two-part mixture processes: (1) species abundance using count data, and (2) species occurrence (presence-absence) with a binary distribution predicting true absence of individuals, where zero counts were used in both modeling processes (Hilbe 2011). We compared ZIP and ZINB with Poisson and NB GLMs via BIC and Vuong's test, again using biologically-relevant covariates within each of the four predictor categories based on species type. If a zero-inflated model was required, we fit the same variables for both the abundance and occurrence portions of the zero-inflated models, limiting variable combinations for possible models.

Once we identified the initial distributional form of the model, we estimated univariable models for all 27 covariates. We then identified the best combination model using BIC, considering all variables within each of the four predictor categories. All models were compared to the null model. For any covariates that appeared non-linear, we fit a quadratic term and compared BIC with the linear model form. Once we determined top models in each predictor category, we evaluated all possible combinations among the covariate category groups. During model development, if direction of coefficients fluctuated across models they were deemed uninformative parameters and removed from further consideration (Arnold 2010). We calculated variance inflation factors (VIF) to ensure lack of multicollinearity among covariates in the top model, and covariates were removed and the model re-estimated if VIF scores for individual covariates exceeded 3.0 (Zuur et al. 2010). We calculated a chi-square distributed likelihood ratio test on the top GLM to test goodness-of-fit (Hosmer and Lemeshow 1989), comparing the null and reduced model residual deviance. Furthermore, we ranked all final candidate GLMs based on BIC and model present weights (w_i) for the top 10 models, and designated any candidate models based on ΔBIC < 2.0, because of the strength of support these models provide for making inferences (Burnham and Anderson 2002). Finally, we estimated incidence rate ratios (IRR) from our final candidate multivariable GLMs by exponentiating the un-standardized β-coefficients, to quantify how a change in the predictor affects the response (Hilbe 2015).

Post hoc we were interested in how our results would differ if an offset term was not applied. The offset acted as a correction factor (Kery 2010) accounting for variation in detection and survey effort across years and sites. We compared all models with and without the offset term, to discern additional variation not attributed by differing annual survey effort. We performed all statistical tests using Program R 3.1.3 (2015).

Predictive Performance

We used a leave-one-out cross-validation technique to evaluate performance of the top ten candidate GLMs for each species (cv.glm function in the package “boot” in Program R; (Ripley 2010). This technique is recommended in order to produce a relatively unbiased estimate of prediction error, and can identify models that are overfit (i.e., the size of the training dataset is too small in comparison with overall model complexity; Olden and Jackson 2000, Olden et al. 2002). The resulting mean prediction error estimate (delta, Δ) was then compared among the top ten candidate models; a well-fit model with the best predictive performance has the smallest delta (Efron and Tibshirani 1993, Davison and Hinkley 1997).

RESULTS

Field Surveys

We sampled the 68 point count sites a total of 214 times during June and July of the 2014 and 2015 field seasons (Mt. Evans, n = 37 point count sites in 2014 and 37 in 2015; RMNP, n = 31 point count sites in 2014 and 28 in 2015). Each point count site had one sampling occasion during 2014 and all sites were sampled twice in 2015, though some RMNP sites were sampled a third time in 2015 due to fewer sites. American pipit and white-crowned sparrow were the most abundant of the five breeding species on the 68 point count sites (Table 2.3). We found naïve occurrence of American pipit, brown-capped rosy-finch, and white-crowned sparrow greater at Mt. Evans, while occurrence for horned lark and white-tailed ptarmigan were greater at RMNP (Table 2.3). However, occurrence differed by year at the study sites (Table 2.4).

Detection Probabilities

All five breeding species had detection probabilities estimated using habitat and environmental covariates based on the biology of each species and their habitat requirements, ensuring we had covariates that would represent all 4 predictor categories for comparison purposes (Table 2.5) (MacKenzie et al. 2002).

American pipit

The best American Pipit model had a hazard-rate key function with cosine adjustment and data partitioned into 10 bins, using an initial grouping bin out to 35 m, followed by 15 m intervals between each bin, with a truncation distance of 170 m (Appendix 1). This resulted in 449 of the 497 detections being retained for pipit count-based models (Table 2.6, Table 2.7). The top detection model based on BIC included distance to road and time. Goodness-of-fit model statistics ($\chi^2 = 6.4$, $p = 0.27$) and the detection probability plot (Appendix 1) indicated this model had good fit. Detection probability was low (0.17, 95% CI = 0.15, 0.18), and the mean density of American pipits was estimated at 1.50 birds/ha (95% CI = 1.29, 1.74).

Brown-capped rosy-finch

The best brown-capped rosy-finch model had a hazard-rate key function with cosine adjustment and data partitioned into 10 bins, using an initial grouping bin out to 30 m, followed by manual manipulation of each bin (range: 5 to 10 m intervals), with a truncation distance of 150 m (Appendix 2). This resulted in only 15 of the 20 detections being retained for brown-capped rosy-finch detection models. The top detection model based on BIC included distance to road, observer, and time. Goodness-of-fit model statistics ($\chi^2 = 5.5$, $p = 0.14$) and the detection probability plot (Appendix 2) indicated this model had reasonable fit. Detection probability for brown-capped rosy-finch was low (0.17, 95% CI = 0.01, 1.00). The overall density of brown-capped rosy-finch was estimated at 0.06 birds/ha (95% CI = 0.002, 1.47).

Horned lark

The best horned lark model had a hazard-rate key function with cosine adjustment and data partitioned into 10 bins, using an initial grouping bin out to 60 m, followed by 10 m intervals between each bin, with a truncation distance of 130 m (Appendix 3). This resulted in 64 of the 73 detections being retained for horned lark count-based models (Table 2.6, Table 2.7). The top detection model based on BIC included rock, snow cover, and time. Goodness-of-fit model statistics (χ^2 = 8.8, p = 0.06) and the detection probability plot (Appendix 3) indicated weak model fit. Detection probability for horned lark was low (0.17, 95% CI = 0.11, 0.26). The overall density of horned lark was estimated at 0.16 birds/ha (95% CI = 0.09, 0.29).

White-crowned sparrow

The best white-crowned sparrow model had a hazard-rate key function with cosine adjustment and data partitioned into 10 bins, using an initial grouping bin out to 40 m, followed by 20 m intervals between each bin, with a truncation distance of 220 m (Appendix 4). This resulted in 235 of the 259 detections retained for white-crowned sparrow count-based models (Table 2.6, Table 2.7). The top detection model based on BIC included krummholz, willow species, distance to road, and observer. Goodness-of-fit model statistics (χ^2 = 4.92, p = 0.09) and the detection probability plot (Appendix 4) indicated sufficient model fit. Detection probability for white-crowned sparrow was low (0.11, 95% CI = 0.09, 0.14). The overall density of white-crowned sparrow was estimated at 0.62 birds/ha (95% CI = 0.47, 0.81).

White-tailed ptarmigan

The best ptarmigan model had a hazard-rate key function with cosine adjustment and data partitioned into 10 bins, using an initial grouping bin out to 60 m, followed by manual manipulation of each bin (range: 15 to 30 m intervals), with a truncation distance of 315 m (Appendix 5). This resulted in 14 of the 16 detections retained for white-tailed ptarmigan detection models. The top model based on BIC included herbaceous species, total mean height, and time. Goodness-of-fit model statistics (χ^2 = 4.21, p = 0.38) and the detection probability plot (Appendix 5) indicated adequate model fit. Detection probability for white-tailed ptarmigan was low (0.08, 95% CI = 0.01, 0.85). The overall density of white-tailed ptarmigan was estimated at 0.02 birds/ha (95% CI = 0.002, 0.23).

Model Selection and Evaluation

Few correlations existed between covariates, however woody species cover and total percent cover of shrubs and small trees were highly correlated ($r = |0.88|$), as well as a slight correlation among woody and willow species cover ($r = |0.71|$). All covariates were retained due to the biological importance for a variety of the avian species of interest; however, we ensured none of the variables with correlation $\geq |0.70|$ remained in the same model. A restricted number of species could be assessed in this analysis, due to smaller sample sizes recorded at point count sites and lack of variation in alpine avian count data. Thus, we could only use GLMs to model three of the five breeding species: 1) American pipit; 2) horned lark; and 3) white-crowned sparrow. We did not have enough data to consider predators and non-predators as covariates in bird count models.

American Pipit

Quadratic forms were considered for multiple covariates, but non-quadratic forms of all covariates were retained based on lower BIC values. The NB GLM outperformed the Poisson GLM across three of the four predictor categories according to BIC and Vuong’s test ($z = 2.97$, $p = 0.002$). However, the Poisson appeared to be the better model for biotic factors (BIC = 726.82, 731.79, respectively). Estimates of the mean and variance (2.16 and 2.43, respectively) confirmed slight overdispersion, thus we retained the NB GLM as the final model structure.

Several univariable models demonstrated strong effects on pipit density (Table 2.8). The top count model, consisted of biotic and temporal factors, including percent woody species, percent ericaceous shrubs, percent Engelmann spruce, and year (BIC = 694.35; Table 2.9). This top model outcompeted the next best model (ΔBIC = 3.18; Table 2.9), had no multicollinearity (all VIF scores < 3.0), and fit the data well (χ^2 = 160.83, df = 5, p = <0.001). Assessment of the dispersion parameter (ϴ = 0.0001) for this top model was not different than zero, indicating the negative binomial was the appropriate model form for the data (Hilbe 2015). The top model without site performed better than the model with site (BIC = 694.35, 699.38, respectively), and we make inferences from the pooled study site model. Our top count model indicated, pipit density was negatively related to cover of woody species (β = -0.72, 95% CI = -0.93, -0.53; Table 2.10; Figure 2.4), ericaceous shrubs (β = -0.19, 95% CI = -0.34, -0.06; Table 2.10; Figure 2.5), and Engelmann spruce (β = -0.22, 95% CI = -0.36, -0.10; Table 2.10; Figure 2.6), and higher densities were predicted later in the year (positive with Julian date; Table 2.10; Figure 2.7).

Horned Lark

Due to excessive zeros we first fit zero-inflated Poisson and NB models, and then we subsequently compared them to Poisson and NB GLMs. Once considering non-linear forms of covariates, only the quadratic form of elevation outcompeted the linear form (BIC = 280.11, 280.80, respectively), which was retained for the multivariable analyses. The zero-inflated Poisson (ZIP) exhibited better model fit over zero-inflated NB, Poisson and NB GLMs across all four predictor categories based on BIC and Vuong’s test. The ZIP model was retained as the final model structure for all univariable and multivariable models within and among the four predictor categories.

Several univariable models demonstrated strong effects on horned lark density and occurrence (Table 2.11 and Table 2.12). The top count model, comprised biotic factors, specifically percent woody and herbaceous species (BIC = 251.57; Table 2.13). A moderate

Bayesian weight of the top multivariable model (w_i = 0.43), demonstrated there were other suitable candidate models within a ΔBIC < 2.0 (Table 2.13). An examination of the two other candidate models (Table 2.13), indicated horned lark density and abundance were positively associated with study site, and negatively associated with woody species and rock cover, as well as Julian date. Conversely, in the second best model (w_i = 0.39, Table 2.13), horned lark occurrence was negatively associated with woody species and rock cover. The model with the lowest Bayesian weight (w_i = 0.17, Table 2.13) demonstrated horned lark occurrence was negatively associated with woody species cover, but positively associated with Julian date. Our top three competing models included woody species cover, so we assessed the relative importance between each of the variables in these models (Burnham and Anderson 2002) (package "MuMIn" in Program R; Bartoń 2015). Although minimal, the relative variable importance of herbaceous cover was 0.43 compared to 0.39 for rock cover, and 0.17 for Julian Date, with Julian date and site receiving equal relative variable importance (1.00). This demonstrated herbaceous cover did not explain much more variation than rock cover. However, due to our top model having a lower BIC than the second candidate model (BIC = 251.57, 251.75, respectively) we continued all analyses with our top ranked model (Herb + Woody + Site; Table 2.13). There was no multicollinearity in this top model as individual VIF scores < 3.0, and the top model demonstrated it fit the data well (χ^2 = 53.34, df = 6, p = < 0.001). The inclusion of site increased model fit and was retained as the final model structure (BIC = 251.57, 264.85, respectively). The top model resulted in negative relationships between horned lark abundance and herbaceous cover (β = -0.08, 95% CI = -0.33, 0.17; Table 2.14) and woody species cover (β = -3.37, 95% CI = -6.73, -0.01; Table 2.14), and a positive relationship between horned lark abundance and site (β = 0.56, 95% CI = -0.12, 1.24; Table 2.14). Alternatively, horned lark occurrence was greater when herbaceous species cover was higher (β = -0.36, 95% CI = -0.80, 0.08; Table 2.14), where the occurrence portion is predicting zeros or true absences. We also found a study site effect (β = -1.00, 95% CI = -1.66, -0.34; Table 2.14). Horned lark absence was positively associated with woody species cover (β = 0.81, 95% CI = -4.27, -5.89; Table 2.14).

White-crowned sparrow

Quadratic forms were considered for several covariates, but we kept the non-quadratic forms for all covariates based on lower BIC values. The NB GLM out-performed the Poisson GLM across all four predictor categories according to BIC and Vuong's test (z = 4.55, p = < 0.001). The variance exceeded the mean (1.85 vs. 1.15), demonstrating slight overdispersion, therefore we retained the NB GLM as our final model type.

Several univariable models demonstrated strong effects on white-crowned sparrow density and occurrence (Table 2.15). The top count model included abiotic, biotic and anthropogenic covariates (BIC = 561.62, Table 2.16). A greater BIC weight of the top model (w_i = 0.62; Table 2.16), demonstrated there was another suitable candidate model within a ΔBIC < 2.0. An examination of the other candidate model (w_i = 0.38; Table 2.16), indicated white-crowned sparrow density was positively associated with distance to road, Engelmann Spruce, height of grass and herbaceous species, and willow cover, but was negatively associated with rock cover and wind. Again we looked at relative variable importance in our top two competing models since both included all of the same covariates except for rock cover. Distance to road, Engelmann Spruce, height of grass and herbaceous species, willow cover, and wind received equal and largest relative variable importance (1.00), whereas rock cover received less importance (0.42). Thus, we continued our analyses with our top ranked model (Distance to

Road + Engelmann Spruce + Grass/Herb Height + Willow + Wind; Table 2.16). Multicollinearity was not apparent in this top model since individual VIF scores < 3.0. The top model had good fit to the data ($\chi^2 = 85.71$, $p = < 0.001$) and overdispersion was not apparent (ɵ = 0.51; Hilbe 2015). Our post hoc analysis demonstrated the top model without site outperformed the model with site (BIC = 561.62, 621.23, respectively), and further analyses for white-crowned sparrow were combined across sites. Our top count model showed white-crowned sparrow density was positively associated with distance to road (β = 0.30, 95% CI = 0.13, 0.47; Table 2.17; Figure 2.9), percentages of Engelmann spruce (β = 0.31, 95% CI = 0.14, 0.47; Table 2.17; Figure 2.10), height of grass and herbaceous species (β = 0.30, 95% CI = 0.13, 0.48; Table 2.17; Figure 2.11), and willow species cover (β = 0.41, 95% CI = 0.25, 0.57; Table 2.17; Figure 2.12); however, it was negatively associated with wind (β = -0.34, 95% CI = -0.55, -0.14; Table 2.17; Figure 2.13).

Assessment of predictive performance

While the top ranked American pipit count model outcompeted all other models, cross-validation indicated that several lower ranked models had lower prediction errors (Table 2.9). Thus, despite the comparatively lower prediction errors of ranked models number 2, 3, and 7 (Table 2.9) the inclusion of more parameters in those models may have increased the predictive power, but reduced model parsimony. Since our top ranked pipit model was more parsimonious than models number 2, 3, and 7, and was not competitive with other candidate models (Table 2.9), this denoted our top ranked model exhibited sufficient model predictive performance. Similarly, the top ranked horned lark count model was competitive with two models. However, cross-validation showed several other models ranked lower with lower prediction errors (Table 2.13). Our top model had the same mean prediction error as several other models (Δ = 0.72,

Table 2.13). Although our top ranked model had fewer predictor covariates than some of the other ranked models, it was competitive with other candidate models (Table 2.13). Since we previously determined herbaceous cover had a greater relative importance than percentage of rock, this further demonstrated our top ranked horned lark model exhibited satisfactory model performance.

The top ranked white-crowned sparrow model also outcompeted other models. Nonetheless, our cross-validation results demonstrated several lower ranking models with lower prediction errors (Table 2.16). Our top model resulted in the fourth lowest prediction error ($\Delta = 5.94$) compared to the seventh, eighth and ninth ranked models, all of which included similar covariates except for rock cover (Table 2.16). This suggested when data were parsed, including an extra covariate in our top model, may have reduced the prediction success for the data that trained particular folds, thus reducing our predictive power. Nonetheless, we retained our top model structure for white-crowned sparrows (Table 2.16).

DISCUSSION

Our results indicate the environmental heterogeneity produced by isolated or combined effects of alpine habitat structural components can influence the abundance and occurrence of American pipit, horned lark, and white-crowned sparrows in these two alpine regions of Colorado. Structure of vegetation and quality of local habitat, have been found to affect and be prominent indicators of abundance and occupancy of avian species (MacArthur et al. 1962). Ecologists face many challenges when trying to identify specific environmental attributes that determine species-habitat relationships, due to species' mobility, different spatial and temporal habitat requirements, and some species being able to occupy a range of areas. Consequently, many patterns and processes (i.e., climate, habitat structure, predation, foraging) can often be operating in conjunction with one another to define these species-habitat relationships (Peterson et al. 1998). Our mean density estimates for each breeding species were similar to density estimates from previous studies for each species (Braun and Giesen 1992; Johnson et al. 2000; Beason et al. 2005; Stanek 2009; Table 2.18), suggesting our top count-based models accurately estimated biologically realistic density estimates for these breeding avifauna. Furthermore, our results indicate a varied response of both density and abundance of selected alpine avifauna to abiotic, biotic, spatial and temporal factors. American pipit and white-crowned sparrows were the most abundant species we sampled in these two alpine areas of Colorado, suggesting if suitable habitat remains, these two species will likely continue to breed across these sampled alpine regions.

Birds undoubtedly have a connection with the structure and function of their surrounding habitat, and the mechanisms shaping avian distribution are complex (Block and Brennan 1993). As temperatures increase, shrubs and trees are expected to encroach into open habitat and there are projected vegetation shifts upward in elevation, where alpine species' distribution are anticipated to change in response to unsuitable habitat (Chamberlain et al. 2013). Specifically, climate modeling scenarios have found with an increase of 3.3°C by 2080, alpine habitat will be reduced and alpine bird distribution is estimated to decrease by 78% (Chamberlain et al. 2013). As a result, alpine species in general may be more at risk due to climate change if suitable habitat is limited (Chamberlain et al. 2016). Understanding current factors influencing existing alpine avifauna is essential in recognizing certain relationships as they change, especially in light of anticipated warming climate trends. In the following sections, we examine and discuss the factors influencing density and occurrence for three of the five breeding alpine birds throughout our two alpine study areas in Colorado.

American Pipit

Biotic and temporal factors influenced American pipit density across Colorado's alpine ecosystem (Table 2.10). However, other factors from our univariable NB GLMs, showed diverse relationships affecting pipit counts differently (Table 2.8). American pipit density was negatively associated with woody species percentage (Table 2.8). The predominant woody species in these two study regions consisted of willow (*Salix*) species, Engelmann spruce (*Picea engelmannii*), and krummholz (both willow and spruce) (Braun 1980, Zeigenfuss 2006). American pipits rely on open, heterogeneous sites dominated by grasses and sedges, and sparse woody and shrub species (Pattie and Verbeek 1966, MacDonald et al. 2013). Our results corroborate past research, and provided insight with how alpine pipit populations may be affected if vegetation structure is altered. Engelmann spruce cover and height increased while willow and overall shrub cover and height decreased from 1971 to 1996 at our Trail Ridge study site (Zeigenfuss 2006). Continued increases in spruce would likely result in lower pipit densities, unless willow was significantly reduced to create more open habitats. However, losses of willow could have negative consequences for other bird species in the alpine, like white-tailed ptarmigan (Hoffman 2006) and potentially other processes (e.g.; snowmelt patterns, soil chemistry; Holtmeier and Broll 1992, Jumpponen et al. 1998). American pipit density is predicted to decrease at our study sites as species of woody shrubs, willow, and Engelmann spruce increase (Table 2.8). Alpine species that rely on these open, grassland habitats, could have decreased distributions and density if vegetation and fauna shift up in elevation, constricting essential habitat necessary for important life cycles (Chamberlain et al. 2013). American pipit density increased with elevation (Table 2.8), suggesting that if climate change causes community shifts, could result in potential competitive interactions with other alpine species that are highly competitive foragers in these same open alpine areas (e.g., horned lark; Kingery 1998).

Our results were contrary to our expectation that American pipit density would be greater when rock cover was less abundant (Table 2.1 and Table 2.8). Although rocks are important protective cover for pipit nests (Verbeek 1970, Hendricks and Norment 1994), a large abundance of rock cover has been found to negatively affect pipit density (e.g., Melendez and Laiolo 2014) and also decrease habitat use by nesting pipits in Wyoming (Hendricks 1987). Although increased rock cover is not an important habitat feature for nesting pipits (MacDonald et al. 2016), abundant rock cover could conceivably be important for pipits to forage on insects and arachnids. Many of the rocky and areas in our study sites appeared to be abundant with spiders, particularly when snow began to dissipate (S. Spear, unpubl. obs.). Arachnids are one of the staple arthropods pipits forage on and provide to nestlings (Hendricks 1987, Frey-Roos et al. 1995). Perhaps selection for higher percentages of rock cover are also important for pipits as a tactic for thermoregulation, as many alpine songbirds have been found to utilize dark, rocky areas during colder temperatures to increase and regulate their body temperature (Martin 2001a). Conceivably, abundant rock could allow American pipits to be less conspicuous to aerial avian predators (e.g., peregrine falcon, *Falco peregrinus*; Northern harrier, *Circus cyaneus*) that frequent these alpine areas.

Pipit density decreased as temperature (◦F) increased, however, temperature exhibited a weak effect (β = -0.08, 95% CI = -0.17, 0.02). Although temperature did not affect pipit abundance within our two-year study, temperature data from snowpack telemetry (SNOTEL) sites (Mt. Evans: Echo Lake, site 936; RMNP: Lake Irene, site 565) demonstrated 2015 was warmer compared to 2014 (1.97◦F and 2.27◦F, respectively, 2014: June-10 – Jul-12; 2015: June-

15 – July-07). While the effect of temperature was weak, we are uncertain how projected increasing temps in Colorado (Lukas et al. 2014) might affect pipits.

All covariates within our top count model had a strong effect (Table 2.10). While pipit density decreased greatly with increasing cover of woody species (β = -0.72, 95% CI = -0.93, -0.53; Figure 2.4), cover of ericaceous shrub species (primarily *Vaccinium caespitosum*, S. Spear, unpubl. obs.) also had negative effects (β = -0.19, 95% CI = -0.34, -0.06; Figure 2.5). However, dwarf shrubs such as *Vaccinium vitisideae, V. uva-ursi, and V. myrtillus* have been shown to reduce prey (e.g., insects) availability and increase search times for alpine water pipit (Brodmann et al. 1997). This study provides one plausible explanation for the negative relationship between ericaceous shrubs and American pipit density in our alpine study sites. Surprisingly, our calculated IRRs illustrated American pipit density will decrease by 40% for each 10% increase of woody species (Table 2.10, Figure 2.4). We also found for every 10% increase of ericaceous shrub species and Engelmann spruce, pipit density would decrease by ~9% and ~7%, respectively (Table 2.10, Figure 2.5 and Figure 2.6).

Distance sampling requires that the assumption of population closure is met (Cassey 1999). Our top pipit model found that density increased with Julian date (range: 161-193). It is likely that changes in breeding phenology stages (Kingery 1998) and activity of birds resulted in increased pipit detections and predicted abundance over time. During the breeding season, there is considerable overlap of American pipit courtship (Julian date range: 170-188), occupied pipit nests by adults (Julian date range: 173-202), and pipits feeding nestlings (Julian date range: 171-225; Figure 2.7; Kingery 1998). It is possible more pipits were detected later in the season due to adults actively feeding nestlings. Furthermore, it is important to note that American pipit density increased from 2014 to 2015 (Figure 2.8, Table 2.10). This may be related to interannual variation in climate or other processes not tied to breeding grounds, but could also be linked to mechanistic changes in habitat or food-supply, which we did not track.

Horned lark

Biotic and spatial predictors influenced overall density and occurrence of horned lark in these alpine regions in Colorado (Table 2.14). However, covariates appeared to explain more about occurrence than abundance within the ZIP models based on confidence intervals (Table 2.11). Our results supported our expectation that horned lark density and occurrence would be positively correlated with abundant grasses (Table 2.1 and Table 2.12). Grass is important for horned lark nest construction and protection, and for forage opportunities (e.g., seed heads and insects; Verbeek 1967).

Our results matched our expectations and other research that horned larks are using areas with less snow cover (Table 2.11 and Table 2.12). Previous studies have found horned larks in the alpine occurred more regularly (e.g., 94.5% of the time) in snow-free and drier sites; however, use of sites with snow occurred later in the afternoon by horned larks who were taking advantage of wind-blown insects from lower elevations onto snowfields (Norvell and Creighton 1990). Our results show that for every 10% increase in snow cover, horned lark true absence will increase by 60%, indicating they will only tolerate up to a certain percentage of snow cover (Table 2.11). If annual precipitation and climate trends continue to vary in these two alpine regions, ultimately minimizing snow cover, horned larks may benefit in these alpine regions. On the contrary, because our surveys were conducted between 0700 and 1300 hr (Mountain Standard Time), based on findings by Norvell and Creighton (1990) it is possible horned lark abundance and occurrence would have been greater during the mid- to late afternoon in our study sites, warranting further research to see if there is a temporal component with regard to importance of snowfields for horned larks in these alpine regions.

Our results showed an interesting relationship between horned larks and distance to road (Table 2.12). Horned larks were using roads and in greater abundance at closer proximity to roads. It is possible habitat conditions (i.e., access to displaying along open roads; less predators; availability of insects and other forage) may be more favorable for horned larks closer to roads. Thus, as recreational use continues to grow in these two alpine regions, where visitors are often limited to traveling close to the road, future research should incorporate if habitat conditions nearest roads should be conserved for horned larks.

Covariates within our top ZIP GLM had varying and some strong effects (Table 2.14). Both occurrence (β = 0.81, 95% CI = -4.27, 5.89) and abundance (β = -3.37, 95% CI = -6.73, -0.01) of horned larks decreased with woody species cover. Our results demonstrated for every 1% decrease in woody species cover, horned lark abundance decreased by 16% (Table 2.14). Horned lark abundance (β = -0.08, 95% CI = -0.33, 0.17) declined with increased herbaceous cover, whereas occurrence (β = -0.36, 95% CI = -0.80, 0.08) increased with herbaceous cover, consistent with previous research that have found horned larks often select territories and forage sites in open areas that consist of abundant, shorter grass and forbs (Braun 1980, Martin 2001a). Although this top model's weight of evidence was moderately high (w_i = 0.43), there were two other candidate models to compare this top model to (Table 2.13). Percentage of woody species was prevalent throughout the candidate models, with percentage of rock as well as Julian date present in ranked models 2 and 3, respectively. These other top candidate models indicated abiotic, biotic, spatial and temporal predictor categories affected both the count-based and occurrence portions of the zero-inflated models. For our top ranked zero-inflated model, we could not gain adequate representation of effects of percentage of herbaceous and woody species on horned larks at each study site, since there were vastly different total detections between Mt. Evans and Rocky Mountain National Park (Table 2.3, Table 2.4).

White-crowned sparrow

Abiotic, biotic and anthropogenic predictors shaped density of white-crowned sparrows at these two alpine sites in Colorado (Table 2.17). Similar to American pipit, elevation strongly affected white-crowned sparrow density (β = -0.45, 95% CI = -0.66, -0.23, Table 2.15). However, white-crowned sparrow density had a negative relationship with elevation. The IRR we calculated for white-crowned sparrow density in response to elevation demonstrated that for every 10-m increase in elevation, white-crowned sparrow density would decrease by ~1% (Table 2.15), nearly the inverse rate we found American pipit (Table 2.8). While these species do co-occur, it is unlikely one species competes for resources due to a lack of niche overlap. Other species such as dark-eyed Juncos (*Junco hyemalis*) have territories that coincide with white-crowned sparrows, where they will actively chase juncos to remove them from these habitats (Chilton et al. 1995). With higher densities of white-crowned sparrows at lower elevations (Table 2.15), they could displace species like juncos that have a specific niche envelope at these lower elevations. Samples sizes for juncos from our surveys were low (n = 14) throughout 2014 and 2015, however we detected them from 3,193 to 3,741m; white-crowned sparrows detections ranged from 3,155 to 4,094m.

Results from our top NB GLM supported our expectation that white-crowned sparrows would be positively associated with small trees and shrubs (Table 2.1 and Table 2.17, Figure 2.10 and Figure 2.12). However, we found percentage of bare ground and litter, grass species (Table 2.15), and ericaceous shrubs (e.g., *Vaccinium caespitosum*) to negatively affect white-crowned sparrow density; however only percentage of ericaceous shrubs lacked a strong effect (β = -0.21, 95% CI = -0.47, 0,04). White-crowned sparrow occurrence is influenced more by the assemblage of bare ground and grasses and shrubs, rather than specific varieties of species for each vegetation type (DeWolfe and DeWolfe 1962). Conceivably, the relationship between white-crowned sparrow density decreasing at higher percentages of bare ground, litter and grass, could be a result of inadequate composition of those habitat elements in our study sites.

Contrary to our predictions, white-crowned sparrow density increased in response to snow cover, although it was a weak effect (β = 0.18, 95% CI = -0.03, 0.40). Water is one of the important habitat requirements for white-crowned sparrows (DeWolfe and DeWolfe 1962), and these birds have been found to consume snow for moisture (Morton 2002, S. Spear, unpubl. obs.), which could partially explain our observed increase in density with snow cover. Although white-crowned sparrows are considered habitat-specialists (Braun 1980), they are known generalist foragers (Morton 1967, Norment and Fuller 1997) and often exploit snow-covered surfaces to capture and forage on insects, similar to other alpine avifauna (Morton 2002). Snowmelt has been occurring earlier in Colorado's mountains over the past 30 years (Clow 2010) despite overall snowpack remaining consistent (Lukas et al. 2014). Advancement of snowmelt anticipated with climate warming could cause white-crowned sparrows to rely further on their generalist abilities for foraging and acquisition of water resources, while compensating for those variable snowpack trends.

We found white-crowned sparrow densities were greatest at moderate distances from roads (β = 0.30, 95% CI = 0.13, 0.47; Table 2.17), specifically between 1,500 and 3,000 m (Figure 2.9) supporting our predictions. Unlike horned larks, white-crowned sparrows may be adversely impacted by the highly traveled roadways.

Following many of our expectations, we found a strong, positive relationship between white-crowned sparrow density and percent of Engelmann spruce and willow (*Salix*) based on our top count model (Table 2.17, Figure 2.10, Figure 2.11). Trees and shrubs in the alpine are important for white-crowned sparrows for breeding and nesting protection (Pattie and Verbeek 1966, Norment 1993) and for establishing breeding territories (Pattie and Verbeek 1966). Mountain white-crowned sparrows can shift nest building from trees to newly leafed-out willows (Morton et al. 1993). Differences of willow are apparent among the two study sites. Notably, declines in willow species abundance by as much as 20% have been found in the alpine regions of Rocky Mountain National Park from 1971 to 1996, which have corresponded to an increase in elk (*Cervus canadensis*) densities (Braun et al. 1991, Zeigenfuss 2006). Elk are not hunted in Rocky Mountain National Park, resulting in exponential increases in elk populations in the park (Zeigenfuss et al. 2011), with roughly 75% of these populations spending summers in the alpine and subalpine and up to 200 individuals wintering in the alpine in RMNP (Zeigenfuss 2006). Hunting is allowed at Mt. Evans, which has allowed elk populations to decline and stay below population objectives of 2,500 individuals (Kraft 2015). Since willow makes up a considerable portion of elk summer and winter diets in the alpine (Hobbs et al. 1982, Zeigenfuss 2006) and if browsing by elk continues to decline willow abundance in alpine areas such as RMNP, white-crowned sparrow density and nesting may be adversely impacted in that region. However, these benefits could be negated if Engelmann spruce cover continues to increase and expands into more alpine areas of the park. Overall, our calculated IRRs (Table 2.17) illustrated for every 10% increase in both Engelmann spruce and willow species, white-crowned sparrow density would increase by 10%.

Offset vs. non-offset models

While including detectability and variation in study area size or survey effort between point count sites has been deemed effective for modeling count response (Buckland et al. 2009, Kery 2010), there is limited knowledge as to the specific differences of how models perform with and without this term. When we compared our top count models with and without the offset post hoc, our results were thought-provoking. Two of the three birds had the same covariates enter their respective top count models with and without the offset; however, differences were evident in strength and direction of covariates (American pipit: Table 2.10 and Table 2.19; horned lark: Table 2.14 and Table 2.20; white-crowned sparrow: Table 2.17 and Table 2.21). Thus, including an offset term is important to increase the capability of directly and accurately modeling these avian species-habitat relationships by accounting for variation with sampling design and predictor covariates.

CONCLUSIONS

Limited knowledge exists regarding high elevation birds and the associations they have with their surrounding mountain habitats, often resulting from restricted access because of terrain and less sampling being conducted in high elevation regions (Boyle and Martin 2015). Our models documented specific fine-scale factors influencing three of the five alpine avian breeding species' populations in these two alpine areas of Colorado. Globally there is already clear evidence of avian species exhibiting range shifts from lower elevations and reduced abundance in relation to climate change, however further research on more fine-scaled species-habitat associations, such as ours, are necessary to understand how alpine breeding avian species will respond across various climate-change scenarios (La Sorte and Jetz 2010).

Our separation of predictor covariates into four predictor categories allowed us to analyze which predictor category influenced these bird species the most. Abiotic and biotic factors interact to determine habitat and use of habitat for many of these species, as has been shown for species in other habitats (Martin 2001b). Thus, these factors should not be assessed independently in order to truly understand the relationships breeding avian species have with their surrounding environment in these alpine regions of Colorado, and that anthropogenic, spatial, and temporal components should be incorporated given the differences in site characteristics and temporal variability each site exhibited throughout this sampling timeframe.

While abiotic factors such as temperature exhibited weak effects on these three birds' abundance and occurrence, temperature variability was evident within the sampling period within the two years of our study. Further, long-term studies at this fine scale would help to discern if projected increases in temperature will cause a mismatch between tolerable and suitable climate and habitat conditions for any of these alpine avian species. Climate change can affect many important biological processes such as altering the synchrony between breeding times and peak food availability (Visser and Both 2005). Assessment of availability or prevalence of forage and prey are important aspects to consider in future research to determine if these alpine avian species are able to remain stable in viable habitats. Moreover, as we continue to lay this groundwork, we can adapt our focus and management based on the complexity of the alpine ecosystem, mechanisms behind avian populations, and projected climate change.

LITERATURE CITED

Aldridge, C. L., S. E. Hanser, S. E. Nielsen, M. Leu, D. J. Saher, and S. T. Knick. 2011. Detectability adjusted count models of songbird abundance. Pp 141-220 in Hanser, S.E., M. Leu,S.T. Knick, and C.L. Aldridge (Eds). Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Allen Press, Lawrence, KS.

Arnold, T.W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criteria. Journal of Wildlife Management 74:1175-1178.

Bartoń, K. 2015. Package 'MuMIn'.[online] CRAN: https://cran.r-project.org/web/packages/ MuMIn/MuMIn.pdf [May 2, 2016].

Beason, J., R. Levad, and T. Leukering. 2005. Monitoring Colorado's birds: the 2004 field season report. Unpublished report on file at the San Juan Public Lands Center, Durango, CO. 60 pp.

Beers, T.W., P.E. Dress, and L.C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64: 691-692.

Beniston, M., and D.G. Fox. 1996. Impacts of climate change on mountain regions. In Climate-Change 1995, impacts, adaptations and mitigations of climate change: Scientific-technical analysis. Intergovernmental Panel of Climate Change (IPCC), edited by R.T. Watson, M.C. Zinyowera, and R.H. Moss. Cambridge University Press, Cambridge.

Bibby, C., M. Jones, and S. Marsden. 1998. Expedition Field Techniques. Bird Surveys. Expedition Advisory Centre, Royal Geographical Society, London.

Block, W.M., and L.A. Brennan. 1993. The habitat concept in ornithology. Current Ornithology 11: 35-91.

Bowman, W. D., and T.R. Seastedt [Eds]. 2001. Structure and Function of an Alpine Ecosystem – Niwot Ridge, Colorado. Oxford University Press, Inc. New York, New York, USA.

Boyle, W.A., and K. Martin. 2015. The conservation value of high elevation habitats to North American migrant birds. Biological Conservation 192:461-476.

Braun, C. E. 1971. Habitat requirements of Colorado white-tailed ptarmigan. Proceedings of the Western Association of State Game and Fish Commissioners. Pp. 284-292.

Braun, C.E. 1980. Alpine Bird Communities of Western North America: Implications for Management and Research. In Workshop Proceedings: Management of Western Forests and Grasslands for Nongame Birds (R. M. Deraff, technical coordinator). USDA Forest Service General Technical Report. INT-86. Pp. 280-291.

Braun, C.E., D.R. Stevens, K.M. Giesen, and C.P. Melcher. 1991. Elk, white-tailed ptarmigan and willow relationships – A management dilemma in Rocky Mountain National Park: Transactions of the 56th North American Wildlife and Natural Resources Conference. Pp. 74-84.

Braun, C.E., and K.M. Giesen. 1992. Population dynamics of white-tailed ptarmigan. Wildlife Research Report, April 1992, Part 1. Colorado Division of Wildlife, Fort Collins, CO, USA.

Braun, C. E., K. Martin, and L.A. Robb. 1993. White-tailed ptarmigan (Lagopus leucurus). In A. Poole, & F. Gill (Eds.), The birds of North America, Number 68. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Brodmann, P.A., H-U Reyer, K. Bollmann, A.R. Schläpfer, and C. Rauter. 1997. The importance of food quantity and quality for reproductive performance in alpine water pipits (Anthus sp. spinoletta). Oecologia 109:200-208.

Brown, J.H. 2001. Mammals on mountainsides: elevational patterns of biodiversity. Global Ecology & Biogeography 10:101-109.

Brunetti, M., G. Lentini, M. Maugeri, T. Nanni, I. Auer, R. Böhm, and W. Schöener. 2009. Climate variability and change in the Greater Alpine Region over the last two centuries based on multi-variable analysis. International Journal of Climatology 29:2197-2225.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, New York, USA.

Buckland, S.T., R.E. Russell, B.G. Dickson, V.A. Saab, D.N. Gorman, & W.M. Block. 2009. Analyzing designed experiments in distance sampling. Journal of Agricultural,Biological, and Environmental Statistics 14:432-442.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Edition. Springer-Verlag, New York, NY.

Cassey, P. 1999. Estimating animal abundance by distancing sampling techniques. Conservation Advisory Science Noies No. 237, Department of Conservation, Wellington.

Chamberlain, D.E., M. Negro, E. Caprio, and A. Rolando. 2013. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biological Conservation 167:127-135.

Chamberlain, D.E., M. Brambilla, E. Caprio, P. Pedrini, and A. Rolando. 2016. Alpine bird distributions along elevational gradients: the consistency of climate and habitat effects across geographic regions. Oecologia 181: 1139 - 1150.

Chapin, F.S., and C. Körner. 1996. Arctic and Alpine Biodiversity: Its Patterns, Causes and Ecosystem Consequences. In Functional Roles of Biodiversity: A Global Perspective (H.A. Mooney, J.H. Cushman, E. Medine, O.E. Sala, and E.-D. Schulze, Eds). John Wiley & Sons Ltd. Pages 7-32.

Chernov, Y.I. 1995. Diversity of the arctic terrestrial fauna. In Chapin, F.S., III and C. Körner [Eds]. Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Springer, Berlin, Germany. Pages 81-95.

Chilton, G., M.C. Baker, C.D. Barrentine, and M.A. Cuningham. 1995. White-crowned Sparrow. In The birds of North America, no. 183 (A. Poole and F. Gills, Eds). Academy of Natural Science, Philadelphia, and American Ornithological Union, Washington, D.C.

Choate, T.S. 1963. Habitat and population dynamics of white-tailed ptarmigan in Montana. Journal of Wildlife Management 27:684-699.

Clarke, J.A., and R.E. Johnson. 1992. The influence of spring snow depth on white-tailed ptarmigan breeding success in the Sierra Nevada. Condor 94:622-627.

Clow, D.W. 2010. Changes in the Timing of Snowmelt and Streamflow in Colorado: A Response to Recent Warming. Journal of Climate 23:2293-2306.

Coxe, S., S.G. West, and L.S. Aiken. 2009. The Analysis of Count Data: A Gentle Introduction to Poisson Regression and Its Alternatives. Journal of Personality Assessment 91:121-136.

Davison, A.C., and D.V. Hinkley. 1997. Bootstrap methods and their application. Cambridge University Press, Cambridge.

DeWolfe, B.B., and R.H. DeWolfe. 1962. Mountain White-crowned Sparrows in California. Condor 64.

Dirnböck, T., F. Essl, and W. Babitsch. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biology 17:990-996.

EEA (European Environment Agency). 2010. Europe’s Ecological Backbone: Recognising the True Value of our Mountains. EEA Report 6/2010. Copenhagen.

Efron, B., and R.J. Tibshirani. 1993. An Introduction to the Bootstrap. Chapman & Hall, New York.

Essl, F., M. Staudinger, O. Stöhr, L. Schratt-Ehrendorfer, W. Rabitsch, and H. Niklfeld. 2009. Distribution patterns, range size and niche breadth of Austrian endemic plants. Biological Conservation 142:2547-2558.

Evans, D. M., S. M. Redpath, S. A. Evans, D. A. Elston, and P. Dennis. 2005. Livestock grazing effects the egg size of an insectivorous passerine. Biology Letters 1:322-325.

Foppen, R., and R. Reijnen. 1994. The effects of car traffic on breeding bird populations in woodland. II. Breeding dispersal of male willow warblers (Phylloscopus trochilus) in relation to proximity of a highway. Journal of Applied Ecology 31:95-101.

Frey-Roos, F., P.A. Brodmann, and H.-U. Reyer. 1995. Relationships between food resources, foraging patterns, and reproductive success in the water pipit, Anthus sp. spinoletta. Behavioral Ecology 6(3): 287 - 295.

Fuller, R.J. 2001. Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. Forestry 74:289-298.

Grabherr, G., M. Gottfried, A. Gruber, and H. Pauli. 1995. Patterns and current changes in alpine plant diversity. In Chapin, F.S., III and Körner, C. [Eds.]: Artic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Springer, Berlin, Pp. 167 – 181.

Greenland, D., and M. Losleben. 2001. Climate. In Bowman, W.D., and T.R. Seastedt [Eds]. 2001. Structure and Function of an Alpine Ecosystem – Niwot Ridge, Colorado. Oxford University Press, Inc. New York, New York, USA.

Hendricks, P. 1987. Habitat Use by Nesting Water Pipits (Anthus spinoletta): A Test of the Snowfield Hypothesis. Arctic and Alpine Research 19:313-320.

Hendricks, P., and C.J. Norment. 1994. Hatchability of American Pipit eggs in the Beartooth Mountains, Wyoming. Wilson Bulletin 106:392-399.

Hilbe, J.M. 2011. Negative binomial Regression. Cambridge, UK: Cambridge University Press.

Hilbe, J.M. 2015. Modeling Count Data. New York: Cambridge University Press

Hobbs, N.T., D. Baker, J.E. Ellis, and D.M. Swift. 1982. Composition and quality of elk summer diets in Colorado. Journal of Wildlife Management 46:694-703.

Hoffman, R.W. 2006. White-tailed Ptarmigan (Lagopus leucura): A Technical Conservation Assessment. Prepared for the USDA Forest, Rocky Mountain Region, Species Conservation Project, Pp. 1- 72.

Holtmeier, F., and G. Broll. 1992. The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra eco-tone on Niwot Ridge, Colorado Front Range, U.S.A. Arctic and Alpine Research 24: 216 - 228.

Hosmer, J., D.W., & S. Lemeshow. 1989. Applied Logistic Regression. New York, NY: John Wiley & Sons.

Johnson, R.E., P. Hendricks, D.L. Pattie, and K.B. Hunter. 2000. Brown-capped Rosy-Finch (Leucosticte australis), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology.

Jumpponen, A., K. Mattson, J.M. Trappe, and R. Ohtonen. 1998. Effects of established willows on primary succession on Lyman Glcier forefront, north Cascade Range, Wasnginton, U.S.A.: evidence of simultaneous canopy inhibition and soil facilitation. Arctic and Alpine Research 30: 31 - 39.

Kery, M. 2010. Introduction to WINBUGS for Ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Burlington, MA: Academic Press.

Kingery, H.E.E. 1998. Colorado Breeding Bird Atlas. Colorado Springs, CO: Colorado Bird Atlas Partnership; Copublished by Colorado Division of Wildlife.

Körner, C., and W. Larcher. 1988. Plant life in cold climates. In Plants and temperatures, S.P. Long and F.I. Woodward. Cambridge, England: The Company of Biologists.

Körner, C. 1995. Alpine plant diversity: A global survey and functional interpretations. In Chapin, F.S., III and C. Körner [Eds]. Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Springer, Berlin, Germany, Pp. 45 - 62.

Kraft, B. 2015. Mount Evans Elk Herd Management Plan Data Analysis Unit E-39: Game Management Units 39, 391, 46, and 461. Prepared for By Colorado Parks and Wildlife.

Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. Journal of Ecology 90:68-77.

Kullman, L. 2003. Recent reversal of neoglacial climate cooling trend in the Swedish Scandes as evidence by Birch tree-limit rise Global and Planetary Change 36:77-88.

La Sorte, F.A., and W. Jetz. . 2010. Avian distribution under climate change: towards improved projections. The Journal of Experimental Biology 213:862-869.

Lindén, A., and S. Mäntyniemi. 2011. Using the negative binomial distribution to model overdispersion in ecological count data. Ecology 97.

Lukas, J., J. Barsugli, N. Doesken, I. Rangwala, and K. Wolter. 2014. Climate Change in Colorado: A Synthesis to Support Water Resources Mangement and Adaptation. University of Colorado, Boulder: Western Water Assessment, Cooperative Institute for Research in Environmental Sciences (CIRES).

MacArthur, R.H., J.W. MacArthur, and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. The American Naturalist 96: 167 - 174.

MacDonald, E.C., A.F. Camfield, M. Martin, S. Wilson, and K. Martin. 2013. Extended incubation recesses by alpine-breeding Horned Larks: a strategy for dealing with inclement weather? Journal of Field Ornithology 84:58-68.

MacDonald, E.C., A.F. Camfield, M. Martin, S. Wilson, and K. Martin. 2016. Nest-site selection and consequences for nest survival among three sympatric songbirds in an alpine environment. Journal of Ornithology 157: 393 - 405.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle, and C.L. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83.

Marques, F.F., and S.T. Buckland. 2003. Incorporating covariates into standard line transect analyses. Biometrics 59:924-935.

Marques, T.A., L. Thomas, S.G. Fancy, and S.T. Buckland. 2007. Improving estimates of bird density using multiple-covariate distance sampling. Auk 124:1229-1243.

Martin, K., and K.L. Wiebe. 2004. Coping Mechanisms of Alpine and Arctic Breeding Birds: Extreme Weather and Limitations to Reproductive Resilience. Integrative and Comparative Biology 44:177-185.

Martin, K.M. 2001a. Wildlife in Alpine and Sub-alpine Habitats. Pp 285-310 in D.H. Johnson and T.A. O’Neil (Managing Directors). Wildlife-Habitat Relationships.

Martin, T.E. 2001b. Abiotic vs. Biotic Influences on Habitat Selection of Coexisting Species: Climate Change Impacts? . Ecology 82:175-188.

Marty, E., and M. Mossoll-Torres. 2012. Point-count method for estimating rock ptarmigan spring density in the Pyrenean chain. European Journal of Wildlife Research 58:357-363.

Melendez, L., and P. Laiolo. 2014. The role of climate in constraining the elevational range of the Water Pipit Anthus spinoletta in an alpine environment. The International Journal of Avian Science 156:276-287.

Meshinev, T., I. Apostolova, E. Koleva. 2000. Influence of warming on timberline rising: a case study on Pinus peuce Griseb. in Bulgaria Phytocoenologia 30.

Moiseev, P.A., S.G. Shiyatov. 2003. Vegetation dynamics at the treeline ecotone in the Ural highlands, Russia. In Nagy, L., G. Grabherr, C. Kömer, and D. B. A. Thompson [Eds]. Alpine Biodiversity in Europe – A Europe-wide Assessment of Biological Richness and Change Ecological Studies 167:423-435.

Morton, M.L. 1967. Diurnal feeding patterns in White-crowned Sparrows, Zonotrichia leucophrys gambelii. Condor 69:491-512.

Morton, M.L., J. Hortsmann, and J. Osborn. 1972. Reproductive cyle and nesting success of the Mountain White-crowned Sparrow (Zonotrichia leucophrys oriantha) in the central Sierra Nevada. Condor 74: 152-163.

Morton, M. L., K.W. Sockman, and L.E. Peterson. 1993. Nest Predation in the Mountain White-crowned Sparrow. The Condor 95:72-82.

Morton, M. L. 2002. The Mountain White-crowned Sparrow: migration and reproduction at high altitude. Camarillo, CA: Cooper Ornithological Society.

Norment, C. J. 1993. Nest-site characteristics and nest predation in Harris' Sparrows and White-crowned sparrows in the Northwest Territories, Canada. The Auk 110:769-777.

Norment, C.J., and M.E. Fuller. 1997. Breeding-season fugivory by Harris' Sparrows (Zonotrichia querula) and White-crowned Sparrows (Zonotrichia leucophrys) in a low-arctic ecosystem. Canadian Journal of 75:670-679.

Norvell, J.R., and P.D. Creighton 1990. Foraging of Horned Larks and Water Pipits in Alpine Communities. Journal of Field Ornithology 61:434-440.

Olden, J.D., and D.A. Jackson. 2000. Torturing data for the sake of generality: how valid are our regression models? . Ecoscience 7:501-510.

Olden, J.D., D.A. Jackson, and P.R. Peres-Neto. 2002. Predictive models of fish species distributions: a comment on proper validation and chance predictions. Transactions of the American Fisheries Society 131:329-336.

Pattie, D.L., and N.A.M. Verbeek. 1966. Alpine Birds of the Beartooth Mountains. The Condor 68:167-176.

Peterson, G., C.R. Allen, and C.S. Holling. 1998. Ecological Resilience, Biodiversity, and Scale. Ecosystems 1: 6-18.

Potts, J.M., and J. Elith. 2006. Comparing species abundance models Ecological Modeling 199:153-163.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ripley, B. 2010. Package 'boot' [online] CRAN: http://cran.r-project.org/web/packages/boot/index.html [May 9, 2016].

Schmidt, J., R.K. 1998. Behavior of white-tailed ptamrigan during the breeding season. In A.T. Bergerud, & M.W. Gradson (Eds.), Adaptive strategies and population ecology of northern grouse, Volume I: Population Studies (pp. 270-299). University of Minnesota Press, MN, USA.

Siegel, R.B., J. H. Pyle, A. J. Thorne, C. A. Holguin, C. A. Howell, S. Stock, and M. W. Tingley 2014. Vulnerability of birds to climate change in California's Sierra Nevada. Avian Conseration and Ecology 9:7.

Stanek, J.R. Breeding habitat selection by rosy-finches in the San Juan Mountains, Colorado, M.S., Department of Zoology and Physiology, May 2009, University of Wyoming. Laramie, Wyoming.

Sturm, M., C. Racine, and K. Tape. 2001. Climate change – increasing shrub abundance in the Arctic. Nature 411:546-547.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques, and K.P. Burnham 2010. Distance software: design and analysis of distance sampling surveys estimating population size. Journal of Applied Ecology 47:5-14.

Ver Hoef, J. M., and P.L. Boveng. 2007. Quasi-poisson vs. Negative binomial Regression: How Should We Model Overdispersed Count Data? . Ecology 88:2766-2772.

Verbeek, N.A.M. 1967. Breeding Biology and Ecology of the Horned Lark in Alpine Tundra The Wilson Bulletin 79:208-218.

Verbeek, N.A.M. 1970. Breeding Ecology of the Water Pipit. The Auk 87:425-451.

Visser, M.E., and C. Both. 2004. Global climate change leads to mistimed avian reproduction. Advances in Ecological Research 35:89-110.

Visser, M.E., and C. Both. 2005. Review. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society Series B 272:2561-2569.

Walker, M. 1995. Patterns and causes of arctic plan community diversity. In Chapin, F.S., III and C. Körner [Eds]. Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Springer, Berlin, Germany, Pp. 3 – 20.

Wilson, S., and K. Martin. 2005. Songbird use of high-elevation habitat during the fall post-breeding and migratory periods. Ecoscience 12:561-568.

Yaacob, W.F.W., M.A. Lazim, and Y.B. Wah. 2010. A Practical Approach in Modelling Count Data. Proceedings of the Regional Conference on Statistical Sciences (RCSS) June 2010 Pp. 176 – 183.

Zeigenfuss, L.C. 2006. Alpine plant community trends on the elk summer range of Rocky Mountain National Park, Colorado: an analysis of existing data. U.S. Geological Survey, Fort Collins Science Center, Open-file Report 2006-1122, 21 pp.

Zeigenfuss, L., T. Johnson, and Z. Wiebe. 2011. Monitoring plan for vegetation responses to elk management in Rocky Mountain National Park: U.S. Geological Survey Open-File Report 2011-1013, 94 pp.

Zuur, A.F., E.N. Ieno, and C.S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3-14.

Table 2.1 – Predictions posited for first hypothesis that abiotic and biotic factors will be strong effects in defining the occurrence and abundance of five alpine breeding avian species during their breeding seasons. Predictions are based on known attributes determining breeding distribution and factors important to these five breeding alpine avifauna. (+) and (-) indicate positive and negative associations, respectively, of predicted bird species relative to specific attributes at sites within two alpine areas in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP).

Species	**Scientific Name**	**Prediction Number**	**Predictions – Abundance and Occurrence Will Be:**	**References**
American pipit	*Anthus rubescens*	1	(+) with open, heterogeneous sites composed of higher percentages of grasses and forbs (-) with increased rock cover percentage (-) with warmer temperatures	(Pattie & Verbeek 1966; Verbeek 1970; Melendez & Laiolo 2014)
Brown-capped rosy-finch	*Leucosticte australis*	2	(+) with open areas with minimal to no snow cover (+) with higher percentages of grass cover, cliffs and bare ground (+) with higher elevations	(Pattie & Verbeek 1966; Johnson et al. 2000; Stanek 2009)
Horned lark	*Eremophila alpestris*	3	(+) with areas of abundant grasses and exposed rock (-) with higher percentages of snow	(Verbeek 1967; Norvell & Creighton 1990)
White-crowned sparrow	*Zonotrichia leucophrys oriantha*	4	(+) with areas of higher percentage of shrubs/subshrubs, small trees, grass, and bare ground (+) with areas with lower percentages of snow cover	DeWolfe & DeWolfe 1962; Morton, Horstmann & Osborn 1972)
White-tailed ptarmigan	*Lagopus leucura*	5	(+) with higher elevation ranges (+) with higher percentages of rocks, talus, and herbaceous species (+) with lower percentages of snow cover (+) with areas with shorter willow (*Salix)* species	(Choat 1963; Braun 1971; Clarke & Johnson 1992; Braun et al. 1993; Hoffman 2006)

Table 2.2 – Description of predictor covariates, including predictor category and covariate type, in avian point counts conducted during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP).

No.	**Covariate**	**Predictor Category**	**Description**
1	Aspect	Abiotic	Aspect (degrees) measured at point count site
2	Bare/Litter	Biotic	% of bare ground and litter present at point count site
3	Cliff	Abiotic	% of cliffs present at point count site
4	Dead/Down	Biotic	% of dead and downed material present at point count site
5	Distance to Road	Anthropogenic	Distance to road (meters) from point count site
6	Elevation	Abiotic	Elevation (meters) at point count site
7	Engelmann Spruce	Biotic	% of Engelmann spruce (*Picea engelmannii*) present at point count site
8	Ericaceous Shrub	Biotic	% of ericaceous shrubs present at point count site
9	Grass	Biotic	% of grass present at point count site
10	Grass/Herb Height	Biotic	Mean grass and herbaceous height (centimeters) at point count site
11	Herb	Biotic	% of herbaceous species (i.e., forbs) present at point count site
12	Julian Date	Spatial/Temporal	Date point count site was sampled (standard date converted to Julian Date)
13	Krummholz	Biotic	% of krummholz species present at point count site
14	Rock	Abiotic	% of rocks present at point count site
15	Site	Spatial/Temporal	Number that delineated between the 2 study sites (Mt. Evans = 0 or RMNP = 1)
16	Sky	Abiotic	Number associated with particular sky condition at point count site
17	Slope	Abiotic	Slope (degrees) measured at point count site
18	Snow Cover	Abiotic	% of snow cover present at point count site
19	Talus	Abiotic	% of talus present at point count site
20	Temp	Abiotic	Temperature (◦F) measured at point count site
21	Time	Spatial/Temporal	Time point count was initiated at point count site (start time converted to decimal)
22	Total Mean Height	Biotic	Total mean height (meters) of shrubs and small trees present at point count site
23	Total Percent Cover	Biotic	Total % cover of shrubs and small trees present at point count site
24	Willow	Biotic	% of willow (*Salix spp.*) present at point count site
25	Wind	Abiotic	Wind (miles per hour) measured at point count site
26	Woody	Biotic	% of woody species present at point count site
27	Year	Spatial/Temporal	Year point count site was sampled

Table 2.3 - Field survey results for the five breeding avian species during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Survey results shown for each study site for the combined years include the number of point count sites with occurrences (percent), total number of detections of each species, detection distance [meters; mean ($\bar{x}$), standard error (SE)], and total truncated detection distance (m) estimated by program DISTANCE 6.2

Species	**Scientific Name**	**Study Site Both Years**	**Occurrence # sites (%)**	**Total # of Detections**	**Detection Distance By Study Site (m; $\bar{x}$ [SE])**	**Total Truncated Detection Distance (m)**
American pipit	*Anthus rubescens*	Mt. Evans	36 (97)	259	70 (3)	170
		RMNP	28 (90)	238	69 (3)	
		Total	**64 (94)**	**497**		
Brown-capped rosy-finch	*Leucosticte australis*	Mt. Evans	8 (22)	14	62 (100)	150
		RMNP	1 (3)	6	65 (21)	
		Total	**9 (13)**	**20**		
Horned lark	*Eremophila alpestris*	Mt. Evans	4 (11)	5	56 (22)	130
		RMNP	17 (55)	68	53 (6)	
		Total	**21 (31)**	**73**		
White-crowned sparrow	*Zonotrichia leucophrys oriantha*	Mt. Evans	31 (84)	127	69 (4)	220
		RMNP	25 (81)	132	81 (6)	
		Total	**56 (82)**	**259**		
White-tailed ptarmigan	*Lagopus leucura*	Mt. Evans	7 (19)	8	83 (72)	315
		RMNP	8 (26)	8	97 (119)	
		Total	**15 (22)**	**16**		

Table 2.4 – Field survey results for the 5 breeding avian species during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Survey results shown for each study site separated by year include the number of point count sites with occurrences (percent), and total number of detections of each species.

Species	**Scientific Name**	**Year**	**Occurrence # sites (%)**			
			Mt. Evans	**RMNP**	**Total**	**Total # of Detections**
American pipit	*Anthus rubescens*	2014	30 (81)	25 (81)	55 (81)	152
		2015	32 (86)	28 (100)	60 (92)	345
					Total	**497**
Brown-capped rosy-finch	*Leucosticte australis*	2014	7 (19)	1 (3)	8 (12)	11
		2015	3 (8)	2 (7)	5 (8)	9
					Total	**20**
Horned lark	*Eremophila alpestris*	2014	2 (5)	11 (35)	13 (19)	19
		2015	2 (5)	15 (56)	17 (26)	54
					Total	**73**
White-crowned sparrow	*Zonotrichia leucophrys oriantha*	2014	24 (65)	18 (58)	42 (62)	83
		2015	29 (78)	22 (79)	51 (78)	176
					Total	**259**
White-tailed ptarmigan	*Lagopus leucura*	2014	4 (11)	3 (10)	7 (10)	7
		2015	3 (8)	4 (14)	7 (11)	9
					Total	**16**

Table 2.5 – Description of covariates used in determining detection probabilities in program DISTANCE 6.2 for the five breeding bird species: American pipit (*Anthus rubescens*), brown-capped rosy-finch (*Leucosticte australis*), horned lark (*Eremophila alpestris*), white-crowned sparrow (*Zonotrichia leucophrys oriantha*), and white-tailed ptarmigan (*Lagopus leucura*) from point count data collected during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Covariates were chosen based on literature review (see References) describing each species' habitat characteristics.

Species	Scientific Name	Covariate	Predictor Category	References
American pipit	*Anthus rubescens*	Grass	Biotic	Pattie & Verbeek (1966)
		Herb	Biotic	Pattie & Verbeek (1966)
		Woody	Biotic	Melendez & Laiolo (2014)
		Elevation	Abiotic	Verbeek (1970)
		Rock	Abiotic	Melendez & Laiolo (2014)
		Talus	Abiotic	Melendez & Laiolo (2014)
		Temp	Abiotic	Verbeek (1970)
		Wind	Abiotic	Verbeek (1970)
		Distance to Road	Anthropogenic	Foppen & Reijnen (1994)
		Observer	Anthropogenic	----
		Time	Spatial/Temporal	----
Brown-capped rosy-finch	*Leucosticte australis*	Grass	Biotic	Pattie & Verbeek (1966)
		Bare/Litter	Abiotic	Pattie & Verbeek (1966)
		Cliff	Abiotic	Johnson et al. (2000)
		Elevation	Abiotic	Stanek (2009)
		Snow Cover	Abiotic	Johnson et al. (2000)
		Distance to Road	Anthropogenic	Foppen & Reijnen (1994)
		Observer	Anthropogenic	----
		Time	Spatial/Temporal	----

Table 2.5 continued

Species	Scientific Name	Covariate	Predictor Category	References
Horned lark	*Eremophila alpestris*	Grass	Biotic	Verbeek (1967)
		Herb	Biotic	Verbeek (1967)
		Rock	Abiotic	Verbeek (1967)
		Snow Cover	Abiotic	Verbeek (1967); Norvell & Creighton (1990)
		Distance to Road	Anthropogenic	Foppen & Reijnen (1994)
		Observer	Anthropogenic	----
		Time	Spatial/Temporal	----
White-crowned sparrow	*Zonotrichia leucophrys oriantha*	Ericaceous Shrub	Biotic	DeWolfe & DeWolfe (1962)
		Engelmann Spruce	Biotic	DeWolfe & DeWolfe (1962)
		Grass	Biotic	DeWolfe & DeWolfe (1962)
		Krummholz	Biotic	DeWolfe & DeWolfe (1962)
		Willow	Biotic	DeWolfe & DeWolfe (1962)
		Bare/Litter	Abiotic	DeWolfe & DeWolfe (1962)
		Snow Cover	Abiotic	DeWolfe & DeWolfe (1962); Morton, Horstmann, & Osborn (1972)
		Distance to Road	Anthropogenic	Foppen & Reijnen (1994)
		Observer	Anthropogenic	----
		Time	Spatial/Temporal	----

Table 2.5 continued

Species	Scientific Name	Covariate	Predictor Category	References
White-tailed ptarmigan	*Lagopus leucura*	Herb	Biotic	Braun (1971)
		Shrub/Small Tree Total Mean Height	Biotic	Braun (1971); Hoffman (2006)
		Elevation	Abiotic	Braun et al. (1993)
		Rock	Abiotic	Braun (1971); Choate (1963); Hoffman (2006)
		Talus	Abiotic	Braun (1971); Choate (1963); Hoffman (2006)
		Snow Cover	Abiotic	Clarke & Johnson (1992)
		Distance to Road	Anthropogenic	Foppen & Reijnen (1994)
		Observer	Anthropogenic	----
		Time	Spatial/Temporal	----

Table 2.6 - Field survey results for three of the five breeding avian species during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Survey results shown for each study site for the combined years include the number of point count sites with occurrences (percent), total number of detections of each species, and detection distance [meters; mean ($\bar{x}$), standard error (SE)]. Count data was truncated based on total truncated detection distance estimated by program DISTANCE 6.2, and subsequently fit with generalized linear models (GLMs) for each of the 3 bird species.

Species	**Scientific Name**	**Study Site Both Years**	**Occurrence # sites (%)**	**Total # of Detections**	**Detection Distance By Study Site (m; $\bar{x}$ [SE])**	**Total Truncated Detection Distance (m)**
American pipit	*Anthus rubescens*	Mt. Evans	35 (95)	240	70 (3)	170
		RMNP	28 (90)	209	69 (3)	
		Total	**63 (93)**	**449**		
Horned Lark	*Eremophila alpestris*	Mt. Evans	4 (11)	5	56 (22)	130
		RMNP	16 (52)	59	53 (6)	
		Total	**20 (29)**	**64**		
White-crowned sparrow	*Zonotrichia leucophrys oriantha*	Mt. Evans	31 (84)	125	69 (4)	220
		RMNP	24 (77)	110	81 (6)	
		Total	**55 (81)**	**235**		

Table 2.7 - Field survey results for the three of the five breeding avian species during June to July of 2014 and 2015 at sites within two alpine areas in Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Survey results shown for each study site separated by year include the number of point count sites with occurrences (percent), and total number of detections of each species. Count data was truncated based on total truncated detection distance estimated by program DISTANCE 6.2, and subsequently fit with generalized linear models (GLMs) for each of the 3 bird species.

Species	**Scientific Name**		**Occurrence # sites (%)**			
		Year	**Mt. Evans**	**RMNP**	**Total**	**Total # of Detections**
American pipit	*Anthus rubescens*	2014	27 (73)	24 (77)	51 (75)	132
		2015	31 (84)	28 (100)	59 (91)	317
					Total	**449**
Horned Lark	*Eremophila alpestris*	2014	2 (5)	10 (32)	12 (18)	17
		2015	2 (5)	14 (36)	16 (25)	47
					Total	**64**
White-crowned sparrow	*Zonotrichia leucophrys oriantha*	2014	19 (51)	16 (52)	35 (52)	70
		2015	29 (78)	20 (71)	49 (75)	165
					Total	**235**

Table 2.8 – Results of top univariable negative binomial generalized linear models (GLMs) conducted on all covariates within four predictor categories ranked by Bayesian Information Criteria (BIC) within each predictor category, for American pipit (*Anthus rubescens*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Models listed include an offset term for detection calculated from the mean detection probability in program DISTANCE 6.2. Results presented are from standardized data and include predictor categories, covariate model, number of parameters (k), predictor (β) estimates, 95% confidence intervals (CI), log-likelihood (LL), and BIC. We only listed covariate univariable models for parameter estimates where lower and upper confidence intervals did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of American pipit density in response to each covariate and predictor category type.

Category	**Covariate Model**	**k**	**β estimate**	**95% CI**	**IRR**	**LL**	**BIC**
Abiotic	Elevation	3	0.35	(0.24 , 0.47)	1.002	-393.43	802.87
	Rock	3	0.16	(0.04, 0.28)	1.01	-405.60	827.21
Biotic	Woody	3	-0.94	(-1.17, -0.73)	0.95	-353.79	723.60
	Total Percent Cover	3	-0.71	(-0.94, -0.52)	0.96	-376.22	768.46
	Willow	3	-0.48	(-0.64, -0.33)	0.99	-388.11	792.23
	Total Mean Height	3	-0.49	(-0.68, -0.32)	0.73	-390.74	797.49
	Engelmann Spruce	3	-0.36	(-0.51, -0.21)	0.99	-397.43	810.86
	Ericaceous Shrub	3	-0.29	(-0.46, -0.14)	0.99	-401.60	819.22
	Grass	3	0.13	(0.01, 0.26)	1.01	-406.76	829.54
Spatial/Temporal	Year	3	0.22	(0.10, 0.34)	1.60	-403.33	822.68
	Julian Date	3	0.14	(0.01, 0.27)	1.02	-403.64	829.29

Table 2.9 – Results of top ten multivariable negative binomial generalized linear models (GLMs) sorted by ascending Bayesian Information Criteria (BIC), for American pipit (*Anthus rubescens*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP), to compare the estimated prediction error (p_{Err}) produced from the leave-one-out cross-validation test to further confirm model fit and verify top model predictability if applied to new a new data set. Results presented are from unstandardized data with model rank based on ascending BIC, covariate model structure, number of parameters (k), log-likelihood (LL), BIC, change in BIC value from top model (ΔBIC), and Bayesian weight (w_i). Each ranked model includes an offset term (ratio of counts to survey effort), calculated from mean detection probability in program DISTANCE 6.2.

Rank	Covariate Model	k	LL	BIC	ΔBIC	w_i	p_{Err}
1	Woody + Ericaceous Shrub + Engelmann Spruce + Julian Date + Year	7	-328.49	694.35	0.00	1.00	1.60
2	Elevation + Woody + Ericaceous Shrub + Engelmann Spruce + Julian Date + Year	8	-327.42	697.53	3.18	0.00	1.57
3	Wind + Woody + Ericaceous Shrub + Engelmann Spruce + Julian Date + Year	8	-327.48	697.66	3.31	0.00	1.57
4	Woody + Engelmann Spruce + Julian Date + Year	6	-333.22	698.47	4.12	0.00	1.66
5	Wind + Woody + Ericaceous Shrub + Engelmann Spruce + Year	7	-331.15	699.66	5.31	0.00	1.72
6	Woody + Ericaceous Shrub + Engelmann Spruce + Year	6	-334.22	700.47	6.12	0.00	1.84
7	Wind + Elevation + Woody +Ericaceous Shrub + Engelmann Spruce + Julian Date + Year	9	-326.25	700.53	6.18	0.00	1.54
8	Woody + Julian Date + Year	5	-338.40	703.49	9.14	0.00	1.74
9	Wind + Elevation + Woody + Ericaceous Shrub + Engelmann Spruce + Year	8	-330.43	703.56	9.21	0.00	1.72
10	Elevation + Woody + Ericaceous Shrub + Engelmann Spruce + Year	7	-333.77	704.89	10.54	0.00	1.85

Table 2.10 – Results of top multivariable negative binomial generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for American pipit (*Anthus rubescens*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed includes an offset term for detection calculated from mean detection probability in program DISTANCE 6.2, along with covariates: woody species percentage (Woody), ericaceous shrub percentage, Engelmann spruce (*Picea engelmannii*) percentage, Julian date, and year. Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of American pipit density in response to each covariate. Any IRRs not provided were due to not being relevant in this analysis.

Covariate	**β estimate**	**95% CI**	**IRR**
(Intercept)	0.14	(0.03, 0.25)	---
Woody	-0.72	(-0.93, -0.53)	0.96
Ericaceous Shrub	-0.19	(-0.34, -0.06)	0.99
Engelmann Spruce	-0.22	(-0.36, -0.10)	0.99
Julian Date	0.16	(0.07, 0.26)	1.02
Year	0.19	(0.10, 0.29)	1.52

Table 2.11 – Results of top univariable zero-inflated Poisson (ZIP) generalized linear models (GLMs) conducted on all covariates within four predictor categories, sorted by ascending Bayesian Information Criteria (BIC) within each predictor category, for horned lark (*Eremophila alpestris*) data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Models listed include an offset term for detection calculated from mean detection probability in program DISTANCE 6.2. Results presented are from standardized data and include predictor categories, covariate model, number of parameters (k), predictor (β) estimates, 95% confidence intervals (CI), log-likelihood (LL), and BIC. We only listed covariate univariable models for parameter estimates where lower and upper confidence intervals did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of horned lark density and abundance in response to each covariate and predictor category type. Section (A) represents the count portion (abundance) of the zero-inflated Poisson model, while section (B) represents the binomial portion (presence-absence) of the zero-inflated Poisson models.

	Category	**Covariate Model**	**k**	**β estimate**	**95% CI**	**IRR**	**LL**	**BIC**
(A) Abundance								
	Anthropogenic	Distance to Road	2	-0.41	(-0.74, -0.09)	1.00	-126.64	274.66
	Spatial/Temporal	Year	2	0.28	(0.01, 0.56)	1.83	-127.09	275.57
(B) Occurrence								
	Abiotic	Snow Cover	2	0.96	(0.03, 1.88)	1.06	-127.44	276.27
	Abiotic	Rock	2	0.58	(0.02, 1.13)	1.04	-128.31	278.01
	Abiotic	Wind	2	-0.39	(-0.75, -0.03)	0.94	-128.68	278.74
	Biotic	Herb	2	-0.70	(-1.09, -0.32)	0.96	-124.05	269.49
	Biotic	Grass/Herb Height	2	0.63	(0.11, 1.15)	1.24	-126.49	274.37
	Spatial/Temporal	Site	2	-0.99	(-1.63, -0.35)	----	-117.70	256.80
	Spatial/Temporal	Year	2	0.40	(0.02, 0.77)	2.32	-127.09	275.57

Table 2.12 – Results of univariable zero-inflated Poisson (ZIP) generalized linear models (GLMs) conducted on all covariates within four predictor categories, sorted by ascending Bayesian Information Criteria (BIC) within each predictor category, for horned lark (*Eremophila alpestris*) data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Models listed include an offset term for detection calculated from mean detection probability in program DISTANCE 6.2. Results presented are from standardized data and include predictor categories, covariate model, predictor (β) estimates, number of parameters (k), log-likelihood (LL), lower and upper 95% confidence intervals (CI), and BIC. We only listed covariate univariable models to compare against our predictions to determine the response in horned lark abundance and occurrence based on our hypotheses (Table 2.1). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Section (A) represents the count portion (abundance) of the zero-inflated Poisson model, while section (B) represents the binomial portion (presence-absence) of the zero-inflated Poisson models.

	Category	**Covariate Model**	**k**	**β estimate**	**95% CI**	**LL**	**BIC**
(A) Abundance							
	Abiotic	Snow Cover	3	0.05	(-0.67, 0.77)	-127.44	276.27
	Biotic	Grass	3	0.19	(-0.08, 0.46)	-128.03	277.45
	Biotic	Rock	3	0.01	(-0.34, 0.35)	-128.31	278.01
	Anthropogenic	**Distance to Road**	3	-0.41	(-0.74, -0.09)	-126.64	274.66
(B) Occurrence							
	Abiotic	**Snow Cover**	2	0.96	(0.03, 1.88)	-127.44	276.27
	Biotic	Grass	2	-0.33	(-0.70, 0.03)	-128.03	277.45
	Biotic	**Rock**	2	0.58	(0.02, 1.13)	-128.31	278.01
	Anthropogenic	Distance to Road	2	0.08	(-0.36, 0.52)	-126.64	274.66

Table 2.13 – Results of top ten multivariable zero-inflated Poisson (ZIP) generalized linear models (GLMs) sorted by ascending Bayesian Information Criteria (BIC), for horned lark (*Eremophila alpestris*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP), to compare the estimated prediction error (p_{Err}) produced from the leave-one-out cross-validation test to further confirm model fit and verify top model predictability if applied to new a new data set. Results presented are from unstandardized data with model rank based on ascending BIC, covariate model structure, number of parameters (k), log-likelihood (LL), BIC, change in BIC value from top model (ΔBIC), and Bayesian weight (w_i). Each ranked model includes an offset term (ratio of counts to survey effort), calculated from mean detection probability in program DISTANCE 6.2.

Rank	**Covariate Model**	**k**	**LL**	**BIC**	**ΔBIC**	w_i	p_{Err}
1	Herb + Woody + Site	5	-104.40	251.57	0.00	0.43	0.72
2	Rock + Woody + Site	5	-104.49	251.75	0.18	0.39	0.72
3	Woody + Julian Date + Site	5	-105.30	253.39	1.82	0.17	0.76
4	Snow Cover + Woody + Year + Site	6	-101.94	257.35	5.78	0.00	0.79
5	Snow Cover + Rock + Woody + Site	6	-102.03	257.54	5.97	0.00	0.72
6	Snow Cover + Woody + Distance to Road + Site	6	-102.45	258.37	6.80	0.00	0.68
7	Rock + Woody + Year + Site	6	-102.47	258.41	6.84	0.00	0.75
8	Herb + Woody + Distance to Road + Site	6	-102.49	258.45	6.88	0.00	0.64
9	Rock + Woody + Distance to Road + Site	6	-102.56	258.60	7.03	0.00	0.63
10	Herb + Woody + Year + Site	6	-102.61	258.68	7.11	0.00	0.78

Table 2.14 – Results of top multivariable zero-inflated Poisson (ZIP) generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for horned lark (*Eremophila alpestris*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed is results of multivariable analyses with an offset term, along with covariates: herbaceous species percentage (Herb), woody species percentage (Woody), and study site (Site). Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of horned lark density and occurrence in response to each covariate. Any IRRs not provided were due to not being relevant in this analysis. Section (A) represents the count portion (abundance) of the zero-inflated Poisson model, while section (B) represents the binomial portion (presence-absence) of the zero-inflated Poisson models.

	Covariate	**β estimate**	**95% CI**	**IRR**
(A) Abundance	(Intercept)	-2.09	(-3.88, -0.30)	---
	Herb	-0.08	(-0.33, 0.17)	0.99
	Woody	-3.37	(-6.73, -0.01)	0.84
	Site	0.56	(-0.12, 1.24)	3.06
(B) Occurrence	(Intercept)	0.74	(-1.79, 3.26)	---
	Herb	-0.36	(-0.80, 0.08)	0.98
	Woody	0.81	(-4.27, 5.89)	1.04
	Site	-1.00	(-1.66, -0.34)	0.14

Table 2.15 – Results of top univariable negative binomial generalized linear models (GLMs) conducted on all covariates within four predictor categories, sorted by ascending Bayesian Information Criteria (BIC) within each predictor category, for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Models listed include an offset term for detection calculated from mean detection probability in program DISTANCE 6.2. Results presented are from standardized data and include predictor categories, covariate model, number of parameters (k), predictor (β) estimates, 95% confidence intervals (CI), log-likelihood (LL), and BIC. We only listed covariate univariable models for parameter estimates where lower and upper confidence intervals did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of white-crowned sparrow density in response to each covariate and predictor category type.

Category	Covariate Model	k	β estimate	95% CI	IRR	LL	BIC
Abiotic	Elevation	3	-0.45	(-0.66, -0.23)	0.99	-324.71	665.39
	Wind	3	-0.44	(-0.68, -0.21)	0.94	-325.97	667.91
	Rock	3	-0.42	(-0.69, -0.16)	0.97	-327.86	671.68
	Slope	3	-0.24	(-0.49, 0.01)	0.96	-331.05	678.07
	Slope^2	4	-1.31	(-2.46, -0.42)	0.99	-326.54	674.37
	Bare/Litter	3	-0.21	(-0.43, 0.00)	0.99	-331.06	678.08
Biotic	Willow	3	0.53	(0.36, 0.70)	1.02	-316.32	648.61
	Woody	3	0.52	(0.35, 0.71)	1.03	-316.70	649.36
	Total Percent Cover	3	0.51	(0.32, 0.72)	1.03	-318.88	653.73
	Grass/Herb Height	3	0.43	(0.24, 0.64)	1.16	-323.76	663.49
	Total Mean Height	3	0.43	(0.21, 0.66)	1.32	-325.79	667.54
	Grass	3	-0.32	(-0.54, 0.10)	0.98	-328.81	673.58
	Engelmann Spruce	3	0.29	(0.09, 0.50)	1.01	-328.89	673.74
	Herb	3	-0.25	(-0.46, -0.04)	0.99	-330.28	676.53
Anthropogenic	Distance to Road	3	0.46	(0.25, 0.69)	1.00	-323.59	663.16
Spatial/Temporal	Year	3	0.28	(0.08, 0.49)	1.03	-329.47	674.91
	Julian Date	3	0.23	(0.01, 0.45)	1.85	-330.74	677.44

Table 2.16 – Results of top ten multivariable negative binomial generalized linear models (GLMs) sorted by ascending Bayesian Information Criteria (BIC), for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP), to compare the estimated prediction error (p_{Err}) produced from the leave-one-out cross-validation test to further confirm model fit and verify top model predictability if applied to new a new data set. Results presented are from unstandardized data with model rank based on ascending BIC, covariate model structure, number of parameters (k), log-likelihood (LL), BIC, change in BIC value from top model (ΔBIC), and Bayesian weight (w_i). Each ranked model includes an offset term (ratio of counts to survey effort), calculated from mean detection probability in program DISTANCE 6.2.

Rank	**Covariate Model**	**k**	**LL**	**BIC**	**ΔBIC**	w_i	p_{Err}
1	Distance to Road + Engelmann Spruce + Grass/Herb Height + Willow + Wind	7	-262.18	561.62	0.00	0.62	5.94
2	Distance to Road + Engelmann Spruce + Grass/Herb Height + Rock + Willow + Wind	8	-259.99	562.60	0.98	0.38	6.51
3	Distance to Road + Grass + Grass/Herb Height + Willow + Wind	7	-260.58	563.70	2.12	0.00	7.97
4	Distance to Road + Grass + Grass/Herb Height + Rock + Willow + Wind	8	-260.58	563.70	2.13	0.00	9.20
5	Distance to Road + Engelmann Spruce + Grass + Grass/Herb Height + Rock + Willow + Wind	9	-258.23	564.40	2.75	0.00	7.00
6	Distance to Road + Grass/Herb Height + Rock + Willow + Wind	7	-263.75	564.80	3.14	0.00	8.76
7	Engelmann Spruce + Grass/Herb Height + Willow + Wind	6	-266.44	564.80	3.20	0.00	4.40
8	Distance to Road + Engelmann Spruce + Willow + Wind	6	-266.54	565.00	3.39	0.00	4.55
9	Engelmann Spruce + Grass/Herb Height + Rock + Willow + Wind	7	-263.92	565.10	3.48	0.00	5.06
10	Engelmann Spruce + Grass + Grass/Herb Height + Rock + Willow + Wind	8	-261.59	565.80	4.15	0.00	6.37

Table 2.17 - Results of top multivariable negative binomial generalized linear models (GLMs) based on lowest Bayesian Information Criteria (BIC), for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed includes an offset term, calculated from mean detection probability in program DISTANCE 6.2, along with covariates: distance to road (m), Engelmann spruce (*Picea engelmannii*) percentage, Julian date, and year. Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Incidence Rate Ratios (IRRs), calculated from unstandardized data, are also provided in order to determine the rate of white-crowned sparrow density in response to each covariate. Any IRRs not provided were due to not being relevant in this analysis.

Covariate	**β estimate**	**95% CI**	**IRR**
(Intercept)	-0.90	(-1.00, -0.62)	---
Distance to Road	0.30	(0.13, 0.47)	1.00
Engelmann Spruce	0.31	(0.14, 0.47)	1.01
Grass/Herb Height	0.30	(0.13, 0.48)	1.11
Willow	0.41	(0.25, 0.57)	1.01
Wind	-0.34	(-0.55, -0.14)	0.95

Table 2.18 – Comparisons of our estimated density estimates, calculated in program DISTANCE 6.2, from count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP), for the five known alpine breeding avian species in Colorado's alpine, with density estimates from previous research. Results presented include estimated density {birds/hectare (ha)}, 95% confidence intervals (CI), and researched density {birds/hectare (ha)} with their associated references for each avian species.

Species	**Scientific Name**	**Estimated Density (birds/ha) (95% CI)**	**Researched Density (birds/ha) (95% CI)**	**References**
American pipit	*Anthus rubescens*	1.50 (1.29, 1.74)	1.16 (0.89, 1.51)	(Beason, Levad, and Leukering 2005)
Brown-capped rosy-finch	*Leucosticte australis*	0.06 (0.002, 1.47)	0.10 (0.05, 0.19)	(Beason, Levad, and Leukering 2005)
			1.91 (1.36, 2.80)	(Stanek 2009)
Horned lark	*Eremophila alpestris*	0.16 (0.09, 0.29)	0.26 (0.16, 0.44)	(Beason, Levad, and Leukering 2005)
White-crowned sparrow	*Zonotrichia leucophrys oriantha*	0.62 (0.47, 0.81)	1.10 (0.77, 1.56)	(Beason, Levad, and Leukering 2005)
White-tailed ptarmigan	*Lagopus leucura*	0.02 (0.002, 0.23)	0.02 - 0.14 Mt. Evans = 0.06 RMNP = 0.09	(Braun, Martin, and Robb 1993) (Braun and Giesen 1992)

Table 2.19 - Results of top multivariable negative binomial generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for American pipit (*Anthus rubescens*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed is results of multivariable analyses without an offset term, along with covariates: woody species percentage (Woody), ericaceous shrub percentage, Engelmann spruce (*Picea engelmannii*) percentage, Julian date, and year. Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero.

Covariate	**β estimate**	**95% CI**
(Intercept)	0.61	(0.49, 0.72)
Woody	-0.56	(-0.77, -0.38)
Ericaceous Shrub	-0.10	(-0.25, 0.02)
Engelmann Spruce	-0.20	(-0.34, -0.07)
Julian Date	0.17	(0.08, 0.27)
Year	0.03	(-0.06, 0.13)

Table 2.20 - Results of top multivariable zero-inflated (ZIP) generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for horned lark (*Eremophila alpestris*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed is results of multivariable analyses without an offset term and herbaceous species percentage (Herb), woody species percentage (Woody), and study site (Site). Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero. Section (A) represents the count portion (abundance) of the zero-inflated Poisson model, while section (B) represents the binomial portion (presence-absence) of the zero-inflated Poisson models.

	Covariate	**β estimate**	**95% CI**
(A) Abundance	(Intercept)	-2.35	(-4.28, -0.42)
	Herb	0.05	(-0.25, 0.35)
	Woody	-3.90	(-6.49, -1.32)
	Site	0.66	(-0.57, 1.90)
(B) Occurrence	(Intercept)	-1.73	(-12.60, 9.15)
	Herb	-0.47	(-1.23, 0.29)
	Woody	-4.79	(-25.25, 15.68)
	Site	-1.01	(-2.56, 0.55)

Table 2.21 – Results of top multivariable negative binomial generalized linear model (GLM) based on lowest Bayesian Information Criteria (BIC), for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) count data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). The top model listed are results of multivariable analyses without an offset term and demonstrates results of different covariates such as distance to road (m), percentage of Engelmann spruce (*Picea engelmannii*), rock, willow, and wind (mph), and study site (Site), compared to the top model with an offset term (Table 2.19). Comparisons depict different covariate results when an offset is (Table 2.19) and is not applied. Results presented are from standardized data and include predictor covariates, predictor (β) estimates, and 95% confidence intervals (CI). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero.

Covariate	**β estimate**	**95% CI**
(Intercept)	-0.11	(-0.28, 0.05)
Distance to Road	0.20	(0.07, 0.33)
Engelmann Spruce	0.28	(0.13, 0.42)
Rock	-0.25	(-0.48, -0.04)
Willow	0.32	(0.20, 0.45)
Wind	-0.31	(-0.49, -0.13)
Site	-0.25	(-0.42, -0.08)

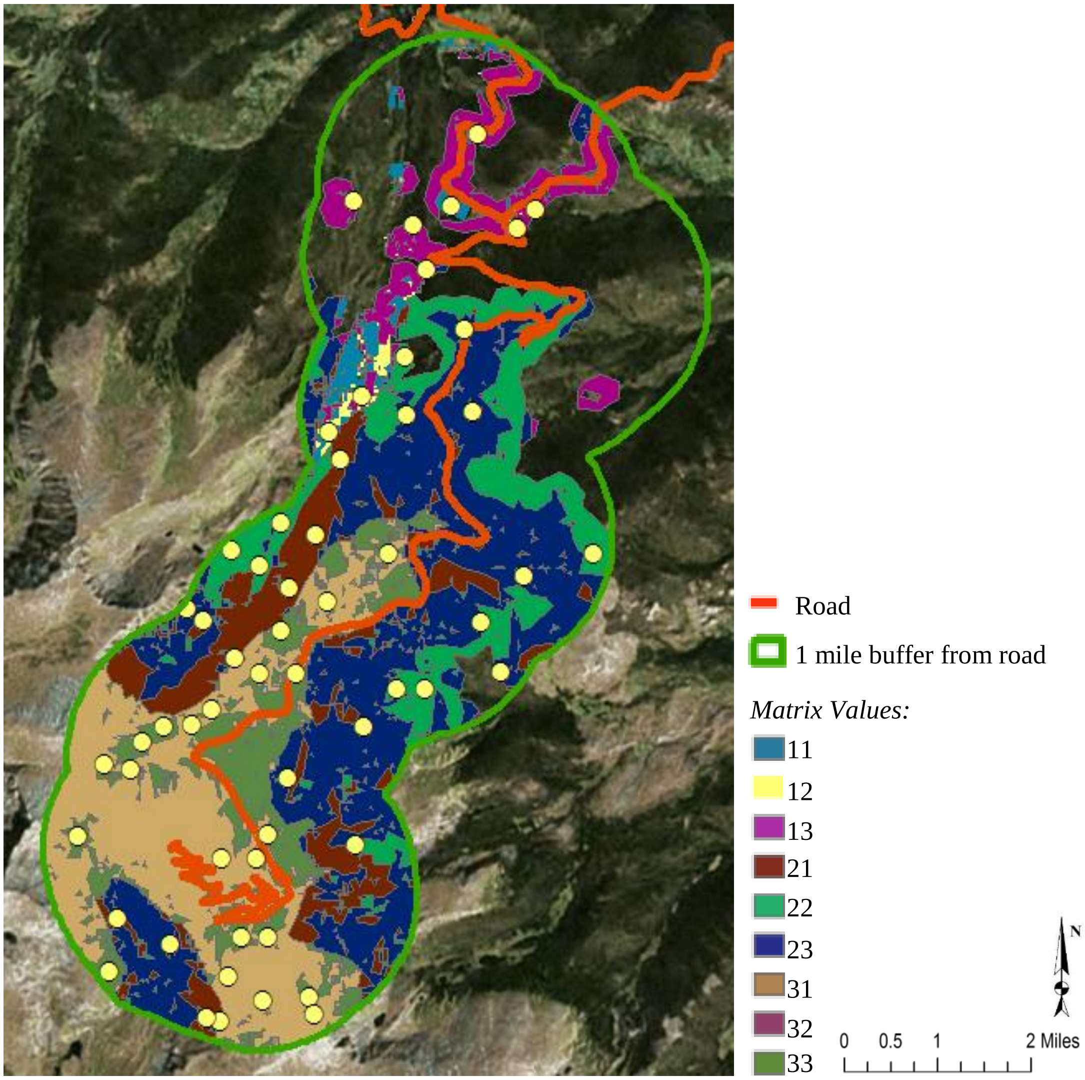


Figure 2.1 – Location of 57 random points for the point count sampling conducted at Mt. Evans in Clear Creek County, Colorado during June to July in 2014 and 2015. Points were randomly generated within each stratum at a distance of 300 m a part. Each stratum was based on low, medium, and high elevation and shrub cover, and defined by various colors and values in matrix scale on right. Matrix Values were estimated from stratified elevation by designating three equal bins beginning at forest edge from low (bin = 10; e.g., Mt. Evans = 2,870 – 3361 m), medium (bin = 20; e.g., Mt. Evans = 3,362 – 3,853 m), and high (bin = 30; e.g., Mt. Evans = 3,854 – 4,345 m) elevations. Land cover data was derived from all Existing Vegetation Types (EVT) found within Landfire, version LF 2010. Stratified elevation was combined with low (1), medium (2), and high (3) shrub and subshrub EVT data, resulting in final Matrix Values. Due to various restrictions, only 37 of the 57 points were accessible.

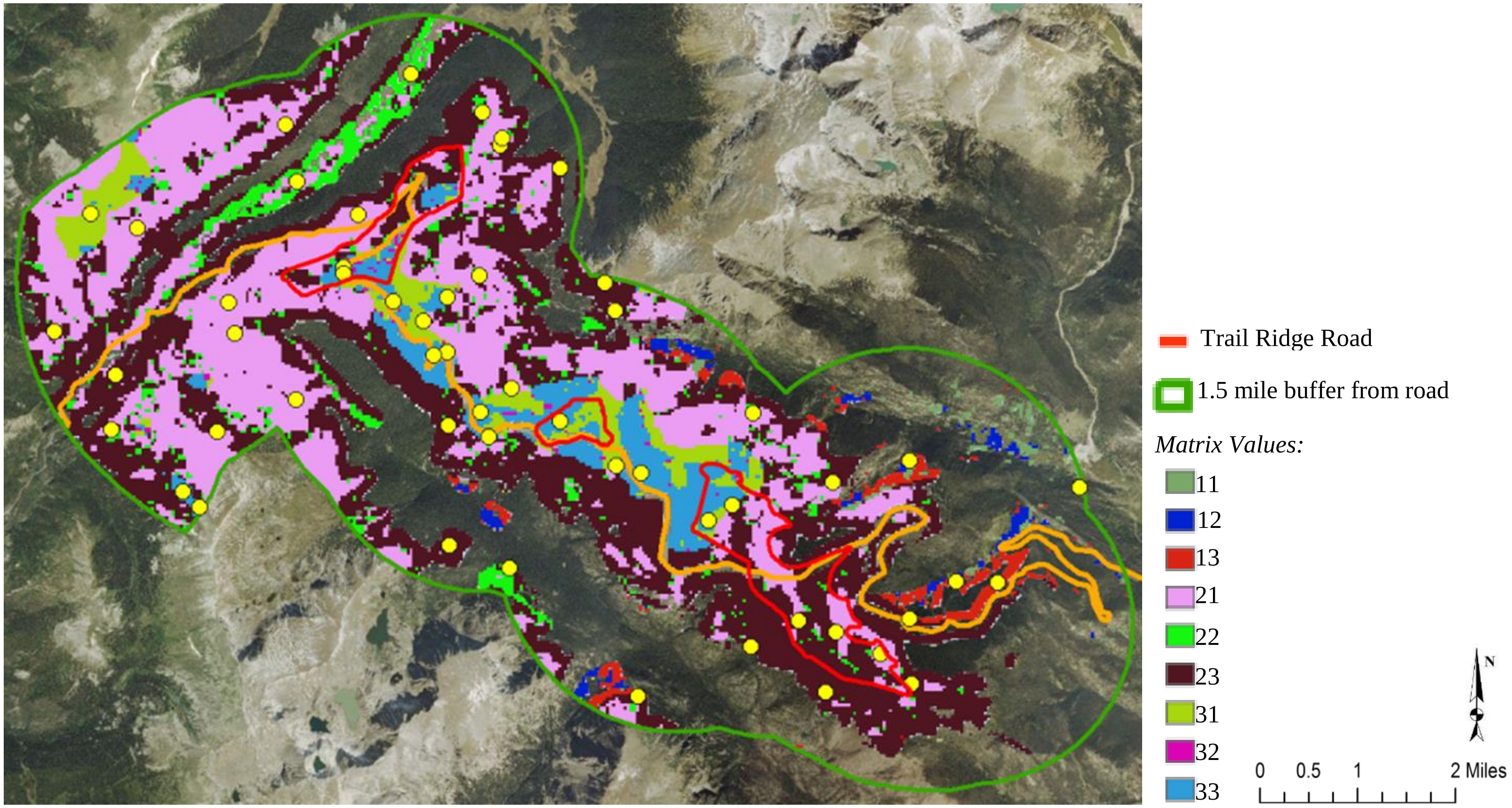


Figure 2.2 – Location of 54 random points for the point count sampling conducted at Trail Ridge Road located in Rocky Mountain National Park (RMNP), Colorado during June to July in 2014 and 2015. Points were randomly generated within each stratum at a distance of 300 m a part. Each stratum was based on low, medium, and high elevation and shrub cover, and defined by various colors and values in matrix scale on right. Matrix Values were estimated from stratified elevation by designating three equal bins beginning at forest edge from low (bin = 10; e.g., RMNP = 2,599 – 3,104 m), medium (bin = 20; e.g., RMNP = 3,104 – 3,610 m), and high (bin = 30; e.g., RMNP = 3,611 – 4,114 m) elevations. Land cover data was derived from all Existing Vegetation Types (EVT) found within Landfire, version LF 2010. Stratified elevation was combined with low (1), medium (2), and high (3) shrub and subshrub EVT data, resulting in final Matrix Values. Due to various restrictions, only 31 of the 54 points were accessible.

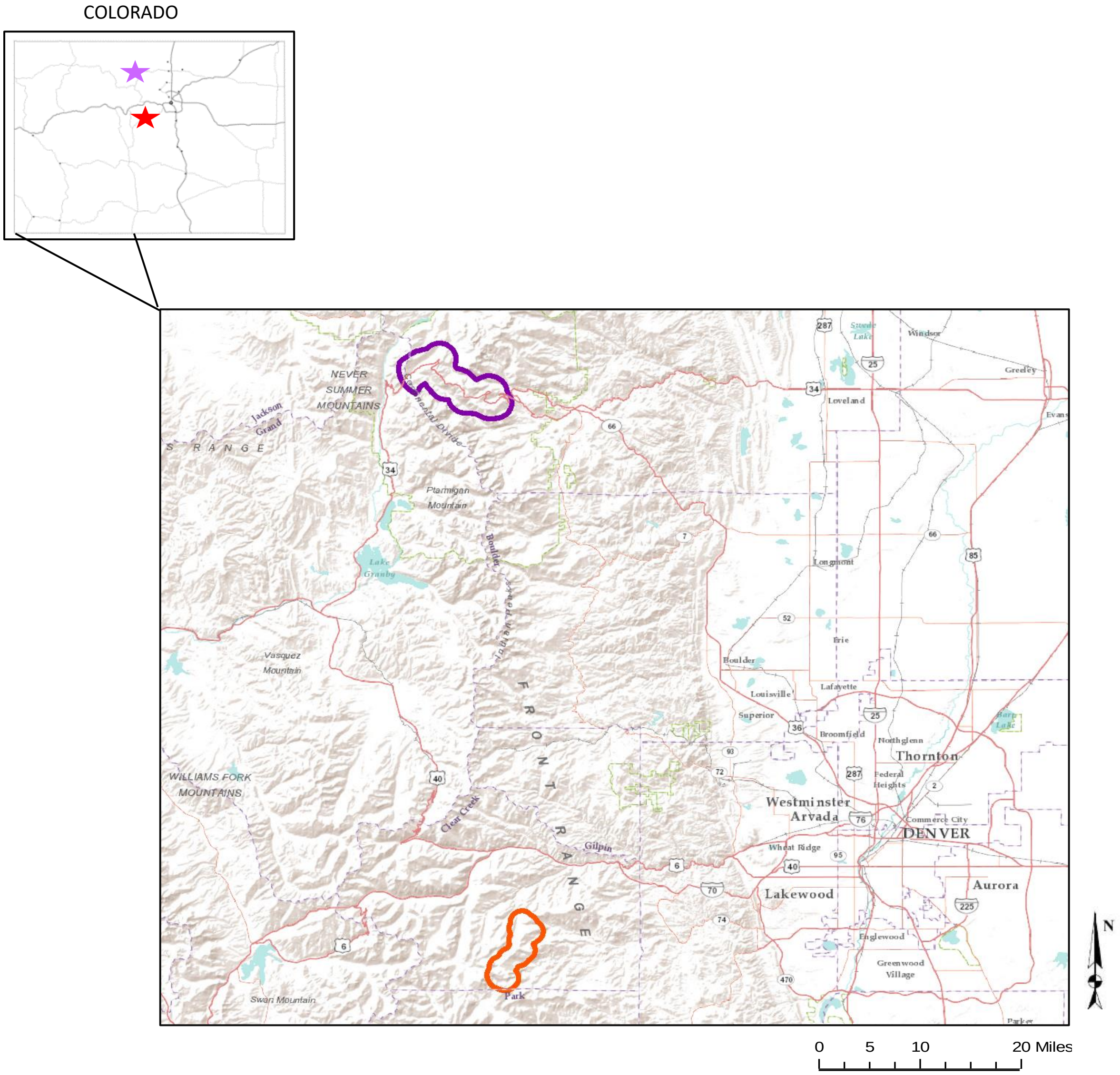


Figure 2.3 - Two alpine study sites in Colorado: (1) Mt. Evans in Clear Creek County (orange polygon) and (2) Trail Ridge Road in Rocky Mountain National Park (RMNP, purple polygon) for point count surveys conducted during June to July of 2014 and 2015, for the five breeding alpine avian species.

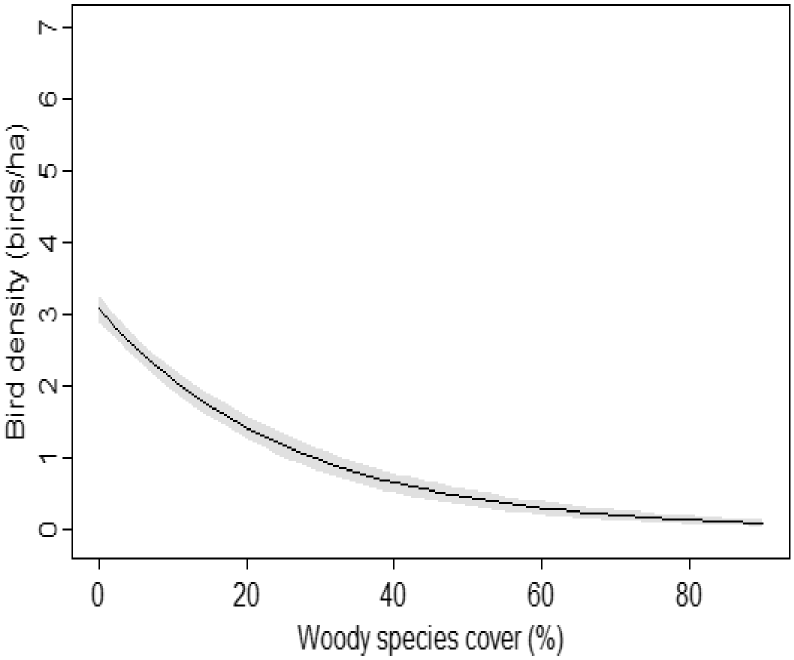


Figure 2.4 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset)] relative to woody species cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a negative relationship between pipit density and woody species cover (%). Plot includes 95% upper and lower confidence intervals (CIs), and holds other covariates in top model at their median.

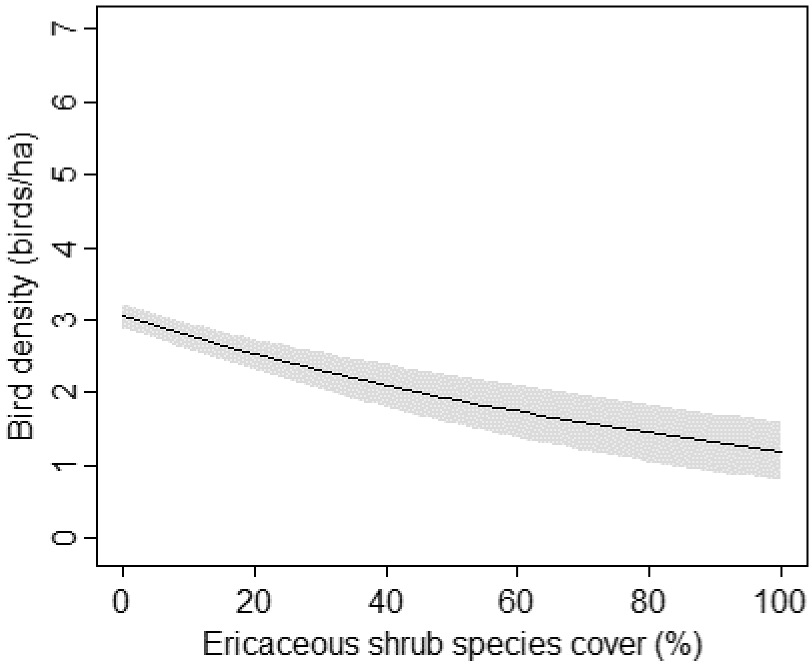


Figure 2.5 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset)] relative to ericaceous shrub species cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a negative relationship between pipit density and ericaceous shrub species cover (%). Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median.

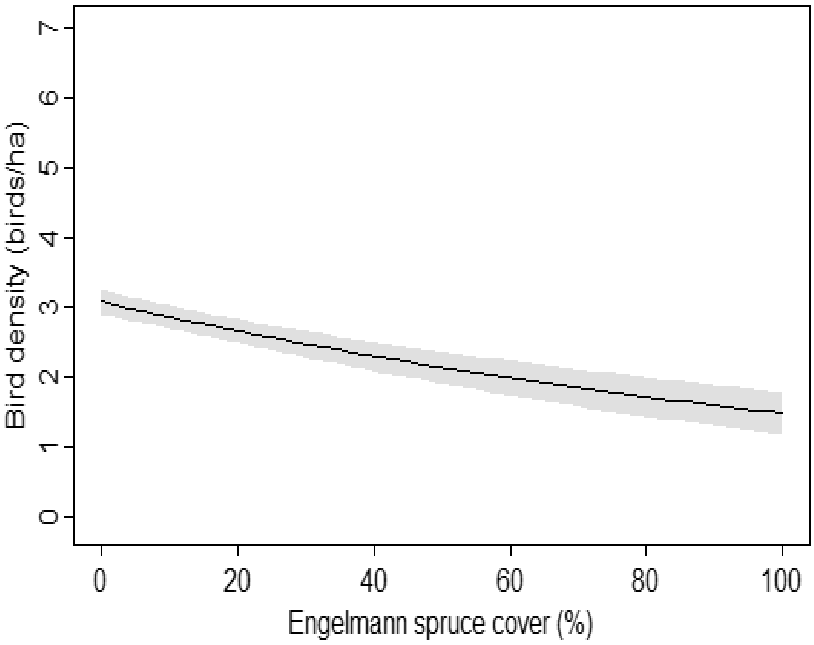


Figure 2.6 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset] relative to Engelmann spruce cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a negative relationship between pipit density and Engelmann spruce percentage (%). Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median.

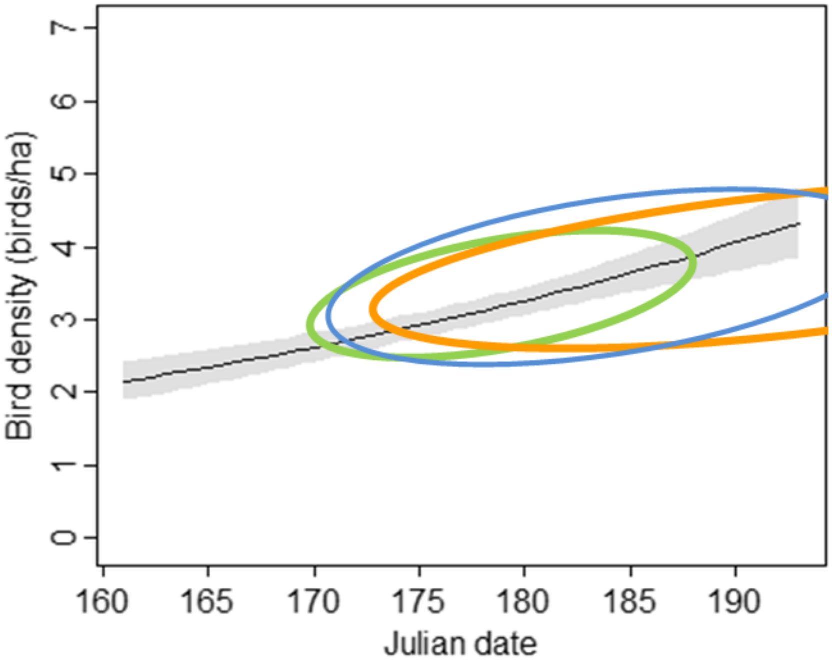


Figure 2.7 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset] relative to Julian date, from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between pipit density and Julian date. Plot includes 95% upper and lower confidence intervals (CIs), and holds other covariates in top model at their median. Colored circles represent the breeding phenology stage of American pipit (Kingery 1998), where green indicates the Julian date range (170-188) associated with pipit courtship, orange indicates the Julian date rage (173-202) associated with the period pipits occupy nests, and blue indicates the Julian date range (171-225) when pipits are feeding their young. Considerable overlap of breeding phenolgy demonstrates why there is a lower pipit density earlier in the breeding season versus toward the end.

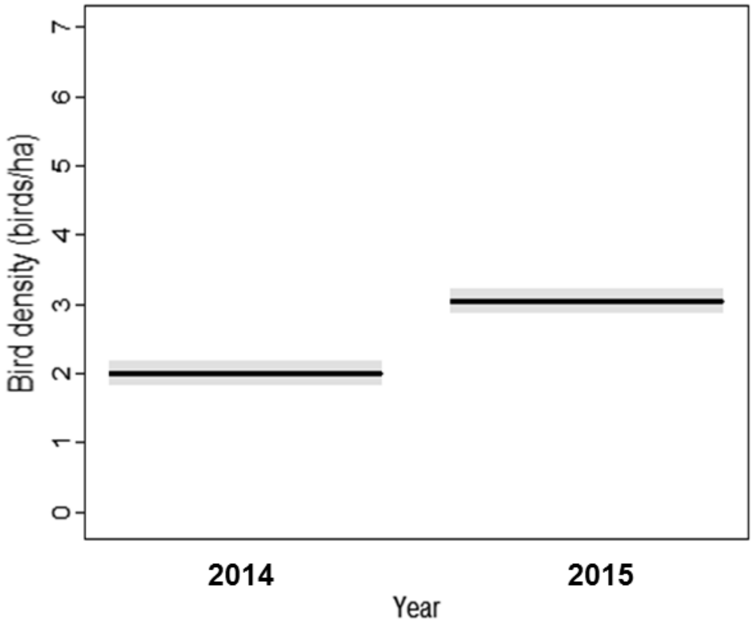


Figure 2.8 – Distribution of American pipit (*Anthus rubescens*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 [woody species cover (WOODY) + ericaceous shrub species cover + Engelmann spruce (*Picea engelmannii*) cover + Julian date + year + offset] relative to year, from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a a greater pipit density in the second year (2015) compared to the first year (2014). Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median.

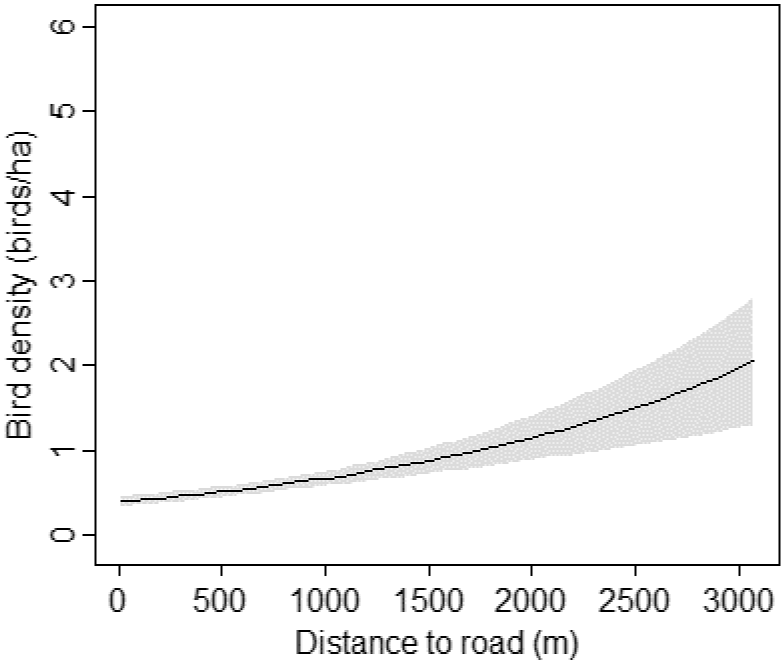


Figure 2.9 – Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to distance to road (m), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between white-crowned sparrow density and distance to road. Plot includes 95% upper and lower confidence intervals (CIs).), and holds other covariates in top model at their median.

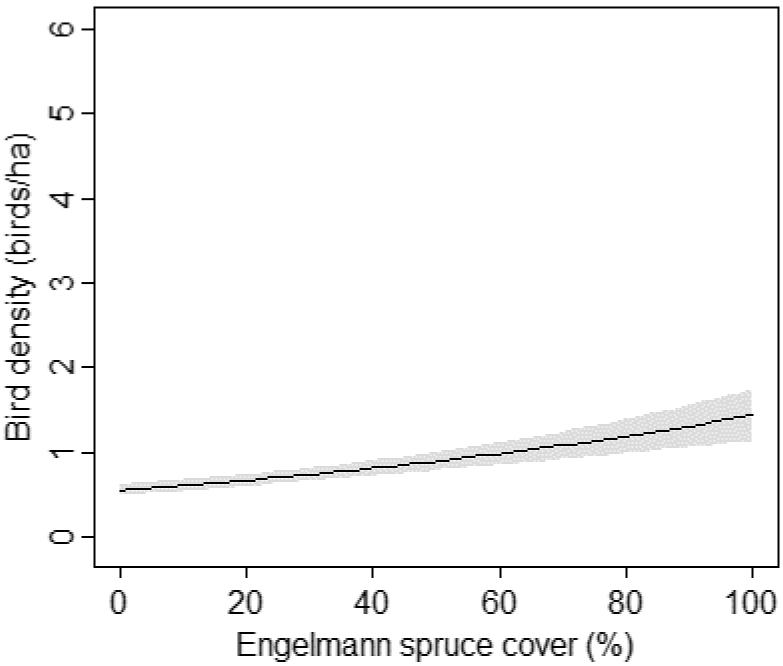


Figure 2.10 – Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to Engelmann spruce cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between white-crowned sparrow density and Engelmann spruce cover. Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median.

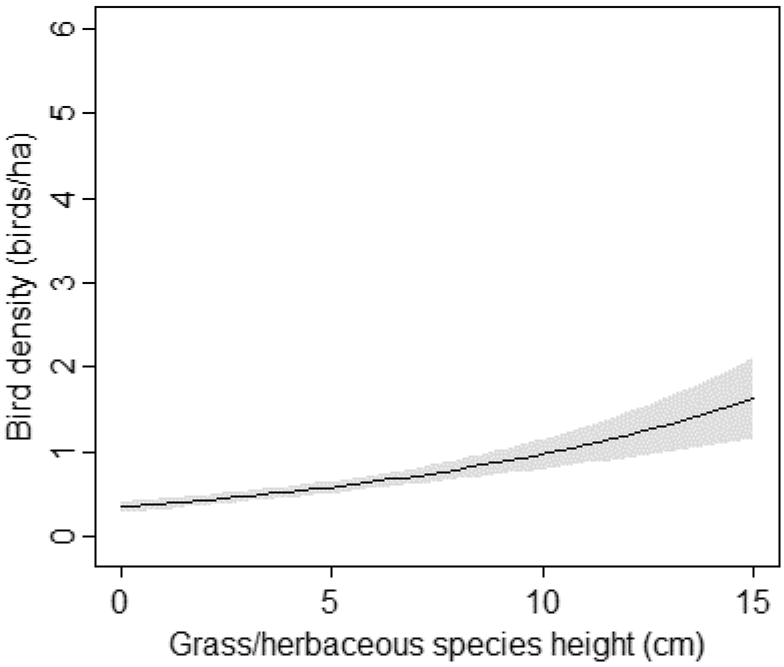


Figure 2.11 – Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to grass and herbaceous species height (cm), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between white-crowned sparrow density and grass and herbaceous species height. Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median.

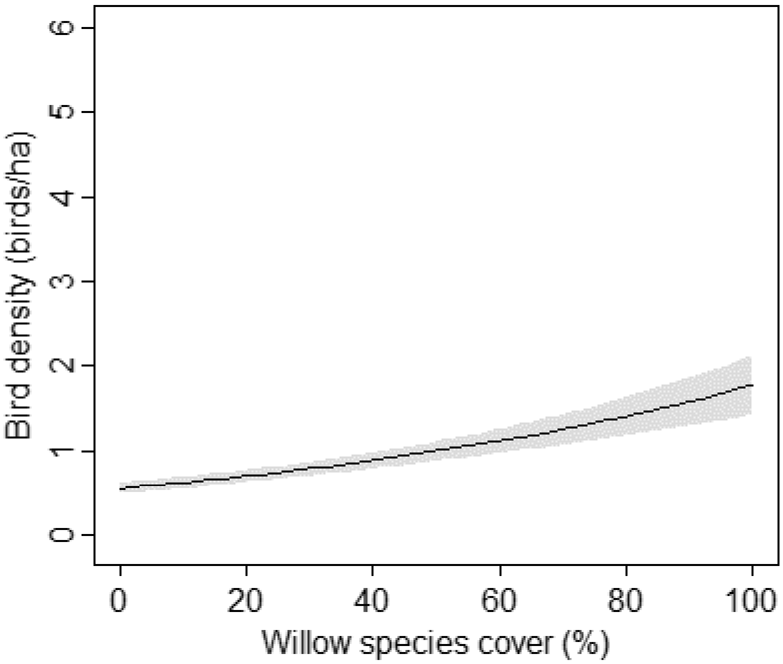


Figure 2.12 – Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to willow species cover (%), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a positive relationship between white-crowned sparrow density and willow species cover. Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median.

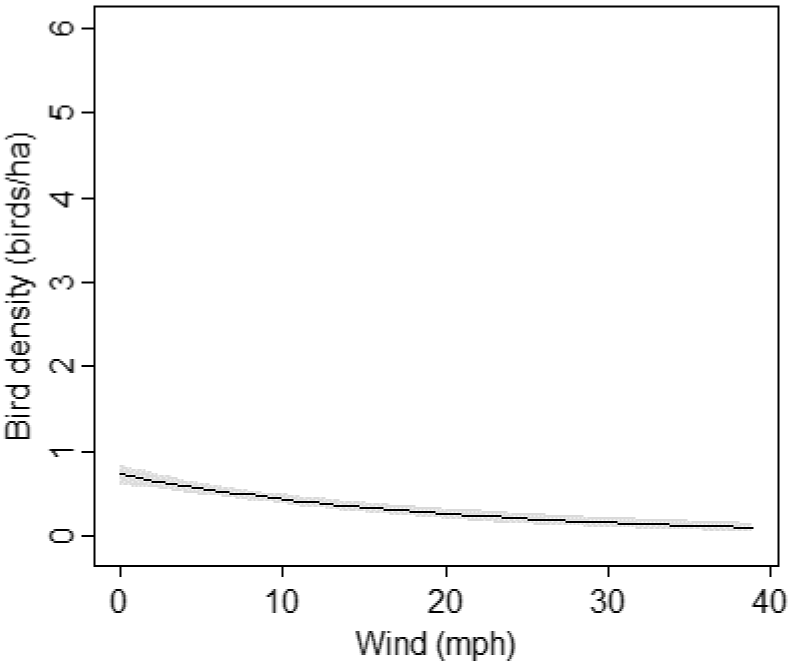


Figure 2.13 - Distribution of white-crowned sparrow (*Zonotrichia leucophrys oriantha*) density (birds/hectare) from top multivariable negative binomial generalized linear model (GLM) plus an offset term calculated from mean detection probability in program DISTANCE 6.2 (distance to road + Engelmann spruce (*Picea engelmannii*) cover + grass and herbaceous species height + willow (*Salix*) species cover + wind + offset) relative to wind (mph), from data collected during June to July in 2014 and 2015 at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot illustrates a negative relationship between white-crowned sparrow density and wind. Plot includes 95% upper and lower confidence intervals (CIs)), and holds other covariates in top model at their median.

CHAPTER 3: PATTERNS OF FINE-SCALE HABITAT SELECTION BY BREEDING WHITE-TAILED PTARMIGAN (*LAGOPUS LEUCURA)* IN COLORADO'S ALPINE

SUMMARY

The alpine ecosystem is an extreme and variable environment both in climate and topography that influences resource availability and duration, and species distribution and persistence. Resource selection by animals is a combination of factors driven by species' biology, their behavioral decisions, and the surrounding habitat, all in a hierarchical context ultimately to enhance survival and fitness. Resource selection and habitat characteristics of white-tailed ptarmigan (*Lagopus leucura*) and other sympatric species have been described to explain their foraging, morphology, and survival in many alpine regions. However, a lapse of information about habitat selection by white-tailed ptarmigan on a fine-sale during two concurrent breeding stages (nesting and brood-rearing), exists in Colorado's alpine. In particular, few studies have tested whether nest and brood-site selection by white-tailed ptarmigan is driven by smaller-scale components that include species of vegetation and arthropod forage. To assess these fine-scale habitat preferences, we analyzed paired use-available resource selection for nest (n = 122) and brood (n = 108) sites. We used conditional logistic regression and Bayesian Information Criteria (BIC) model selection for data collected in two alpine areas of Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park during 2014 and 2015. We evaluated resource selection at mesohabitat (patch) and microhabitat (site) scales. We found nest-site selection at the patch scale was best predicted by forage forbs, rock and gravel, and shrub cover (%). We also found forage forbs cover explained more variation in our top model when compared to models with specific vegetation species. Our results suggested brood-site selection at the patch level was driven by rock and gravel cover (%) as well as

proximity to shrubs (m). Analysis of a subset of our brood data (*n* = 34) revealed hens selected brood habitat that contained insect species (*Cicadellidae*) over vegetation cover (%), likely to meet dietary requirements of chicks. Hens placed their nests at lower elevations and selected for less graminoid cover (%) at the site scale. Our results demonstrate how and where white-tailed ptarmigan are currently selecting these different breeding sites in Colorado's alpine, giving us insight into consequences this alpine endemic bird may face if their breeding habitat is altered by climate change.

INTRODUCTION

Climatic regimes in alpine ecosystems are extreme and rapidly changing, ultimately affecting and driving both habitat suitability and availability for many wildlife species in these regions (Beniston et al. 1997). Variability in abiotic factors in alpine habitat, such as climate and topography, dictates many of the biotic processes found there. Short-term, intermittent climate fluctuations will likely not be impactful to alpine vegetation because many plant species are slow-growing with prolonged life cycles (Pauli et al. 1999) and can cope with changes at this scale. However, as climate change continues over longer periods of time, it is predicted that response patterns (e.g., biodiversity, species distribution and persistence) of already sensitive alpine vegetation and habitat could be more significant (Gottfried et al. 1998; Theurillat and Guisan 2001).

Identifying relationships between species and their habitats provides a strong foundation in understanding basic ecological framework (Guisan and Zimmermann 2000). Understanding these interactions and how climate change may impact these associations is a growing conservation concern (Dawson et al. 2011). Climate change poses many risks to avian species in high mountain regions, particularly endemic species that breed in the alpine zone. Climate change has already been shown to have varying and significant impacts to bird abundance, distribution, phenology, and survival (e.g., Crick 2004; Gregory et al. 2009). In Colorado over the past three decades, average annual temperatures have increased by 2.0˚F across the state and by 1.6˚F in Colorado's north-central mountains alone, and timing of snowpack melt has shifted two to three weeks earlier in the year over a 29 year period in Colorado's high mountain regions (Ray et al. 2008; Clow 2010; Lukas et al. 2014). For every 1˚F rise in temperature, vertical migrations of treelines have been estimated at shifting 170 m into the alpine (EPA 1997), eventually limiting and/or expanding habit for both subalpine and alpine species. Organisms are expected to track these shifts, potentially causing them to disperse into novel areas with limited or unsuitable habitats necessary to sustain important biotic interactions (Lodge 1993). Habitat structure, particularly vegetation, is an essential component driving the relationship between birds and their environment, which can influence foraging, reproduction, and survival both directly and indirectly (Wiens 1969; Cody 1985). Determining the attributes defining habitat selection by breeding alpine avifauna and the important habitats driving their breeding relationships is vital for conservation of these species. Understanding how avian habitat selection, use, and fitness are affected by specific abiotic and biotic factors is particularly important because of how these responses may be impacted by climate change (Martin 2001).

Here we analyze nest and brood site habitat selection by white-tailed ptarmigan (*Lagopus leucura*; hereafter ptarmigan), the smallest grouse species endemic to the alpine (Braun et al. 1993; Hoffman 2006). However, ptarmigan can move below treeline into mesic meadows throughout the year if suitable forage and habitat are present (Braun 1971; Braun et al. 1976; Herzog 1977, 1980). Nesting season for white-tailed ptarmigan occurs from early-June to early-August, peaking in mid-June to mid-July, whereas brood-rearing ranges between late-June to late-September, peaking mid-July to mid-September (Hoffman 2006). While ptarmigan use a broad range of plant assemblages and components of alpine habitat, willow is a critical component throughout much of the ptarmigan life cycle, providing food and cover (Braun 1971; Braun 1980; Hoffman 2006).

Like many species, birds are not randomly distributed throughout habitats; selection of sites is driven by a combination of behavioral aspects, habitat factors and ecological requirements (Hildén 1965). Habitat selection is a hierarchy of an individual’s behavioral decisions about environmental features it will use at various scales that optimizes fitness and survival (Hutton 1985). Although often misinterpreted, habitat selection can depict patterns of habitat use (Jones 2001). Various studies have analyzed habitat selection by ptarmigan species in other alpine areas, specifically white-tailed ptarmigan in Canada (Fedy and Martin 2011), sympatric ptarmigan species (e.g., willow (*Laguopus* lagopus), rock (*Lagopus muta*), and white-tailed; Wilson and Martin 2008), and rock ptarmigan in the Italian Alps (Nelli et al. 2013) and Japan (Sawa et al. 2011). Other studies in Colorado have focused on winter forage and habitat characteristics of ptarmigan (Geisen and Braun 1992), nest site selection relative to ptarmigan hen morphology, predation, and microclimate (Wiebe and Martin 1998), and crop contents of ptarmigan (May and Braun 1972). Despite these contributions, fine-scale habitat selection by ptarmigan during both nesting and brooding periods, have yet to be fully evaluated. Microscale habitat selection (e.g., nest-site selection) hinges on decisions that directly influence an individual’s fitness, reproductive success and survival (Jones 2001). Furthermore, brood-rearing is an essential stage early in a juvenile’s life, especially for white-tailed ptarmigan who already have a short window to forage in the alpine; this social learning between hens and chicks acts as training both increasing survival and development of chicks (Allen and Clarke 2005). Therefore, resource selection functions allow us to link habitats and resources selected with fitness, as attributes associated with reproduction and survival and habitat selection are similar and often overlap (McLoughlin et al. 2006).

Habitat selection, along with fitness and survival of ptarmigan, is known to be driven by at least three mechanisms: available forage, concealment from predators, and thermal regulation (Hoffman 2006). Specifically, thick vegetation can often increase predation risk of hens and nests, and rocks followed by willow are the predominant ground cover of their nest sites (Braun 1971, Wiebe and Martin 1998). Research has shown body condition and size associated with vegetative cover, have been drivers in white-tailed ptarmigan nest-site selection (Wiebe and Martin 1998). Temperature constraints are an important aspect of white-tailed ptarmigan physiology where ptarmigan are highly vulnerable to heat stress (Hoffman 2006). Additionally, ptarmigan lose on average 60 percent of their metabolic heat when ambient temperatures are high (Johnson 1968). Previous research documented white-tailed ptarmigan nests warmed rapidly in the morning and maintained cool temperatures throughout the day if the nest site was composed of rock and was east-facing (Wiebe and Martin 1997). Furthermore, ptarmigan hens tend to move less than an average of 1,000 m between their nest and brood locations, resulting in some hens using brood sites near their nesting locations as long as suitable habitat is present (Braun 1969, Giesen 1977, Schmidt 1988, Hoffman 2006).

Understanding which resource conditions are required by ptarmigan will help inform management of alpine habitats and provide insights into potential impacts of climate change on fine-scale resources. Defining small-scale habitat characteristics important to species, especially species with specialized habitat preferences, not only depict how organisms are using the habitat, but is a suitable approach to identify which habitat components a species prefers (Graf et al.

2005). Therefore we developed biological hypotheses and predictions that were placed largely on the defining, ecological factors listed above for ptarmigan and are itemized in Table 3.1.

We first hypothesized that habitat characteristics defining habitat selection by ptarmigan for nest and brood sites will be different among sampled populations at each study site, with vegetation largely driving these differences. We predicted ptarmigan will use different sites for nests and broods, based on habitat characteristics (e.g., percentage of rock cover, specific vegetation forage). Although brood-rearing sites often overlap or border breeding territories (Braun 1969, Giesen 1977, Schmidt 1988, Hoffman 2006), as the summer progresses hens and broods typically move upslope to access more suitable habitat and forage for broods.

Second, we hypothesized nest and brood site selection by ptarmigan will vary across study sites, likely due to difference in availability of resources. Previous findings indicated white-tailed ptarmigan both use and select habitat in a more specialized manner that consists of mesic areas with abundant willow (Frederick and Gutierrez 1992, Giesen and Braun 1992, Allen and Clarke 2005, Wilson and Martin 2008). Habitat use and selection can be differentiated by selection being hierarchical decisions with outcomes of habitat use when resources are encountered (Krausman 1999). We predicted willow species will not be an important determinant of ptarmigan nest or brood site selection at our northern study site, Rocky Mountain National Park, due to lower observed abundance of willow at that study site. We also predicted the following forage species will be an important component of ptarmigan nest and brood site habitat selection: sedges (*Carex spp.*), alpine avens (*Geum rossii*), bistort species (*Bistorta bistortoides* and *Polygonum viviparum*), mountain-meadow cinquefoil (*Potentilla diversifolia*), buttercups (*Ranunculus spp.*), willows (*Salix spp.)*, and clovers (*Trifolium spp*). These forage species have been found to comprise the majority of female white-tailed ptarmigan diets in

Colorado, with spring diets mostly composed of willow (*Salix spp.*, 85%) and summer diets consisting mainly of Alpine bistort (*Polygonum viviparum*, 54%) (May and Braun 1972). These results mirror a ptarmigan food-calling study in Rocky Mountain National Park, which found hens chose and called chicks to foraging sites based on presence of *Salix spp.* and *Polygonum viviparum*, both of which encompassed the majority of chicks' diets, with chicks consuming ~38% and ~22%, respectively (Allen and Clarke 2005).

STUDY AREA

Two study areas were selected for sampling throughout 2014 and 2015 for comparative purposes, primarily due to both sites contributing to ptarmigan research since the mid-1960s and because they provided enough distinction among sites to determine if site-specific differences were evident in habitat selection by ptarmigan. Located in central Colorado in Clear Creek County, the Mt. Evans study site within the Mt. Evans Wilderness Area, encompasses 9.2 km^2 of alpine habitat and is bisected by a 14-mile long scenic byway. Rocky Mountain National Park (hereafter, RMNP) located in north-central Colorado, is bisected by Trail Ridge Road, of which approximately 11 miles is within alpine habitat, with our study area comprising 9.11 km^2 of this region. Mt. Evans' alpine area ranges in elevation from roughly 3,300 to 4,300 m, and 3,300 to 3,700 m across the alpine region of Trail Ridge Road. Distance between the two study sites is <100 km apart, resulting in comparable climate patterns including extreme variability in wind, temperature, and precipitation. Alpine plant communities in these study sites consist of graminoids (e.g., *Carex* and *Poa spp.*), forbs (e.g., *Geum rossii, Bistorta bistortoides*, and *Trifolium spp.*), shrubs (e.g., *Salix spp*), small trees (e.g., *Picea engelmannii*), riparian corridors, rock, bare ground, and persistent snowfields, with many of these plants being rare or endemic to this region (Braun 1980; Kraft 2016).

METHODS

Field surveys

To assess habitat selection, we employed a use-available resource selection framework where use locations were compared to available locations, allowing robust inference that denotes choices made by species (Jones 2001). Use locations were defined as locations where ptarmigan were found and observed, whereas available locations were sites that fell within accessible and pertinent areas (Manley et al. 2002), both biologically and spatially for ptarmigan. Habitat selection is scale-dependent and is inherently hierarchical (Boyce 2006). We first located birds in late spring and early summer (mid-May to early-June in 2014 and 2015) by playing territorial male calls throughout each study area. As the season progressed and male responses diminished, we focused our search efforts in areas that consisted of abundant willows, intermittent snowfields, and rock cover. Once located, hens were captured with a modified telescopic noose pole (Zwickel and Bendell 1967). To identify nest and brood site use locations, we affixed 4 g very high frequency (VHF) necklace radio-transmitter collars (Holohil, Carp, ON) to all hens captured as well as an aluminum state band and distinctive color combination leg bandettes. Birds were classified into two age categories: sub-adult (< 1 yr old) and adult (> 1 yr old), by presence or absence, respectively, of pigmentation on outer primaries 9 and 10 (Braun and Rogers 1967). We tracked birds throughout each study area and the individual was identified by frequency and band combination, and use locations were recorded with a handheld Garmin GPS unit in place. We attempted to relocate birds a minimum 3 times each week, which helped us determine when a hen began nesting and when hatching at nest sites occurred. Incubation at ptarmigan nests typically range between 22 – 25 days (Giesen et al. 1980; Martin et al. 1993; Braun et al. 1993). During our visit to the nest, we monitored hens at a distance of ~30 m as to minimize disturbance of the hen in case she was currently laying an egg, which could increase the likelihood of nest abandonment, and to reduce the likelihood of predators being attracted to the nest site by human scent (G. Wann, unpubl. obs). During the nesting period, we designated use sites as either an initial nest site, or if a nest was abandoned, failed, or was predated and a new nest location for a hen was found, was assigned as a re-nest use site. Habitat data on use sites was recorded when the hen and brood were no longer present at the site, right after failure or hatch. Examination of nest sites only occurred one time. During the brooding period, we followed hens to relocate broods, and attempted to relocate broods 2-3 times per week. We designated these locations as brood use sites. Individual brood use sites were only measured once. However, since hens and broods are quite mobile, especially as chicks get older (Hoffman 2006) several different brood use locations of the same hen, if obtainable, were measured throughout the field season. Thus, we analyzed selection at two local scales including: (1) a mesohabitat scale (i.e., habitat patch surrounding nest and brood sites; hereafter patch scale) and (2) a microhabitat scale (i.e., central location of nest sites; hereafter site scale) (Johnson 1980; Jones 2001). Since chicks are precocial, and thus highly mobile shortly after hatching (Hoffman 2006), we decided not to measure habitat selection at the site scale as we felt the patch scale was more representative of their movement range and patterns, especially given the brood typically is scattered over a larger patch area.

Available or random locations for both nest and brood sites were chosen based off of randomly generated distances between 50-350 m from the center point of the use location, and at randomly generated directions ranging from 0°-360°. This range of distances has been shown to encompass the availability within an individual’s territory (Fedy and Martin 2011).

We measured a variety of abiotic and biotic characteristics at each use and available nest and brood site (Table 3.1). Upon arrival at each site, the actual location of the use and available sites, were designated as the center point (T2-5M, Figure 3.1). Because we wanted to measure fine-scale habitat attributes, we selected Daubenmire plots to do so (Canfield 1941; Daubenmire 1959; Hoffman 2006). We sampled along three 10 m long transects (Figure 3.1) with a ¼ m^2 Daubenmire plot at three sampling points distributed every 5 m along each transect. Transects were positioned 10 m apart, perpendicular to the natural slope of the site. At each Daubenmire plot, percent cover and height of tallest habitat characteristic were measured (Table 3.2) and the top four dominant vegetation species were recorded, dominance rankings (four was most dominant). Lastly, Sticky Aphid Whitefly Trap paper was used at brood use and available sites only, at all four corners of the sample area (Figure 3.1) to gain insight into insects that are available at foraging sites for ptarmigan. Wire mesh covers were placed over the flypaper to ensure wildlife, especially ptarmigan chicks, would not get stuck on the paper. Flypaper was deployed at Mt. Evans during both the 2014 and 2015 seasons; due to park restrictions we were limited to only sampling insects in 2015 at RMNP.

DATA ANALYSES

Habitat selection data

We included all nine sample plots along line transects to represent the patch scale, averaging covariates from those plots. The site scale data encompassed only the centralized location (i.e., T2-5M; Figure 3.1) of a nest. We used a Pearson's correlation matrix to assess correlation ($|r \geq 0.7|$) among our predictor variables (Table 3.2). We visually assessed covariates for non-linearities and considered biologically relevant relationships. Aspect was included as a continuous variable after it was transformed to a linear value by: aspect transformed =

sin[measured aspect + (90 – maximum aspect assigned)] + 1, where values closer to zero were southwest aspects (azimuth of 225 degrees, maximum aspect assigned) and closer to two were more northeastern aspects (azimuth of 45 degrees) (Beers et al. 1966). Within the study areas slopes that face more southwest were warmer and drier, and slopes facing more northeastern were cooler and wetter. Additionally, predictor covariates were standardized prior to model fitting, by subtracting the variable mean from the individual value of the variable and then dividing it by its standard deviation.

Vegetation data

We identified vegetation to genus and species and ranked these based on dominance within each plot. Rankings were summed to give an overall "weighted rank" for each vegetation species, delineating dominance. We estimated the relative abundance of plants at sites by summing the vegetation species' count and dividing by the total number of sampled plots per site. Analyzing specific vegetation species was important to isolate if ptarmigan are selecting nest and brood sites based on vegetation species preference. Again, data were standardized using the same format as above, prior to fitting models. Correlation among vegetation species was explored via a Pearson's correlation matrix.

Insect data

We collected individual insects at both use and available brood sites that were counted on each trap and organized based on genus, if discernable, or to insect order or family. These data were analyzed only at the patch scale, because flypaper traps were arranged on the four outside corners, rather than the center point of each sample site. To account for lost insect traps (e.g., traps taken by animals) and for differences in range of days the traps were deployed, insect abundances were adjusted (divided) by the total trap days (total days out x number of traps recovered). Likewise, data were standardized using the same format as above, prior to model fitting. We also explored correlation among insects via a Pearson's correlation matrix.

Statistical analyses

We used conditional logistic regression (package "clogit" in Program R; Therneau 2015) to compare use (case) to available or random (control) ptarmigan nest and brood locations. Our sampling design prevented issues of contamination, where available locations including areas that were actually used (Keating and Cherry 2004; Johnson et al. 2006) contrasted locations used by ptarmigan with other potential available sites (paired) in the surrounding area (conditional). We evaluated our *a priori* hypotheses with both univariable and multivariable case-control logistic regression models considering all covariates (Table 3.2) fit at the patch and site scales. Covariates were first evaluated individually within four predictor categories (abiotic, biotic, spatial and temporal) to reduce the number of variables with our hypothesized predictor categories. We assessed all combinations of predictors within each category and identified a top model. All combinations of covariates from top models within the predictor categories were then evaluated across categories to isolate a final top model considering combinations, using Bayesian information criterion (BIC). BIC selects for more parsimonious models and simplifies the amount of variables we had for interpretation purposes (Burnham and Anderson 2002; Johnson and Omland 2004). We ranked candidate models using Bayesian model weights (w_i), with comparisons of competing models within 2 ΔBIC (Burnham and Anderson 2004). However, we moved forward with analyses based on our top model and not on competing models. We assessed collinearity among covariates in our top model by calculating variance inflation factors (VIFs) of each covariate, where overall VIFs > 10 indicated correlation among covariates; these predictors were removed and the models refit to determine if collinearity persisted among remaining covariates (Montgomery and Peck 1992).

We wanted to verify if including specific vegetation species dominance explained more variation in habitat selection by ptarmigan rather than overall percentage of vegetation cover. If top models included a vegetation cover category (e.g., forage or other forbs, graminoids, shrubs; Table 3.2), we removed the cover category from the top model and replaced it with the specific vegetation species we determined, prior to field sampling, that comprised those cover categories. To verify this, we compared BICs among the original top model and the models with substituted vegetation species.

Using a similar approach, once a top brood model was identified, we evaluated if the inclusion of specific insect species would further explain ptarmigan brood habitat selection instead of habitat and vegetative components alone, using a subset of our brood data we collected insects for. Though this was on a subset of the sampled sites, we first refit the top brood model from the full dataset at the patch scale, to the reduced data to ensure parameter estimates did not vary. We then analyzed univariable and multivariable models of insect species to determine how selection is being driven by insects alone. We then included the insect species with the habitat characteristics in our top model to see if the addition of another forage source explained selection by hens and broods. Again, BICs were compared across models.

Model predictive accuracy and validation

We analyzed receiver operating characteristic (ROC) curves integrated with the area under the curve (AUC) to assess each models' performance and predictive accuracy (Fielding and Bell 1997; Cumming 2000; Baasch et al. 2010). ROC plots illustrate the fraction of nest and brood sites selected by ptarmigan (true positives) versus the fraction of dependent random, available nest and brood locations incorrectly classified (false positives). An AUC of 0.50 indicates limited to no predictive power (Hosmer and Lemeshow 2000). Acceptable predictive power is where $0.70 \leq \text{AUC} \leq 0.80$, whereas excellent predictive power is where $\text{AUC} \geq 0.80$, with an AUC of 1.0 depicting perfect discrimination (Hosmer and Lemeshow 2000).

RESULTS

We captured and collared 51 ptarmigan hens during 2014 to 2015 (nine were sub-adults and 21 were adults in 2014; 11 were sub-adults and 18 were adults in 2015; 8 of these hens were measured in both 2014 and 2015). Of these hens, 28 nested in 2014 (Mt. Evans = 15; RMNP = 13) and 29 hens nested in 2015 (Mt. Evans = 18; RMNP = 11). There were 15 hens with broods in 2014 (Mt. Evans = 10; RMNP = 5), and 16 hens with broods in 2015 (Mt. Evans = 8; RMNP = 8). There were five hens that re-nested as a result of abandoned, failed or predated nests, two in 2014 (Mt. Evans = 2; RMNP = 0), and three re-nesting attempts in 2015 (Mt. Evans = 3; RMNP = 0). Both re-nests in 2014 were adult hens, whereas re-nests in 2015 were by one sub-adult and two adults.

Apparent nest success in our study was 64% (18 out of 28) in 2014, with a 73% nest success (11 out of 15) at Mt. Evans and a 54% nest success (7 out of 13) at RMNP. In 2015, apparent nest success was 55% (16 out of 29), with a 44% nest success (8 out of 18) at Mt. Evans and a 73% nest success (8 out of 11) at RMNP. There were two hens that re-nested in 2014 and both were successful, whereas in 2015 67% of the re-nests (2 out of 3) were successful, all of which were located at Mt. Evans.

We collected resource information at use and available sites of 51 hens, which resulted in 230 nest and brood sites sampled, that we used for the patch and site scale analyses. We used twenty-three habitat predictors (Table 3.2) in our conditional logistic regression models for both the nest and brood analyses. Exploration of the Pearson's correlation matrix indicated graminoids height and cover were correlated (*r* = 0.72) at the patch scale for nests and were also correlated (*r* = 0.71) at the patch scale for broods. We also found that height of shrubs and shrub cover were correlated (*r* = 0.83) at the patch scale for broods. However, no covariates were correlated at the site scale. Variable exploration indicated a quadratic term of rock and gravel cover should be used in univariable and multivariable models for both nests and broods at the patch scale. No quadratic term was necessary at the site scale for nests and all modeling could continue with linear terms for the nest analysis at this scale.

We recorded and measured dominance for eighty-five vegetation species across our 230 sampled sites (Table 3.3). Eight vegetation species were considered highly correlated at nest sites at the patch scale. These species included: *Angelica grayi* and *Rhodiola rhodantha* (*r* = 0.95); *Cercocarpus montanus* and *Pedicularis* spp. (*r = 0.95*); *Sibbaldia procumbens* and *Taraxacum officinale* (*r = 0.80*); and *Achillea alpicola* and *Ericaceace* spp. (*r* = 0.76). We also found shrub cover to be highly correlated with willow (*Salix* spp.) (*r* = 0.80), further indicating willows are the predominant shrub cover in our study sites. Fourteen species were highly correlated at brood sites at the site scale. These species included: *Angelica grayi* and *Heterotheca pumila (r* = 0.89), *Carex albonigra* and *Pedicularis groenlandica (r* = 0.82), *Cirsium scopulorum* and *Carex pyrenacia (r* = 0.70), *Geranium* spp. and *Heterotheca pumila (r* = 0.89), *Mertensia alpina* and *Achillea alpicola (r* = 0.87), *Psychrophila leptosepala* and *Erigeron melanocephalus (r* = 0.95), and Unknown Forbs species and *Juncus* spp. *(r = 0.*73). Two vegetation species were considered highly correlated at nests at the site scale, which included: *Mertensia alpina* and *Androsace chamaejasme (r* = 0.74). Evaluation of the percent dominance of plants at all sampled sites indicated that species ≥ ~13% dominance per breeding site type had sufficient data to utilize in our multivariable modeling analyses.

Due to the limited number of broods in our study (*n* = 31) and park service permits, we were only able to collect insects at 34 use and random brood sites. We collected and classified twenty-four insect types primarily to insect family, with some classified down to genus and species (Table 3.4). Correlation was evident among six insect types, which included: *Coccinellidae* and *Bombyliidae* (*r* = 0.84); *Hesperitidae* and *Geomitridae* (*r* = 0.80*)*; and *Ichneumonidae* and *Coccinellidae* (*r* = 0.75). Two insect types were weakly correlated (*r* = 0.69; *Phoridae* and *Cynipoidea.*), however we decided to allow them to occur in the same model. Further evaluation of adjusted abundances of insects resulted in four species (No. 1-4; Table 3.4) that could be used for additional univariable and multivariable analyses.

There were no strong differences in habitat and environmental covariates between use and random nest sites at the patch and site scales (Table 3.5 and Table 3.6). Aspect (transformed), elevation, slope, and wind were all very similar between nest use and random sites (Table 3.5). However, the average distance to boulders at use sites was less than random sites (Table 3.5), the average distance to snow or snowfields was greater at use versus random nest sites (Table 3.5); whereas the average distance to standing water and shrubs were shorter at use nest sites compared to random sites (Table 3.5).

Likewise, aspect (transformed), elevation, slope, and wind were comparable among use and random brood sites (Table 3.5). The average distance to boulders, snow and snowfields, and standing water were all similar at brood use and random locations; however distance to shrubs was greater at use brood sites versus random locations (Table 3.5).

Comparisons among transformed aspect in nest and brood sites demonstrated nest use locations were more northeast-facing compared to random nest sites that were on more southwest aspects, and brood use and random locations were more northeast-facing as well (Table 3.5). Elevation was slightly lower in use and random nest sites compared to use and random brood sites (Table 3.5). The average distance to boulders and standing water were greater at nest use and random sites compared to use and random brood locations; however nest use and random sites were in closer proximity to snow and snowfields and shrubs than brood use and random sites (Table 3.5).

Patch scale nest habitat selection

We collected data on nests at 61 use and 61 random locations throughout 2014 and 2015. Univariable models demonstrated weak effects of most predictors (Table 3.7) on patch-scale habitat selection by ptarmigan at nest sites. Ptarmigan hens selected sites with a more southwest aspect (β = 0.08, 95% CI = -0.24, 0.40), increasing slopes (β = 0.06, 95% CI = -0.32, 0.44), more forage forbs cover (β = 0.33, 95% CI = -0.18, 0.83), further distances from snow and snowfields (β = 0.33, 95% CI = -0.47, 1.13), and taller forage forbs (β = 0.16, 95% CI = -0.41, 0.72) (Table 3.7). Shrub cover was also positive and contributed significantly to selection of nest sites at this scale (β = 0.65, 95% CI = 0.08, 1.22; Table 3.7). However, elevation (β = -0.66, 95% CI = -1.54, 0.22), wind speed (β = -0.19, 95% CI = -0.75, 0.36), percent bare ground and litter (β = -0.13, 95% CI = -0.64, 0.39), percent other forage forbs cover (β = -0.22, 95% CI = -0.67, 0.22), percent rock and gravel cover (β = -0.38, 95% CI = -0.86, 0.09), graminoid height (β = -0.34, 95% CI = -0.95, 0.27), and distance to boulders (β = -0.12, 95% CI = -0.49, 0.25), distance to standing water (β = -0.06, 95% CI = -0.74, 0.63), and distance to shrubs (β = -0.39, 95% CI = -1.04, 0.26) all demonstrated negative effects on habitat selection at nest sites (Table 3.7).

Graminoid cover was also negative (β = -0.60, 95% CI = -1.14, 0.07; Table 3.7) and had a strong effect on nest site selection at the patch scale.

When developing the multivariable model for patch-scale habitat selection, hens strongly selected for more forage forbs cover (β = 1.42, 95% CI = 0.44, 2.40; Figure 3.2), lower percent rock and gravel cover (β = 3.41, 95% CI = 0.94, 5.87, Figure 3.2; rock and gravel^2, β = -3.20, 95% CI = -5.60, -0.81), and more shrub cover (β = 2.35, 95% CI = 1.02, 3.67; Figure 3.2) (Table 3.8 and Table 3.10). There was no correlation among forage forbs and shrub cover in the top multivariable model (VIF < 10.0).

Since there were coverage categories (i.e., forage forbs and shrubs) in the top model, we substituted vegetation species that were included in each category. Ten forage forb species had dominance ≥ ~13% (*Arenaria fendleri ,Arenaria obtusiloba, Artemisia artica, Bistorta bistortoides, Geum rossii, Polygonum viviparum, Potentilla diversifolia, Trifolium dasyphyllum, Trifolium parryi, Trifolium* spp.*;* Table 3.3). Only one shrub species (i.e., *Salix* spp.; Table 3.3) had non-zero counts which could be used for the shrub cover category in our top model. Given that we had two coverage categories in our top multivariable nest model, our substitution was a three-step approach resulting in the following model structures: (1) eight forage forb species listed above combined with percent rock and gravel (quadratic) and percent shrub cover; (2) the eight forage forb species models above, but replacing *Salix* spp. for the percent shrub cover; and (3) percent forage forb combined with percent rock and gravel (quadratic) + *Salix* spp. Of those top models from each of the three categories, the original top patch-scale model for nest selection had overwhelming support (w_i =1.0; Table 3.8). Our results indicated our top model including cover categories out-competed the other three models (Table 3.8). We compared the top 10 models of each of the four modeling scenarios above, and found no competitive models with our top nest model (w_i =1.0; Table 3.9). Finally, the area under the ROC curve for this top model was 0.86, which indicated outstanding predictive power of the model.

Site scale nest habitat selection

Cover and height of vegetation varied between nest and random locations at the site scale (Table 3.11). Several predictors in our univariable models had strong effects on nest site selection at the site scale. For instance, percent forage forbs cover (β = -0.65, 95% CI = -1.12, -0.18), percent graminoids cover (β = -0.80, 95% CI = -1.36, -0.25), and percent shrub cover (β = 1.93, 95% CI = 0.66, 3.20), along with height of graminoids (β = -0.62, 95% CI = -1.10, -0.13) and height of shrubs (β = 7.85, 95% CI = 2.97, 12.72) were all significant contributors to these models (Table 3.11). Aspect (transformed) (β = 0.08, 95% CI = -0.25, 0.42), slope (β = 0.08, 95% CI = -0.36, 0.52), distance to snow and snowfields (β = 0.35, 95% CI = -0.47, 1.18) all showed positive effects (Table 3.11). Conversely, elevation (β = -0.67, 95% CI = -1.56, 0.22), wind speed (β = -0.22, 95% CI = -0.83, 0.38), percent bare ground cover (β = -0.29, 95% CI = -0.75, 0.17), percent litter cover (β = -0.08, 95% CI = -0.56, 0.30), percent other forage forbs cover (β = -0.21, 95% CI = -0.63, 0.21), percent rock and gravel cover (β = -0.20, 95% CI = -0.60, 0.20), distance to boulders (β = -0.12, 95% CI = -0.49, 0.25), distance to standing water (β = -0.06, 95% CI = -0.74, 0.63), distance to shrubs (β = -0.39, 95% CI = -1.04, 0.26), height of forage forbs (β = -0.30, 95% CI = -0.73, 0.12) , and height other forage forbs (β = -0.10, 95% CI = -0.49, 030) all demonstrated negative effects on habitat selection at nest sites at this scale (Table 3.11).

Our top multivariable model for nest site habitat selection at the site scale resulted in elevation (β = -0.79, 95% CI = -1.78, 0.20; Figure 3.3) and percent graminoid cover (β = -0.87, 95% CI = -1.47, -0.26; Figure 3.3), where graminoid cover was a strong predictor of nest site habitat selection at this scale (Table 3.12 and Table 3.13). Multicollinearity among these predictors was not apparent (VIF = 1.03 for both). Although there was a cover category in this top model, we did not have adequate sample sizes of vegetation species that comprised this category to conduct further analyses at the graminoid species level. We compared the candidate models with the top model, which demonstrated there were three competitive models (ΔBIC < 2.0; Table 3.12). The area under the ROC curve for our top nest model at this scale was 0.75, denoting acceptable predictive performance.

Patch scale brood habitat selection

We collected data on 54 brood sites and 54 random brood locations throughout 2014 and 2015. Vegetation attributes were not considerably different among use and random locations at the patch scale (Table 3.6). Univariable models indicated no strong effects on habitat selection by ptarmigan at brood locations. Ptarmigan hens and broods selected brood sites at the patch scale based on increasing slopes (β = 0.29, 95% CI = -0.25, 0.84), forage forbs cover (β = 0.45, 95% CI = -0.03, 0.93), percent graminoids (β = 0.07, 95% CI = -0.33, 0.47), percent litter (β = 0.13, 95% CI = -0.36, 0.62), and percent shrub cover (β = 0.05, 95% CI = -0.39, 0.48), along with distance to snow and snowfields (β = 0.22, 95% CI = -0.68, 1.12), and height of vegetation (Table 3.14). Whereas aspect (transformed) (β = -0.07, 95% CI = -0.47, 0.33), elevation (β = -0.63, 95% CI = -1.68, 0.43), wind speed (β = -0.17, 95% CI = -0.68, 0.33), percent bare ground (β = -0.22, 95% CI = -0.75, 0.31), percent other forage forbs (β = -0.26, 95% CI = -0.72, 0.20), percent rock and gravel (β = -0.16, 95% CI = -0.56, 0.20), distance to boulders (β = -0.18, 95% CI = -1.05, 0.69), distance to standing water (β = -0.10, 95% CI = -0.69, 0.49), and distance to shrubs (β = -0.63, 95% CI = -1.28, 0.02) had negative relationships (Table 3.14).

The top model for brood site habitat selection included distance to shrubs (β = -0.79, 95% CI = -1.50, -0.08; Figure 3.4), along with rock and gravel linear (β = 2.78, 95% CI = 0.72, 4.84; Figure 3.4) and quadratic (β = -2.96, 95% CI = -5.18, -0.74) terms where all contributed strongly to the model (Table 3.15 and Table 3.16). No correlation was found in distance to shrubs in our top model (VIF = 1.15), however multicollinearity was apparent in percentage of rock and gravel linear and quadratic terms (VIF = 14.66, 14.17, respectively). Ignoring that correlation, we kept all three covariates in the top model for further evaluation. As no coverage categories were represented in the top model, further analyses of specific vegetation species were not conducted. Comparisons among the top 10 candidate models indicated no competitive models (Table 3.15).

When we fit the covariates from our top brood model to our reduced data set that we had collected insect samples on (n = 34), it confirmed the same relationships between the predictors and our response (Table 3.17). Direction and magnitude of the effect of coefficients was very similar in most cases. Distance to shrubs was attenuated, with β = -0.79 and confidence intervals that did not overlap zero (95% CI = -1.50, -0.80) in the full data set to β = -0.35 with confidence intervals slightly overlapping zero (95% CI = -1.32, 0.62) in the reduced data set. Beta estimates of percent rock and gravel were similar in the full (rock and gravel linear: β = 2.78, 95% CI = 0.72, 4.84; rock and gravel quadratic: β = -2.96, 95% CI = -5.18, -0.74) versus the reduced (rock and gravel linear: β = 2.67, 95% CI = -0.66, 5.99; rock and gravel quadratic: β = -2.44, 95% CI = -5.60, 0.72) data set, but the confidence intervals increased and strength of effect diminished moving from a full to reduced data set. Univariable models of insect species demonstrated a weak effect for all four insect species (Table 3.18). The top multivariable model of insect species alone resulted in *Cicadellidae* (β = 1.70, 95% CI = 0.70, 43.34) and *Muscidae* (β = 1.41, 95% CI = 0.46, 36.42) (BIC = 24.96; Table 3.19). When we fit the covariates in our top brood model

(Table 3.17) in additional multivariable models with the four insect species we had adequate data for (Table 3.18), this resulted in *Cicadellidae* (β = 1.87, 95% CI = -0.54, 4.28; Figure 3.5) and linear (β = 3.43, 95% CI = -0.42, 7.28; Figure 3.5) and quadratic (β = -2.95, 95% CI = -6.38, 0.49) terms of rock and gravel coverage in the top model (BIC = 24.88, Table 3.20). However, predictors in this model were not significant contributors to brood site habitat selection (Table 3.21). Our top brood model from the full dataset had reasonable predictive power (ROC = 0.79). Our top model from our reduced dataset including insect species, had exceptional predictive power (ROC = 0.84).

DISCUSSION

Apparent nest success throughout our study (2014 = 64%; 2015 = 55%) was similar to previous work in these and other areas of Colorado (~57%; Giesen et al. 1980), and was comparable to ranges outside of Colorado (i.e., 19 to 61%; Clarke and Johnson 1992). However, apparent nest success of re-nests in our study at Mt. Evans was high (2014 = 100%; 2015 = 67%) compared to previous success of re-nesting attempts at Mt. Evans and its vicinity (~32 to 39%; Sandercock et al. 2005). Although, we realize our apparent nest success of re-nests would be lower if we had calculated daily survival rates similar to Sandercock et al. (2005). Interestingly, the pattern of nest success between Mt. Evans (73%) and RMNP (54%) in 2014 was contrary to that in 2015, where Mt. Evans was less than RMNP (44% and 73%, respectively). Although we did not analyze environmental and habitat covariates that could have contributed to differences in nest success, our results emphasize the variability of demography throughout our study.

Patch scale nest habitat selection

It was without surprise that we found ptarmigan nest selection at the patch scale was driven by percent forage forbs, rock and gravel, and shrubs (Table 3.10). Our top model demonstrated the probability of nest site selection at the patch scale increased as percent forage forbs increased (Figure 3.2). Furthermore, the odds ratio [exp(β)] indicated for a standard deviation increase in forage forbs cover, the odds of nest-site selection at the patch scale was 4.15 times greater when the other variables were held constant (Table 3.10; Figure 3.2). However, forage forbs never occurred above 66% at study sites. Thus, we are unsure if this trend is maintained as forage forbs reach 100% cover, but it is also unlikely that 100% forb cover across our patch scale occurs in these alpine systems. While ptarmigan can take multiple day and nighttime recesses from the nest (Giesen and Braun 1979; Wiebe and Martin 1997, 2000; Hoffman 2006), it is important hens have food resources to maintain body condition to assist with further egg laying and incubation. Since ptarmigan hens and broods tend to stay near the nest site after eggs hatch (< 1 week), and due to the precocial nature of ptarmigan chicks (Braun 1969, May and Braun 1972, Giesen 1977, Schmidt 1988, Hoffman 2006), it is possible hens choose nest sites that will have adequate forage for her and her brood immediately following hatching until they reach brood-rearing sites.

Given that we were able to explore vegetation species due to the inclusion of cover categories in our top model of nest sites at the patch scale, we were not surprised by the ten forage forb species that were most dominant in our sample sites (Table 3.3). Six of the ten species, specifically alpine avens (*Geum rossii),* clovers (*Trifolium parryi* and *Trifolium dasyphyllum*), bistort (*Bistorta bistortoides* and *Polygonum viviparum*), and cinquefoil (*Potentilla diversifolia*) have been found to be principal food sources for females during summer, with alpine bistort (*Polygonum viviparum*) the greatest food source of hens during this time (May and Braun 1972). Interestingly, alpine avens was the most dominant forage forb and alpine bistort was the fifth ranked forage forb species in our patch-level nest sample sites (38.52%, 18.85%, respectively, Table 3.3). Although sedges (*Carex* spp.) have been found to comprise among the second highest food source of ptarmigan hens along with willows in summer months (May and Braun 1972), graminoids were not in our top model. However, *Carex* spp. was the third most dominant overall species in our nest sample sites at this scale (27.87%, Table 3.3). If warming temperatures along with decreased precipitation in the alpine continue, *Carex* spp. could outcompete and dominate *Geum rossii* (Winkler et al. 2016). Since we found both to be relatively dominant in our sample sites compared to other species, this shift in plant community may not be completely disadvantageous to ptarmigan at first glance. However, experimental warming at Niwot Ridge, approximately 108 km from Mt. Evans, predicted negative responses in forbs, cushion plants, and succulents to increased temperatures (Winkler et al. 2016), all of which are known and potential ptarmigan forage (i.e., succulents such as stonecrop, *Sedum lanceolatum;* S. Spear, unpubl. obs; May and Braun 1972; Hoffman 2006). A *Carex*-dominated community could reduce the variation in forage types available to ptarmigan, which may limit resources for ptarmigan. This could be particularly harmful to both hens and chicks as *Polygonum viviparum* has been found to comprise ~21% of chicks' and ~30% of hens' diets in RMNP (Allen and Clarke 2005). In RMNP, *Polygonum viviparum* and *Carex* spp. cover were found to both be increasing in RMNP over 25 years (1971-1996; Zeigenfuss 2006), which may offset negative effects to ptarmigan at least in RMNP, if palatable forage forbs such as bistort are thriving in spite of increases of *Carex* spp. From analyzing specific vegetation species, we found much support of our third prediction in our second hypothesis (Table 3.1). Surprisingly when we replaced the cover categories in our top model (i.e., forage forb and shrub cover) with vegetation species that comprised those categories, there were no competing models with our top nest site model (Table 3.8). This suggested the community of forage forbs and shrubs and willows contributes more to nest site selection at the patch scale, rather than importance of an individual species.

Odds ratios indicated for a standard deviation increase in rock and gravel cover, the odds of patch-scale nest site selection was 30.25 times greater up until a threshold of rock and gravel cover, but then nest site selection decreased by 0.04 (Table 3.10; Figure 3.2) holding the other covariates constant. The top model also suggested odds of nest site selection at this scale, was 10.46 times greater for a standard deviation increase in percent shrub cover (Table 3.10; Figure 3.2) holding the other predictors constant. Our results demonstrated there are more factors dictating how and where ptarmigan are selecting nest sites at this coarser scale. Ptarmigan seem to be looking beyond their immediate nest site location to select resources in the surrounding area, which can contribute to their fitness (i.e., reproduction and survival). Our top model suggested probability of selection of nest sites at the patch scale was moderate until rock and gravel cover was approximately 25-30% (Figure 3.2). Rock and gravel cover may play different roles in habitat selection for ptarmigan, but we did not differentiate between these in the field. Due to harsh conditions, much of the alpine consists of open gravel areas that consist of small stones (Bowman and Seastedt 2001). Ptarmigan, like many birds, have been known to ingest gravel (or grit) that collects in the gizzard and aids in digesting food, particularly woody species such as *Salix* (May and Braun 1973). Ptarmigan hens, on average, have been found to maintain more grit in their gizzard than males, particularly during nesting season, with quartz being the dominant grit type (May and Braun 1973). Differences in grit amount in male and female ptarmigan was theorized as a nutrient source for hens during egg-laying; however, reasons behind the disparity are unknown (May and Braun 1973; Hoffman 2006). Thus, future work could assess if rock and gravel size present, affects nest selection by ptarmigan.

There was a positive and strong overall trend between nest selection and shrub cover at the patch scale (Table 3.10, Figure 3.2). Shrubs and willows did not exceed 93% in our study, but due to the overall trend it is likely nest site selection by ptarmigan would continue to favor higher shrub and willow coverage. Frederick and Gutiérrez (1992) found a similar relationship with willow and shrub cover for white-tailed ptarmigan in the Sierra Nevada in California. They found the probability of nest site selection at the same patch scale as ours (i.e., 0.02 ha) increased as willow cover increased. Willow being a strong predictor in our top nest model at this scale was not surprising, seeing as willow is a staple food source throughout much of their life cycles and an important element for protective cover from predators and the elements, often driving breeding areas (Braun 1971, Schmidt 1988, Clarke and Johnson 1992, Hoffman).

Site scale nest habitat selection

Hens selected most strongly for placement of nest site at the site scale at lower elevations with less graminoid cover (Figure 3.3). Earlier research in Colorado found the majority of nests (84%) were located at elevations ranging from 3,536 to 3,811 m (Braun 1971). Other studies found nests in Colorado ranged from 3,383 to 3,901 m (Giesen et al. 1980), and 3,467 to 4,161 m (Wiebe and Martin 1998). While the mean elevation of nests from earlier studies (3,618 m, Giesen et al. 1980) was similar to our mean elevation (3,652 m), the lowest elevation our nests sites were found at was 3,196 m at Mt. Evans. Further comparison of our results to Braun (1971) demonstrated ~30% of our nests were found at elevations ranging from 3,196 to 3,536 m, ~49% found between 3,538 and 3,791 m, and ~21% of nests found at 3,835 to 4,112 m. With the threat of climate change altering species distributions in alpine habitat, these results provide us insight that ptarmigan can nest in lower elevations of our study sites. However, if advancement of treelines and elevational shifts of vegetation and other species occurs as a result of climate change, it is likely this change in habitat structure will further limit white-tailed ptarmigan suitable habitat and intensify competition with ptarmigan and other species (Fedy and Martin 2011). Given our results showed a negative association between graminoids and ptarmigan nest site selection (Table 3.13), if climate change induces interspecific competition between graminoids and known forage forb species, increases in graminoids (site model) and reduction of forbs (patch model) could restrict habitat quality for ptarmigan at our study sites. When we compared the two competing models with our top nest site selection model at the site scale, the secondary model was highly competitive with our top model (w_i = 0.41, 0.42, respectively, Table 3.12). Much like our top model, the second ranked model including bare ground and graminoid cover negatively affected nest site selection, with graminoids exhibiting the stronger effect of the two covariates (Table 3.12). Presence and increase in bare ground could be detrimental to the plant and alpine community (Zeigenfuss 2006), and if bare ground increases as has been documented over 25 years in RMNP (1971-1996, Zeigenfuss 2006), ptarmigan nesting habitat quality could be reduced, as predicted by our models. Bare ground could allow for other vegetation species to move in, such as invasive exotic plants, which may further deteriorate suitable habitat for ptarmigan nest sites.

The differences between our mesoscale and microscale nest site selection models represented biologically relevant patterns of how ptarmigan are choosing nest sites and territories, which varied across scales considered. Across a larger area (patch scale), cover of forage forbs, rock and gravel, and shrubs are all important predictors of nesting habitat. Within those habitat patches, nest sites are placed at lower elevation sites with less grass cover. Our results, like with many habitat selection analyses, allow us to specify if birds are hierarchically structuring their selection of habitats and resources (Kristan 2006). Habitat selection should be analyzed across multiple spatial scales, because important habitat features may be incorrectly estimated as evidenced by Jedlikowski and Brambilla (2017) who found water depth was important at multiple scales for a marsh-nesting waterbird, the little crake (*Zaoprnia parva*), but not a strong driver of selection at a territory scale.

Patch scale brood habitat selection

Hens selected for patch-scale brood habitat that was closer to willows and shrubs and with sufficient rock cover (Table 3.16). Throughout much of the year, willow is the dominant food source for adult ptarmigan (Weeden 1967; May and Braun 1972; Hoffman 2006). In summer, willow has been found to have higher caloric content than herbaceous plants (4.76-5.25 kcal g^{-1} dry weight vs. 3.92-5.00 kcal g^{-1} dry weight; May 1975; Hoffman 2006). Larger substrates such as willows and rocks provide protection from inclement weather, predators, and aid in reducing potential heat stress (Hoffman 2006). For species in the alpine, thermoregulation is crucial and may play a more prominent role in habitat preference and use (Zerba and Morton 1983; Wiebe and Martin 1998). Ptarmigan in our study appear to be selecting brood sites in areas that will provide them both adequate cover and access to sufficient food sources. This was further defined, because *Salix* spp. was ~78% more dominant than other shrub/small trees species, specifically *Picea engelmannii*, at sites broods and hens selected. We found overall ptarmigan brood site selection at the patch scale decreased as distance to shrubs increased ($\beta = -0.79$; Figure 3.4). However, our results indicated patch-scale brood site selection reached a threshold around 0.5-0.6 when distance to shrubs were ~30-40 m, but declined steadily at distances greater than 40 m (Figure 3.4). We found support for our first hypothesis and first prediction, that nest and brood site characteristics are different, where we did see vegetation driving these differences. We also found support of our second hypothesis that willows were important to both nest and brood site habitat selection by ptarmigan. However, we did not find a study site effect. Similar selection patterns for willow (i.e., more abundance and in closer proximity) at both study sites, suggests it is important for ptarmigan during both breeding stages. If loss of willow continues at Rocky Mountain National Park (Zeigenfuss 2006), this could be more problematic for white-tailed ptarmigan in our northern study site if they cannot find willows. This may also link to reduced ptarmigan population densities over time (Braun et al. 1991, Zeigenfuss 2006, Wann et al. 2016)

Probability of brood site selection in response to rock and gravel cover was positive until a threshold, similar to nest site selection at this scale, and then declined rapidly once rock and gravel cover exceeded ~30% (Figure 3.4). Notably brood sites typically have an excess of 50% rock ground cover (Hoffman 2006). In places such as RMNP, where rock cover was found to increase toward the end of a 25-year sampling period (Zeigenfuss 2006), this could put limitations on areas that have sufficient rock cover for ptarmigan and hinder their selection of nest and brood sites. This variability in our results between nest and brood-site selection could be due to the inherent mobility of hens and broods during this later life stage. The similarity of brood-site selection at the patch scale relative to distance to shrubs and rock and gravel cover (Figure 3.4) and the odds ratio of both predictors (OR = 16.12, 0.45, respectively, Table 3.16), indicated for a standard deviation increase in rock and gravel cover, the odds of brood site selection was 16.12 times greater, but 0.45 times smaller for a standard deviation increase in shrub cover (Table 3.16). Both of these factors perhaps act as refugia from weather and predators, as a means of reducing heat stress, or for acquiring grit for digestion during browsing on these woody species (May and Braun 1973).

When we included the four insect species in our top model for our reduced dataset (*n* = 34), results indicated insect species and rock and gravel cover explained more variation than distance to shrubs and rock and gravel cover (Table 3.21, Table 3.17, respectively). This demonstrated the importance of collecting and analyzing data on more than just vegetative forage during this post-breeding period, especially since invertebrates are an important food source up to three weeks after chicks hatch (May 1975). Because insects represent a limited portion of adult ptarmigan diets (Hoffman 2006), our results indicated brood site selection is driven by chick requirements as well. Furthermore, results of our top model including insect species revealed both insects, specifically *Cicadellidae,* and rock and gravel drive selection of brood sites (Table 3.21). Odds ratios of this model suggested for a standard deviation increase in *Cicadellidae*, brood site selection is 6.51 times greater when holding the other covariates constant (Table 3.21). We found probability of broods and hens selecting sites was highest when rock and gravel cover was ~20-25% and then steadily declined as rock and gravel cover increased (Figure 3.5). Again selection of brood sites is occurring to an upper limit of rock and gravel cover, similar to brood site selection in the full data set (*n* = 108). Perhaps too much rock cover provides more protection for ambush predators (e.g., weasels) or perches for opportunistic scavengers/predators (e.g., ravens) to prey upon broods. Interestingly, we found selection of brood sites gradually increased as abundance of *Cicadellidae* increased (Figure 3.5). Since there were nine competing models with our top model and three of the four abundant insect species were represented throughout the competitive models (Table 3.20), this further denoted insects, particularly different insect species within similar or different orders (e.g., *Diptera, Hemiptera, and Hymenoptera*), are driving brood site selection in these two alpine regions. Grouse chicks need substantial nutrients in the first few weeks of their life to aid in rapid growth and survival

(May 1975; Moss 1997; Hoffman 2006). All of the species (*Cicadellidae*, *Muscidae, Cynipoidea* and *Phoridae*; Table 3.20) in our competing models are relatively small in size (*Cicadellidae* = 0.3 to 2.0 cm; *Muscidae* = 0.2 to 1.2 cm; *Cynipoidea* = 1.0 to 9.0 mm; *Phoridae* = 0.6 – 6.0 mm; McGavin 2000), and due to the small nature of chicks during this time, perhaps these insects are easier for chicks to capture and ingest due to insect size. Despite our limitations with obtaining a larger sample size of brood sites with insects, we still achieved a sample adequate to develop new information regarding arthropod influence on brood site habitat selection by white-tailed ptarmigan, a focus that has received little attention.

In the next decades, alpine temperatures are expected to continue to warm (IPCC 2013). Insect species that are limited spatially (i.e., by elevation) or by climatic regimes, especially cold-adapted and high elevation species, are expected to be more vulnerable than other species (Butterfield and Coulson 1997). Under climate change, effects to insects could be indirect through impacts to plants or direct by altering life cycles, phenology and distribution of invertebrate species. Our findings and the fact that white-tailed ptarmigan may depend on insect species of concern, may limit white-tailed ptarmigan if insect species in the alpine decrease or shift in abundance and phenology as result of warming temperatures.

CONCLUSIONS

Habitat selection by white-tailed ptarmigan in these two alpine regions of Colorado throughout these two important breeding stages is a trade-off between presence and availability of food resources (percent forage forbs, shrub cover, distance to shrubs, percent graminoids), protective cover or thermoregulatory aid (rock cover, distance to shrubs), and abiotic components (elevation). By evaluating selection at two spatial scales, it increased our understanding of the selection process of white-tailed ptarmigan. We investigated the site (i.e., specific resources used) and the patch (i.e., an area around the used site), which explained how selection by ptarmigan is linked to these selection processes and our results. Additionally, our hierarchical analyses on two sequential scales allowed us to identify existence of patterns across scales (Wiens 1985). Greater emphasis should be placed on what is driving resource selection by ptarmigan in these areas to identify additional patterns that will lead to better conservation and management of white-tailed ptarmigan and their habitat in these regions.

Although general trends did emerge, we found some new differences in our results of habitat selection by ptarmigan in alpine areas of Colorado. While highly mobile species such as birds have been forecast to disperse into novel and potentially unsuitable areas in response to climate change (Martin 2001), how climate change will affect alpine breeding birds such as white-tailed ptarmigan is unclear. We suggest long-term monitoring programs continue on ptarmigan preferred breeding habitats and urge land managers to set conservation priorities and devise strategies to combat the threats the alpine ecosystem and its species face in response to continued warming in these regions.

LITERATURE CITED

Allen, T., and J.A. Clarke. 2005. Social learning of food preferences by White-tailed Ptarmigan chicks. Animal Behaviour 79: 305 – 310.

Baasch, D.M., A.J. Tyre, J.J. Millspaugh, S.E. Hygnstrom, and K.C. Vercauteren. 2010. An evaluation of three statistical methods used to model resource selection. Ecological Modeling 221: 565 – 574.

Beers, T.W., P.E. Dress, and L.C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64: 691 - 692.

Beniston, M., H.F. Diaz, and R.S. Bradley. 1997. Climatic change at high elevation sites: an overview. Climate Change 36: 233 – 251.

Bowman, W.D., and T.R. Seastedt [Eds]. 2001. Structure and Function of an Alpine Ecosystem – Niwot Ridge, Colorado. Oxford University Press, Inc. New York, New York, USA.

Boyce, M.S. 2006. Scale for resource selection functions. Diversity and Distributions 12: 269-276.

Braun, C.E. and G.E. Rogers. 1967. Determination of age and sex of the southern white-tailed ptarmigan. Game Information Leaflet 54. Colorado Division of Game, Fish and Parks, Fort Collins, CO.

Braun, C.E. 1969. Population dynamics, habitat, and movements of white-tailed ptarmigan in Colorado. Dissertation. Colorado State University, Fort Collins, CO, USA.

Braun, C. E. 1971. Habitat requirements of Colorado white-tailed ptarmigan. Proceedings of the Western Association of State Game and Fish Commissioners 51: 284 – 292.

Braun, C.E., R.W. Hoffman, and G.E. Rogers. 1976. Wintering areas and winter ecology of white-tailed ptarmigan in Colorado. Special Report 38. Colorado Division of Wildlife, Fort Collins, CO, USA.

Braun, C.E. 1980. Alpine Bird Communities of Western North America: Implications for Management and Research. In Workshop Proceedings: Management of Western Forests and Grasslands for Nongame Birds (R. M. Deraff, technical coordinator). USDA Forest Service General Technical Report. INT-86. Pp. 280-291.

Braun, C.E., Stevens, D.R., Giesen, K.M., and Melcher, C.P., 1991, Elk, white-tailed ptarmigan and willow relationships—A management dilemma in Rocky Mountain National Park: Transactions of the 56th North American Wildlife and Natural Resources Conference, v. 56, p. 74–84.

Braun, C.E., K. Martin, and L.A. Robb.1993. White-tailed ptarmigan (*Lagopus leucura*). In: A. Poole (Ed.) The birds of North America. Cornell Lab of Ornithology, Ithica. Retrieved from the birds of North America. http:/bna.birds.cornell.edu/bna/species/068.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Edition. Springer-Verlag, New York, NY.

Burnham, K.P., and D.R. Anderson. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33(2): 261 – 304.

Butterfield, J., and J.C. Coulson. 1997. Terrestrial invertebrates and climate changeg: physiological and life-cycle adaptations. In: *Past and Future Raid Environmental Change* (eds Huntly, B., W. Cramer, A.V. Morgan, H.C. Prentice, and J.R.M. Allen), Springer, Berlin.

Canfield, R.H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39: 388-394.

Clarke, J.A., and R.E. Johnson. 1992. The Influence of Spring Snow Depth on White-tailed Ptarmigan Breeding Success in the Sierra Nevada. The Condor 94: 622 – 627.

Clow, D.W. 2010. Changes in the Timing of Snowmelt and Streamflow in Colorado: A Response to Recent Warming. Journal of Climate 23:2293-2306.

Cody, M.L. 1985. Habitat Selection in Birds. Academic Press, New York.

Crick, H.Q.P. 2004. The impact of climate change on birds. Ibis 146(Suppl. 1): 48 – 56.

Cumming, G.S. 2000. Using between-model comparisons to fine-tune linear models of species ranges. Journal of Biogeogrpahy 27: 441 – 455.

Daubenmire, R.F. 1959. A canopy-coverage method of vegeation analysis. Northwest Science 33: 43-64.

Dawson, T.P., S.T. Jackson, J.I. House, I.C. Prentice, and G.M. Mace. 2011. Beyond Predictions: Biodiversity Conservation in a Changing Climate. Science 332: 53-57.

EPA (Environmental Protection Agency). 1997. Climate Change and Colorado. Climate and Policy Assessment Division (2111).

Fedy, B., and K. Martin. 2011. The Influence of Fine-scale habitat Features on Regional Variation in Population Performance of Alpine White-tailed Ptarmigan. The Condor 113(2): 306 – 315.

Fielding, A.H., and J.F. Bell. 1997. A review of the methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38 – 49.

Frederick, G.P., and R.J. Gutierrez. 1992. Habitat use and population characteristics of the White-tailed Ptarmigan in the Sierra Nevada, California. Condor 94: 889 – 902.

Giesen, K.M. 1977. Mortality and dispersal of juvenile white-tailed ptarmigan. Thesis. Colorado State University, Fort Collins, CO, USA.

Giesen, K.M., and C.E. Braun. 1979. Nesting behavior of female white-tailed ptarmigan in Colorado. Condor 81: 215-217.

Giesen, K. M., C. E. Braun, and T. A. May. 1980. Reproduction and nest-site selection by white-tailed ptarmigan in Colorado. Wilson Bulletin 92: 188 – 199.

Geisen, K.M., and C.E. Braun. 1992. Winter home range and habitat characteristics of white-tailed ptarmigan in Colorado. The Wilson Bulletin 104(2): 263 – 272.

Gottfried M., H. Pauli, and G. Grabherr. 1998. Prediction of vegetation patterns at the limits of plant life: a new view of the alpine–nival ecotone. Arctic Alpine Research 30: 207–21.

Graf, R.F., K. Bollmann ,W. Wuter, and H. Bugmann. 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. Landscape Ecology 20: 703 – 717.

Gregory, R.D., S.G. Willis, F. Jiguet, P. Vorisek, A. Kivanova, A. Van Strien, B. Huntley, Y.C. Collingham, D. Couvet, and R.E. Green. 2009. An indicator of the impact of climate change in European bird populations. PLoS ONE 4(3): e4678

Guisan, A., and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modeling 135: 147 – 186.

Herzog, P.W. 1977. Summer habitat use by white-tailed ptarmigan in southwestern Alberta. Canadian Field-Naturalist 91: 367 – 371.

Herzog, P.W. 1980. Winter habitat use by white-tailed ptarmigan in southwestern Alberta. Canadian Field-Naturalist 94: 159 – 162.

Hildén, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2: 53 – 75.

Hoffman, R.W. 2006. White-tailed Ptarmigan (Lagopus leucura): A Technical Conservation Assessment. Prepared for the USDA Forest, Rocky Mountain Region, Species Conservation Project, Pp. 1- 72.

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression. Wiley, New York.

Hutton, R.L. 1985. c. Pages 455 – 476 *in* Habitat Selection in Birds (M. L. Cody, Editor). Academic Press, New York.

IPCC (Intergovernmental Panel on Climate Change) 2013. Climate change 2013: the physical science basis. Contrib. Working Grp I to the 5th Assess. Rep. of the Intergovernmental Panel on Climate Change. – Cambridge Univ. Press.

Jedlikowski, J., and M. Brambilla. 2017. The adaptive value of habitat preferences from a multi-scale spatial perspective: insights from marsh-nesting avian species. PeerJ 5:e3164; DOE 10.7717/peerj.3164.

Johnson, R.E. 1968. Temperature regulation in the white-tailed ptarmigan, *Lagopus leucurus.* Comparative Biochemistry and Physiology 24: 1003 – 1014.

Johnson, D.H. 1980. The comparison and usage of availability measurements for evaluating resource preference. Ecology 61: 65 – 71.

Johnson, J.B., and K.S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19(2): 101 – 108.

Johnson, C.J., S.E. Nielsen, E.H. Merrill, T. L. McDonald, and M.S. Boyce. 2006. Resource Selection Functions Base on Use-Availability Data: Theoretical Motivation and Evaluation Methods. Journal of Wildlife Management 70(2): 347 – 357.

Jones, J. 2001. Habitat Selection Studies in Avian Ecology: A Critical Review. The Auk 118(2): 557 – 562.

Keating, K.A., and S. Cherry. 2004. Use and Interpretation of Logistic Regressin in Habitat-Selection Studies. Journal of Wildlife Management 68(4): 774 – 789.

Kraft, B. 2016. Mount Evans Elk Herd Management Plan Data Analysis Unit E-39. Game Management Units 39, 391, 46, and 461. Colorado Parks and Wildlife. Northeast Region, CO.

Krausman, R.P. 1999. Some basic principles of habitat use, grazing behavior of livestock and wildlife. Idaho Forest, Wildlife and Range Experiment Station Bulletin 70: 85–90.

Kristan, W.B. 2006. Sources and expectations for hierarchical structure in bird-habitat associations. Condor 108: 5-12.

Lodge, D.M. 1993. Species invasions and deletions: community effects and responses to climate and habitat change. In P.M. Kareiva, J.G. Kingsolver, and R.B. Huey (Eds.), Biotic interactions and global change (pp.367-387). Sundersland, Massachusetts, USA: Sinauer Associates.

Lukas, J., J. Barsugli, N. Doesken, I. Rangwala, and K. Wolter. 2014. Climate Change in Colorado: A Synthesis to Support Water Resources Mangement and Adaptation. University of Colorado, Boulder: Western Water Assessment, Cooperative Institute for Research in Environmental Sciences (CIRES).

McGavin, G.C. 2000. Insects, Spiders, and Other Terrestrial Arthropods. Dorling Kindersley Ltd., New York, New York.

Mac Nally, R., A.F. Bennett, J.R. Thomson, J.Q. Radford, G. Unmack, G. Horrocks, and P.A. Vesk. 2009. Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. Diversity and Distributions 15: 720 – 730.

Manly, B.F., L.L. McDonald, D.L.Thomas, T.L. McDonald, and W.P. Erikson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Chapman and Hall, New York, New York, USA.

Martin, K., R.F. Holt, and D.W. Thomas. 1993. Getting by on high: ecological energetics of arctic and alpine grouse. Pages 33 – 41 *in* C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, editors. Life in the cold III: ecological, physiological, and molecular mechanisms. Westview Press, Boulder, CO, USA.

Martin, T.E. 2001. Abiotic vs. Biotic Influences on Habitat Selection of Coexisting Species: Climate Change Impacts? Ecology 82(1): 175 – 188.

May, T.A., and C.E. Braun. 1972. Seasonal Foods of Adult White-Tailed Ptarmigan in Colorado. The Journal of Wildlife Management 36(4): 1180 – 1186.

May, T.A., and C.E. Braun. 1973. Gizzard stones from adult white-tailed ptarmigan (*Lagopus leucurus*) in Colorado. Arctic and Alpine Research 5: 49-57.

May, T.A. 1975. Physiological ecology of White-tailed Ptarmigan in Colorado. Ph.D. Dissertation. University of Colorado, Boulder, Colorado.

May, T. A. and C.E. Braun. 1992. Seasonal Foods of Adult White-tailed Ptarmigan in Colorado. The Journal of Wildlife Management 36(4): 1180 – 1186.

McGavin, G.C. 2000. DK Handbooks: Insects, Spiders, and Other Terrestrial Arthropods. Dorling Kindersley Publishing, East Rutherford, NJ, USA.

McLoughlin, P.D., M.S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society 276: 1449-1454.

Montgomery, D.C., and E.A. Peck. 1992. Introduction to Linear Regression Analysis. Wiley, New York.

Moss, R. 1997. Grouse and ptarmigan nutrition in the wild and in captivity. Proceedings of the Nutrition Society 56: 1137-1145.

Nelli, L., A. Meriggi, and A. Franzoi. 2013. Habitat selection by breeding rock ptarmigan *Lagopus muta helvitica* males in the western Italian Alps. Wildlife Biology 19(4): 382 – 389.

Orians, G.H., and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137(Supplement): 29 – 49.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37 – 42.

Pauli, H., M. Gottfried, and G. Grabherr. 1999. Vascular plant distribution patterns at low temperature limites of plant life – the alpine-niveal ecotone of Mount Schrankogel (Tyrol, Austria). Phytocoenologia 29: 297 – 32.

Ray, A.J., J.J. Barsugli, and K.B. Averyt. 2008. Climate change in Colorado: a synthesis to support water resources management and adaptation. A report by the western water assessment for the Colorado water conservation board. CU-NOAA Western Water Assessment, Boulder, CO.

Reid, S., and R. Tibshirani. 2013. Package ‘clogitL1’ [online] CRAN: https://cran.r-project.org/ web/packages/clogitL1/index.html [November 16, 2016].

Revermann, R., N. Zbinden, H. Schmid, R. Spaar, B. Schröder. 2011. Suitable habitat for ptarmigan (Lagopus muta helvita Thienemann 1829) in the Swiss Alps and its response to rapid climate change in the 21st century – a multiscale approach.

Sandercock, B.K., K. Martin, and S.J. Hannon. 2005. Demographic consequences of age structure in extreme environments: population models for arctic and alpine ptarmigan. Oecologia 146: 13 – 24.

Sawa, Y., Y. Takeuchi, and H. Nakamura. 2011. Nest site selection and nesting biology of Rock Ptarmigan *Lagopus muta japonicas* in Japan. Bird Study 58(2): 200 – 207.

Schmidt, Jr., R.K. 1988. Behavior of white-tailed ptarmigan during the breeding season. Pages 270-299 in A.T. Bergerud and M.W. Gratson, editors. Adaptive strategies and population ecology of northern grouse, volume I: population studies. University of Minnesota Press, MN, USA.

Storch, I. 2000. Conservation status and threats to grouse worldwide: an overview. Wildlife Biology 6: 195 – 204.

Storch, I. 2002. On spatial resolution in habitat models: can small-scale forest structure explain Capercaillie numbers? Conservation Ecology 6(1): 6.

Therneau, T.M. 2015. Package ‘clogit’ [online] CRAN: https://cran.r-project.org/web/packages/survival/survival.pdf [August 9, 2016].

Theurillat, J.P., and A. Guisan. 2001. Potential impact of climate change on vegetation in the European Alps: a review. Climate Change 50: 77 – 109.

Walther, G.R., E. Post, P. Coney, A. Menze, C. Parmesan, R.J.C. Beebee, J.M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416: 389 – 395.

Wann, G.T., C.L. Aldridge, and C.E. Braun. 2016. Effects of Seasonal Weather on Breeding Phenology and Reproductive Success on Alpine Ptarmigan in Colorado. PLoS ONE 11(7): e0158913. doi: 10.1371/journal.pone.0158919.

Weeden, R.B. 1967.Seasonal and geographic variation in the foods of adult white-tailed ptarmigan. Condor 69: 303-309.

Wenger, S.J., and J.D. Olden. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods in Ecology and Evolution 3(2): 260 – 267.

Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wiebe, K.L., and K. Martin. 1997. Effects of predation, body condition and temperature on incubation rhythms of white-tailed ptarmigan. Wildlife Biology 3: 143 – 151.

Wiebe, K.L., and K. Martin. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. Animal Behavior 56: 1137 – 1144.

Wiebe, K.L., and K. Martin. 2000. The use of incubation behavior to adjust avian reproductive costs after egg laying. Behavioral Ecology and Sociobiology 48: 463-470.

Wiens, J.A. 1985. Habitat selection in variable environments: shrub-steppe birds. Pages 227-251 *in* Habitat Selection in Birds (M. L. Cody, Editor). Academic Press, New York.

Winkler, D.E., K.J. Chapin, and L.M. Kueppers. 2016. Soil moisture mediates alpine life form and community productivity responses to warming. Ecology 97(6) 1553-1563.

Williams, K.J., L. Belbin, M.P. Austin, J.L. Stein, and S. Ferrier. 2012. Which environmental variables should I use in my biodiversity model? International Journal of Geographical Information Science 26(11): 2009 – 2047.

Wilson, S., and K. Martin. 2008. Breeding habitat selection of sympatric White-tailed, Rock and Willow Ptarmigan in the southern Yukon Territory, Canada. Journal of Ornithology 149: 629 – 637.

Zeigenfuss, L.C. 2006. Alpine plant community trends on the elk summer range of Rocky Mountain National Park, Colorado: an analysis of existing data. U.S. Geological Survey, Fort Collins Science Center, Open-file Report 2006-1122, 21 pp.

Zerba, E., and M.L. Morton 1983. Dynamics of incubation in mountain white-crowned sparrows. Condor 85: 1-11.

Zwickel, F.C., and J.F. Bendell. 1967. A snare for capturing blue grouse. Journal of Wildlife Management 31: 202 – 204.

Table 3.1 – Hypotheses and predictions posited to assess nest and brood site habitat selection by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Evaluation of habitat selection was conducted at two scales: (1) mesohabitat scale (habitat patch surrounding nest and brood sites), and (2) microhabitat scale (central location of nest and brood sites) to determine at which order of scale factors of habitat selection by white-tailed ptarmigan are most important.

Hypothesis Number	Hypothesis	Prediction Number	Prediction
1	Nest and brood site habitat characteristics at use sites will be different among sampled populations at each study site	1	Ptarmigan will use different nest and brood sites (e.g., % of rock cover, specific vegetation forage), will vegetation driving these differences
2	Habitat characteristics (i.e., presence of willow [*Salix spp.*]) will be important to habitat selection of nest and brood sites, but will be different depending upon study site	2	Willow (*Salix spp.*) will not be important for ptarmigan nest and brood site habitat selection at Rocky Mountain National Park
		3	The following forage species will be defining characteristics of ptarmigan nest and brood sites: - Sedges (*Carex spp.*) - Alpine avens (*Geum rossii*) - Bistort species (*Bistorta bistortoides* and *Polygonum viviparum*) - Mountain-meadow cinquefoil (*Potentilla diversifolia*) - Buttercup species (*Ranunculus spp.*) - Willows (*Salix spp.*) - Clovers (*Trifolium spp.*)

Table 3.2 – Description of predictor covariates, including predictor category and covariate type, for the evaluation of habitat selection by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Evaluation of habitat selection was conducted at two scales: (1) mesohabitat scale (habitat patch surrounding nest and brood sites), and (2) microhabitat scale (central location of nest site) to determine at which order of scale factors of habitat selection by white-tailed ptarmigan are most important.

No.	**Covariate**	**Predictor Category**	**Description**
1	Aspect	Abiotic	Aspect (degrees) of nest or brood site
2	Bare Ground	Abiotic	% of bare ground cover measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
3	Boulder Distance	Abiotic	Distance to (m) nearest boulders at nest or brood site
4	Dominant Species	Biotic	Top 4 dominant species recorded at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
5	Elevation	Abiotic	Elevation (m) of nest or brood site
6	Forage Forbs	Biotic	% of forage forbs cover measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
7	Forage Forbs Height	Biotic	Height of tallest forage forbs measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
8	Graminoids	Biotic	% of graminoid cover measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
9	Graminoid Height	Biotic	Height of tallest graminoid measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
10	Hen Age	Biotic	Age of hen when nest or brood site was measured (sub-adult; SA = 0 or adult; A = 1)
11	Litter	Abiotic	% of litter cover at each measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
12	Other Forage Forbs	Biotic	% of other forb cover measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
13	Other Forb Height	Biotic	Height of tallest other forb measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
14	Rock/Gravel	Abiotic	% of rock or gravel cover measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
15	Shrub Cover	Biotic	% of shrubs cover measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
16	Shrub Height	Biotic	Height of tallest shrubs measured at each designated Daubenmire plot along upper, middle, and lower transect lines at nest or brood site
17	Site	Spatial	Number that delineated between the 2 study sites (Mt. Evans = 0 or RMNP = 1)
18	Slope	Abiotic	Slope (degrees) of nest or brood site
19	Snow/Snowfield Distance	Abiotic	Distance to (m) nearest snow/snowfield at nest or brood site
20	Standing Water Distance	Abiotic	Distance to (m) nearest standing water at nest or brood site
21	Shrub Distance	Biotic	Distance to (m) nearest shrubs at nest or brood site
22	Wind Speed	Abiotic	Average of 3 wind speeds (mph) taken at nest or brood site
23	Year	Temporal	Year nest or brood site was sampled

Table 3.3 – Dominance of specific vegetation species for the evaluation of nest and brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Dominance of vegetation species was calculated from a weighted dominance rank within each ¼ m^2 Daubenmire plot, and summed across the nine plots at each sampled site, and then divided by the number of sampled sites depending upon the breeding stage (nest sites: *n* = 122; brood sites: *n* = 108).

No.	**Scientific Name**	**Common Name**	**Coverage Category**	**Dominance of Plants Per Breeding Site (%)**			
				Nest Sites		**Brood Sites**	
				Use	**Available**	**Use**	**Available**
1	*Achillea alpicola*	Alpine Yarrow	Other Forb	4.10	5.74	1.85	2.78
2	*Agropyron* spp.	Wheatgrass Spp.	Graminoid	0.00	0.00	0.00	3.70
3	*Androsace chamaejasme*	Rock Jasmine	Forage Forb	1.64	0.82	0.00	1.85
4	*Angelica grayi*	Angelica	Other Forb	0.82	0.00	0.00	0.93
5	*Aquilegia alpina*	Blue Columbine	Forage Forb	0.82	0.00	0.00	0.00
6	*Arenaria fendleri*	Fendler's Sandwort	Forage Forb	19.67	18.03	13.89	14.81
7	*Arenaria obtusiloba*	Alpine Sandwort	Forage Forb	13.93	11.48	19.44	25.00
8	*Artemisia arctica*	Boreal Sagebrush	Forage Forb	37.70	31.15	37.96	34.26
9	*Artemisia scopulorum*	Alpine Sagebrush	Forage Forb	6.56	4.92	6.48	7.41
10	*Artemisia* spp.	Alpine sagebrush spp.	Forage Forb	1.64	1.64	3.70	4.63
11	*Bistorta bistortoides*	American Bistort	Forage Forb	22.13	25.41	20.37	19.44
12	*Campanulaceae rotundifolia*	Mountain Hairbell	Forage Forb	0.82	0.82	0.00	0.00
13	*Carex albonigra*	Black-and-white Sedge	Graminoid	8.20	10.66	5.56	3.70
14	*Carex nigricans*	Alpine Black Sedge	Graminoid	12.30	11.48	11.11	13.89
15	*Carex norvegica*	Norway Sedge	Graminoid	4.92	6.56	5.56	5.56
16	*Carex pyrenacia*	Pyrennian Sedge	Graminoid	0.00	0.00	0.93	0.93
17	*Carex* spp.	Sedge Spp.	Graminoid	27.87	29.51	29.63	27.78
18	*Castillega occidentalis*	Yellow Paintbrush	Other Forb	7.38	7.38	9.26	8.33
19	*Cerastium alpinum*	Alpine Chickweed	Forage Forb	5.74	4.10	0.00	2.78
20	*Cercocarpus montanus*	Alder-leaf Mountain Mahogany	Shrub/Tree	0.00	0.82	0.00	0.00

Table 3.3 continued

No.	**Scientific Name**	**Common Name**	**Coverage Category**	**Dominance of Plants Per Breeding Site (%)**			
				Nest Sites		**Brood Sites**	
				Use	**Available**	**Use**	**Available**
21	*Cirsium scopulorum*	Frostball Thistle	Other Forb	5.74	5.74	5.56	2.78
22	*Claytonia lanceolata*	Lanceleaf Spring Beauty	Forage Forb	0.82	0.82	1.85	1.85
23	*Claytonia megarhiza*	Alpine Spring Beauty	Forage Forb	1.64	1.64	0.00	0.93
24	*Deschampsia caespitosa*	Tufted Hairgrass	Graminoid	25.41	24.59	27.78	22.22
25	*Dryas octopetala*	Mountain Dryad	Forage Forb	8.20	4.10	9.26	11.11
26	*Ericaceace* spp.	Heath spp.	Shrub/Tree	3.28	0.82	0.00	0.00
27	*Erigeron melanocephalus*	Black-Headed Daisy	Forage Forb	1.64	1.64	0.00	0.93
28	*Erigeron simplex*	One-Headed Daisy	Forage Forb	9.02	7.38	8.33	5.56
29	*Erysimum capitatum*	Alpine Wallflower	Forage Forb	0.82	0.00	0.00	0.93
30	*Gaultheria humifusa*	Alpine Wintergreen	Other Forb	0.00	1.64	0.00	0.00
31	*Gentianodes algida*	Arctic Gentian	Forage Forb	3.28	4.92	12.04	8.33
32	*Geranium* spp.	Geranium spp.	Other Forb	0.82	0.82	0.00	0.93
33	*Geum rossii*	Alpine Avens	Forage Forb	38.52	41.80	48.15	46.30
34	*Heterotheca pumila*	Alum Root	Other Forb	0.00	0.00	0.93	0.93
35	*Juncus* spp.	Rush spp.	Graminoid	0.00	0.82	0.93	0.00
36	*Kobresia myosuroides*	Kobresia	Graminoid	22.95	25.41	29.63	32.41
37	*Lepidium montanum var alpinum*	Alpine Peppergrass	Graminoid	9.84	9.84	6.48	12.04
38	*Luzula spicata*	Spike Woodrush	Graminoid	0.00	0.00	0.93	3.70
39	*Luzula* spp.	Wood-rush spp.	Graminoid	0.00	0.82	0.93	0.00
40	*Mertensia alpina*	Alpine Bluebells	Forage Forb	4.92	3.28	1.85	1.85
41	*Mertensia lanceolata*	Greenleaf Chiming Bells	Forage Forb	4.10	4.10	5.56	7.41
42	*Moss* spp.	Moss spp.	Forage Forb	0.00	1.64	2.78	1.85
43	*Oreoxis alpina*	Alpine Parsley	Forage Forb	0.00	2.46	0.00	0.93
44	*Oxyria digyna*	Alpine Sorrel	Forage Forb	1.64	0.82	2.78	0.93
45	*Paronychia pulvinata*	Alpine Nailwort	Other Forb	0.00	0.00	0.93	0.93

Table 3.3 continued

No.	**Scientific Name**	**Common Name**	**Coverage Category**	**Dominance of Plants Per Breeding Site (%)**			
				Nest Sites		**Brood Sites**	
				Use	**Available**	**Use**	**Available**
46	*Pedicularis groenlandica*	Elephant Head	Forage Forb	2.46	2.46	0.00	0.93
47	*Pedicularis* spp.	Lousewort spp.	Forage Forb	0.82	1.64	0.93	0.00
48	*Pedicularis sudetica*	Alpine Lousewort	Forage Forb	0.00	0.82	0.00	0.00
49	*Penstemon whippleanus*	Alpine Dusky Beardtongue	Other Forb	0.82	0.00	0.00	0.93
50	*Phlox condensata*	Alpine Phlox	Forage Forb	1.64	3.28	0.93	1.85
51	*Picea engelmannii*	Engelmann Spruce	Shrub/Tree	15.57	10.66	3.70	3.70
52	*Poa alpina*	Alpine Bluegrass	Graminoid	20.49	18.85	11.11	11.11
53	*Poa* spp.	Bluegrass Spp.	Graminoid	18.03	18.03	32.41	25.00
54	*Polemonium reptans*	Jacob's Ladder	Other Forb	6.56	1.64	0.00	0.93
55	*Polemonium viscosum*	Sky Pilot	Other Forb	0.00	0.00	0.00	1.85
56	*Polygonum viviparum*	Alpine Bistort	Forage Forb	18.85	20.49	22.22	21.30
57	*Potentilla diversifolia*	Mountain-Meadow Cinquifoil	Forage Forb	15.57	21.31	17.59	14.81
58	*Primula parryi*	Parry's Primrose	Forage Forb	0.00	0.82	0.00	0.00
59	*Psychrophila leptosepala*	Marsh Marigold	Forage Forb	0.00	1.64	0.93	0.93
60	*Pulsatilla alpina*	Alpine Pasque Flower	Other Forb	0.82	0.00	0.00	0.93
61	*Ranunculus adoneus*	Snow Buttercup	Other Forb	0.82	0.00	0.00	0.00
62	*Rhodiola rhodantha*	Queen's Crown	Other Forb	0.82	0.82	0.00	0.00
63	*Rhydebergia grandiflora*	Old Man of the Mountain	Other Forb	4.92	5.74	1.85	3.70
64	*Salix arctica*	Willow	Shrub/Tree	2.46	0.82	0.93	1.85
65	*Salix* spp.	Willow Spp.	Shrub/Tree	23.77	20.49	16.67	20.37
66	*Saxifraga oregano*	Snowball Saxifrage	Forage Forb	2.46	0.82	0.00	0.00
67	*Saxifraga rhomboidea*	Brook Saxifrage	Forage Forb	0.82	0.00	0.93	0.93
68	*Sedum lanceolatum*	Yellow Stonecrop	Forage Forb	12.30	8.20	4.63	8.33
69	*Sedum rosea*	King's Crown	Forage Forb	5.74	5.74	4.63	7.41
70	*Sibbaldia procumbens*	Creeping Sibbaldia	Forage Forb	1.64	0.00	0.00	0.00

Table 3.3 continued

No.	Scientific Name	Common Name	Coverage Category	Dominance of Plants Per Breeding Site (%)			
				Nest Sites		**Brood Sites**	
				Use	**Available**	**Use**	**Available**
71	*Silene acaulis*	Moss Campion	Forage Forb	8.20	6.56	10.19	6.48
72	*Taraxacum officinale*	Dandelion	Forage Forb	0.82	0.82	0.00	0.00
73	*Trifolium dasyphyllum*	Alpine Clover	Forage Forb	16.39	16.39	20.37	18.52
74	*Trifolium nanum*	Dwarf Clover	Forage Forb	3.28	3.28	6.48	2.78
75	*Trifolium parryi*	Parry's Clover	Forage Forb	18.03	18.85	27.78	27.78
76	*Trifolium* spp.	Clover Spp.	Forage Forb	13.11	8.20	12.04	13.89
77	*Trisetum spicatum*	Spike Trisetum	Graminoid	11.48	5.74	5.56	4.63
78	*Trisetum* spp.	Oatgrass spp.	Graminoid	2.46	0.82	2.78	0.93
79	*Vaccinium* spp.	Bilberry/Blueberry spp.	Other Forb	6.56	2.46	1.85	1.85
80	*Viola* spp.	Violet spp.	Other Forb	0.82	0.82	0.00	0.00
81	----	Unknown Forb	Other Forb	3.28	9.02	2.78	3.70
82	----	Unknown Grass	Graminoid	2.46	3.28	0.93	0.93
83	----	Unknown Shrub/Tree	Shrub/Tree	0.00	0.82	0.00	0.00
84	----	Unknown spp.	---	0.00	0.82	0.00	0.00

Table 3.4 – Abundance of insects collected for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Abundance of insects was calculated from counts of insects on flypaper traps positioned on the four outside corners of each sampled site (Figure 3.1). Abundances were adjusted (divided) by the total trap days (total days x number of traps recovered). Insects are listed in order of most to least dominant.

No.	**Insect Family or Species**	**Common Name**	**Insect Order**	***Adjusted* Abundance**		
				Use	**Available**	**Total**
1	*Muscidae*	House Flies	*Diptera*	353.67	290.78	644.45
2	*Phoridae*	Hump-backed Flies	*Diptera*	111.45	170.14	281.59
3	*Cynipoidea*	Gall Wasp	*Hymenoptera*	46.47	49.91	96.37
4	*Cicadellidae*	Leafhopper	*Hemiptera*	35.06	26.31	61.36
5	*Aeropedellus clavatus*	Club-horned Grasshopper	*Orthoptera*	19.02	9.63	28.64
6	*Boloria* spp.	Butterflies and Moths	*Lepidoptera*	6.24	2.44	8.69
7	*Formicidae*	Ant	*Hymenoptera*	3.37	1.22	4.59
8	*Eulophidae*	Parasitic Wasp	*Hymenoptera*	1.92	2.17	4.09
9	*Parnassius smintheus*	Rocky Mountain Parnassian	*Lepidoptera*	1.31	1.87	3.18
10	*Carabidae*	Ground Beetle	*Coleoptera*	1.18	1.49	2.67
11	*Arachnid* spp.	Spiders	*Araneae*	1.27	0.81	2.09
12	*Colias meadii*	Mead's Sulphur Butterfly	*Lepidoptera*	0.79	1.2	1.99
13	*Other Coleoptera* spp.	Beetle	*Coleoptera*	0.43	0.42	0.85
14	*Syrphidae*	Hoverfly	Diptera	0.1	0.63	0.73
15	*Mecoptera* spp.	Scorpion Flies	*Mecoptera*	0.5	0.12	0.63
16	*Other* spp.	----	----	0.57	0	0.57
17	*Hesperitidae*	Skipper	*Lepidoptera*	0.56	0	0.56
18	*Ichneumonidea*	Ichneumon Wasp	*Hymenoptera*	0.18	0.21	0.39
19	*Tenthredinidae*	Saw Flies	Hymenoptera	0.3	0.08	0.38
20	*Bombyliidae*	Bee Fly	*Diptera*	0.12	0.19	0.31
21	*Geomitridae*	Geometrid Moth	*Lepidoptera*	0.23	0.08	0.31
22	*Tipulidae*	Crane Flies	Diptera	0.2	0.08	0.28
23	*Coccinellidae*	Ladybird	*Coleoptera*	0	0.06	0.06
24	*Noctuidae*	Butterflies and Moths	*Lepidoptera*	0	0	0

Table 3.5 – Habitat and environmental characteristics measured at nest and brood use and available (random) sites for the evaluation of habitat selection by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Data are equivalent across the patch and site scales, due to measurements taken at center point (T2 – 5M; Figure 3.1**)** of sampled sites. Values are means (±1 SE).

Covariate	**Predictor Category**	**Patch and Site Scale**			
		Nest	**Random**	**Brood**	**Random**
Aspect (transformed)	Abiotic	1.04 (0.09)	0.97 (0.08)	1.07 (0.07)	1.11 (0.07)
Elevation (m)	Abiotic	3652.15 (26.49)	3684.11 (23.03)	3716.78 (18.91)	3744.48 (16.64)
Slope (º)	Abiotic	14.36 (1.29)	13.85 (1.21)	14.44 (0.82)	13.13 (0.81)
Wind (mph)	Abiotic	3.31 (0.52)	3.69 (0.65)	3.99 (0.41)	4.43 (0.40)
Distance To (m)					
Boulder	Abiotic	4.10 (1.02)	5.56 (1.99)	3.23 (0.53)	3.46 (0.97)
Snow/Snowfield	Abiotic	179.82 (32.04)	174.14 (31.47)	213.65 (16.62)	211.46 (29.57)
Standing Water	Abiotic	129.44 (27.36)	139.22 (29.67)	93.92 (11.36)	94.50 (19.30)
Shrub	Biotic	12.53 (5.02)	18.67 (7.57)	70.72 (11.48)	59.99 (16.40)

Table 3.6 – Vegetation characteristics measured at nest and brood locations and paired dependent available (random) at the patch scale, and measured at nests at the site scale, for the evaluation of habitat selection by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Values are means (±1 SE).

Covariate	**Predictor Category**	**Patch Scale**				**Site Scale**	
		Nest	**Random**	**Brood**	**Random**	**Nest**	**Random**
Cover (%)							
Bare Ground	Abiotic	7.28 (1.14)	7.84 (1.21)	6.14 (0.49)	6.79 (0.58)	6.64 (1.42)	9.16 (1.83)
Forage Forbs	Biotic	23.07 (1.79)	20.77 (1.62)	31.62 (1.13)	27.09 (1.28)	15.03 (2.09)	25.34 (2.85)
Graminoid	Biotic	14.69 (1.34)	18.42 (1.68)	20.40 (1.09)	19.62 (1.20)	11.54 (1.96)	23.15 (2.98)
Litter	Abiotic	7.73 (0.92)	8.20 (1.05)	10.81 (0.72)	10.22 (0.64)	8.56 (1.60)	9.38 (1.51)
Other Forage Forbs	Biotic	3.37 (0.48)	4.34 (0.87)	2.09 (0.17)	2.71 (0.34)	2.25 (0.85)	3.49 (0.94)
Rock/Gravel	Abiotic	22.46 (2.12)	26.98 (2.85)	25.45 (1.30)	28.20 (2.01)	18.57 (3.00)	22.39 (3.07)
Shrub	Biotic	22.14 (3.26)	14.39 (2.79)	4.75 (0.99)	4.43 (0.68)	38.38 (5.03)	7.44 (2.44)
Height (cm)							
Forage Forbs	Biotic	10.90 (0.66)	10.55 (0.80)	13.42 (0.50)	11.73 (0.57)	11.38 (1.34)	13.80 (1.35)
Graminoid	Biotic	13.08 (0.88)	13.93 (0.92)	15.81 (0.54)	14.63 (0.67)	12.16 (1.30)	16.57 (1.23)
Other Forage Forbs	Biotic	4.64 (0.46)	4.32 (0.48)	4.66 (0.29)	4.31 (033)	3.72 (0.84)	4.25 (0.84)
Shrub	Biotic	28.23 (6.56)	20.00 (7.95)	3.60 (0.89)	2.93 (0.42)	53.77 (20.24)	5.66 (1.65)

Table 3.7 – Results of univariable case-control logistic regression models for the evaluation of nest habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine study sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data with parameter estimates (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's *z*-statistic, Bayesian Information Criteria (BIC). The parameter estimate with bold text showed a strong effect based confidence intervals that did not overlap zero.

Covariate Model	Predictor Category	β	95% CI	exp(β)	Wald's z	BIC
Aspect (transformed)	Abiotic	0.08	(-0.24, 0.40)	1.08	0.47	88.46
Elevation (m)	Abiotic	-0.66	(-1.54, 0.22)	0.52	-1.47	85.73
Slope (º)	Abiotic	0.06	(-0.32, 0.44)	1.06	0.31	88.58
Wind (mph)	Abiotic	-0.19	(-0.75, 0.36)	0.82	-0.69	88.19
Cover (%)						
Bare Ground	Abiotic	-0.13	(-0.64, 0.39)	0.88	-0.48	88.44
Forage Forbs	Biotic	0.33	(-0.18, 0.83)	1.39	1.27	86.98
Graminoid	**Biotic**	**-0.60**	**(-1.14, -0.07)**	**0.55**	**-2.22**	**83.15**
Litter	Abiotic	-0.11	(-0.58, 0.36)	0.90	-0.45	88.47
Other Forage Forbs	Biotic	-0.22	(-0.67, 0.22)	0.80	-0.98	87.55
Rock/Gravel	Abiotic	-0.38	(-0.86, 0.09)	0.68	-1.58	86.04
Rock/Gravel^2	Abiotic	-1.69	(-3.43, 0.03)	0.19	-1.92	85.40
Shrub	**Biotic**	**0.65**	**(0.08, 1.22)**	**1.91**	**2.22**	**82.71**
Distance To (m)						
Boulder	Abiotic	-0.12	(-0.49, 0.25)	0.89	-0.62	88.26
Snow/Snowfield	Abiotic	0.33	(-0.47, 1.13)	1.40	0.82	87.97
Standing Water	Abiotic	-0.06	(-0.74, 0.63)	0.95	-0.16	88.65
Shrub	Biotic	-0.39	(-1.04, 0.26)	0.68	-1.18	87.10
Height (cm)						
Forage Forbs	Biotic	0.16	(-0.41, 0.72)	1.17	0.54	88.38
Graminoid	Biotic	-0.34	(-0.95, 0.27)	0.71	-1.09	87.44
Other Forage Forbs	Biotic	0.12	(-0.30, 0.55)	1.13	0.56	88.36
Shrub	Biotic	0.30	(-0.25, 0.85)	1.35	1.06	87.41

Table 3.8 – Results of candidate multivariable case-control logistic regression models for the evaluation of nest site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Models listed are comparisons among top nest model versus other models when coverage categories (i.e., forage forb and shrub and willow percentage) are substituted with specific vegetation species. Results presented are model rank based on ascending Bayesian Information Criteria (BIC), with covariate model structure, number of parameters (k), chi-square likelihood ratio test statistic (χ^2), and Bayesian weight (w_i).

Rank	**Model**	***k***	**χ^2**	**BIC**	**ΔBIC**	**w_i**
1	Forage Forbs Cover + Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover	4	27.56	73.45	0.00	1.00
2	*Arenaria obtusiloba*+ Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover	4	20.05	80.95	7.50	0.00
3	Forage Forbs Cover + *Salix* spp.	2	7.83	84.95	11.50	0.00
4	Rock/Gravel Cover + Rock/Gravel^2 Cover + *Salix* spp. + *Trifolium parryi*	4	14.73	86.28	12.83	0.00

Table 3.9 – Results of candidate multivariable case-control logistic regression models including species specific vegetation for the evaluation of nest site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Models listed are the top 10 models compared among the 4 modeling scenarios: (1) top nest model including forage forb percentage + rock and gravel percentage + rock and gravel^2 percentage + shrub and willow percentage; (2) nine forage forb species + rock and gravel percentage + rock and gravel^2 percentage + shrub and willow percentage; (3) nine forage forb species + rock and gravel percentage + rock and gravel^2 percentage + *Salix spp.*; and (4) forage forb percentage + rock and gravel percentage + rock and gravel^2 percentage + *Salix spp.* Results presented are model rank based on ascending Bayesian Information Criteria (BIC), with covariate model structure, number of parameters (*k*), chi-square likelihood ratio test statistic (χ^2), and Bayesian weight (w_i).

Rank	**Model**	***k***	χ^2	**BIC**	**ΔBIC**
1	Forage Forbs Cover + Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover	4	27.56	73.45	0.00
2	Forage Forbs Cover + Shrub Cover	2	17.30	75.49	2.04
3	Forage Forbs Cover + Rock/Gravel Cover + Shrub Cover	3	18.58	78.32	4.87
4	Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover	3	17.36	79.54	6.09
5	*Arenaria obtusiloba* + Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover	4	20.05	80.95	7.50
6	*Geum rossii* + Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover	4	20.02	80.99	7.54
7	*Arenaria obtusiloba* + *Geum rossi* + Rock/Grave Cover + Rock/Gravel^2 Cover + Shrub Cover	5	23.76	81.36	7.91
8	Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover + *Trifolium parryi*	4	18.36	82.65	9.20
9	*Arenaria obtusiloba* + Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover + *Trifolium parryi*	5	22.23	82.89	9.44
10	Rock/Gravel Cover + Rock/Gravel^2 Cover + Shrub Cover + *Trifolium dasyphyllum*	4	17.91	83.09	9.64

Table 3.10 – Results of top multivariable case-control logistic regression model for the evaluation of nest site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data with estimated beta-coefficients (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's z-statistic. The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero.

Covariate	β	95% CI	exp(β)	Wald's z
Forage Forb Cover	1.42	(0.44, 2.40)	4.15	2.84
Rock/Gravel Cover	3.41	(0.94, 5.87)	30.25	2.71
Rock/Gravel^2 Cover	-3.20	(-5.60, -0.81)	0.04	-2.62
Shrub Cover	2.35	(1.02, 3.67)	10.46	3.48

Table 3.11 – Results of univariable case-control logistic regression models for the evaluation of nest site habitat selection at the site scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data with estimated beta-coefficients (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's z-statistic, Bayesian Information Criteria (BIC). The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero.

Covariate Model	Predictor Category	β	exp(β)	SE	95% CI	Wald's z	BIC
Aspect (transformed)	Abiotic	0.08	1.09	0.17	(-0.25, 0.42)	0.49	89.13
Elevation (m)	Abiotic	-0.67	0.51	0.45	(-1.56, 0.22)	-1.47	85.70
Slope (º)	Abiotic	0.08	1.08	0.23	(-0.36, 0.52)	0.36	88.55
Wind (mph)	Abiotic	-0.22	0.80	0.31	(-0.83, 0.38)	-0.73	88.12
Cover (%)							
Bare Ground	Abiotic	-0.29	0.75	0.23	(-0.75, 0.17)	-1.25	86.98
Forage Forbs	Biotic	-0.65	0.52	0.24	(-1.12, -0.18)	-2.68	79.44
Graminoid	Biotic	-0.80	0.45	0.29	(-1.36, -0.25)	-2.82	76.72
Litter	Abiotic	-0.08	0.93	0.19	(-0.56, 0.30)	-0.40	88.52
Other Forage Forbs	Biotic	-0.21	0.81	0.21	(-0.63, 0.21)	-1.00	87.57
Rock/Gravel	Abiotic	-0.20	0.82	0.20	(-0.60, 0.20)	-0.97	87.71
Shrub	Biotic	1.93	6.92	0.65	(0.66, 3.20)	2.99	56.23
Distance To (m)							
Boulder	Abiotic	-0.12	0.89	0.19	(-0.49, 0.25)	-0.62	88.26
Snow/Snowfield	Abiotic	0.35	1.42	0.42	(-0.47, 1.18)	0.84	87.93
Standing Water	Abiotic	-0.06	0.95	0.35	(-0.74, 0.63)	-0.16	88.65
Shrub	Biotic	-0.39	0.68	0.33	(-1.04, 0.26)	-1.18	87.10
Height (cm)							
Forage Forbs	Biotic	-0.30	0.74	0.22	(-0.73, 0.12)	-1.41	86.57
Graminoid	Biotic	-0.62	0.54	0.25	(-1.10, -0.13)	-2.50	81.03
Other Forage Forbs	Biotic	-0.10	0.91	0.20	(-0.49, 0.30)	-0.49	88.43
Shrub	Biotic	7.85	2554.44	2.49	(2.97, 12.72)	3.15	64.04

Table 3.12 – Results of multivariable case-control logistic regression models for the evaluation of nest site habitat selection at the site scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are model rank based on ascending Bayesian Information Criteria (BIC), with covariate model structure, number of parameters (k), chi-square likelihood ratio test statistic (χ^2), and Bayesian weight (w_i).

Rank	**Model**	***k***	χ^2	**BIC**	**ΔBIC**	w_i
1	Elevation + Graminoid Cover	2	15.53	77.26	0.00	0.42
2	Bare Ground Cover + Graminoid Cover	2	15.46	77.32	0.06	0.41
3	Bare Ground + Elevation + Graminoid Cover	3	17.88	79.01	1.75	0.17
4	Forage Forbs Height + Graminoid Cover	2	12.03	80.76	3.50	0.00
5	Bare Ground Cover + Forage Forbs Height + Graminoid Cover	3	15.71	81.18	3.92	0.00
6	Elevation + Forage Forbs Height + Graminoid Cover	3	15.66	81.24	3.98	0.00
7	Bare Ground Cover + Elevation + Forage Forbs Height + Graminoid Cover	4	18.12	82.88	5.62	0.00
8	Elevation + Forage Forbs Height	2	5.27	87.51	10.25	0.00
9	Bare Ground Cover + Forage Forbs Height	2	4.44	88.35	11.09	0.00
10	Bare Ground Cover + Elevation	2	4.06	88.73	11.47	0.00

Table 3.13 – Results of multivariable case-control logistic regression model for the evaluation of nest site habitat selection at the site scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data with estimated beta-coefficients (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's z-statistic. The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero.

Covariate	**β**	**95% CI**	**exp(β)**	**Wald's z**
Elevation	-0.79	(-1.78, 0.20)	0.45	-1.57
Graminoid Cover	-0.87	(-1.47, -0.26)	0.42	-2.82

Table 3.14 – Results of univariable case-control logistic regression models for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data with estimated beta-coefficients (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's z-statistic, Bayesian Information Criteria (BIC).

Covariate Model	**Predictor Category**	**β**	**95% CI**	**exp(β)**	**Wald's z**	**BIC**
Aspect (transformed)	Abiotic	-0.07	(-0.47, 0.33)	0.94	-0.32	78.75
Elevation (m)	Abiotic	-0.63	(-1.68, 0.43)	0.53	-1.17	76.77
Slope (º)	Abiotic	0.29	(-0.25, 0.84)	1.34	1.06	77.69
Wind (mph)	Abiotic	-0.17	(-0.68, 0.33)	0.84	-0.68	78.35
Cover (%)						
Bare Ground	Abiotic	-0.22	(-0.75, 0.31)	0.80	-0.81	78.18
Forage Forbs	Biotic	0.45	(-0.03, 0.93)	1.57	1.84	74.91
Graminoid	Biotic	0.07	(-0.33, 0.47)	1.07	0.34	78.73
Litter	Abiotic	0.13	(-0.36, 0.62)	1.14	0.53	78.56
Other Forage Forbs	Biotic	-0.26	(-0.72, 0.20)	0.77	-1.10	77.45
Rock/Gravel	Abiotic	-0.16	(-0.56, 0.24)	0.85	-0.80	78.20
Rock/Gravel^2	Abiotic	-2.62	(-4.76, -0.47)	0.07	-2.39	73.64
Shrub	Biotic	0.05	(-0.39, 0.48)	1.05	0.21	78.81
Distance To (m)						
Boulder	Abiotic	-0.18	(-1.05, 0.69)	0.83	-0.41	78.68
Snow/Snowfield	Abiotic	0.22	(-0.68, 1.12)	1.25	0.48	78.61
Standing Water	Abiotic	-0.10	(-0.69, 0.49)	0.91	-0.32	78.74
Shrub	Biotic	-0.63	(-1.28, 0.02)	0.53	-1.91	74.11
Height (cm)						
Forage Forbs	Biotic	0.37	(-0.08, 0.83)	1.45	1.60	76.04
Graminoid	Biotic	0.27	(-0.20, 0.74)	1.31	1.11	77.56
Other Forage Forbs	Biotic	0.17	(-0.32, 0.66)	1.19	0.69	78.36
Shrub	Biotic	0.11	(-0.33, 0.56)	1.12	0.50	78.58

Table 3.15 – Results of candidate multivariable case-control logistic regression models for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are model rank based on ascending Bayesian Information Criteria (BIC), with covariate model structure, number of parameters (k), chi-square likelihood ratio test statistic (χ^2), and Bayesian weight (w_i).

Rank	**Model**	k	χ^2	**BIC**	**ΔBIC**	w_i
1	Shrub Distance + Rock/Gravel Cover + Rock/Gravel^2 Cover	3	15.45	71.38	0.00	1.00
2	Rock/Gravel Cover + Rock/Gravel^2 Cover	2	9.20	73.64	2.26	0.00
3	Shrub Distance + Forage Forbs Cover + Rock/Gravel Cover + Rock/Gravel^2 Cover	4	16.12	74.70	3.32	0.00
4	Shrub Distance + Forage Forbs Cover	2	7.55	75.29	3.91	0.00
5	Forage Forbs Cover + Rock/Gravel Cover + Rock/Gravel^2 Cover	3	10.50	76.33	4.95	0.00
6	Shrub Distance + Rock/Gravel Cover	2	4.79	78.05	6.67	0.00
7	Forage Forbs Cover + Rock/Gravel Cover	2	3.94	78.90	7.52	0.00
8	Shrub Distance + Forage Forbs Cover + Rock/Gravel Cover	3	7.74	79.09	7.71	0.00

Table 3.16 – Results of multivariable case-control logistic regression model for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data with estimated beta-coefficients (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's z-statistic. The parameter estimate with bold text showed a strong effect based on lower and upper confidence intervals that did not overlap zero.

Covariate	**β**	**95% CI**	**exp(β)**	**Wald's z**
Shrub Distance	-0.79	(-1.50, -0.08)	0.45	-2.18
Rock/Gravel Cover	2.78	(0.72, 4.84)	16.12	2.64
Rock/Gravel^2 Cover	-2.96	(-5.18, -0.74)	0.05	-2.62

Table 3.17 – Results of multivariable case-control logistic regression model for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data from the reduced data set (n = 34) that insects were collected from. Covariates used in the model are the same predictors in the top brood-site selection model using the full data set (n = 122; see Table 3.16) Results include estimated beta-coefficients (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's z-statistic.

Covariate	**β**	**95% CI**	**exp(β)**	**Wald's z**
Shrub Distance	-0.35	(-1.32, 0.62)	0.70	-0.71
Rock/Gravel Cover	2.67	(-0.66, 5.99)	14.40	1.57
Rock/Gravel^2 Cover	-2.44	(-5.60, 0.72)	0.09	-1.51

Table 3.18 – Results of univariable case-control logistic regression models for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data from the reduced data set (n = 34) that insects were collected from. Results include covariate models of insect species, estimated beta-coefficients (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's z-statistic, Bayesian Information Criteria (BIC).

Covariate Model	Predictor Category	β	95% CI	exp(β)	Wald's z	BIC
Cicadellidae	Biotic	1.33	(-0.57, 3.24)	3.80	1.37	24.02
Cynipoidea	Biotic	-0.74	(-2.23, 0.74)	0.48	-0.98	25.19
Muscidae	Biotic	0.83	(-1.01, 2.66)	2.28	0.88	25.56
Phoridae	Biotic	0.05	(-0.90, 1.00)	1.05	0.10	26.39

Table 3.19 – Results of multivariable case-control logistic regression models including specific insects for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data from the reduced data set (n = 34) that insects were collected from. Results presented are model rank based on ascending Bayesian Information Criteria (BIC), with covariate model structure, number of parameters (k), chi-square likelihood ratio test statistic (χ^2), and Bayesian weight (w_i).

Rank	**Model**	k	χ^2	**BIC**	**ΔBIC**	w_i
1	*Cicadellidae* + *Muscidae*	2	4.27	24.96	0.00	0.36
2	*Cicadellidae* + *Cynipoidea*	2	3.91	25.33	0.37	0.30
3	*Cicadellidae* + *Cynipoidea* + *Muscidae*	3	6.04	26.03	1.07	0.21
4	*Cicadellidae* + *Phoridae*	2	2.38	26.85	1.89	0.14
5	*Cynipoidea* + *Muscidae*	2	2.08	27.16	2.20	0.00
6	*Cynipoidea* + *Phoridae*	2	1.68	27.56	2.60	0.00
7	*Cicadellidae* + *Cynipoidea* + *Phoridae*	3	4.29	27.78	2.82	0.00
8	*Muscidae* + *Phoridae*	2	0.85	28.38	3.42	0.00
9	*Cicadellidae* + *Cynipoidea* + *Muscidae* + *Phoridae*	4	6.49	28.41	3.45	0.00
10	*Cynipoidea* + *Muscidae* + *Phoridae*	3	2.59	29.48	4.52	0.00

Table 3.20 – Results of multivariable case-control logistic regression models including specific insects for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data from the reduced data set (n = 34) that insects were collected from. Covariates included in multivariable models are from the top brood model (Table 3.17) including four insect species (Table 3.18). Results presented are model rank based on ascending Bayesian Information Criteria (BIC), with covariate model structure, number of parameters (k), chi-square likelihood ratio test statistic (χ^2), and Bayesian weight (w_i).

Rank	**Model**	***k***	**χ^2**	**BIC**	**ΔBIC**	**w_i**
1	*Cicadellidae* + Rock/Gravel Cover + Rock/Gravel^2 Cover	3	7.19	24.88	0.00	0.15
2	*Cicadellidae* + *Muscidae*	2	4.27	24.96	0.08	0.15
3	Rock/Gravel Cover + Rock/Gravel^2 Cover	2	3.97	25.26	0.38	0.13
4	*Cicadellidae* + *Cynipoidea*	2	3.91	25.32	0.44	0.12
5	*Cicadellidae* + Rock/Gravel Cover	2	3.24	25.99	1.11	0.09
6	*Cicadellidae* + *Cynipoidea* + *Muscidae*	3	6.04	26.03	1.15	0.09
7	*Cicadellidae* + *Cynipoidea* + Rock/Gravel Cover	3	5.97	26.10	1.22	0.08
8	*Cicadellidae* + Shrub Distance	2	2.76	26.48	1.60	0.07
9	*Cicadellidae* + *Cynipoidea* + Rock/Gravel Cover + Rock/Gravel^2 Cover	4	8.29	26.61	1.73	0.06
10	*Cynipoidea* + Shrub Distance	2	2.62	26.61	1.73	0.06

Table 3.21 – Results of multivariable case-control logistic regression models including specific insects for the evaluation of brood site habitat selection at the patch scale by white-tailed ptarmigan (*Lagopus leucura*) from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Results presented are from standardized data from the reduced data set (n = 34) that insects were collected from. Results include estimated beta-coefficients (β), 95% confidence intervals (CI), odds ratios [exp(β)], Wald's z-statistic.

Covariate	**β**	**95% CI**	**exp(β)**	**Wald's z**
Cicadellidae	1.87	(-0.54, 4.28)	6.51	1.52
Rock/Gravel Cover	3.43	(-0.41, 7.28)	31.02	1.75
Rock/Gravel^2 Cover	-2.95	(-6.38, 0.49)	0.05	-1.68

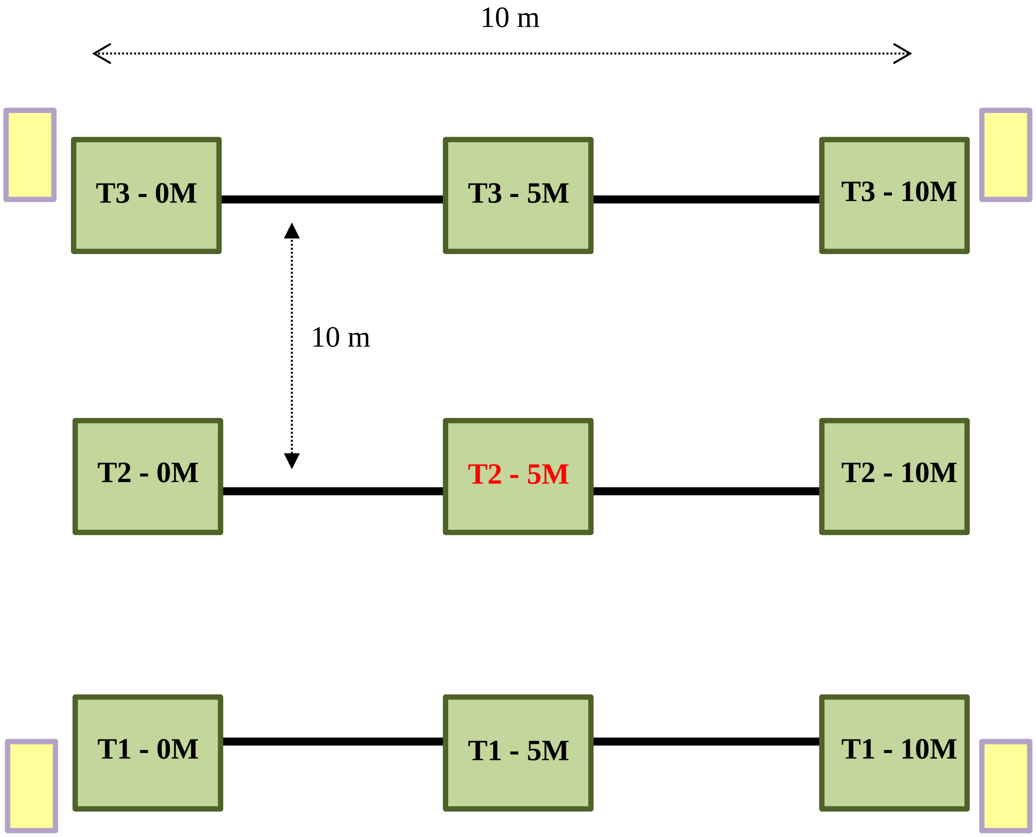


Figure 3.1 – Sampling design used to measure habitat selection of nest and brood sites by white-tailed ptarmigan (*Lagopus leucura*) during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Transects (black lines) were positioned perpendicular to topographic aspect of sites, 10 m a part and running 10 m in length. A ¼ m^2 Daubenmire plot (green squares) was used every 5 m along each transect line, measuring specific elements of habitat (see Table 3.2). Yellow rectangles illustrate Sticky Aphid Whitefly Trap paper to collect insects at brood sites. Fly paper was affixed to the ground via stakes at each of the four corners of the site, and left for at least 3 days. The Daubenmire plot labeled as "T2-5M" represents the actual location of the nest or brood location, and was designated as the centralized point of the use and available locations.

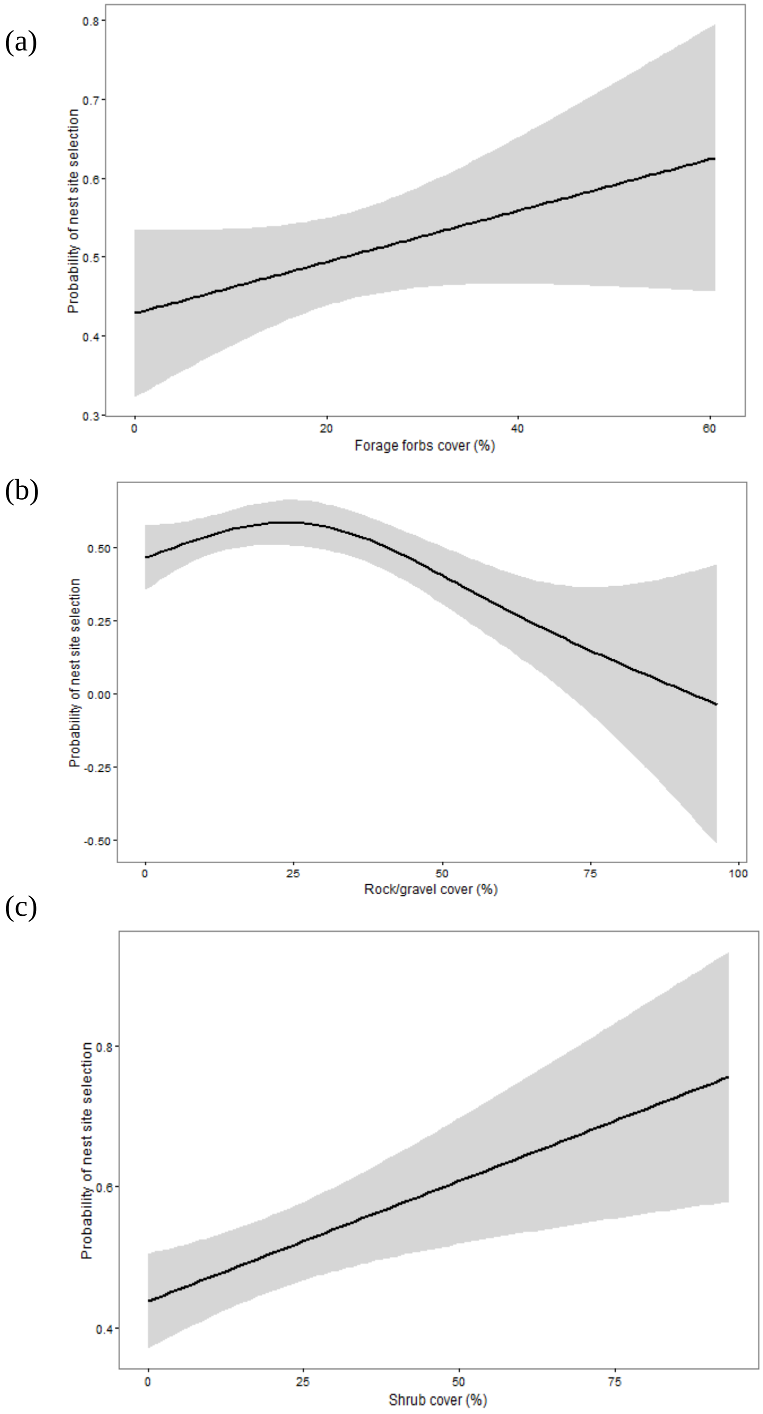


Figure 3.2 – Predicted response of nest site selection by white-tailed ptarmigan (*Lagopus leucura*) at the patch scale relative to the three predictor covariates in the top model: (a) forage forbs cover (%), (b) rock and gravel cover (%), and (c) shrub cover (%) at sample sites, from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Trends and their 95% confidence intervals were depicted using the ggplot2 package in Program R 3.1.3 with generalized additive model (GAM) smoothing function (Wickham 2009). GAM plots compare predictions made from the top case-control logistic regression model and then plotted against the actual values of each covariate.

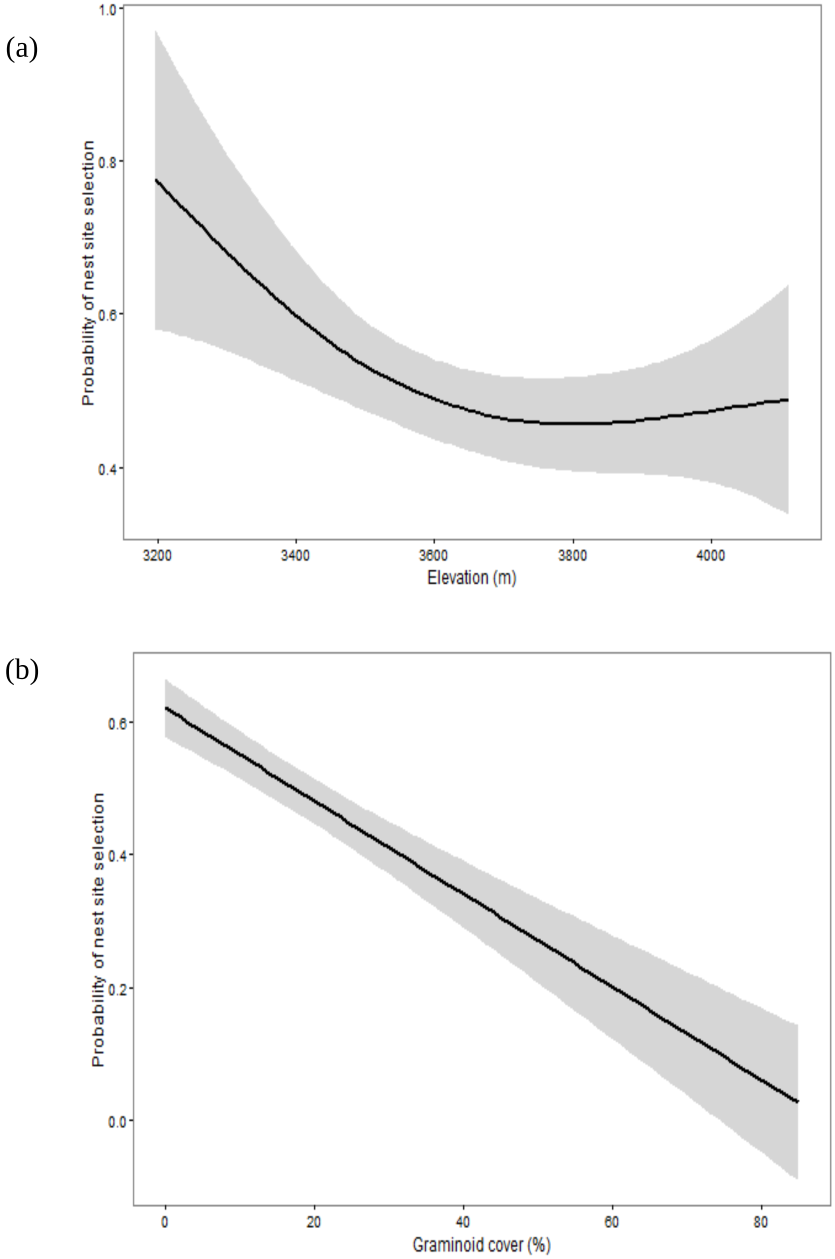


Figure 3.3 – Predicted response of nest site selection by white-tailed ptarmigan (*Lagopus leucura*) at the site scale relative to the two predictor covariates in top model: (a) elevation (m), and (b) graminoid cover (%) at sample sites, from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Trends and their 95% confidence intervals were depicted using the ggplot2 package in Program R 3.1.3 with generalized additive model (GAM) smoothing function (Wickham 2009). GAM plots compare predictions made from the top case-control logistic regression model and then plotted against the actual values of each covariate.

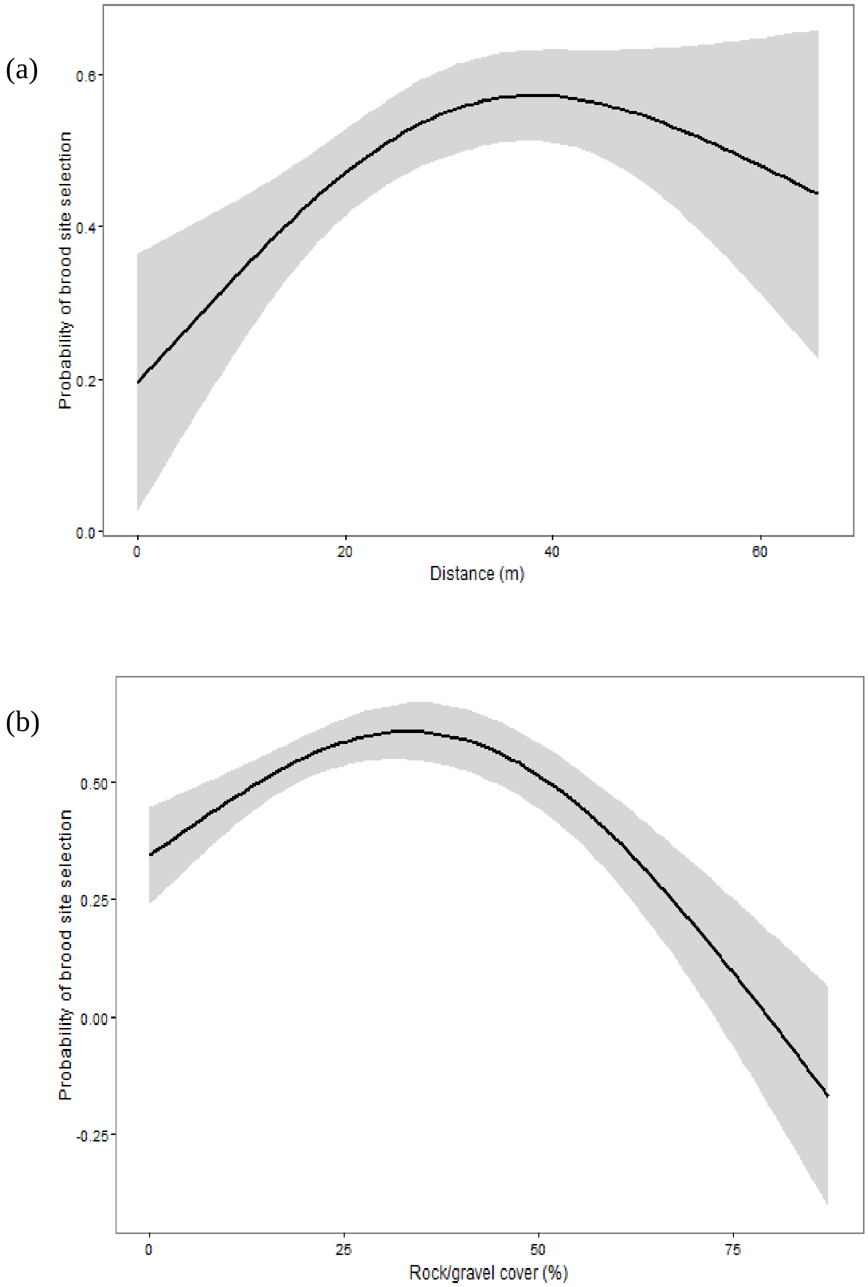


Figure 3.4 – Predicted response of brood site selection by white-tailed ptarmigan (*Lagopus leucura*) at the patch scale relative to the two predictor covariates in top model: (a) distance to (m) shrubs, and (b) rock and gravel cover (%) at sample sites, from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Trends and their 95% confidence intervals were depicted using the ggplot2 package in Program R 3.1.3 with generalized additive model (GAM) smoothing function (Wickham 2009). GAM plots compare predictions made from the top case-control logistic regression model and then plotted against the actual values of each covariate.

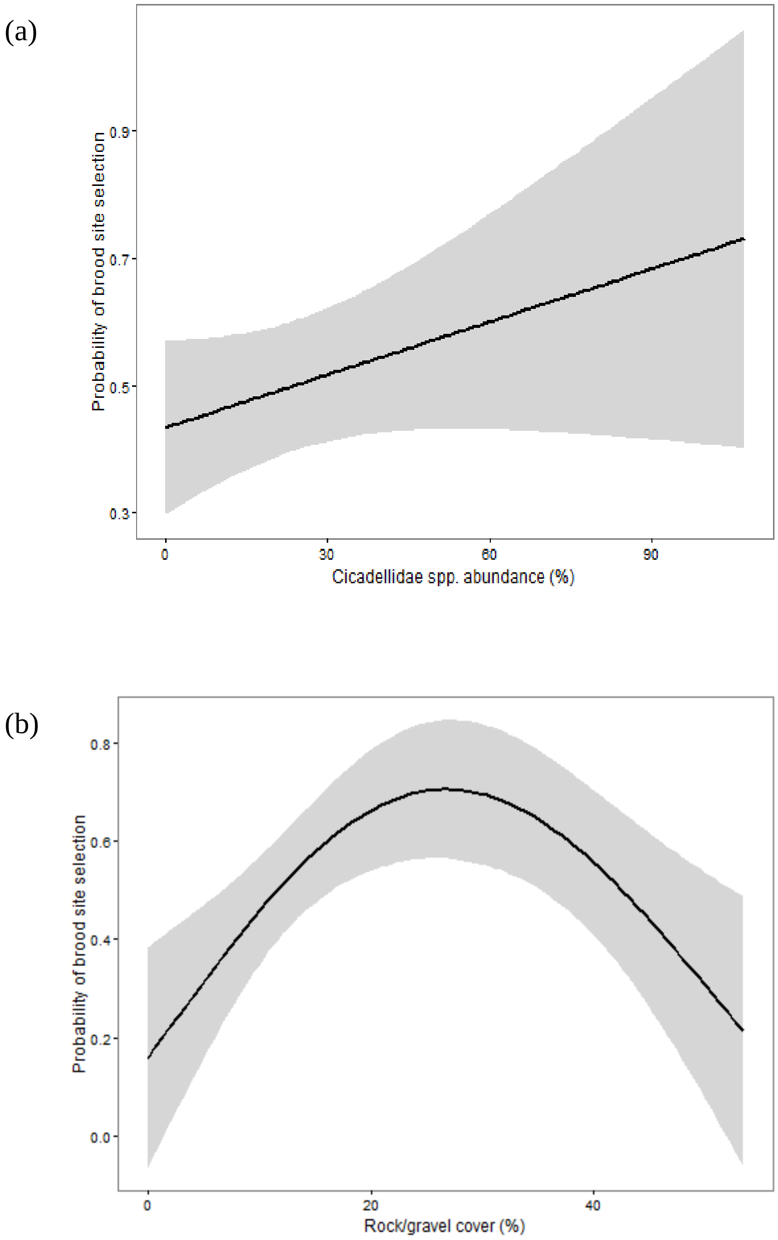


Figure 3.5 – Predicted response of brood site selection by white-tailed ptarmigan (*Lagopus leucura*) at the patch scale relative to the two predictor covariates in top model: (a) *Cicadellidae* abundance (%), and (b) rock and gravel cover (%) at sample sites, from data collected during mid-June to end of August 2014 and 2015 at two alpine sites in Colorado: Mt. Evans in Clear Creek County and Trail Ridge Road in Rocky Mountain National Park (RMNP). Top model fit to reduced data (*n* = 34) set including collected insect samples. Trends and their 95% confidence intervals were depicted using the ggplot2 package in Program R 3.1.3 with generalized additive model (GAM) smoothing function (Wickham 2009). GAM plots compare predictions made from the top case-control logistic regression model and then plotted against the actual values of each covariate.

CHAPTER 4: CONCLUSIONS

SUMMARY

Biota that are topographically isolated to high mountaintops have specialized adaptations to withstand such harsh alpine environments and shorter growing seasons, that distributional shifts could force them into habitats where their specializations no longer increase their survival (Xu et al. 2009). Additionally, species endemic to and already found in high elevations have limited range available for vertical migration (Beniston 2003, Hennessy et al. 2003, Walther et al. 2005). In many ecosystems, the context of habitat and species traits together primarily regulate species distributions, rather than directly by climate. Thus, effects of climate change can indirectly affect species through habitat changes. Climate change in the alpine is thought be occurring more rapidly than in lower elevations (Beniston et al. 1997, Diaz and Bradley 1997) and is liable to persist. Under climate change, these "sky islands" could become increasingly fragmented into smaller habitat and potentially be lost if up-slope migration of subalpine species encroaches into the alpine. Therefore, shifts of treelines into alpine areas as a result of climate change, could be especially impactful to alpine birds, especially if suitable habitat becomes restricted or degraded (Chamberlain et al. 2013). Predicted response of rock ptarmigan (Lagopus muta helvetica) breeding habitat in the Swiss Alps has been estimated to decline by two-thirds if increased temperature exceeds 4◦C (Revermann et al. 2012). Changes to habitat can be particularly detrimental to birds during their breeding season when they are trying to acquire the resources they need to facilitate and ensure reproductive success. Alpine birds could also respond to climate change by advancement of their breeding phenology as has already been seen by white-tailed ptarmigan in Colorado (Wann 2012), instead of or coupled with altering their distribution. In fact, phenological mismatch between lower elevation plants shifting to an earlier growing season with earlier onset of snow melt, has led American Robins to migrate upslope an average of 14 days earlier (Inouye et al. 2000). This can be particularly problematic if species are initiating their migration from lower elevations earlier, but arrive in summer breeding grounds at higher elevations when winter is still present and resources are sparse. Our findings demonstrated a surprising relationship between white-crowned sparrows and snow cover, helping to link how certain alpine birds will respond with changes in snow cover in the alpine. Ultimately, these effects are difficult to infer without first understanding species' relationship with their environment, as well as both the direct and indirect effects to species and their habitats. Our work has provided some insight of the underlying relationships breeding avifauna have with the alpine environment that will guide management in both the short- and long-term perspective, especially if alpine habitat is altered by climate change.

In the second chapter, I estimated the response of alpine passerine abundance and occurrence to fine-scale habitat and environmental characteristics. These analyses enabled us to isolate not only which features influenced alpine breeding birds the most in our study sites, but what predictor categories were most influential. The results indicated factors not confined to only abiotic and biotic categories drove relationships between all three of the breeding birds we modeled. This was important in helping our understanding that along with abiotic and biotic components, space, time, and anthropogenic factors also affect these alpine species of interest in very different ways. While none of the top models specifically included temperature as a component driving these alpine breeding bird relationships, we did find one of the three birds' abundance to respond negatively due to increased temperatures in these two alpine areas. This could be a concern, given climate change projections in this region.

In the third chapter, I analyzed fine-scaled habitat selection by white-tailed ptarmigan during two important breeding stages and at two successive spatial scales. Our results largely supported many of our initial expectations that forage components and protective cover influenced ptarmigan in our two study sites. Results on specific vegetation and insect forage components demonstrate that if climate change indirectly or directly affects other biota in the alpine, especially species that ptarmigan rely on, white-tailed ptarmigan will be adversely impacted if these resources are depleted. Although white-tailed ptarmigan are considered more alpine generalists, they are presumably more susceptible than other species in this region due to them being an annual resident in the alpine (Braun 1980). Our results shed further light that habitat heterogeneity is important throughout ptarmigan breeding stages, although ptarmigan require resources at different spatial scales across life stages (i.e., at immediate nest sites vs. patches surrounding immediate nest sites).

Colorado contains sizeable, suitable alpine habitat (i.e., ~770,000 ha) sufficient to sustain the largest white-tailed ptarmigan population in the lower 48 states (Hoffman 2006). Thus, the information we gathered in our study helps to understand the relationship ptarmigan have with their surrounding environment during these two important life stages, providing insights as to how ptarmigan may respond elsewhere if climate change alters important alpine habitat.

RESEARCH NEEDS

Data collected for alpine birds were on a fine-scale over a shorter time frame (i.e., two sample years and shorter, annual sampling windows). Although not addressed specifically in this research, in order to discern if there are climate change effects to these alpine species, managers should determine the affiliations alpine avifauna have with their surrounding habitat at various spatial scales over more extensive time periods. This will give managers awareness of which individuals or species guilds will be displaced and when these shifts actually occur. Our study did incorporate temperature data, but the temporal scale was too narrow to determine if any detrimental and strong effects impacted species in these regions. Nonetheless, these baseline data established the foundation necessary for informing the design of future alpine habitat and species monitoring programs and research.

To build upon this groundwork, future research should be developed to include landscape composition and configuration variables as predictors, which is reasonable provided birds are also influenced at multiple spatial scales (e.g., landscape and patch; Mazerolle and Villard 1999). A viable approach would be to use moving window analyses with FRAGSTATS to calculate patch and landscape variables at cells within grids of our study sites. Then models (i.e., GLMs, conditional logistic regression) can be applied based on covariates in our top models to create a continuous probability surface (McGarigal et al. 2012) of abundance, occurrence and resource selection responses in these two alpine regions. Thus, predictions can be made on the extent of current suitable alpine habitat for these avian species, across broader landscapes, allowing us to understand how these two alpine regions and species distributions may change in response to changing climates. Analyzing these responses across various extents is crucial not only to determine at which scale habitats and species are most responsive, but for conservation decisions and at what scales these decisions and priorities should be set at.

LITERATURE CITED

Beniston, M., H.F. Diaz, and R.S. Bradley. 1997. Climatic change at high-elevation sites: an overview. Climatic Change 36: 233-252

Beniston, M. 2003. Climatic change in mountain regions: A review of possible impacts. Climatic Change 59: 5-31.

Braun, C. E. 1980. Alpine Bird Communities of Western North America: Implications for Management and Research. In Workshop Proceedings: Management of Western Forests and Grasslands for Nongame Birds (R. M. Deraff, technical coordinator). USDA Forest Service General Technical Report. INT-86. Pp. 280-291.

Chamberlain, D.E. M. Negro, E. Caprio, and A. Rolando. 2013. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biological Conservation 167: 127-135.

Diaz, H.F., and R.S. Bradley. 1997. Temperature variations during the last century at high-elevation sites. Climatic Change 36: 253-279.

Hennessy K., Fitzharris B., B.C. Bate1s, Harvey N., Howden S. M., Hughes L., Salinger J. & Warrick R. (2007) Australia and New Zealand. In: Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. v. d. Linden and C. E. Hanson) pp. 507-40. Cambridge University Press, Cambridge.

Hoffman, R. W. 2006. White-tailed Ptarmigan (Lagopus leucura): A Technical Conservation Assessment. Prepared for the USDA Forest, Rocky Mountain Region, Species Conservation Project, Pp. 1- 72.

Inouye, D.W., B. Barr, K.B. Armitage, and B.D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Sciences 97(4): 1630-1633.

Mazerolle, M.J., and M.A. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6: 117-1240

McGarigal, K., S.A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html

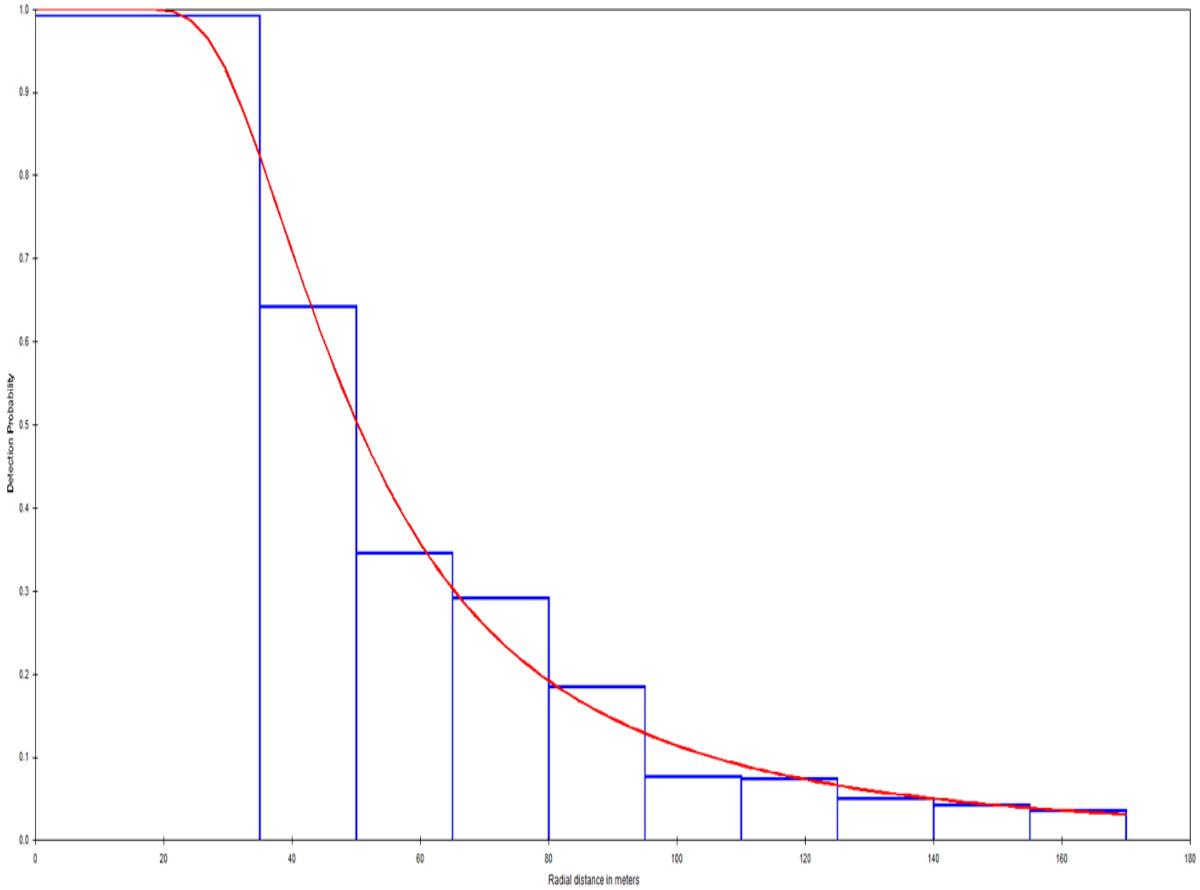
Revermann, R., H. Schmid, N. Zbinden, R. Spaar, and B. Schrörder. 2012. Habitat at the mountain tops: how long can Rock Ptarmigan Lagopus muta Helvetica survive rapid climate in the Swiss Alps? A multi-scale approach. Journal of Ornithology 153: 891-905.

Walther, G.-R., S. Beissner, and C.A. Burga. 2005. Trends in the upward shift of alpine plants. Journal of Vegetation Science 16: 541 – 548.

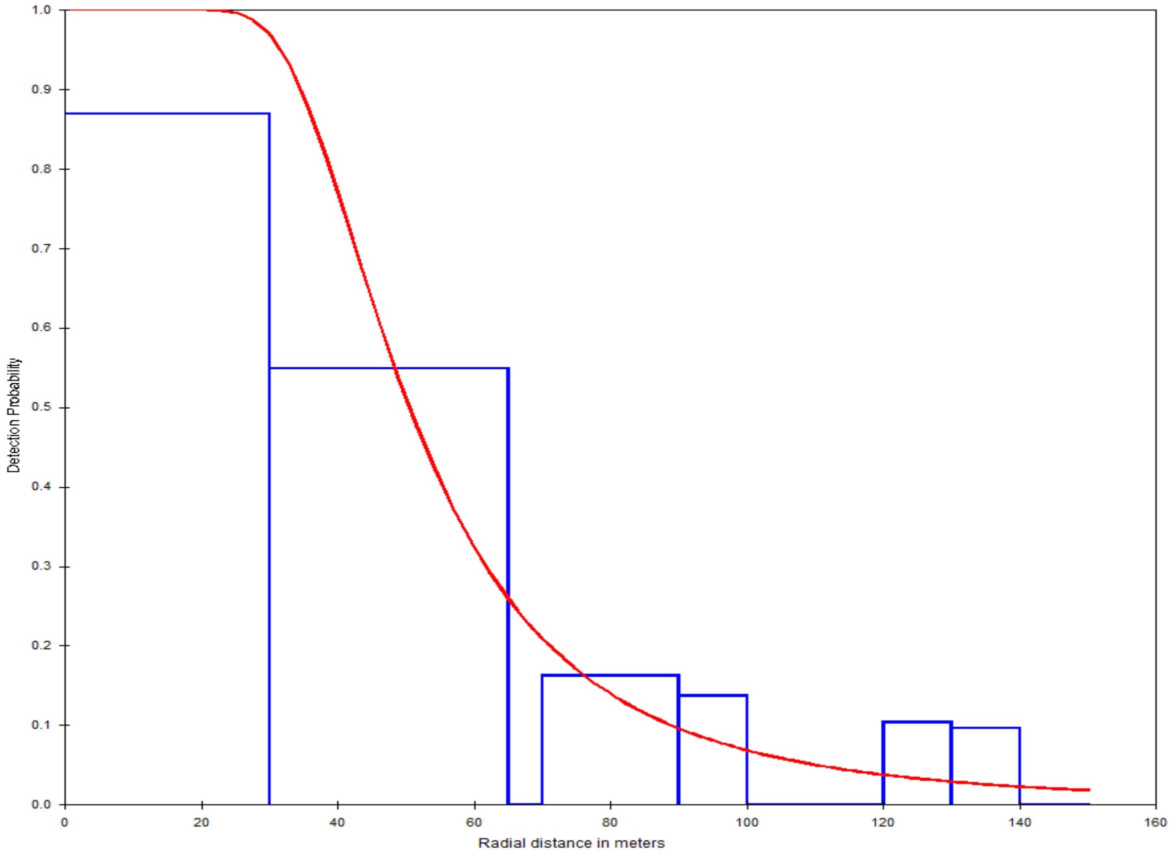
Wann, G. T. 2012. Long-term Demography of a White-tailed Ptarmigan (Lagopus leucura) Population in Colorado. Department of Ecosystem Science. Diploma Thesis, Pp 125.

Xu, J., R. E. Grumbine. A. Shrestha, M. Eriksson, X. Yang, Y. Wang, and A. Wilkes. 2009. The Melting Himalayas: Cascading Effects of Climate Change on Water, Biodiversity, and Livelihoods. Conservation Biology 23(3): 520 – 530.

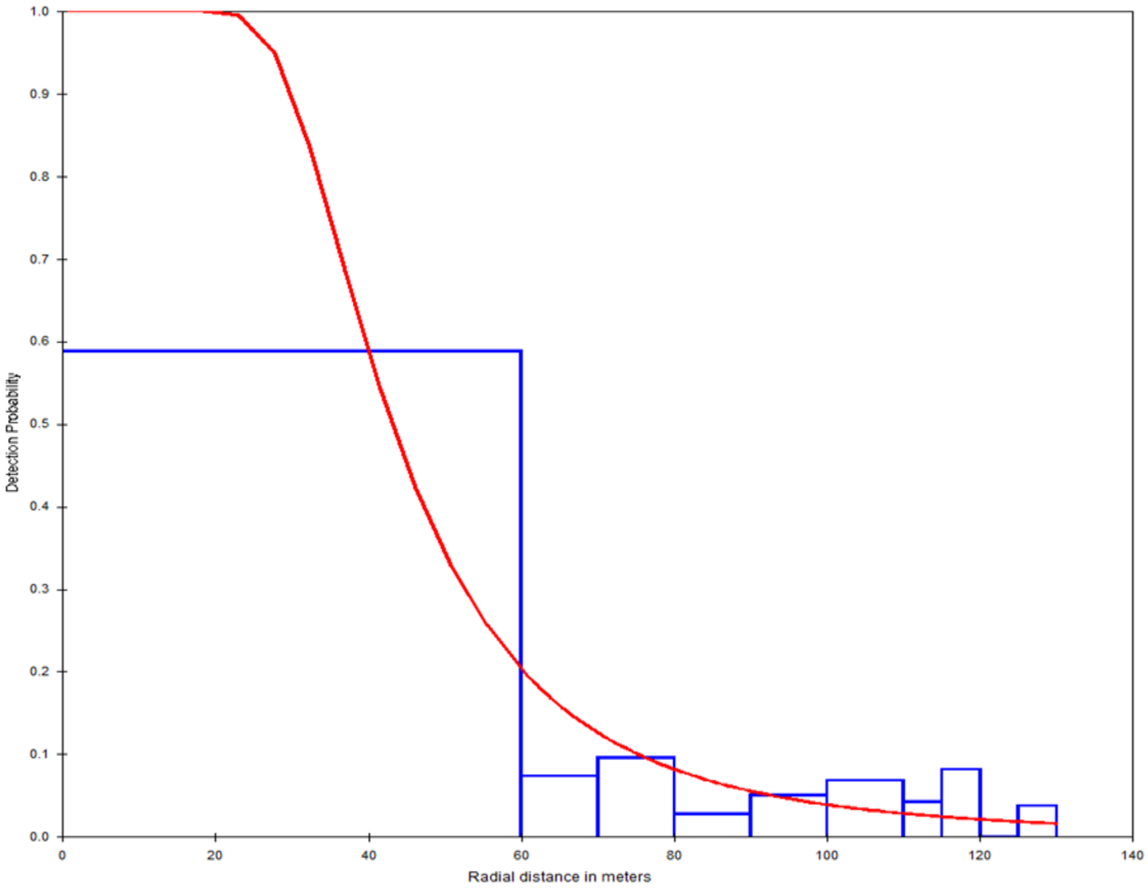
APPENDICES



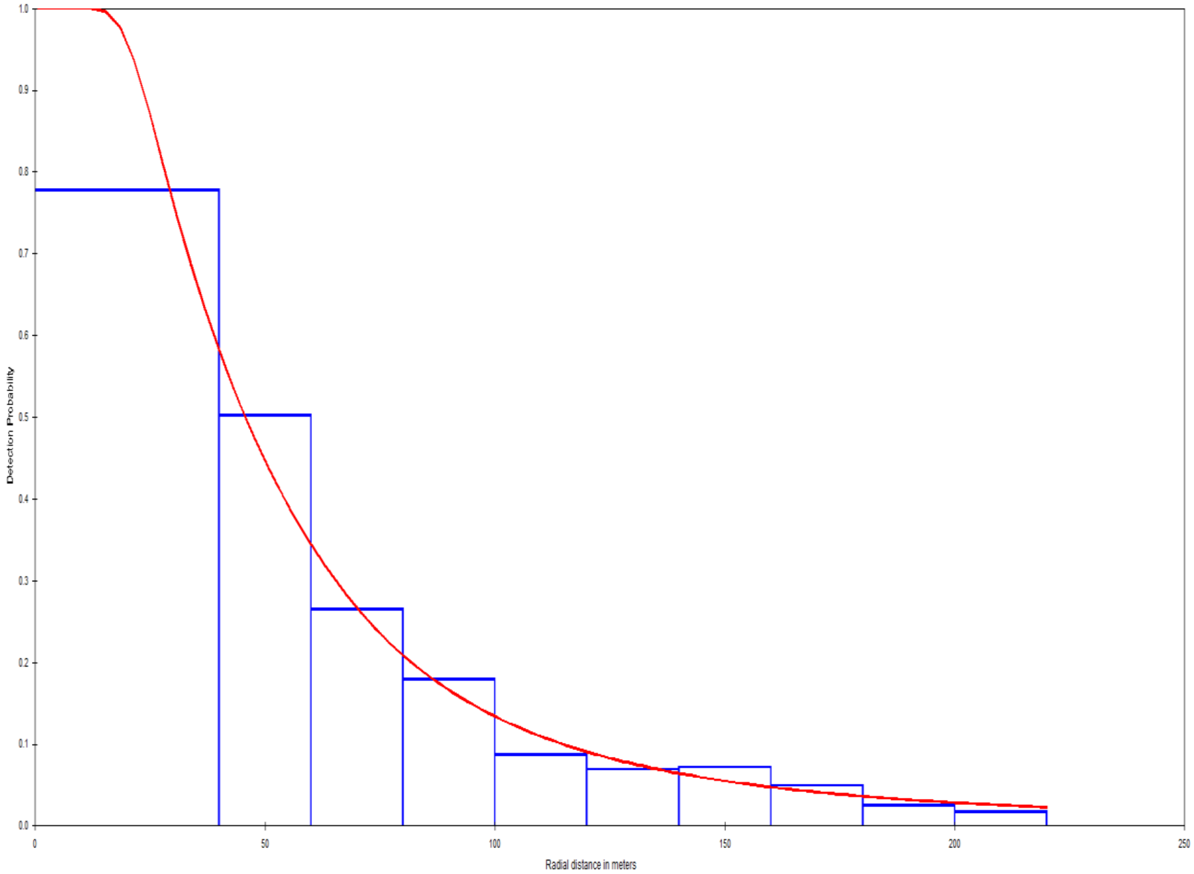
Appendix 1 – Detection probability plot for American pipit (*Anthus rubescens*) from program DISTANCE 6.2 from data collected at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot depicts the distribution from a hazard-rate key function with cosine adjustment separated into 10 bins, using an initial cut point of 35 m, followed by 15 m between each bin thereafter, with a truncation distance of 170 m. Top model included distance to road (m) and time of count (hour and minutes). After truncation, the total observations used in top model were 449 pipits.



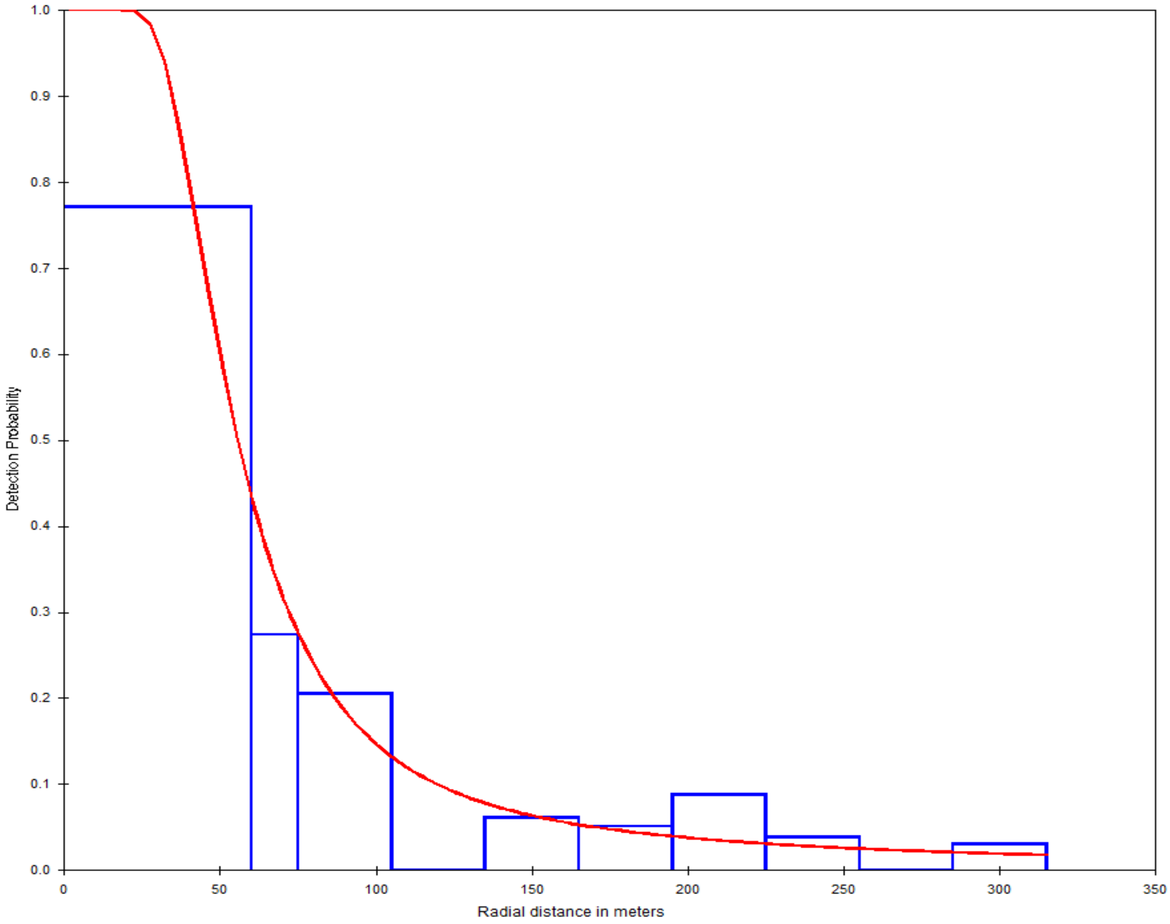
Appendix 2 – Detection probability plot for brown-capped rosy-finch (*Leucosticte australis*) from program DISTANCE 6.2 from data collected at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot depicts the distribution from a hazard-rate key function with cosine adjustment separated into 10 bins, using an initial cut point of 30 m, followed by manual manipulation of each bin thereafter (range: 5- to 10 m intervals), with a truncation distance of 150 m. Top model included distance to road (m), observer, and time of count (hour and minutes). After truncation, the total observations used in top model were 15 brown-capped rosy finches.



Appendix 3 – Detection probability plot for horned lark (*Eremophila alpestris*) from program DISTANCE 6.2 from data collected at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot depicts the distribution from a hazard-rate key function with cosine adjustment separated into 10 bins, using an initial cut point of 60 m, followed by 10 m between each bin thereafter, with a truncation distance of 130 m. Top model included percentage of rock and snow cover, and time of count (hours and minutes). After truncation, the total observations used in top model were 64 horned larks.



Appendix 4 – Detection probability plot for white-crowned sparrow (*Zonotrichia leucophrys oriantha*) from program DISTANCE 6.2 from data collected at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot depicts the distribution from a hazard-rate key function with cosine adjustment separated into 10 bins, using an initial cut point of 40 m, followed by 20 m between each bin thereafter, with a truncation distance of 220 m. Top model included percentage of krummholz and willow species, distance to road (m), and observer. After truncation, the total observations used in top model were 235 white-crowned sparrows.



Appendix 5 – Detection probability plot for white-tailed ptarmigan (*Lagopus leucura*) from program DISTANCE 6.2 from data collected at sites within two alpine areas of Colorado: Mt. Evans (n = 37) in Clear Creek County and Trail Ridge Road (n = 31) in Rocky Mountain National Park (RMNP). Plot depicts the distribution from a hazard-rate key function with cosine adjustment separated into 10 bins, using an initial cut point of 40 m, followed by manual manipulation of each bin thereafter (range: 15- to 30 m intervals), with a truncation distance of 315 m. Top model included percentage of herbaceous species, total mean height (of shrubs and small trees; m), and time (hour). After truncation, the total observations used in top model were 14 white-tailed ptarmigan.