THESIS

LONG-TERM DEMOGRAPHY OF A WHITE-TAILED PTARMIGAN (*LAGOPUS LEUCURA*) POPULATION IN COLORADO

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ABSTRACT

LONG-TERM DEMOGRAPHY OF A WHITE-TAILED PTARMIGAN (*LAGOPUS LEUCURA*) POPULATION IN COLORADO

Animals endemic to alpine habitats have been receiving increasing attention in recent years due to concerns over sensitivities of high elevation systems to climate warming. Long-term datasets are needed to assess trends in populations of alpine endemic species, but such datasets are rare, primarily due to logistical challenges that constrain data collection in these environments. Long-term datasets also provide critical information on impacts of altered climate because they span multiple decades under which climate varies. To accurately forecast or predict the impacts of warming on alpine animals, it is necessary to first understand how they have responded to climate variation in the past.

Here, I present a demographic analysis on 43 years (1968-2010) of long-term data for the white-tailed ptarmigan (*Lagopus leucura*) at an alpine study site in central Colorado. Spring warming was found to advance breeding phenology an average of 10 days over the course of study, and temperature and precipitation were found to be the primary factors affecting timing of nesting. Weather conditions experienced immediately post-hatch were found to have the strongest effects on reproductive success, with seasonal effects being of secondary importance. Both the number of rain days occurring post-hatch and warm and dry seasonal conditions were found to negatively correlate with reproductive success. Reproductive success declined from the mid-1970s through 2008,

but the mechanism behind this decline is not entirely understood. Winter precipitation was the weather variable that had the strongest effect on survival of breeding age white-tailed ptarmigan, and survival was reduced during years of low winter cumulative precipitation. Annual rates of population change were greatest during the first decade of study but tended to be lower during subsequent decades. The average annual rate of population change was close to 1, but there was a high amount of variability among years.

Several of the weather variables that were found to most strongly impact reproductive success and survival in white-tailed ptarmigan are expected to change in coming decades. Warming summers are a concern given the potential impact on standing snowfields and the potential to reduce brood-rearing habitats. Higher temperatures in the winter may decrease snowpack which was found to negatively affect survival. I discuss the implications for future climate change on white-tailed ptarmigan. Further, I discuss a recently developed method for combining multiple data sources, and explore how these methods can be applied to white-tailed ptarmigan population modeling in the future.

ACKNOWLEDGMENTS

This project depended heavily on a number of people for its successful completion. Dr. Cameron Aldridge and Dr. Tom Hobbs provided crucial guidance throughout every step of the research process. Both Dr. Aldridge and Dr. Hobbs proved to be excellent graduate advisors with great levels of enthusiasm for teaching and ecology. My graduate committee members, Dr. Barry Noon and Dr. Cameron Ghalambor, greatly improved the quality of the thesis manuscript through their thoughtful review and critiques of its content. Dr. Clait Braun was responsible for the collection of the majority of data used in this manuscript. In addition, Dr. Braun taught me everything I know about the biology of white-tailed ptarmigan, and I am deeply indebted for everything he has done to help me become a better ecologist, including his patience in answering my incessant (and often repeated) questions about white-tailed ptarmigan biology. Dr. Larissa Bailey, Dr. Paul Doherty, and Dr. Gary White provided valuable help and suggestions with the demographic analysis.

I was very fortunate to have excellent field support during the 2010 and 2011 field seasons. Chad Young (2010) and Jeremy Austin (2011) both proved to be excellent field companions during many cold treks across windy alpine tundra. Both Chad and Jeremy had an excellent attitude and great sense of humor which substantially enhanced the field experience. I wish them the best in their future endeavors.

Both my parents, Tom and Kathy, were highly supportive throughout my graduate education. I am not sure they fully understand my interest in wildlife, even at this stage, but nonetheless, they have always encouraged me to follow my interests and have shown great enthusiasm for my career path.

Dr. Michael Monahan and the University of Denver's High Altitude Lab at Echo Lake provided critical field support throughout multiple years of the research project. It is not an understatement to say that without Dr. Monahan and the University of Denver's support, this project may well have ended prematurely. Dr. Monahan personally went out of his way during multiple years to make certain the lab facilities were available for our use, and a most sincere thanks are in order for his generosity.

I was fortunate to have many excellent laboratory and office mates during my time as a graduate student. In particular, I would like to acknowledge the late Kathryn Herbener for her encouragement and willingness to help out a new student during my first year at Colorado State University. Kathy was an incredibly generous and lovely human being, and she will be sorely missed.

Funding for this project was provided by multiple sources. Colorado Parks and Wildlife (CPW) were one of the few wildlife agencies in the country to support long-term research of white-tailed ptarmigan. There is no question that the contribution to the biology of white-tailed ptarmigan would have been greatly diminished without support from CPW. The U. S. Geological Survey (USGS) provided support for data collection beginning in 2008. The USGS is also responsible for the majority of my graduate support provided for this project. The Rocky Mountain Nature Association provided valuable financial graduate support during the summer of 2010 for which I am very thankful. Additional graduate support was provided by the Natural Resource Ecology Laboratory at Colorado State University through the James E. Ellis Scholarship and a Graduate Fellowship through the Program in Research and Scholarly Excellence.

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Chapter Two:

Impacts of weather on nesting phenology and fecundity of white-tailed ptarmigan*

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*In prep: *Journal of Animal Ecology*

Chapter Three:

Long-term trends in survival, growth, and population recruitment of a white-tailed ptarmigan population in Colorado*

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CHAPTER 1: WHITE-TAILED PTARMIGAN IN COLORADO

INTRODUCTION

Predicting how populations will respond to climate change in the future depends in a fundamental way on understanding how they responded to past weather and climate events. Establishing mechanistic links between historic climate and demography offers a particularly promising route to forecasting population dynamics in a warmer world. In practice, making this linkage is difficult because there are very few detailed studies of populations spanning a sufficient interval of time to capture responses to altered climate. Thus, exploiting multi-decade datasets offers opportunities to gain meaningful insight into the ways environmental stochasticity affects populations of interest.

Long-term demographic studies provide ecologists with opportunities to assess natural fluctuations in demographic rates over time and better understand the factors affecting population regulation (Lindenmayer et al. 2012). Over the past several decades the challenge of understanding responses of organisms to climate warming has raised the importance of long-term studies to assess the risks of climate change (Parmesan and Yohe 2003). For the majority of species, however, datasets spanning multiple decades do not exist, and few inferences can be drawn from the effects of recent warming on populations. In alpine systems the lack of long-term datasets is particularly noticeable. Very few studies have published long-term demographic trends in alpine-endemic species, but of the few that have there have been significant findings relevant to climate

change research. For example, Ozgul et al. (2010) exploited several decades of demographic data for yellow-bellied marmots in Colorado. Results from this research indicated that spring warming directly affected date of emergence from hibernation, which in turn led to increased weight gains and survival in yellow-bellied marmots. Over the past decade the size of the population of yellow-bellied marmots studied nearly doubled. Thus, climate warming can have a direct effect on the demographics of alpine animals.

The white-tailed ptarmigan (*Lagopus leucura*) occurs throughout alpine habitats in Colorado and western North America (Braun et al. 1971). It is one of only a few North American species adapted to live nearly its entire life history near or above treeline (Braun et al. 1993). Before the 1960s, little was known about the biology of white-tailed ptarmigan, and few studies were available presenting information on basic life history characteristics, such as breeding, dispersal, and diet. In the mid-1960s Colorado Division of Wildlife (now Parks and Wildlife) initiated studies of the species at several locations in Colorado, including Mt. Evans (Clear Creek County), Crown Point (Larimer County), and Rocky Mountain National Park (Larimer County). Monitoring of the species has continued at Mt. Evans through 2011 and currently represents the longest time series of demographic data available for an alpine avian species (and perhaps any avian species) in North America. Alpine habitat where the species can be found is increasingly thought to be in jeopardy from warming trends in temperature. Indeed, cold temperatures that define these habitats are already being lost in North America (Diaz and Eischeid 2007). Unfortunately, there is little known about how these warming trends have affected alpine

species, primarily due to a paucity of demographic data available for alpine animals (Chamberlain et al. 2012).

Here, 43 years of demographic data for a population of white-tailed ptarmigan is analyzed and presented. In chapter 2 I analyze reproductive data in the form of counts of chicks observed annually, and test the effects of different weather variables over differing post-hatch and seasonal scales. Warming predicted from downscaled climate models and its potential effect on reproduction in white-tailed ptarmigan is considered. Chapter 3 presents annual estimates of apparent survival, recruitment, and population growth across the study period. Open population mark-recapture models are utilized for the analysis. Winter climate data is used to test the influence of precipitation and temperature on apparent survival. Chapter 4 summarizes the findings of my research, and also includes a discussion of a recently developed analytical approach that combines count and demographic data into a single analysis to obtain estimates of vital rates and population size which can be used to forecast population size with multiple sources of uncertainty.

I hope the research presented is both informative and useful to land stewards and biologists charged with managing alpine habitats in Colorado. The presentation of annual demographic estimates provide informative information of long-term trends in a studied alpine species in the southern Rockies, while the use of weather and climate covariates provide insight into the potential effects of continued climate warming on the species. Still, a considerable amount of work is needed to understand the likely consequences of climate change on white-tailed ptarmigan. This study was correlative in nature, and it is important to note that the data analyzed were not collected in an experimental manner with a climate analysis in mind, and thus causation cannot be

directly addressed with respect to the effects of weather and climate variables on reproduction and demographic vital rates. The addition of site-specific weather data and known-fate data offer the potential to substantially increase our understanding of the role weather and climate play in regulating white-tailed ptarmigan populations when combined with an experimental design.

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CHAPTER 2: IMPACTS OF WEATHER ON NESTING PHENOLOGY AND FEECUNDITY OF WHITE-TAILED PTARMIGAN

SUMMARY

We used 43 years of demographic data (1968-2010) to investigate the impacts of weather and seasonal climate on nesting phenology and reproductive success of white-tailed ptarmigan (*Lagopus leucura*), in central Colorado, USA. The average median date of hatch in our study population advanced an average of 10 days over the study period (β_{YEAR} = -0.24, SE = 0.075, R^2 = 0.19), and reproductive success, as measured by the annual number of chicks per hen, declined from 1968 to 2008 (β_{YEAR} = -0.03, SE = 0.010, R^2 = 0.14). We found no evidence that timing of nesting impacted reproductive success at our study site, and post-hatch weather conditions did not change over the course of study. The number of rain days occurring post-hatch had a negative relationship with reproductive success, and warm and dry conditions over the course of the breeding season negatively affected reproductive success. Our best predictive models all included the number of post-hatch rain days, and variables used to measure seasonal warm and dry conditions were of secondary importance. We attribute the observed decline in reproductive success in part to warmer breeding seasons, but there were processes that we failed to model that had a substantial role in fecundity of our study population. Projected downscaled climate data available for our study area indicates a continued increase in temperatures during the spring and summer

periods. The biggest threat to reproductive success in our study population appears to be continually warmer breeding seasons which may affect plant forage and habitats used by broods.

KEY WORDS alpine, breeding phenology, climate, reproductive success, weather, white-tailed ptarmigan

INTRODUCTION

Recent changes to the earth's climate have been demonstrated to have a direct impact on many aspects of avian life history traits (Crick 2004, Møller et al. 2006, Gienapp 2008). Until recently, the majority of studies investigating the influence of climate change on avian species have focused primarily on advanced nesting phenology and geographic shifts due to changing abiotic factors (Crick and Sparks 1999, Brommer 2004, Hitch and Leberg 2007, La Sorte and Thompson 2007). Understanding how climate and weather events affect vital demographic parameters, such as fecundity and survival, are of high importance but still poorly understood in the context of future climate change. In addition, species occurring in different ecosystems will likely be affected differently, because observed and forecasted changes have affected and will affect ecosystems differently (IPCC 2007). High elevation alpine systems are thought to be particularly vulnerable to warming due to their habitat boundaries being defined largely by cold temperatures (Diaz and Eischeid 2007). Unfortunately, given the difficulty of accessing these locations due to high snow accumulation early in the breeding season, studies of breeding birds in alpine habitats are uncommon, and little is known about how changing

climate trends have affected alpine-avian species. A prerequisite for predicting the consequences of projected climate change is to first understand how climate has influenced vital parameters in the past. Thus, long-term data sets containing information to estimate these vital parameters are necessary to gain meaningful inference. Parameters of high interest for species that are relatively short-lived include metrics of reproductive success.

Weather events are known to influence the reproductive success of several species in the family Tetraoninae (Steen et al. 1994, Clark and Johnson 1992, Novoa et al. 2008). Of particular relevance are studies conducted on species in the genus *Lagopus*, all of which occur in habitats that undergo seasonal extremes in climatic conditions. These studies indicate that weather events occurring over short- and long-time periods can directly impact productivity in ptarmigan populations (Erikstad and Andersen 1983, Novoa et al. 2008). White-tailed ptarmigan (*Lagopus leucura*), are endemic to alpine habitats and are well adapted to the harsh conditions that occur above treeline (Braun et al. 1993). However, reproductive success in this genus is still susceptible to unfavorable weather events due to the inability of chicks to thermoregulate without the aid of brooding by hens during the first weeks of life (Myhre et al. 1975). In addition, annual variation in seasonal weather may impact resource availability (Körner 1999). Thus, we might expect that alterations in breeding season weather will result in detectable changes in annual fecundity of white-tailed ptarmigan. Previous work with a diverse group of avian species has demonstrated that warming temperature trends in the spring are highly correlated with breeding phenology (reviewed by Crick and Sparks 1999, and Dunn 2004). However, few of these studies have demonstrated the consequences of altered

breeding phenology, and the adaptive nature of these responses is still largely unknown. Nesting phenology has been linked to reproductive success in rock ptarmigan (*Lagopus muta*; Novoa et al. 2008), and similar findings in the closely related white-tailed ptarmigan might be expected.

Our objectives were first to examine the effect of recent spring warming trends on timing of nesting of white-tailed ptarmigan, as measured by the median date of hatch, and the potential consequences of any observed effect with respect to reproductive success. Second, we investigated how local weather conditions impact reproductive success in white-tailed ptarmigan in terms of annual chick production. Our third objective was to understand the consequences of future changes in climate for our study area. We use the term post-hatch weather to refer to events occurring over short-time windows (≤ 4 weeks), and seasonal weather to specify conditions averaged over longer time periods (> 4 weeks). *A priori* predictions were made on all weather covariates used in our analysis. Our expectations were that warm and dry conditions occurring immediately after hatch would be beneficial to reproductive success, but seasonal warm conditions would have a negative effect on reproductive success due to drying effects which might affect vegetation and ultimately influence resource availability.

STUDY AREA

Productivity and nesting phenology of white-tailed ptarmigan were studied at Mt. Evans, an alpine site in central Colorado. The Mt. Evans study area includes long-term data spanning 1968–2010. The study area is within the Mt. Evans Wilderness Area (Arapahoe National Forest) in Clear Creek County and ranges in elevation from 3,292 m to the summit of Mt. Evans at 4,347 m (Braun 1969). The total study area consists of 9.2 km^2

of alpine habitat, which is contiguous with alpine habitat on virtually all sides. The study area was expanded to 13.2 km^2 from years 1987 to 1996.

The vegetation is primarily alpine tundra with cushion plant stands (*Silene* spp.), Dryas stands (*Dryas octopetala*), and Kobresia (*Kobresia simpliciuscula*), hairgrass (*Deschampsia caespitosa*), sedge-grass (*Carex* spp.), and clover meadows (*Trifolium* spp.) being the dominant vegetative communities (Braun 1969). Semi-permanent snowfields are typically present throughout the summer months at high elevations below ridge lines, although in low winter precipitation years or warmer than average summers they can melt out completely (Clait E. Braun, personal observation).

Annual climate typically includes prevailing westerly winds and precipitation dominating in the form of snow and sleet in late September through May, rain through June and early- to mid-September, and low daily minimum temperatures occurring from November through March (Braun and Rogers 1971). January is the coldest month with temperatures averaging -13.2 º C, and July is the warmest month with temperatures averaging 8.2 º C. However, low temperatures and snow can occur during any month of the year, including July and August.

METHODS

Focal Species

The white-tailed ptarmigan is the only species in the genus *Lagopus* endemic to North America. It is well adapted to the extreme environments found in the alpine and has several behavioral and physiological characteristics that allow it to survive in habitat dominated by snow and low temperatures during the winter months (Braun and Schmidt 1971, Braun et al. 1993). White-tailed ptarmigan can be classified into two age classes.

The identification of yearlings (< 12 months in age), and adults (> 12 months in age) is made based on the presence of pigmentation in primaries 9 and 10 (Braun and Rogers 1967). Most females apparently breed as yearlings (Wiebe and Martin 1998), and renesting can occur if a first nest is lost early, but white-tailed ptarmigan do not rear multiple broods within a season (Braun et al. 1993).

Data Collection

Breeding success was measured by counts of chicks obtained in August and September from 1968 to 2010 (Appendix A). Field work was greatly reduced in 1999 at Mt. Evans due to logistical constraints and, productivity data for that year are not included in the analysis. In addition, sample sizes in 1969 and 1971 were inadequate to draw inference regarding reproductive success during those years, and data from those years were removed from the reproductive analysis. Weather data for 2009 and 2010 were only available during the spring months at the time of analysis. Thus, all modeling of reproductive success was based on data spanning 1968-2008 with the exception of the aforementioned years which were not used, while modeling of breeding phenology was based on data spanning 1968-2010, excluding the year 1999.

Broods were located by searching all suitable habitats within study area boundaries and broadcasting chick distress calls to elicit responses from hens with broods (Braun et al. 1973). Once broods were located we attempted to capture all observed chicks using a noose or noose carpet (Zwickel and Bendell 1967). Each captured chick was marked with an aluminum state band containing a unique identification number with the exception of chicks that were too small to hold a band. Unmarked hens were also captured and marked with unique combinations of colored bandettes for identification

during subsequent resightings. We were usually able to assign chicks to individual hens if broods were re-encountered at later times in the season. Various body measurements were recorded from captured chicks, including length measurements for primaries 1-10 (measured to the nearest millimeter). Chick ages can be accurately predicted to within 1-2 days based on length of primaries 1-10 (Giesen and Braun 1979a), and it was from these measurements that we based our estimates of breeding phenology. Most yearling and adult female ptarmigan attempt to nest at least once in a season (Wiebe and Martin 1998). Thus, hens without broods observed during counts either had a nest depredated, experienced brood failure, or were separated from their chicks after hatch. There were no chicks captured in 1999 and hence breeding phenology could not be assessed for that year.

It is important to note that we were unable to monitor nests in this study, and all measures of reproductive success were dependent on observations of chicks and hens in August and September. Nest initiation dates vary among individuals and among years in white-tailed ptarmigan (Martin and Wiebe 2004). This variation in timing of nesting may bias our estimates of reproductive success if the number of chicks observed in August and September are lower simply because of attrition attributed to earlier nesting, and hence a longer gap occurring between the date of hatch and the date of observation. However, we measured the number of days between the median hatch date and the median date of observation of broods for each year in our study, and regressed this measure on year and found that there was no significant change in the number of days occurring between these two events. We made an attempt to begin banding chicks at roughly six weeks of age as this is a time when the legs of chicks are large enough to

hold bands. Based on our observations of the progression of nuptial molt observed in hens in the spring, we were usually able to tell if nesting would occur early or late for a given year (Clait E. Braun, personal observation), which would in turn inform us of when to begin the collection of reproductive data. Thus, it is unlikely bias was introduced in our estimates of reproductive success due to annual variation in timing of nesting of white-tailed ptarmigan and timing of summer data collection. It is also important to note that our method of locating broods depended on the use of broadcasting chick distress calls to illicit a response from hens. This method might positively bias our estimates of reproductive, because hens with chicks or hens that only recently lost chicks are more likely to respond to chick distress calls (Clait E. Braun, personal observation). However, hens that lost chicks early in the nesting season are typically found in either mixed flocks of males and females, or sometimes together with hens that have broods. In both cases detection is not likely to be severely affected, because our experience indicates that both mixed flocks and broods have similar detection probabilities. Hence, our experience indicates that we find both successful and unsuccessful hens in our study area without any apparent heavy bias favoring the former.

Weather Data

Weather data were collected from the Niwot Ridge Long Term Ecological Research (LTER) site, the closest location available to our study area that included the weather variables of interest which dated to the beginning of our study. The D1 weather station at Niwot Ridge is at an elevation and topographic position similar to the study locations at Mt. Evans. This study area is ~ 45 km south by southwest of the D1 weather station. We acknowledge that weather is likely to vary between these site locations, though we

believe that data from Niwot Ridge offered the best option for representing weather conditions experienced by birds at our study area. Temperature data from 1998 to 2008 were available at a nearby snowpack telemetry (SNOTEL) site ~ 10 km from the center of our study area and indicate that SNOTEL and D1 weather station data are highly correlated ($r = 0.93$) even though the SNOTEL site is at an elevation roughly 650 m below the average territory elevation. Precipitation data were not directly comparable among sites as recordings of daily accumulated precipitation did not occur at the SNOTEL site.

We used downscaled climate models for our study area available from the Natural Resources Ecology Laboratory at Colorado State University (Dennis S. Ojima, personal communication) to explore likely future trajectories of timing of nesting by white-tailed ptarmigan. The data set used included daily simulations of surface temperatures on a 1 km grid over the conterminous United States. A grid cell was selected that occurred in the center of the Mt. Evans study area. Projected data were available for years 2012 to 2049.

Nesting Phenology

We used temperature and precipitation data as explanatory variables and the median date (Julian) of nest hatching as the response variable in a linear regression analysis to investigate the influence of spring weather conditions on nesting phenology. Median date of hatch was based on calculating ages of captured chicks and backdating to obtain estimates of hatching dates (Giesen and Braun 1979a). The average of all estimated chick ages was calculated when multiple chicks were encountered with a single hen to obtain a brood hatch date. Mixed flocks containing multiple hens and chicks were

encountered at times, in which case brood hatch dates could not be obtained by taking the average among chicks unless the age differences between chicks were sufficiently large to make segregating into sibling-related groups possible. If segregation into sibling-related groups was not possible, each estimated chick age was taken to represent a brood hatch date. White-tailed ptarmigan hens will adopt chicks if they are encountered without a hen (Wong et al. 2009), and large differences in chick ages within groups is an indication of this occurring. Renesting is relatively uncommon by white-tailed ptarmigan, but second nesting attempts can occur and may potentially bias estimates of timing of nesting (Giesen et al. 1980). We used the median brood age rather than the mean to reduce the potential influence of outliers on our estimates of timing of nesting. Estimates of hatch dates were not available for hens that lost their nests or broods before counting occurred in August. Thus, our estimates of the median date of hatch were only representative of hens that successfully reared broods until the time of counting.

Linear regression was used to examine if breeding phenology advanced temporally over the study period. Regressions were implemented in R (R Development Core Team 2006) using the linear model function. Weather data used as explanatory variables for timing of nesting included the sum of maximum temperature (warmth sum = WS), cumulative spring precipitation (CSP), and number of spring growing degree days (SGDD), all summed over specified time windows. The choice of temperature explanatory variables was based on previous studies relating weather data to nesting phenology (McCleery and Perrins 1998, Dunn and Winkler 1999, Hussell 2003). Previous work has demonstrated that weather events occurring up to 2 months prior to the onset of nesting may have a strong effect on breeding phenology in avian species

(McCleery and Perrins 1998). The average nest initiation date in our study population was previously estimated to occur in early June (Braun et al. 1993). Thus, we defined a searchable time period to be roughly two months prior to this date, between Julian day 91 (1 Apr during non-leap years) and 159 (8 Jun during non-leap years). This fixed time period was used to search for appropriate sized windows to sum the three explanatory variables over. We searched temporal windows of varying length for the best correlation between each of our three weather variables and the median date of hatch. Window sizes were varied between 10 and 68 days and all possible windows of these sizes within the defined searchable space were considered. This search was done separately for each explanatory variable. The window period for each explanatory variable that had the highest correlation with median hatch date was chosen for regression analysis. A cumulative winter precipitation explanatory variable (CWP) was included in the analysis due to the potential effect of snow on available nesting habitat (Clarke and Johnson 1992). This variable was the sum of daily winter precipitation occurring over the months October through March. Several additive and interactive models were considered in the candidate model set, in addition to models that only included single variables. Quadratic trends were also considered for all variables. The variables SGDD, CSP, and WS were all correlated ($r > 0.50$), and these variables were not considered in the same additive or interactive models due to problems of multicollinearity. Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to select the most parsimonious candidate model (Burnham and Anderson 2002). Akaike weights (w_i) were used to assess relative support for each candidate model, given the data. We made *a priori* predictions on the direction of coefficients (positive or negative slope) for every model tested (Table 2.1).

Predictions for future breeding phenology were made using projected climate data for years 2012 to 2049. The number of growing degree days and warmth sums were considered for the predictive model, but precipitation data were not examined because climate model simulations tended to have a high amount of uncertainty (Dennis S. Ojima, personal communication). We included our best temperature model parameterized on past phenology data to predict the average advance in nesting over the next four decades using the simulated data as a covariate. We were conservative in making inferences from these predictions as a few of the simulated data points were beyond the range of values used in the parameterization of the model.

Phenology and Reproductive Success

The relationship between reproductive success and timing of nesting was examined by taking the ratio of total chicks and total hens (chicks/hen) and regressing against the median date of hatch. The ratio of the total number of chicks to total successful hens (average brood size) was also regressed against the annual median date of hatch. Model selection was not used to examine either of these models, because there were only two models to compare and the primary interest was in magnitude of model coefficient estimates. Thus, a frequentist approach using significance testing was used. A significant positive beta coefficient for the median date of hatch explanatory variable would lend support for a beneficial effect of delayed nesting, whereas a significant negative beta coefficient would suggest a non-beneficial effect of earlier nesting. 95% confidence intervals were used to assess if they included 0; a confidence interval not including 0 or only marginally including 0 would lend support to an effect of timing of nesting on fecundity.

Weather and Reproductive Success

We investigated the influence of post-hatching and seasonal conditions on reproductive success of white-tailed ptarmigan using weather variables occurring over set windows centered on the median date of hatch in addition to seasonal weather variables. Four explanatory variables were used. Sum of minimum temperature (T_{min}), sum of maximum temperature (T_{max}), number of rain days (N_{rain}), and an index representing post-hatch warm/dry and cold/wet conditions (PHIndex = sum of average temperature/sum of cumulative precipitation) were considered to represent post-hatching weather experienced by ptarmigan broods. The index was standardized by subtracting the mean and dividing by the standard deviation. These variables were calculated over time windows of 11, 15, 19, and 23 days. These time windows were selected based on previous research with capercaillie (*Tetrao urogallus*) that suggested time periods of ~ 10 days are useful to capture weather patterns as opposed to monthly time windows which may fail to capture relevant short-term weather events (Moss 1985). However, it was unknown if 10-day windows were appropriate for ptarmigan chicks. Thus, larger windows up to 23 days in length were also considered. Window sizes were odd numbered to keep the summed, counted, and averaged variables symmetric around the median date of hatch. The primary purpose of examining different time windows was to find the strongest relationship between the response and predictor variables, because we had no *a priori* reason to believe a 10- or 23-day window might be more appropriate. Each post-hatch explanatory variable was modeled for each of the four time windows, and the time window for the univariate model having the lowest AIC_c was used for subsequent modeling.

Variables summed and averaged over longer time periods in the spring (1 Apr to 15 Jun) and summer (16 Jun to 15 Aug) were considered to represent seasonal conditions that can affect the quality of habitat available to hens during egg laying (spring) and chicks during early growth stages to age of thermoregulation (summer). A longer breeding season time period (1 Apr to 15 Aug) was also considered to represent a total seasonal effect (spring + summer). Seasonal variables included the number of growing degree days (GDD), cumulative precipitation (CP), and a dryness seasonal index (SIndex = GDD/CP) occurring in the spring and summer. We use the numbers 1, 2, and 3 in seasonal variable names, referring to spring, summer, and breeding seasons, respectively. Our approach to selecting the appropriate time period for each explanatory variable was the same as used for the post-hatch variables. Each of the three seasonal explanatory variables was modeled for each of the three seasonal time periods, and the time period for the univariate model having the lowest AIC_c was used for subsequent modeling.

Generalized linear models (GLMs) were implemented in R (R Development Core Team 2006) using the GLM function. Count models were implemented because the data arose from a count process (Appendix B). However, the data indicated overdispersion ($\mu < \sigma^2$), and the Vuong's closeness test was used on the most general model in the dataset under both a Poisson and negative binomial distribution to determine which distribution was the most appropriate (Vuong 1989). Results from this test indicated the negative binomial distribution was most appropriate for our data ($P = 0.001$). We largely followed the methods of Moss et al. (2001) for our statistical analyses of count data. The number of chicks per hen observed in the months August and September was modeled using a negative binomial distribution with total number of chicks as the dependent variable and

total number of hens as an offset (natural log link function). We note that the total number of hens included hens that were unsuccessful and without broods, in addition to successful hens found with broods. There were differences in search effort among years, and as a result, it did not make sense to simply model the annual total number of chicks as these results were not always comparable during years when the search effort was larger. The offset effectively accounts for differences in search effort by modeling the response variable as the log of the ratio of total chicks per total hen. Thus, instead of modeling the counts directly we are modeling an annual rate which is comparable among years.

Our candidate model set included univariate models for all 7 of our explanatory variables, and additive subsets of models that included both post-hatch and seasonal variables. We did not test models with interactions between post-hatch and seasonal variables because time periods used for each was different, and any interactions between different time periods would be difficult to interpret. Model averaging was used to accommodate model uncertainty in the candidate datasets in cases where there was not a clear best model. Concerns of multicollinearity led us to avoid placing variables in the same model that had correlation coefficients > 0.5. *A priori* predictions were made for all model coefficients prior to analysis (Table 2.2). We present McFadden's R^2 values for GLM models where appropriate in figure legends as a pseudo measure of variance explained (Hardin and Hilbe 2001).

RESULTS

Nesting Phenology

Our study population demonstrated a steady advance in timing of nesting from 1968 through 2010 (Fig. 2.1). On average, the median date of hatch advanced 10 days during this time period (β_{YEAR} = -0.24, SE = 0.075, R^2 = 0.19). The strongest correlations for the covariates cumulative spring precipitation, sum of maximum temperature, and number of growing degree days occurred during time windows of Julian days 119-151, 91-159, and 115-159, respectively (Fig. 2.2). Comparisons were made among these three explanatory variables using the models' AIC_c scores and AIC_c weights (Table 2.3). Coefficients for models tested matched *a priori* predictions. Number of spring growing degree days and warmth sum were both negatively correlated with timing of nesting (β_{SGDD} = -0.12, SE = 0.012, R^2 = 0.35; β_{WS} = -0.03, SE = 0.006, R^2 = 0.31) while cumulative spring precipitation was positively correlated with timing of nesting (β_{CSP} = 0.07, SE = 0.017, R^2 = 0.26). The additive model containing the number of growing degree days and winter cumulative precipitation received the majority of support for best predictive model for onset of nesting in white-tailed ptarmigan (w_i = 0.48). The top model that included number of growing degree days and winter cumulative precipitation demonstrated beta coefficients with opposite signs, having negative and positive slopes, respectively.

Downscaled climate data applied to the best univariate temperature-based variable, number of growing degree days, provided predictions of the median hatch day for years 2012 through 2049. A linear regression based on those data points was used to predict the average advance in timing of nesting through 2049 (Fig. 2.3). The

parameterized regression model indicated that an average advance of 5.5 days in timing of nesting is expected over the period 2012-2049, based on projected climate data.

Two indices were tested for a relationship between reproductive success and timing of nesting. The reproductive indices were the annual number of chicks per hen and average brood size; the median date of hatch was used as the response variable. A linear regression indicated that neither annual number of chicks per hen nor average brood size was affected by timing of nesting (all confidence intervals overlapped 0).

Reproductive Success

Annual reproductive success varied widely at our study site (Fig. 2.4) and generally declined from the beginning of study through 2008 (β_{YEAR} = -0.03, SE = 0.010, R^2 = 0.14). The years 2009 and 2010 were among the highest for reproductive success in the time series analyzed. Four different time windows were tested for post-hatch weather variables and three periods were tested for seasonal weather variables. Time windows and periods receiving model support for post-hatch and seasonal weather variables varied. Windows of 15, 19, and 23 days all received model support for one or more of the post-hatch variables, and periods 2 and 3 received support for one or more of the seasonal variables (Table 2.4). The post-hatch window of 11 days and seasonal time period 1 did not receive any support relative to the other time windows and periods tested.

A comparison of univariate models for post-hatch and seasonal weather variables indicated that rain days (N_{rain}) and number of growing degree days (GDD) were the two most important variables tested for the respective post-hatch and seasonal periods with both models receiving the majority of model support relative to post-hatch and seasonal

competing models (Appendix C). Coefficients for models tested tended to match *a priori* predictions. However, post-hatch variables T_{min} and T_{max} had coefficients with slopes in the opposite direction predicted. The AIC_c values for post-hatch weather variables were generally smaller than their seasonal climate variable counter parts. Seventeen models were included in the candidate model set, including univariate models for each of seven post-hatch and seasonal variables, and additive models having both post-hatch and seasonal weather variables combined. There was high model uncertainty among candidate models (Table 2.5). The most parsimonious model in our data set included only rain days (N_{rain}) and received 18% of model support. Models including additional covariates for seasonal index calculated over the entire season (Sind(3)), number of growing degrees during the second half of the season (GDD(2)), and cumulative precipitation during the second half of the season (CP(2)) were all considered reasonable alternatives to the top model with Δ AIC_c values < 2. All of the top models < 2 Δ AIC_c included the rain days covariate, and this appeared to be the most important covariate tested. Models were averaged across the 95% confidence set due to the high amount of model uncertainty (Table 2.6).

DISCUSSION

Nesting Phenology

White-tailed ptarmigan at Mt. Evans advanced their nesting phenology an average of 10 days from 1968 to 2010 (Fig. 2.1; Appendix A). There was clear evidence that conditions experienced in early spring have a strong influence on timing of nesting in this species. However, there was still some uncertainty that we were unable to account for in our models. Undoubtedly timing of nesting is influenced by a variety of factors

experienced by ptarmigan in their environment. For example, the total amount of snow cover is a limiting factor due to its effect of reducing available nesting habitat. Timing of molt is largely affected by photoperiod, and white-tailed ptarmigan hens will not begin egg laying until they have reached full nuptial plumage (Giesen and Braun 1979b). Snow cover may have the added effect of influencing molt timing in ptarmigan as the intensity of light may act to slow the progression of molt (Lindgård and Stokkan 1989). Thus, both photoperiod and snow cover may act as primary factors in timing of nesting by white-tailed ptarmigan with temperature and precipitation being important secondary factors used to fine tune their phenology to local conditions. We found a strong relationship with spring temperature and precipitation on timing of nesting in white-tailed ptarmigan, and the relationships were consistent with our expectations. For example, the estimates of beta coefficients in candidate models all had signs that were in the direction of our *a priori* predictions (Table 2.1). The number of growing degree days that occurred during the window that had the strongest correlation with timing of nesting increased from 1968 to 2010 (β_{YEAR} = 1.60, SE = 0.403, R^2 = 0.27). However, there was no trend in spring precipitation over this same time period (β_{YEAR} = -0.33, SE = 0.730, R^2 = 0.00). Thus, we attribute the observed advancement of timing of nesting primarily to warmer temperatures experienced by birds at Mt. Evans during the spring.

Timing of nesting was not related to reproductive success in our study population as measured by the total number of chicks per hen and average brood size. The consequences of earlier nesting in bird populations have been explored in many different species (Dunn and Winkler 2010). Of particular relevance to this study are published reports of the influence early nesting has on species in Tetraoninae. Novoa et al. (2008)

found rock ptarmigan (*Lagopus muta*) had the highest reproductive success during years of early snowmelt. Clark and Johnson (1992) found that reproductive success of white-tailed ptarmigan populations in the Sierra Nevada correlated negatively with spring snow depth, which in turn was found to delay timing of nesting during years of high snow cover. In contrast, no evidence that differences in annual productivity were related to differences in the onset of timing of nesting for populations of willow ptarmigan (*Lagopus lagopus*) or spruce grouse (*Dendragapus canadensis*) was found (Smyth and Boag 1984, Hannon et al. 1988). Earlier nesting is typically associated with higher reproductive success as individuals that nest early have a tendency to produce larger clutches (Price and Lou 1989). However, potential drawbacks of earlier nesting include increased susceptibility to higher weather variability that occurs early in the season, and the possibility of mistiming the emergence of chicks with peak resource abundance (Both et al. 2006). Hence, the adaptive nature of earlier nesting may differ among different species and across different environments.

We found no evidence that earlier nesting has been beneficial for white-tailed ptarmigan. However, it is important to note that post-hatch weather conditions did not significantly increase or decrease throughout the study for any of the weather variables examined (all confidence intervals overlapped 0). This indicates the ability of hens to adjust timing of nesting based on spring conditions does not appear to be detrimental to reproductive success. Indeed, on average hens are adjusting timing of nesting enough that the post-hatch weather conditions experienced have not changed over the course of study, even though spring conditions have. The ability of white-tailed ptarmigan hens to adjust timing of nesting may be highly important to maintain synchrony with post-hatch

conditions. There may be problems, however, if at some point warmer springs lead to earlier egg laying but post-hatch conditions no longer remain favorable for ptarmigan. For example, Ludwig et al. (2006) found that black grouse in Finland were nesting earlier due to warmer springs, but post-hatch conditions were not changing temporally. This created conditions unfavorable to chicks as they were emerging earlier during colder and wetter conditions, and overall reproductive success in the species declined over several decades. This did not appear to be a problem for our study population, but predicted advancements in timing of nesting of white-tailed ptarmigan at Mt. Evans is of concern given the potential for asynchrony to develop if post-hatch conditions begin to change at different rates than spring conditions. This is an important point to consider given that downscaled climate data for our study site suggest that an average further advance of 5.5 days is expected by the year 2049 at Mt. Evans (Fig. 2.3).

The individual genetic variation that contributes to phenotypic plasticity in the timing of nesting trait is unknown in white-tailed ptarmigan. This is highly important given that springs are projected to continue to warm in coming decades (IPCC 2007, Ray et al. 2008). Although we have presented evidence that white-tailed ptarmigan can adjust timing of nesting based on local conditions, the extent that photoperiod constrains this plastic trait is unknown. If the genetic component of observed variation in timing of nesting is small relative to the environmental component, the ability to continually adapt breeding phenology will be problematic over shorter time spans as evolutionary potential of the trait will be small. Using a special class of mixed models known as 'random regression models' allows for separation of genetic and environmental contributions to an observed plastic trait (Nussey et al. 2008). Unfortunately pedigree information is also

needed for these models, and very large sample sizes are required to obtain parameter estimates (Martin et al. 2011). Our dataset was not large enough to support such an analysis. Thus, the ability of white-tailed ptarmigan to adapt breeding phenology to anticipated climate conditions remains unknown.

Reproductive Success

There was strong evidence that post-hatch weather conditions directly impact reproductive success of white-tailed ptarmigan at Mt. Evans. The number of days with rain occurring during the post-hatch period of three weeks negatively impacted the number of chicks per hen in our study population (Fig. 2.5). This relationship was expected, given the inability of white-tailed ptarmigan chicks to thermoregulate during their first several weeks of life (Myhre et al. 1975). Cold and wet conditions also were unfavorable for reproductive success, and warm and dry conditions were favorable. These results are similar to those reported in other published studies of Tetraoninae (Erikstad and Anderson 1983, Moss 1985, Ludwig et al. 2006). The minimum and maximum temperature variables we examined during post-hatch periods had a negative relationship with reproductive success; both of these variables had small estimated slopes which indicated the effect was minimal. Thus, post-hatch temperature alone appears to be a poor predictor of reproductive success of white-tailed ptarmigan but, together with precipitation, cold temperatures can have a detrimental effect.

Post-hatch weather conditions appeared to be the most important abiotic factor related to reproductive success, although seasonal conditions can influence fecundity of white-tailed ptarmigan. The best seasonal predictor variables were the number of growing degree days, a measure of heat accumulation used to predict plant growth rates,

and seasonal index, a relative measure of temperature and precipitation over the course of a season. Growing degree days are primarily used as measures of plant productivity, but they are also useful as a measure of warmth accumulated at a given area for a specified time. The seasonal index provides information on warm and dry conditions, a probable indicator of dryness.

We hypothesized *a priori* that warmer seasonal conditions would be detrimental to reproductive success due to possible drying effects on alpine vegetation and the potential for semi-permanent snowfields to be either reduced in size or completely depleted. We expected both conditions would lead to desiccation of vegetation and less availability of herbaceous vegetation for chicks. The seasonal dryness index (SIndex) suggested that warm and dry conditions had a negative effect on reproductive success. There were no available data on snowfield size or date of melt out for our study area, but it seems reasonable that warm conditions during the breeding season will directly affect size and persistence of snow fields. We acknowledge that other factors such as topography, solar intensity, and snowpack remaining from the previous winter are also likely to influence snowfield persistence.

The general observed decline in number of chicks per hen from the mid-1970s to 2008 is attributed partially to warmer summers at our study site. There were no trends in precipitation at our study site from 1968-2010, but the number of growing degrees did increase over this same time period. Coefficients for the seasonal growing degree day covariates were negative, indicating lowered reproductive success during warmer breeding seasons. Although our models tended to match our *a priori* predictions, caution should be used in drawing strong inferences from our models, because much of the

variation in the observed data was not explained. This suggests that while weather and climate have an important role in the annual reproductive success of white-tailed ptarmigan at Mt. Evans, other unmeasured factors also had a strong influence. Steen et al. (1994) found that predation was the primary cause of mortality of hazel grouse (*Tetrastes bonasia*), and weather was only the second most important factor for reproductive success. It seems the same, or other factors, might also be driving trends for white-tailed ptarmigan.

Predictions

Downscaled climate projections for Mt. Evans indicate summers will continue to warm over the next several decades (Fig. 2.6). Of particular concern is the influence warming may have on production of alpine vegetation, particularly those species used by ptarmigan broods (May and Braun 1972). The difficulty of predicting future trends in precipitation makes understanding the likely conditions ptarmigan will encounter in the future particularly difficult, especially considering the importance of post-hatch rain days on fecundity. If summers become continually warmer yet precipitation levels remain unchanged, drought conditions are likely to ensue. Increased temperatures during the second half of the breeding season tend to lower reproductive success, based on our modeling of weather effects on white-tailed ptarmigan. Given the predicted changes in temperature, it seems likely reproductive success of white-tailed ptarmigan will suffer if these changes cause drought conditions and lower vegetation production. Despite the fact that we could not model all abiotic processes that are likely to impact white-tailed ptarmigan reproduction, we were still able to develop predictive models using post-hatch and seasonal weather data alone to explain patterns and trends in reproductive success.

Averaging of candidate model coefficients suggest the most general model in the dataset captured the trend (Fig 2.7). Thus, other sources of variation appear to play a substantial role in the reproductive success of white-tailed ptarmigan. Both weather and climate can have an important role in reproductive success of white-tailed ptarmigan, and there is a need to better understand the abiotic processes that impact ptarmigan reproduction. An important step to addressing this problem for white-tailed ptarmigan is to gain a better understanding of the role standing snowfields and the ability to track plant phenology have in shaping reproductive success in the species. Future studies that consider the role of phenotypic plasticity in traits such as timing of nesting in coping with environmental variation will also be important to understand vulnerability to future warming that is expected over coming decades.

Table 2.1. *A priori* linear regression models and predictions for four explanatory variables used to predict timing of nesting for white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado, USA. The model is provided along with a verbal description of the prediction, and the predicted direction of explanatory variables in the model with respect to the sign of the slope for the associated beta coefficients.

Model	Hypothesis	Predicted beta coefficient				
		β_0	β_1	β_2	β_3	β_4
$\beta_0 + \beta_1(\mathrm{WS})$	Advancing effect of warmth sum on timing of nesting	>0	-	-	-	-
$\beta_0 + \beta_1(\mathrm{WS}) + \beta_2(\mathrm{WS}^2)$	Advancing effect of warmth sum on timing of nesting, quadratic form	>0	<0	<0	-	-
$\beta_0 + \beta_1(\mathrm{SGDD})$	Advancing effect of number of spring growing degree days on timing of nesting	>0	-	-	-	-
$\beta_0 + \beta_1(\mathrm{SGDD}) + \beta_2(\mathrm{SGDD}^2)$	Advancing effect of number of spring growing degree days on timing of nesting, quadratic form	>0	<0	<0	-	-
$\beta_0 + \beta_1(\mathrm{CSP})$	Delaying effect of cumulative spring precipitation on timing of nesting	>0	>0	-	-	-
$\beta_0 + \beta_1(\mathrm{CSP}) + \beta_2(\mathrm{CSP}^2)$	Delaying effect of cumulative spring precipitation on timing of nesting, quadratic form	>0	>0	>0	-	-
$\beta_0 + \beta_1(\mathrm{CWP})$	Delaying effect of cumulative winter precipitation on timing of nesting	>0	>0	-	-	-
$\beta_0 + \beta_1(\mathrm{CWP}) + \beta_2(\mathrm{CWP}^2)$	Delaying effect of cumulative winter precipitation on timing of nesting, quadratic form	>0	>0	>0	-	-
$\beta_0 + \beta_1(\mathrm{SGDD}) + \beta_2(\mathrm{CWP})$	Additive effect of spring growing degree days and cumulative winter precipitation on timing of nesting	>0	<0	>0		
$\beta_0 + \beta_1(\mathrm{SGDD}) + \beta_2(\mathrm{CWP}) + \beta_3(\mathrm{SGDD}^2) + \beta_4(\mathrm{CWP}^2)$	Additive effect of spring growing degree days and cumulative winter precipitation on timing of nesting, quadratic form	>0	<0	>0	<0	>0
$\beta_0 + \beta_1(\mathrm{WS}) + \beta_2(\mathrm{CWP})$	Additive effect of warmth sum and cumulative winter precipitation on timing of nesting	>0	<0	>0		
$\beta_0 + \beta_1(\mathrm{WS}) + \beta_2(\mathrm{CWP}) + \beta_3(\mathrm{WS}^2) + \beta_4(\mathrm{CWP}^2)$	Additive effect of warmth sum and cumulative winter precipitation on timing of nesting, quadratic form	>0	<0	>0	<0	>0
$\beta_0 + \beta_1(\mathrm{SGDD}) + \beta_2(\mathrm{CWP}) + \beta_3(\mathrm{SGDD} \times \mathrm{CWP})$	Interactive effect between spring growing degree days and cumulative winter precipitation	>0	<0	>0	<0	-
$\beta_0 + \beta_1(\mathrm{WS}) + \beta_2(\mathrm{CWP}) + \beta_3(\mathrm{WS} \times \mathrm{CWP})$	Interactive effect between warmth sum and cumulative winter precipitation	>0	<0	>0	<0	-

Table 2.2. Univariate generalized linear models and *a priori* predictions for eight explanatory variables used to predict reproductive success for white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado, USA. Post-hatch and seasonal variables are identified, and a verbal prediction along with the predicted direction of the slope is provided for each model.

Model	Hypothesis	Predicted beta coefficient	
		β_0	β_1
Post-hatch			
$\beta_0 + \beta_1(N_{rain})$	Negative effect of rain days on reproduction	>0	<0
$\beta_0 + \beta_1(T_{min})$	Positive effect of warm temperatures on reproduction	>0	>0
$\beta_0 + \beta_1(T_{max})$	Positive effect of warm temperatures on reproduction	>0	>0
$\beta_0 + \beta_1$(PHIndex)	Positive effect of warm dry conditions on reproduction	>0	>0
Seasonal			
$\beta_0 + \beta_1$(GDD)	Negative effect of warm seasons on reproduction	>0	<0
$\beta_0 + \beta_1$(CP)	Positive effect of wet seasons on reproduction	>0	>0
$\beta_0 + \beta_1$(SIndex)	Negative effect of warm dry seasons on reproduction	>0	<0

Table 2.3. Model selection results for 14 predictive models of nesting phenology using weather variables for white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado. Variables tested were number of spring growing degree days (SGDD), cumulative winter and spring precipitation (CWP and CSP, respectively), and warmth sum (WS). Models are ranked based on AIC_c. Also shown are the associated beta coefficients for each variable in the model and associated standard error in parentheses, the number of parameters (K), delta AIC_c (ΔAIC_c), AIC_c weights (w_i), and the amount of variation explained by each model (R^2). Squared terms in the model definition represent both the linear and squared form of the variable indicated.

Table 2.3 Continued.

Model	Intercept	CSP	CSP^2	CWP	CWP^2	SGDD	$SGDD^2$	WS	WS^2	CWP x SGDD	CWP x WS	LL	K	AIC_c	ΔAIC_c	w_i	R^2
SGDD + CWP	200.258	-	-	0.002	-	-0.109	-	-	-	-	-	-130.50	3	270.08	0.00	0.48	0.37
	(4.814)	-	-	(0.006)	-	(0.023)	-	-	-	-	-						
SGDD x CWP	195.600	-	-	0.009	-	-0.061	-	-	-	-7.14E-05	-	-130.44	4	272.54	2.46	0.14	0.37
	(14.490)	-	-	(0.028)	-	(0.144)	-	-	-	(2.10E-04)	-						
WS + CWP	192.100	-	-	3.27E-05	-	-	-	-0.029	-	-	-	-131.98	3	273.05	2.96	0.11	0.32
	(4.240)	-	-	(6.10E-03)	-	-	-	(6.84E-03)	-	-	-						
CSP	182.534	0.068	-	-	-	-	-	-	-	-	-	-133.44	2	273.52	3.44	0.09	0.28
	(2.197)	(0.068)	-	-	-	-	-	-	-	-	-						
CSP + CSP^2	186.800	-6.97E-05	2.23E-04	-	-	-	-	-	-	-	-	-132.76	3	274.60	4.52	0.05	0.33
	(4.309)	(0.006)	(1.96E-04)	-	-	-	-	-	-	-	-						
$SGDD^2$ + CWP^2	209.800	-	-	-0.032	2.62E-05	-0.093	-5.67E-05	-	-	-	-	-130.14	5	274.68	4.60	0.05	0.38
	(16.650)	-	-	(0.004)	(3.56E-05)	(0.110)	(5.25E-04)	-	-	-	-						
WS^2 + CWP^2	204.700	-	-	-0.038	2.90E-05	-	-	-0.029	-4.18E-05	-	-	-130.35	5	275.11	5.02	0.04	0.37
	(14.590)	-	-	(0.047)	(3.56E-05)	-	-	(0.007)	(3.43E-05)	-	-						
WS x CWP	193.100	-	-	-0.001	-	-	-	-0.047	-	-	2.67E-05	-131.88	4	275.43	5.35	0.03	0.33
	(4.916)	-	-	(6.94E-03)	-	-	-	(0.043)	-	-	(6.24E-05)						
SGDD	201.613	-	-	-	-	-0.109	-	-	-	-	-	-135.98	2	278.59	8.50	0.01	0.37
	(2.444)	-	-	-	-	-	-	-	-	-	-						
$SGDD^2$	200.100	-	-	-	-	-0.074	-1.66E-04	-	-	-	-	-135.91	3	280.91	10.83	0.00	0.37
	(5.116)	-	-	-	-	(0.102)	(4.85E-04)	-	-	-	-						
WS^2	193.300	-	-	-	-	-	-	-0.030	-5.06E-05	-	-	-135.97	3	281.01	10.93	0.00	0.37
	(1.161)	-	-	-	-	-	-	(0.006)	(3.13E-05)	-	-						
WS	192.139	-	-	-	-	-	-	-0.029	-	-	-	-137.32	2	281.28	11.20	0.00	0.33
	(0.945)	-	-	-	-	-	-	(0.006)	-	-	-						
CWP	187.200	-	-	0.005	-	-	-	-	-	-	-	-139.97	2	286.58	16.49	0.00	0.01
	(4.876)	-	-	(0.007)	-	-	-	-	-	-	-						
CWP^2	210.500	-	-	-0.071	5.78E-05	-	-	-	-	-	-	-138.90	3	286.87	16.79	0.00	0.06
	-16.950	-	-	-0.053	-4.04E-05	-	-	-	-	-	-						

Table 2.4. Post-hatch and seasonal windows and time periods for which different weather and climate variables were tested at Mt. Evans, Colorado. The top GLM model for each weather or climate variable and window or time period is identified with an 'X'. All subsequent modeling used the windows and time periods identified below for each variable.

	Post-hatch				Seasonal		
	W1 11 days	W2 15 days	W3 19 days	W4 23 days	P1 15 Apr-15 Jun	P2 16 Jun-15 Aug	P3 15 Apr-Aug 15
N_{rain}	-	-	X	-	-	-	-
T_{min}	-	-	-	X	-	-	-
T_{max}	-	X	-	-	-	-	-
PHIndex	-	-	X	-	-	-	-
GDD	-	-	-	-	-	X	-
CP	-	-	-	-	-	X	-
SIndex	-	-	-	-	-	-	X

Table 2.5. Model selection results for 17 predictive models of reproductive success in white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado. Models are ranked by AIC_c, and model variables and their associated beta coefficients and standard errors (±SE) are provided. Time periods are identified for seasonal variables in parentheses. Also shown the number of parameters (*K*), delta AIC_c (ΔAIC_c), and AIC_c weights (w_i). Variables presented include number of rain days (N_{rain}), post hatch index (PHIndex), cumulative precipitation in second period (CP(2)), number of growing degree days in second period (GDD(2)), and the seasonal index for the third period (SIndex(3)). Both indices were standardized by subtracting the mean and dividing by the standard deviation.

Table 2.5 Continued.

Model	N_{rain}	PHInd	CP(2)	GDD(2)	SInd(3)	-2(LL)	K	AIC_c	ΔAIC_c	w_i
N_{rain}	-0.049 (0.028)	-	-	-	-	-144.37	3	295.44	0.00	0.18
SInd(3) + N_{rain}	-0.054 (0.027)	-0.134 (0.100)	-	-	-	-143.51	4	296.23	0.79	0.12
GDD(2) + N_{rain}	-0.049 (0.027)	-	-	-0.012 (0.010)	-	-143.71	4	296.64	1.20	0.10
CP(2) + N_{rain}	-0.058 (0.029)	-	0.022 (0.022)	-	-	-143.83	4	296.86	1.42	0.09
PHInd	-	0.110 (0.097)	-	-	-	-145.38	3	297.47	2.02	0.07
GDD(2)	-	-	-	-0.011 (0.010)	-	-145.46	3	297.62	2.18	0.06
PHInd + N_{rain}	-0.044 (0.031)	0.044 (0.107)	-	-	-	-144.28	4	297.76	2.32	0.06
SInd(3)	-	-	-	-	-0.111 (0.103)	-145.56	3	297.83	2.39	0.05
CP(2) + GDD(2) + N_{rain}	-0.057 (0.028)	-	0.020 (0.022)	-0.010 (0.010)	-	-143.24	5	298.36	2.91	0.04
CP(2) + SInd(3) + N_{rain}	-0.060 (0.029)	-	0.016 (0.022)	-	-0.011 (0.103)	-143.24	5	298.36	2.92	0.04
SInd(3) + PHInd	-	0.118 (0.096)	-	-	-0.118 (0.102)	-144.74	4	298.69	3.24	0.04
SInd(3) + PHInd + N_{rain}	-0.045 (0.031)	0.045 (0.104)	-	-	-0.134 (0.100)	-143.41	5	298.69	3.25	0.04
CP(2)	-	-	0.008 (0.022)	-	-	-146.01	3	298.73	3.28	0.03
GDD(2) + PHInd	-	0.095 (0.098)	-	-0.009 (0.010)	-	-144.95	4	299.12	3.68	0.03
GDD(2) + PHInd + N_{rain}	-0.047 (0.031)	0.021 (0.108)	-	-0.010 (0.010)	-	-143.69	5	299.26	3.82	0.03
CP(2) + GDD(2)2	-	-	0.007 (0.021)	-0.011 (0.010)	-	-145.40	4	300.01	4.56	0.02
CP(2) + SInd(3)	-	-	0.002 (0.023)	-	-0.108 (0.109)	-145.56	4	300.33	4.88	0.02

Table 2.6. Model averaged covariates for predictive models of reproductive success of white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado. Covariates were averaged from models in the 95% candidate set.

Variable	Estimate	SE
Intercept	0.566	0.422
N_{rain}	-0.052	0.029
SInd(3)	-0.124	0.102
GDD(2)	-0.012	0.010
CP(2)	0.016	0.023
PHInd	0.075	0.108

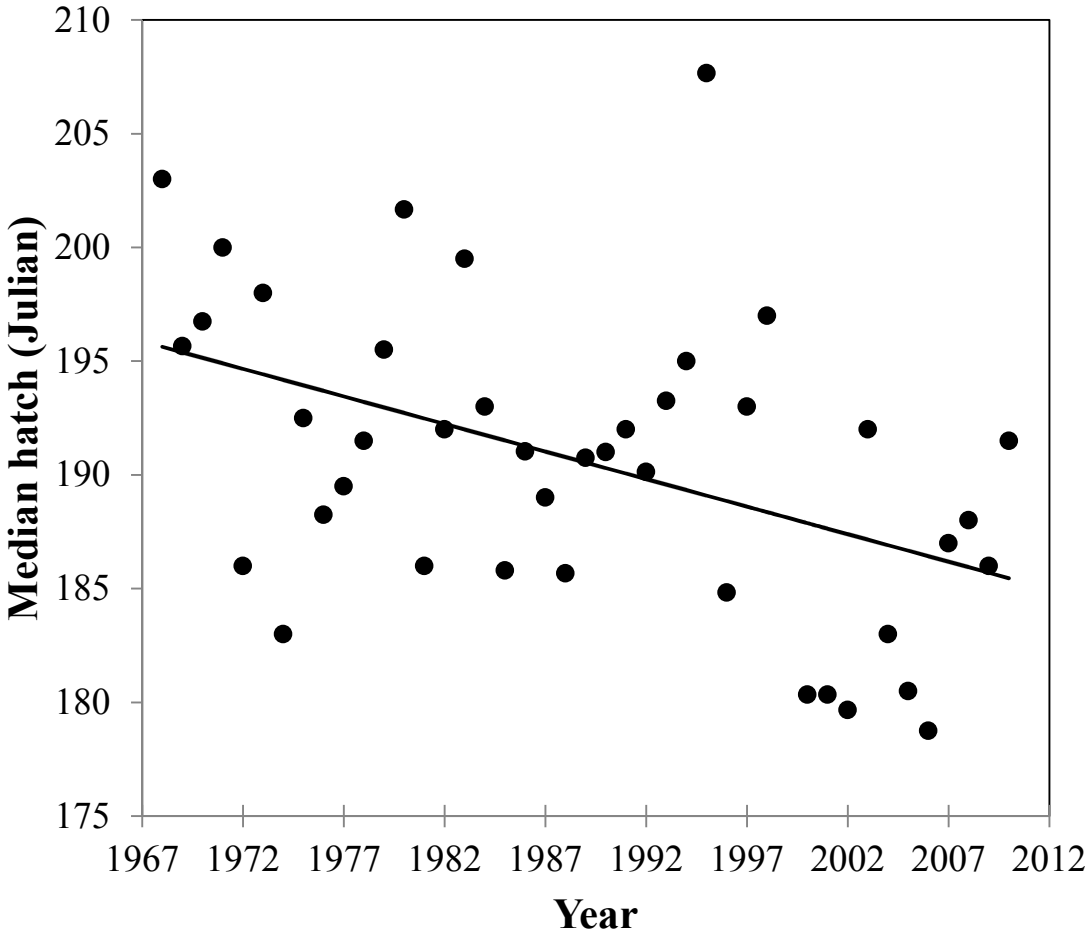

Figure 2.1. Temporal advance of the median date of hatch for white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado from 1968 to 2010. Time on the y-axis is in Julian days, and time units on the x-axis is represented as year. The line represents a linear regression of median date of hatch on year (βyear = -0.242, SE = 0.075, R^2 = 0.19).

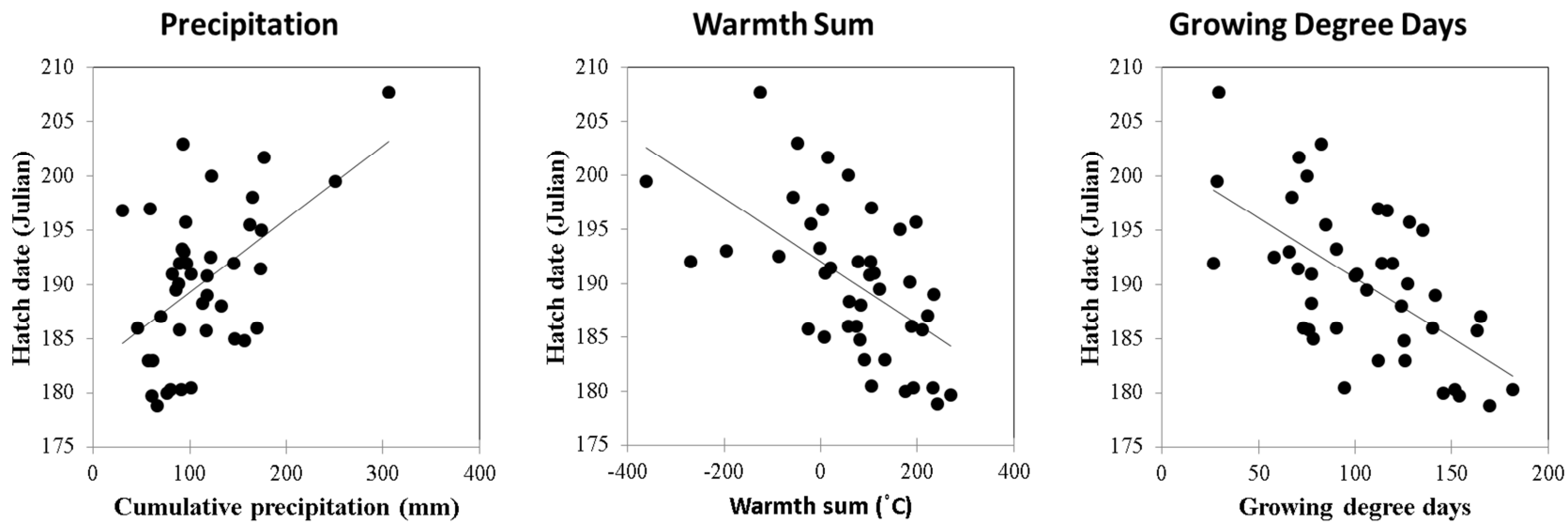

Figure 2.2. Relationships between median date of hatch (Julian days) for white-tailed ptarmigan and three explanatory variables at Mt. Evans in Clear Creek County, Colorado, from 1968 to 2010. The explanatory variables were cumulative spring precipitation (β_{CSP} = 0.067, SE = 0.017, R^2 = 0.27), warmth sum (β_{WS} = -0.029, SE = 0.007, R^2 = 0.33), and number of spring growing degree days (βS_{GDD} = -0.110, SE = 0.022, R^2 = 0.37). Lines represent the best fit linear regressions.

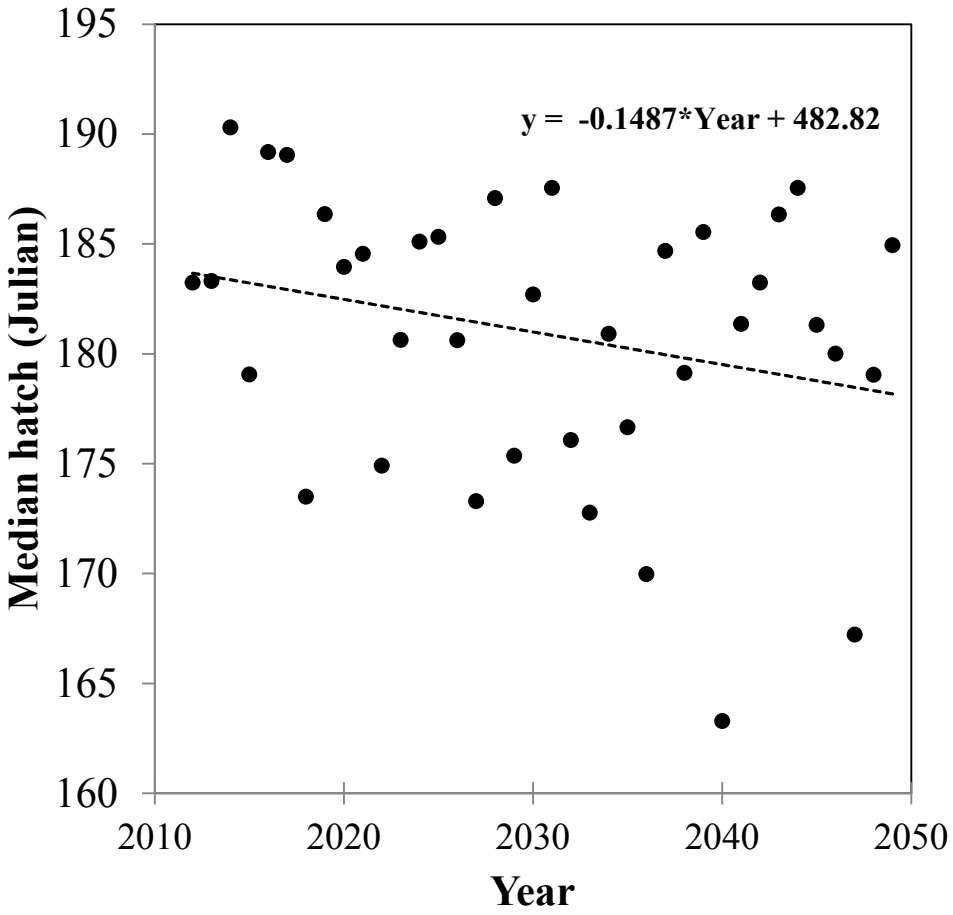

Figure 2.3. Annual predictions for nesting phenology of white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado for years 2012 through 2049. Solid circles represent predicted median hatch dates (y_i) based on the univariate regression model for number of spring growing degree days ($y_i = 201.613 – 0.109*SGGD$). The dashed line was taken from a linear regression between the predicted hatch date and year.

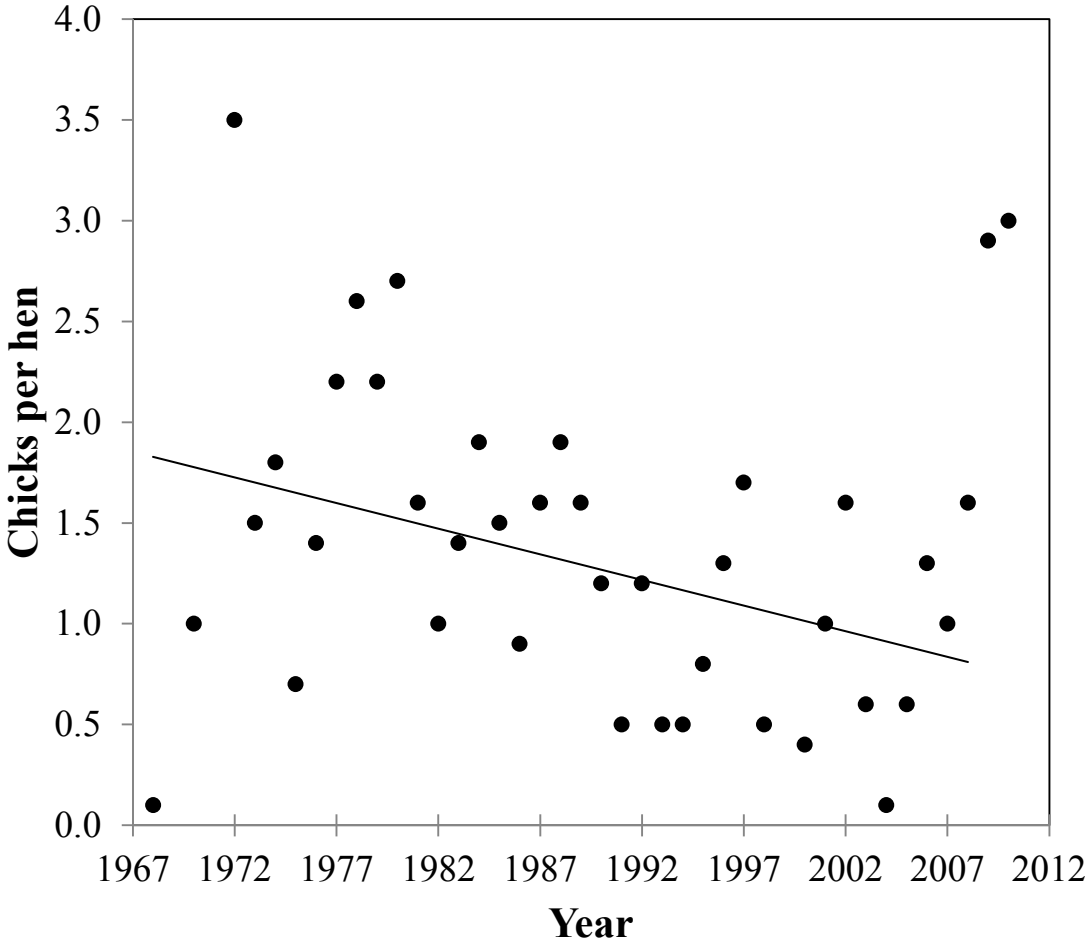

Figure 2.4. Observed number of chicks per hen (solid black circles) for white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado, USA. A trend lines was fit to the observed data points (β_{YEAR} = -0.03, SE = 0.010, R^2 = 0.14).

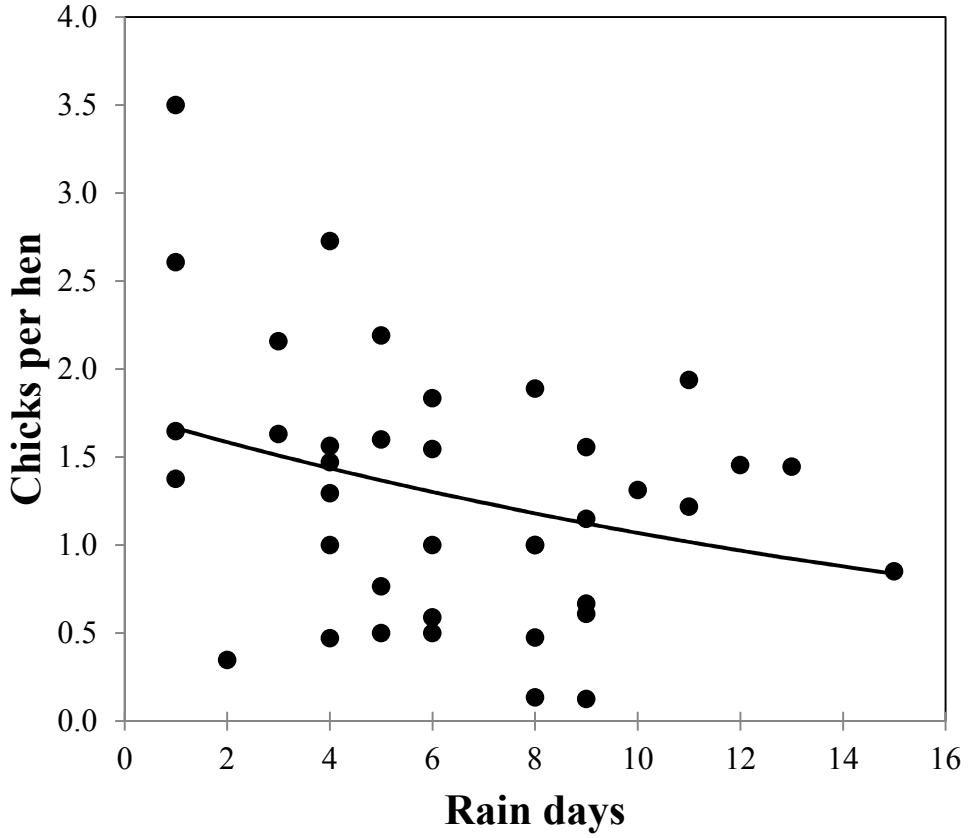

Figure 2.5. Effect of number of rain days on number of chicks per hen at Mt. Evans in Clear Creek County, Colorado, USA. The solid line was fit from the best single predictor model of reproductive success (N_{rain}) and represents the effect of rain days on chicks per hen (β_{rain} = -0.069, SE = 0.010, R^2 = 0.08).

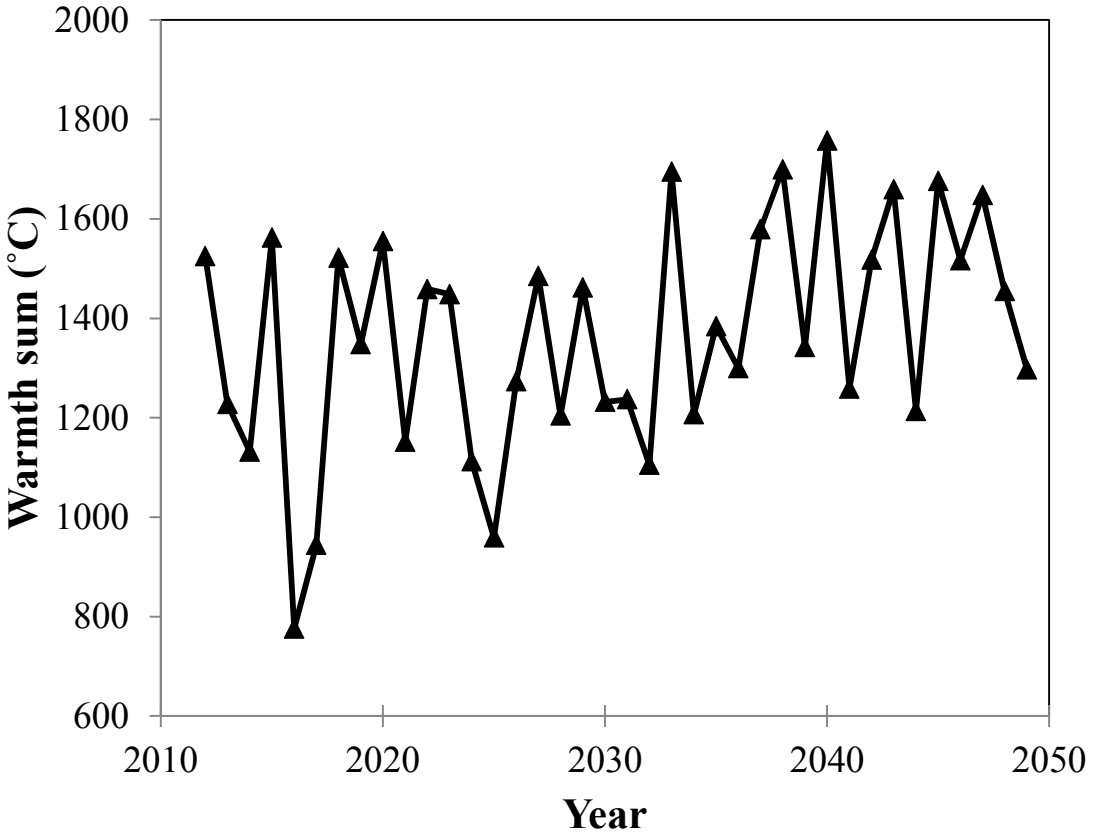

Figure 2.6. Projected sum of maximum temperatures for spring for years 2012 to 2049 at Mt. Evans in Clear Creek County, Colorado, USA. Values were taken by summing temperatures from 16 Jun to 15 Aug.

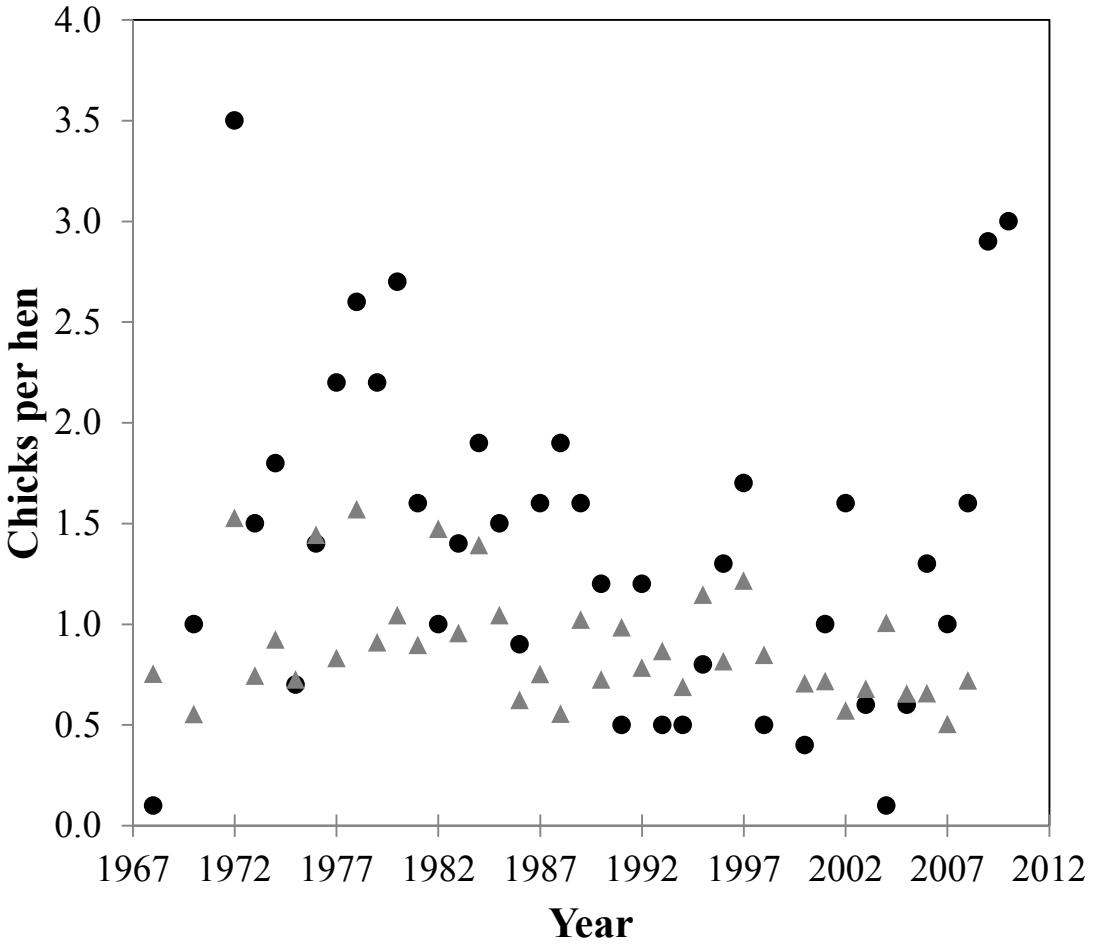

Fig 2.7. Reproductive success and model predictions of white-tailed ptarmigan from 1968 to 2010 at Mt. Evans in Clear Creek County, Colorado, USA. Actual observations (black circles) measure the total number of chicks per hen in a season, and predictions from the most general model {CP(2) + GDD(2) + N_{rain}} with the lowest AIC_c in the candidate set is shown using model-averaged coefficients (gray triangles).

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CHAPTER 3: LONG-TERM TRENDS IN SURVIVAL, GROWTH, AND POULATION RECRUITMENT OF A WHITE-TAILED PTARMIGAN POPULATION IN COLORADO

SUMMARY

High-elevation ecosystems have undergone rapid change in climate during the last century; changes that could threaten viability of alpine species. Lack of long-term datasets needed to understand the effects of climate on population dynamics are rare. We studied a population of white-tailed ptarmigan (*Lagopus leucura*) from 1968 to 2010 in central Colorado, and present annual estimates of survival, rates of population change, and annual recruitment of breeding-age birds into the population. We examined how survival responded to annual variation in winter weather. Trends in annual survival were not apparent and varied widely across years (φ_t: 0.161 to 0.867). Yearling males and females had the highest average annual survival rates (φ_{JuvM} = 0.726 and φ_{JuvF} = 0.628), followed by adult males and females (φ_{AdM} = 0.623 and φ_{AdF} = 0.523). Average annual rates of population change indicated a stable population ($\bar{\lambda}_t$ = 1.036, SE = 0.037), but we cannot rule out declines or increases. The most parsimonious population recruitment model (Pradel's temporal symmetry model) included linear trend and additive sex effects and suggested a decline in recruitment of breeding-age birds into the population and was attributed primarily to hunting restrictions that went into effect in the early 1990s. The decline in recruitment was offset by higher rates of survival towards the last two decades

of the study. The best weather model included winter cumulative precipitation, and weather covariates fit to survival models were able to account for a limited amount of variation in the data (11%). Females were more strongly affected by weather than males in our study population. Our results suggest the population of breeding-age ptarmigan is stable and relatively robust to past variation in climate. However, our best climate survival model indicated lowered survival during low precipitation years, and climate projections for our study area predict warming trends during the winter months. This may have implications for overwinter survival of ptarmigan if temperature affects snowpack and reduces winter habitat at our study site.

KEY WORDS alpine, climate, Colorado, demographics, *Lagopus leucura*, population

INTRODUCTION

High elevation ecosystems are thought to be particularly sensitive to climate warming because their boundaries are defined largely by cold temperatures (Diaz and Eischeid 2007). Considerable uncertainty exists in our understanding of how warming trends have affected high elevation species, although increases in growing season have been shown to impact the demographics of yellow-bellied marmots (*Marmota flaviventris*) (Ozgul et al. 2010), and warmer spring temperatures have been shown to significantly advance the timing of migration of American robins (*Turdus migratorius*) to higher elevations (Inouye et al. 2000). Uncertainty in our ability to describe the influence of climate on population demographics of alpine animals is due primarily to a general lack of data for these species. This paucity of data makes predicting future demographic

trajectories of alpine species difficult. A first step in making predictions on future population trends under projected climate scenarios is to first understand how past climate events have affected alpine-endemic species. Long-term data sets available for alpine species, although rare, offer opportunities to address these needs.

The white-tailed ptarmigan (*Lagopus leucura*) is an alpine-endemic species with populations spanning mountainous habitats in western North America. Their distribution ranges from southern Alaska and northwestern Canada to northern New Mexico (Braun et al. 1993). In Colorado, populations are found in nearly all mountainous habitats occurring above timberline (Braun 1969). White-tailed ptarmigan spend the majority of their life cycle at elevations near or above treeline, and are well adapted to cold climates found at high elevations. The species has many behavioral and physiological traits that help them survive in extreme winter conditions (Braun et al. 1993). The white-tailed ptarmigan has the highest reported annual adult survival rates and the lowest annual fecundity rates of the three *Lagopus* species occurring in North America (Sandercock et al. 2005). Several studies have published findings on the demographic characteristics of white-tailed ptarmigan in Colorado (Braun 1969, Martin et al. 2000, Sandercock et al. 2005), but long-term demographic trends have not been presented, and only abundance trends have been described for one population studied from 1975 to 1999 at Rocky Mountain National Park (Wang et al. 2002). Thus, long-term demographic trends of white-tailed ptarmigan in Colorado and throughout its range in North America are largely unknown. Given recent concerns over the impact of climate change to alpine habitats, the species has recently been petitioned for listing as threatened under the Endangered Species Act, although data to inform a listing decision is lacking. However, the recent

petition to list white-tailed ptarmigan highlights that species dependent on alpine are of high interest to ecologists, primarily due to increased attention focused on warming impacts to high-elevation systems.

The Colorado Division of Wildlife began monitoring white-tailed ptarmigan at multiple locations in Colorado in the 1960s, two of which included populations subsequently monitored for multiple decades (Braun 1969, Braun and Rogers 1971). A study examining population trends at Rocky Mountain National Park was presented by Wang et al. (2002). We examined 43 years of demographic data collected from a population of white-tailed ptarmigan in central Colorado in the form of mark-recapture data. Our objectives were to: (1) estimate annual survival and population recruitment, (2) examine trends in annual population change, and (3) examine the effects of different weather variables on survival. We developed *a priori* hypotheses for our third objective about the predicted direction various weather covariates would have on survival based on our knowledge of white-tailed ptarmigan biology. The predicted direction of the weather covariates are provided in the methods section.

STUDY AREA

The Mt. Evans study site is within the Mt. Evans Wilderness Area in Clear Creek County, Colorado. The study area is approximately 16 km southwest of Idaho Springs and is bisected by the Mt. Evans Scenic Byway, a non-wilderness road corridor that extends to an area below the summit of Mt. Evans. Elevation ranges from 3,292 m to the summit of Mt. Evans at 4,347 m (Braun 1969). The total study area consists of ~4.0 km^2 of alpine habitat. From 1987 to 1996 the study area was expanded to 13.2 km^2 as part of a larger telemetry study. Vegetation of the study area is described in detail in Braun (1969).

Vegetative communities in the study area include cushion plant stands, Dryas stands (*Dryas octopetala*), *Kobresia* meadows (*Kobresia myosuroides*), hairgrass meadows (*Deschampsia caespitosa*), Parry's clover meadows (*Trifolium parryi*), and sedge-grass wet meadows (*Carex* spp.) (Marr 1961, Braun and Rogers 1971). Westerly winds are prevalent, and precipitation throughout the late fall and early spring is in the form of snow or sleet (Sep through May), and rain in the spring and summer (Jun through early- to mid-Sep).

METHODS

Demographic Data

We studied white-tailed ptarmigan at Mt. Evans from 1966 to 2010. Birds were located in spring and summer by broadcasting calls of males and distressed chicks throughout the study area. Hens paired with males could usually be located within a short distance of territorial males in spring and early summer (Braun et al. 1973). We used playback of chick distress calls in mid- to late-summer to locate hens. Male territorial calls also were used during these periods and were frequently successful in locating flocks of birds. Habitat was reduced in spring and early summer due to limited availability of snow-free areas across breeding territories, which in turn reduced the search area where birds could be found. Search effort in mid- to late-summer was maximized by searching suitable habitats that included areas adjacent to snowfields and moist meadows, both of which provide brood habitat, and ridgelines with rock cover are used by flocks of breeding-age birds. The use of broadcast calls was not implemented until 1968 when recordings first became available. Thus, we did not include the first 2 years of demographic data in our

analysis due to estimates potentially being biased low due to lower detection rates in the absence of broadcast calls (Braun et al. 1973).

Breeding-age white-tailed ptarmigan can be assigned to two different age classes based on the presence or absence of pigmentation in outer primaries 9 and 10 (Braun and Rogers 1967). Birds with pigmentation are classified as yearlings (hatched the previous season) and those without are classified as adults (two years of age or older). This was the primary classification tool used to assign an age class for captured birds. We made an attempt to capture all unmarked birds in the study area. All captured birds, including chicks, received a unique aluminum numbered band. Breeding-age birds received additional colored bandettes that allowed identification without need for recapture during subsequent reobservations. Several different measurements were taken from captured birds and used to help assign age and, in some cases sex, of captured birds. We banded the majority of birds from 1 May to 30 September. The midpoint of the sampling period was 15 July for this analysis. During some years birds were located in the winter months. Reobservations occurring outside of the sampling time window were not included in the analysis. For example, if a bird was marked at a time outside of the sampling period but subsequently reobserved at a later time within the sampling period, we took the reobservation or recapture event to represent the first data point for a given bird in our analyses.

The Mt. Evans population experienced varying hunting pressure throughout our study. The implementation of a closed hunting area within ½ mile of the road at Mt. Evans went into effect in 1994 and effectively ended the harvest of birds from our study population (Clait E. Braun, personal observation). A wing collection station was placed

near the entrance to the study area during the hunting season from 1968 to 1998 and a check station was operated on the opening weekend of the hunting season in many years. Hunters were asked to provide band numbers from marked birds they harvested which provided known-fate data for many mortalities. We attempted to control for the effects of hunting when presenting population estimates of the vital rates survival and recruitment. In cases where a bird was harvested and its fate was known, we treated birds used in our survival models as being not released at last capture prior to known harvest. This was an attempt to control for the effects of hunting which was not the focus of this study. The influence of hunting on white-tailed ptarmigan in our study population has been previously described (Braun 1969).

Climate Data

The nearest weather station that had data spanning the entire length of our study period was from the Niwot Ridge Long Term Ecological Research (LTER) D1 weather station. The weather station at Niwot Ridge LTER was approximately 45 km northeast of the study site. The D1 weather station is at an elevation and easterly facing slope comparable to the study area at Mt. Evans. The D1 station presented the best available option for representation of climate conditions experienced at Mt. Evans, and comparisons with temperature data taken from a nearby snowpack telemetry (SNOTEL) station (site 936) available from 1998 to 2010 indicated a high correlation between the two sites ($r = 0.93$).

Estimating Annual Survival

Population Survival Analysis.—We used mark-recapture models implemented in Program MARK using the Cormack-Jolly-Seber (CJS) parameterization to estimate survival between sex and age classes (White and Burnham 1999). Only birds marked or

reobserved at breeding age were included in the analysis, and encounter histories were constructed using 1's (detected by capture or reobservation) and 0's (not detected). The CJS model estimates apparent survival (φ) and probability of recapture (*p*) parameters. We considered the survival parameter to be apparent survival because an individually-marked bird not seen during subsequent years may have emigrated from the study area after its last capture or reobservation. Thus, true mortality cannot be separated from emigration in these models. Models that included age (*a*), time (*t*), and sex (*s*) effects were developed for both the apparent survival and recapture parameters. Trend effects (*T*) and reproductive effects (*r*) were considered separately for the apparent survival and recapture parameters, respectively. Trend effects were used to test if apparent survival either increased or declined across the study period. The reproductive effect (r) was the total number of chicks per total number of hens observed in August and September (total chicks/total hens) calculated for every year of the study. We considered reproductive effect in the structure of the recapture parameter because there may be some bias in capturing or re-observing hens that were reproductively successful as opposed to those which failed to rear young. This was due to the potential for unsuccessful hens to emigrate outside of the study area once a nest or brood failed (Braun 1969, Martin et al. 2000).

We followed the model notation of Lebreton et al. (1992). Examples of this notation include models where survival and probability of capture are a function of time $\{\varphi(t)p(t)\}$ and models where survival and probability of capture are a function of an interaction between sex and time effects $\{\varphi(s*t)p(s*t)\}$. We developed a model set to be tested that included a full model (i.e., the global model) with interactions between sex

and time and an additive age effect in the survival parameter, and additive effects of all three factors in the recapture parameter $\{\varphi(a+s*t)p(a+s+t)\}$. Models that were increasingly more parsimonious in the number of parameters included were also considered in the candidate model set. Our sample sizes were not sufficiently large to support a fully time dependent model as many of the parameters were non-estimable under the fully parameterized structure $\{\varphi(a*s*t)p(a*s*t)\}$. Thus, the global model was a reduced version of the fully saturated model. The total number of possible models to test was large, and we selected the structure of the recapture parameter p by keeping φ in the time-dependent form $\{\varphi(a+s*t)\}$ while testing 12 different *a priori* model structures of p (Table 3.1). An information-theoretic approach was used for model selection (Burnham and Anderson 2002). The structure for p in the model having the lowest AIC_c score was used to test 22 different *a priori* model structures of φ (Table 3.2). These represent our candidate models from which we estimated annual rates of apparent survival.

Climate Survival Analysis.—Models were tested separately for males and females by incorporating seasonal weather covariates to examine the effects of weather on apparent survival. Our interest was in examining the effects of weather on apparent survival parameters, and we did not examine trend effects; we only fit weather covariates to apparent survival parameters. All recapture parameters were modeled with the recapture parameter found to be the most parsimonious in the population survival analysis (Table 1). The starting structure of the apparent survival parameter was of the form $\{\varphi(a+W)p(\text{best})\}$, where '$W$' represents the weather covariate of interest in a given model, and 'best' represents the most parsimonious structure for recapture found in the population survival analysis.

Simple time dependence may have explained more variation in our data than any weather variable. Thus, time (t) models were also maintained in the candidate model set for model comparisons, and the most general model in the candidate model set was $\{\varphi(a+t)p(\text{best})\}$. We examined annual weather variables averaged, counted, or summed over the winter period, defined as occurring from 1 October through 31 March. Variables examined included the total cumulative sum of precipitation (*CP*), average minimum temperature (*MinT*), average maximum temperature (*MaxT*), number of days with maximum temperature above freezing (warm days, *WD*), and quadratic effects for the sum of precipitation variable (CP^2). Additional models with additive effects between the precipitation and temperature-based variables were also tested (Table 3.3). Weather effects during spring and summer could not be tested due to the capture period's length extending over these seasons. Our primary interest was in examining winter weather effects as these were shown to have an impact on adult vital rates in white-tailed ptarmigan studied at Rocky Mountain National Park (Wang et al. 2002). We used analysis of deviance (ANODEV) to examine the amount of deviance explained by the covariates in top models (Skalski et al. 1993). Analysis of deviance estimates the proportion (V) of total deviance in time that is explained by the covariate(s) of interest. It is calculated by subtracting the deviance of a covariate model from a constant model (numerator) and dividing by the deviance of a time dependent model subtracted from a constant model (denominator). An associated F statistic and P value can be used to test the significance of covariates included in a model. Analysis of deviance was used to calculate the amount of deviance explained by each weather covariate in models with delta AIC_c values < 4.

Estimating Rate of Population Change

We used Pradel's temporal symmetry model (Pradel 1996) implemented in Program MARK to estimate annual rates of population change. The Pradel population growth models differ considerably from those structured using a Leslie projection matrix (Caswell 2001). The estimates of annual population growth in a Pradel model are obtained using direct mark-recapture data, whereas those of a Leslie projection matrix are based on demographic rates of survival and fecundity for different age classes averaged over the length of study. The interpretation of the growth estimates (λ) also differs between these models, as estimated λ in a Pradel model indicates if all individuals in the population have been replaced, but the estimated λ from a Leslie projection matrix indicates if all the individuals in a population are replacing themselves (Franklin et al. 2001). In addition, λ estimates from a Pradel model account for open population structures where immigration and emigration events are occurring. A concise overview and comparison of these two models is presented in Anthony et al. (2006), and much of our analytical approach for population change modeling parallels Anthony et al. (2006) and that outlined by Franklin et al. (2004). We use λ_t, to refer to the rate of population change as estimated by the Pradel model, which can be considered the realized rate of population change ($\lambda_t = N_{t+1}/N_t$).

We used the random effects module in Program MARK to estimate the average rate of population change in our population ($\bar{\lambda}_t$) (White et al. 2001). Age effects cannot be included in Pradel models unless age classes are separated into groups with models

estimated separately (Cooch and White 2010). Thus, we pooled data for yearling and adults to increase sample sizes, but maintained groups for males and females. We fit models with interactive sex effects $\{\varphi(s*t)p(s*t)\lambda(s*t)\}$ and without sex effects $\{\varphi(t)p(t)\lambda(t)\}$ to assess the best starting structure of the model using AIC_c. We tested models that were fit with random effects and constraints on λ that included no time effects (.), a linear trend over time (*T*), and quadratic trend (*TT*). The first and last estimates of λ_t are frequently discarded in analyses when using Pradel models, in part due to field crews improving capture abilities and methodologies in subsequent years of study, potential biases from trap and capture responses, and differences in capture probabilities between marked and unmarked birds early in the study (Anthony et al. 2006, Hines and Nichols 2002). Thus, initial estimates can often have substantial error. We discarded non-estimable values of λ_t from the best starting model to fit the constant (.) and trend models (*T* and *TT*) using random effects.

Estimating Population Recruitment

We used Pradel models implemented in Program MARK to investigate annual rates of population recruitment. Population recruitment in the Pradel models in the context of our analysis is defined as the per capita rate of additional breeding age birds (designated B_i) to the population between time *i* and *i* + 1 (Cooch and White 2010). Thus, recruitment (*f*) can be written as: $f_i = B_i/N_i$. It represents the number of breeding-age birds entering the population between time *i* and *i*+1 per individual breeding bird already in the population at time *i*. It is important to note the definition of recruitment used in this analysis applies to birds that have reached breeding age entering the population and is not necessarily a measure of fecundity for the Mt. Evans white-tailed ptarmigan population. However, this

parameter can be interpreted as recruitment into the population from either immigration events or births, but these two processes cannot be separated from the direct estimates of *f*. The relationship between *f* and parameters λ and φ are linear functions of each other in a Pradel model, such that $\lambda = \varphi + f$. This can cause problems if using the λ model ('survival and lambda' model in Program MARK) to derive estimates of *f*, because constraints applied to λ force an inverse relationship between φ and *f*. There may be cases where an inverse relationship between these two parameters is expected, but we wanted to be careful to avoid forcing this relationship in our models. We used the 'recruitment and survival' model implemented in Program MARK for this reason rather than using derived estimates of *f* from φ and λ. We applied constraints directly to the *f* parameter to examine constant (.), linear trend (*T*), and quadratic trend (*TT*). Models with additive sex effects (*s*) were considered in the candidate set. We tested the additional general model $\{\varphi(s*t)p(s*t)f(s*t)\}$ and increasingly parsimonious models (i.e., $\{\varphi(t)p(t)f(t)\}$), but always left the φ and *p* parameters in the time dependent form. There were no *a priori* hypotheses developed to test the effect of weather on recruitment, and climate covariates were not fit to recruitment models.

Evaluating Model Fit

We evaluated goodness of fit for the population analysis using the median c-hat (ĉ) procedure available in Program MARK on the most general model in our data set $\{\varphi(a+s*t)p(a+s+t)\}$ to estimate the variance inflation factor ĉ, which is used to correct for over dispersion by adjusting the width of confidence intervals if the estimated value is > 1. Values > 1 indicate models that suffer from lack of fit and over dispersion, while those that are < 1 indicate under dispersion (Burnham and Anderson 2002). The median

c-hat procedure was also applied separately on male and female data used in the climate survival analysis for the general model $\{\varphi(a+t)p(t)\}$. The median c-hat procedure in Program MARK is not currently available for use on the Pradel temporal symmetry models, and goodness of fit was assessed using Program RELEASE (Burnham et al. 1987) on the most general model $\{\varphi(s*t)p(s*t)\lambda(s*t)\}$ to estimate $\hat{c}$. This was done by pooling degrees of freedom and Chi-square values from Test 2 and 3 which collectively make up the goodness-of-fit test for the fully time-dependent model (Cooch and White 2010). The variance inflation factor from this model was also applied to the population recruitment models. Model adjustments made with $\hat{c}$ were used to adjust the associated AIC_c estimates to a quasi AIC_c value ($QAIC_c$), after correcting for over dispersion.

RESULTS

Survival

Population Survival Analysis.—We used 1,344 marked birds of breeding age in our population analysis of apparent survival and recapture/reobservation probability at Mt. Evans from 1968 to 2010. The number of reobservations or recaptures resulted in 2,763 additional records for a total of 4,107 total observations. Results from the goodness-of-fit test indicated our most general model had some over dispersion, and all model AIC_c values and standard errors were adjusted using the estimated variance inflation factor from the median c-hat procedure ($\hat{c}$ = 1.12). We suspect that over dispersion in our model was due primarily to temporary emigration followed by reobservations or recaptures occurring in subsequent study years.

Apparent survival varied among sex and age classes, and the model that included an additive structure between sex, age, and time in the apparent survival parameter

received nearly all support based on AIC_c weights (Table 3.4). Annual estimates of apparent survival also varied widely (Table 3.5), and there was no evidence of a trend occurring over the years analyzed (Fig. 3.1). Averages of apparent survival over the study period for each sex and age group indicated varying point estimates with subadults having the highest survival among the two age classes, and males having the highest survival. Subadult males had the highest survival (0.73), followed by subadult females (0.63), adult males (0.62), and adult females (0.52) (Table 3.6).

The recapture/reobservation probability averaged over all years was 0.67 but varied widely (Fig. 3.2; Table 3.5). Recapture/reobservation probabilities estimated near the constrained boundaries with the sin and logit links were problematic as it was difficult to tell if those estimates were due to inadequate data or the result of poor estimation that can result when parameters are estimated near the 0 or 1 boundaries. This was an issue for the 1969 and 1973 recapture estimates, both estimated as 1 (SE = 0.00).

Population Climate Analysis.—Of the 1,344 marked birds used in the climate analysis, 602 were females, and 742 were males. Overdispersion was present in both estimates of $\hat{c}$ with the most general model for females having poorer fit than the most general model for males ($\hat{c}$ = 1.36 and $\hat{c}$ = 1.14, respectively). Weather covariates fit to mark-recapture models indicated substantially higher support for those covariates for females than males (results for males are not presented here). The top models accounting for all of the model weight (AIC_c weights) for the male group did not include weather effects but did include time dependence in both apparent survival and recapture/reobservation parameters. Nearly all of the model weight (97%) supported model $\{\varphi(a+t)p(t)\}$. In contrast, models that included weather effects for females accounted for 85% of the AIC_c weights, and the

top model included non-linear winter precipitation with additive age effect $\{\varphi(a+CP^2)p(t)\}$, followed by a model that included the number of warm days and an interaction with age $\{\varphi(a*WD)p(t)\}$(Table 3.7). All temperature model variables were collinear, and model weights were similar among the majority of temperature covariate models tested for females. Covariate models were poorly supported in the male candidate model set, and analysis of deviance was not used in those models. Analysis of deviance results indicated that the best covariate models explained ~ 11% of the deviance (Table 3.8). The covariate model that explained the largest amount of deviance $\{\varphi(a+CP^2)p(\mathrm{t})\}$ had a quadratic relationship between cumulative precipitation and survival (Fig. 3.3), with precipitation levels above and below the mean resulting in the lowest survival for female ptarmigan.

Population Change

Records of birds captured or reobserved during years when the study area was expanded (1987-1998) were discarded from analysis due to effects of inflating annual growth rate estimates. This reduced the total sample size of marked birds of breeding age to 1,288, and the total number of records including recaptures and reobservations was reduced to 3,958. A goodness of fit test performed on the most general model $\{\varphi(s+t)p(s+t)\lambda(s+t)\}$ indicated no evidence of over dispersion with an estimated $\hat{c} = 0.72$ ($\chi^2 = 142.88$, df = 199) and no correction for over dispersion was used. The reduced model $\{\varphi(t)p(t)\lambda(t)\}$ had the highest support based on the minimum AIC_c ($w_i = 1.0$) and was used to develop random effects models for trend fitting (Appendix D). The first three estimates and last estimate of λ_t included high standard errors and were not used to develop the random effects models. Model $\{\varphi(t)p(t)\lambda(T)\}$ had the minimum AIC_c and received the majority

of weight (w_i = 0.44, Appendix D). The average λ_t calculated using random effects from the model $\{\varphi(t)p(t)\lambda(t)\}$ indicated a relatively stationary population from 1971 to 2009 ($\bar{\lambda}_t$ = 1.036, SE = 0.037), although annual estimates taken from the time-dependent model showed substantial variation (Table 3.9, Fig. 3.4).

Population Recruitment

The most parsimonious candidate model included additive sex effects and a quadratic declining trend and received the majority of model support (w_i = 0.87, Appendix D). This model suggested an average decline from 0.551 to 0.213 annual new recruits per male and from 0.637 to 0.281 annual new recruits per female from 1968 to 2010. Model $\{\varphi(s+t)p(s+t)\mathrm{f}(s+t)\}$ was used to calculate the average annual recruitment for males and females with the variance components module in Program MARK. Females had average rates of annual recruitment higher than males (f_{Female} = 0.523, f_{Male} = 0.390).

DISCUSSION

Annual Survival

We did not detect trends in annual survival of white-tailed ptarmigan over the 1968-2010 study period (Fig. 3.1). Our best model included additive effects of age, sex, and time and received overwhelming model support (Table 3.3). The range of annual apparent survival estimates among age and sex classes was highly variable with a large amount of uncertainty in many estimates (Table 3.5). Search efforts among years varied with several field biologists collecting data from 1987 to 1998, and search efforts were less in some years previous to and following that time period. Not surprisingly, uncertainty in annual estimates was lowest when search efforts were highest. Apparent survival estimates averaged over all years indicated subadults had the highest survival at Mt.

Evans, and males had higher survival rates than females (Table 3.6). Previous studies describing survival rates for white-tailed ptarmigan at Mt. Evans and Rocky Mountain National Park have been presented (Braun 1969, May 1975), although those estimates were averaged over a shorter time period and during a time when hunting pressure at Mt. Evans was higher than subsequent years of the study. Our estimates for males are comparable to estimates obtained from nearby populations at Rocky Mountain National Park (RMNP) and Niwot Ridge from 1966 to 1968, with yearlings having higher survival rates than adults (0.76 versus 0.46 at RMNP, and 0.88 versus 0.76 at Niwot Ridge) (Braun 1969). Females at Niwot Ridge were similar, with yearling females having higher survival rates than adults (0.73 versus 0.67). However, reported rates from the RMNP population for females indicated the relationship was in fact opposite, with subadult hens having lower survival rates than adults (0.45 versus 0.70). Sandercock et al. (2005) reported age-specific survival rates for breeding females studied at and near Mt. Evans for 10 years (1987 to 1997). Estimated survival rates from this study indicated yearlings had the lowest annual survival rates (0.423) followed by 3+ year olds (0.465) and 2 year olds (0.643). These estimates are in contrast with our results which indicate yearlings have the highest annual survival estimates, followed by adults. We did not examine models with three age classes due to our interest in testing fully time dependent models to describe annual variation in survival vital rates. Adding an additional age class to our models added considerable complexity and resulted in estimation issues for multiple years in our dataset based on a *post hoc* exploratory analysis. The model used by Sandercock et al. (2005) assumed constant survival across time for all three age classes and avoided the complexity of a fully time dependent model. In addition, the model used

was parameterized on 10 years of data and further partitioned adults into two age groups and only included birds marked in the spring, so the results from their model were not directly comparable to our additive model. Finally, birds from study sites near Mt. Evans were also included in the Sandercock et al. (2005) analysis, and those birds were not included in our data set.

Modeling of the recapture parameter (p) indicated that simple time dependence and no age or sex effects was the most parsimonious model. The average estimate of p from the best model was 0.67 (SE = 0.032). Annual estimates were highly variable (Table 5) and generally lower in the last decade of the study than previous years (Fig. 3.2). Our average estimate of p was considerably lower than previously reported by Sandercock et al. (2005) for females at Mt. Evans ($p = 0.81$), although that analysis spanned a shorter time period (1987 to 1997) during a time when radio collars were being used. We tested models for p that included reproductive effects fit as covariates due to dispersal events by unsuccessful hens (Braun 1969, Martin et al. 2000), but none of those models received support. Our results suggest the influence of reproduction effects on recapture/reobservation probabilities of hens in our study population was of little importance.

There were no major habitat alterations within our study area from 1968 to 2010 of which we were aware, that potentially contributed to annual variation in apparent survival, although recreational visitation undoubtedly increased. Higher levels of recreational visitation may have led to higher mortality rates along the road that bisected the study area, although the lack of a linear trend in the annual survival estimates indicates this was not an issue. There was insufficient mortality-specific data to address

the effect of road traffic on mortality in our study population. One factor that did change throughout the study period at Mt. Evans was hunting pressure. The Colorado Division of Wildlife began implementing a hunting restriction within ½ mile on either side of the Mt. Evans Scenic Byway in 1994 which effectively ended harvest of the Mt. Evans study population (Clait E. Braun, personal observation). This closure was also implemented during 1970-1976, with the exception of 1972 and 1974. In a separate analysis, we fit a model that included a covariate for hunting effect (1 during non-restriction years, 0 during restriction years) and found the groups differed significantly (confidence intervals did not overlap) but, relative to our top fully time dependent model (Table 3.4), the hunting effect model did not receive any of the model weights. We acknowledge that hunting can have a large impact on the demographics of white-tailed ptarmigan (Braun 1969), but it was unlikely the primary source of annual variation in our population during later years.

Climate and Survival

When we replaced time effects with climate covariates in an attempt to explain annual variation in apparent survival, we found that climate affected males and females differently. The climate models were fit to male and female data separately, and model selection results indicated a large discrepancy in model support between sexes. Climate covariate models received the highest support in the female group, but time-variant models were the highest ranked in the male group. A model with a quadratic cumulative precipitation effect in the female group was best supported based on AIC_c (Fig. 3.3). It was difficult to draw inferences from the covariates we chose in our analysis, and the size of the beta coefficients were generally close to zero such that our predictions of negative

or positive slopes were largely inconclusive (Table 3.7). Use of ANODEV indicated the best covariate model explained ~11% of deviance relative to a reduced model (Table 3.8). In addition, the signs for several beta coefficients were unstable, changing signs among different models with confidence intervals overlapping zero.

We anticipated that cumulative winter precipitation would have the largest effect on apparent survival, relative to temperature variables, due to its importance in resource availability and use as snow roosting habitat by white-tailed ptarmigan (Braun et al. 1976). White-tailed ptarmigan frequently use snow burrows to thermoregulate as temperatures below the surface of the snow are warmer than above the surface at night (Braun et al. 1993). The top climate covariate model indicated that survival was highest in average cumulative precipitation years, but reduced in either low or high precipitation years relative to the mean. We predicted that higher winter precipitation would generally be better due to increased roosting habitat availability for ptarmigan, but model results did not lend support to this expectation. It has been shown that flocks in our study area make daily movements between foraging areas and roosting sites (Braun et al. 1976). The distance birds traveled between foraging and roosting sites was higher during years of high winter precipitation. Increased traveling distance may leave birds more susceptible to predators, which could explain lower survival in high precipitation years. Reductions in snow roosting habitat during low precipitation winters may potentially pose threats to ptarmigan if they are unable to find snow of suitable quality in which to burrow. Although our climate models left much of the deviance unexplained, the directions of beta coefficients generally matched our a priori hypotheses, and cumulative winter precipitation was the best covariate tested. Although the cause of lower survival

during low cumulative precipitation years is thought to be a result of reduced roosting habitat, these results suggest a better mechanistic understanding of the effects of winter climate on survival is still needed.

Population Change

We obtained estimates of realized population growth ($\lambda_t = N_{t+1}/N_t$) for years 1970 to 2009 in our data set. Our estimates of realized population growth were obtained using Pradel's temporal symmetry model and are representative of population change in the age classes from which the data were taken. Thus, the annual estimates of realized population growth are representative of annual population growth for birds of breeding age. Annual estimates of realized population growth varied considerably among years, and associated standard errors were high for many of the estimates (Table 3.9). The implementation of random effects models allowed us to fit a trend line to our annual estimates, although the results indicated little overall change in our population across years analyzed (Fig. 4). Although the average realized population growth rate indicated a population growth rate near one, the 95% confidence interval did overlap values less than one, so we cannot rule out a population increase or decline. In addition, the wide variability in estimates indicates high stochasticity in our population.

There was clear evidence of population cycles in the annual rates of change estimated for our population occurring at roughly 12 year intervals (Fig. 3.4). Population cycles in grouse have been well documented for species in the *Lagopus* genus (Bergerud and Gratson 1988, Moss and Watson 2001). Population cycles in these species have been linked to density dependence (Gardarsson 1988, Watson et al. 1998, Watson et al. 2000), climate (Lindström et al. 1996, Watson et al. 2000), and parasites (Watson and Shaw

1991, Hudson et al. 1998, Cattadori et al. 2005). Braun and Willer (1967) found that parasite infection in white-tailed ptarmigan was very low, and it seems unlikely that parasites are responsible for observed cycles in white-tailed ptarmigan. Although there do appear to be some links to climate and vital rates of breeding age white-tailed ptarmigan, the mechanisms behind observed cycles were not explicitly tested. Indeed, until the analysis of this time series it was unclear if white-tailed ptarmigan demonstrated cycles in annual rates of change. It has been observed that grouse occurring in large contiguous habitats where fragmentation has not occurred tend to demonstrate population cycles, whereas those occurring in fragmented habitats demonstrate direct density-dependence (Moss and Watson 2001). This has been attributed partially to source-sink dynamics associated with increased predation events that occur in fragmented habitats. In contrast, grouse occurring in contiguous habitats are thought to be regulated more by delayed density-dependent events given the absence of mortality and dispersal events associated with fragmented habitats (Moss and Watson 2001). Climate is also thought to play a role in population regulation of grouse. Watson et al. (2000) found that rock ptarmigan (*Lagopus mutus*) in years immediately following high June temperatures began declines from peak abundance. Lindström et al. (1996) suggested large-scale climate events were responsible for synchrony of fluctuations in black grouse and capercaillie populations. Based on previous work it seems likely that cycles in population growth rates of white-tailed ptarmigan may be due to delayed density-dependent events and climate events that were not modeled in this analysis. Future research should focus on developing models that describe cycles in white-tailed ptarmigan populations that account for both density-dependence and large-scale climate events.

Population Recruitment

The most parsimonious recruitment model included additive sex effects and indicated a declining quadratic trend in recruitment (Fig. 3.5), suggesting the annual number of breeding age birds added to the population decreased across time. The contributions to recruitment from births and immigration could not be directly separated. Hunting that occurred in our population during the first decades of the study may be responsible for the declining trends in recruitment. Throughout the first decades of the study hunting pressure occurred at varying degrees, and harvests of breeding birds from the population resulted in a high ratio of yearlings to adults. Hunting pressure was highest during the first decade of study, and harvests ceased in the mid-1990s which resulted in a low ratio of yearlings to adults relative to earlier decades. This resulted in a declining trend in the ratio of yearlings to adults (β = -0.01, SE = 0.01). Recruitment likely declined due to higher survival rates in adults during later years of the study, which allowed birds to return to territories held in previous years. In contrast, during years following hunter harvests, yearling birds likely moved into vacant territories previously held by harvested birds. After considering hunting and harvests of breeding birds, it appears that the declining trend in recruitment was primarily the result of reduced availability of territories to subadult birds after the hunting restrictions went into effect in the mid-1990s.

Implications for the Future

There was a large amount of variability in annual demographic rates estimated. Examining these vital rates using climate covariates suggested that males and females are

affected differently at Mt. Evans by climate. This is likely due to differences in distances traveled by sexes from breeding areas (Hoffman and Braun 1975, Hoffman and Braun 1977), and perhaps due to differences in winter habitats used (Giesen and Braun 1993). It is not yet known if this is true for other populations. Our data set analyzed was a long time series, but there was the effect of hunting that occurred at our study site during the majority of the study years. Populations of white-tailed ptarmigan are hunted in many locations throughout the state of Colorado, but the Mt. Evans Scenic Byway makes accessing alpine habitats particularly easy. Thus, hunting pressure was likely higher at this location than other areas throughout the state (Braun 1969). We attempted to control for this influence when fitting climate covariates, but there may have been undetected effects of hunting on the processes underlying the vital rates in our population that we were unable to control. For example, there is evidence that reproductive success rates tend to increase in white-tailed ptarmigan with age (Wiebe and Martin 1997). During hunting periods the ratio of yearlings to adults in the breeding population tended to increase, which might have potentially influenced annual fecundity and subsequent recruitment into the population. It is not completely surprising that winter climate covariates explained a limited amount of variation in the annual survival of white-tailed ptarmigan at Mt. Evans. Winter is the period when white-tailed ptarmigan gain mass (Braun et al. 1976), so they do not appear to be limited by plant forage in wintering areas surrounding Mt. Evans. For this reason, it appears the biggest climate threats to white-tailed ptarmigan during winter months are seasons when snow pack is low, as this will directly affect the availability of snow roosting habitat.

Loss of snowpack in alpine habitats has been widely anticipated under climate change and observed in many areas, including parts of Colorado (IPCC 2007, Pederson et al. 2011), but cumulative precipitation near Mt. Evans did not appear to change for the years of our study. Declines in snowpack expected in future decades may be problematic for wintering populations of white-tailed ptarmigan based on our covariate models. Down-scaled climate models available from the Natural Resource Ecology Laboratory at Colorado State University project an average annual increase in winter temperature of 1.26 ˚C by 2049 (Dennis S. Ojima, personal communication). If increases in temperature affect the amount of accumulated precipitation on the ground, or the condition of snow, there may be an effect on roost site availability for white-tailed ptarmigan. However, future increases in precipitation may offset any winter warming. The down-scaled climate models used have a greater amount of uncertainty in projections for precipitation than they do for temperature (Dennis S. Ojima, personal communication), and it is difficult to predict what winter conditions white-tailed ptarmigan will experience over the coming decades.

Our mark-recapture models fit to climate covariates indicate that white-tailed ptarmigan are relatively robust to the stochastic climate conditions they experienced from 1968 to 2010. This indicates that conditions will have to become more extreme than conditions that occurred during the study if any appreciable effect on birds of breeding age is to be expected. It is important to note, however, that our inferences are limited to breeding-age birds. If climate has an appreciable effect on survival of white-tailed ptarmigan from the interval spanning hatching to the following spring, annual rates of change may be influenced. Unfortunately, return rates for birds banded as chicks are

low, and we could not model annual winter climate effects for ptarmigan banded as chicks. Threats of climate warming to alpine habitats are real and of great concern for species over coming decades, but breeding-age white-tailed ptarmigan at Mt. Evans appear to be stable at present. However, uncertainty in precipitation trends and projected declines in winter snowpack are of concern. Continued monitoring of white-tailed ptarmigan and other alpine-dependent species will be of increasing importance in coming decades.

Table 3.1. Structures of the recapture parameter (p) considered for candidate models for white-tailed ptarmigan at Mt. Evans, CO (1968-2010). The structure of the recapture parameter p was chosen by keeping φ in the general form {φ(a+s*t)} and selecting the model with the structure for p having the minimum $QAIC_c$.

Parameter structure (p)	Model description
Structured with additive effects only	
$a+s+t$	Additive structure with age, sex, and time effects
$a+s$	Additive structure with sex and age effects, no time effect
$a+t$	Additive structure with age and time effects, no sex effect
$s+t$	Additive structure with sex and time effects, no age effect
$a+s+r$	Additive structure with age, sex, and reproduction effects
$a+r$	Additive structure with age and reproduction effects, no sex effect
$s+r$	Additive structure with sex and reproduction effects, no age effect
Structured with a single effect or no effect	
a	Age effect only
s	Sex effect only
r	Reproduction effect only
.	No effects (constant model)

Table 3.2. Structures of the apparent survival (φ) parameter considered for candidate models used to model white-tailed ptarmigan survival at Mt. Evans, CO (1968-2010). The structure of φ was chosen by keeping the recapture parameter (p) in the general form {*p*(*a*+*s*+*t*)} and selecting the model with the structure for φ having the minimum $QAIC_c$.

Parameter structure (ϕ)	Model description
Structured with full or partial interactions	
*a+s*t*	Interaction between sex and time, additive structure of age
*s*t*	Interaction between sex and time, no age effect
*a+s*T*	Interaction between sex and linear trend, additive structure of age
*s*T*	Interaction between sex and linear trend, no age effect
*a+s*TT*	Interaction between sex and quadratic trend, additive structure of age
*s*TT*	Interaction between sex and quadratic trend, no age effect
Structured with additive effects only	
a+s+t	Additive structure with age, sex, and time effects
s+t	Additive structure with sex and time effects, no age effect
a+t	Additive structure with age and time effects, no sex effect
a+s+T	Additive structure with age, sex, and linear trend effects
s+T	Additive structure with sex and linear trend effects
a+T	Additive structure with age and linear trend effects
a+s+TT	Additive structure with age, sex, and quadratic trend effects
s+TT	Additive structure with sex and quadratic trend effects
a+TT	Additive structure with age and quadratic trend effects
a+s	Additive structure with sex and age effects, no time effect
Structured with a single effect or no effect	
a	Age effect only
s	Sex effect only
t	Time effect only
T	Linear trend effect only
TT	Quadratic trend effect only
.	No effects (constant model)

Table 3.3. Developed *a priori* hypotheses and models tested for climate covariates used to model survival of white-tailed ptarmigan at Mt. Evans, CO (1968-2010). A verbal description of the hypothesis is provided, along with the predicted direction of coefficient estimates. Survival was predicted to decrease with age (negative coefficient) and are not represented in the coefficient predictions.

Hypothesis	Model	Model Coefficients	Coefficient Predictions
Positive effect of cumulative precipitation	φ{AGE + CP}	$\beta_0 + \beta_1(\text{AGE}) + \beta 2(\text{CP})$	$\beta_2>0$
Negative effect of cumulative precipitation at low and high years	φ{AGE + CP^2}	$\beta_0 + \beta_1(\text{AGE}) + \beta 2(\text{CP}) + \beta 3(\text{CP}^2)$	$\beta_2>0, \beta_3<0$
Negative effect of number of warm days	φ{AGE + WD}	$\beta_0 + \beta_1(\text{AGE}) + \beta 2(\text{WD})$	$\beta_2>0$
Negative effect of average winter minimum temperature	φ{AGE + MinT}	$\beta_0 + \beta_1(\text{AGE}) + \beta 2(\text{MinT})$	$\beta_2<0$
Negative effect of average winter maximum temperature	φ{AGE + MaxT}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{MaxT})$	$\beta_2<0$
Positive effect of cumulative precipitation, negative effect of of number of warm days	φ{AGE + CP + WD}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_1(\text{WD})$	$\beta_2>0, \beta_3<0$
Positive effect of cumulative precipitation, negative effect of number of warm days, negative effect of their interaction	φ{AGE + CP + WD + CP*WD}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_3(\text{WD}) + \beta_4(\text{CP*WD})$	$\beta_2>0, \beta_3<0, \beta_4<0$
Positive effect of cumulative precipitation, negative effect of minimum temperature	φ{AGE + CP + MinT}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_3(\text{MinT})$	$\beta_2>0, \beta_3<0$
Positive effect of cumulative precipitation, negative effect of minimum temperature, negative effect of their interaction	φ{AGE + CP + MinT + CP*MinT}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_3(\text{MinT}) + \beta_4(\text{CP*MinT})$	$\beta_2>0, \beta_3<0, \beta_4<0$
Positive effect of cumulative precipitation, negative effect of maximum temperature	φ{AGE + CP + MaxT}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_3(\text{MaxT})$	$\beta_2>0, \beta_3<0$
Positive effect of cumulative precipitation, negative effect of maximum temperature, negative effect of their interaction	φ{AGE + CP + MaxT + CP*MaxT}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_3(\text{MaxT}) + \beta_4(\text{CP*MaxT})$	$\beta_2>0, \beta_3<0, \beta_4<0$
Negative effect of cumulative precipitation at low and high years, negative effect of number of warm days	φ{AGE + CP^2 + WD}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_3(\text{CP}^2) + \beta_4(\text{WD})$	$\beta_2>0, \beta_3<0, \beta_4<0$
Negative effect of cumulative precipitation at low and high years, negative effect of minimum temperature	φ{AGE + CP^2 + MinT}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_3(\text{CP}^2) + \beta_4(\text{MinT})$	$\beta_2>0, \beta_3<0, \beta_4<0$
Negative effect of cumulative precipitation at low and high years, negative effect of maximum temperature	φ{AGE + CP^2 + MaxT}	$\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{CP}) + \beta_3(\text{CP}^2) + \beta_4(\text{MaxT})$	$\beta_2>0, \beta_3<0, \beta_4<0$

Table 3.4. Results of model selection from program MARK for 22 candidate models for white-tailed ptarmigan at Mt. Evans, CO (1968-2010). The probability of recapture parameter (*p*) was structured as time dependent with no age or sex effects for all models. $QAIC_c$ was adjusted using a variance inflation factor ($\hat{c}$ = 1.12).

Model	$QAIC_c$	Δ $QAIC_c$	AIC_c w_i	Model likelihood	K
{φ(*a*+*s*+*t*),p(*t*)}	4272.479	0.000	0.995	1.000	86
{φ(*s*+*t*),p(*t*)}	4283.307	10.828	0.004	0.005	85
{φ(*t*),p(*t*)}	4287.717	15.237	0.000	0.001	79
{φ(*a*+*t*),p(*t*)}	4292.571	20.092	0.000	0.000	85
{φ(*a*+*s***t*),p(*t*)}	4319.811	47.332	0.000	0.000	127
{φ(*s***t*),p(*t*)}	4330.823	58.344	0.000	0.000	126
{φ(*a*+*s*+*TT*),p(*t*)}	4343.537	71.057	0.000	0.000	47
{φ(*a*+*s***TT*),p(*t*)}	4344.384	71.905	0.000	0.000	49
{φ(*a*+*s*+*T*),p(*t*)}	4345.225	72.746	0.000	0.000	46
{φ(*a*+*s***T*),p(*t*)}	4346.010	73.531	0.000	0.000	47
{φ(*s*+*a***T*),p(*t*)}	4346.785	74.305	0.000	0.000	47
{φ(*a*+*s*),p(*t*)}	4359.821	87.342	0.000	0.000	45
{φ(*s*+*TT*),p(*t*)}	4362.344	89.865	0.000	0.000	46
{φ(*s***TT*),p(*t*)}	4363.282	90.803	0.000	0.000	48
{φ(*s*+*T*),p(*t*)}	4363.954	91.475	0.000	0.000	45
{φ(*a*+*TT*),p(*t*)}	4364.772	92.293	0.000	0.000	46
{φ(*s***T*),p(*t*)}	4365.044	92.565	0.000	0.000	46
{φ(*a*+*T*),p(*t*)}	4367.092	94.613	0.000	0.000	45
{φ(*s*),p(*t*)}	4375.488	103.009	0.000	0.000	44
{φ(*TT*),p(*t*)}	4377.557	105.078	0.000	0.000	45
{φ(*a*),p(*t*)}	4379.975	107.496	0.000	0.000	44
{φ(.),p(*t*)}	4390.270	117.791	0.000	0.000	43

Table 3.5. Year-specific estimates and standard errors from model $\{\varphi(a+s+t)p(t)\}$ used to model survival of white-tailed ptarmigan at Mt. Evans, CO (1968-2010). Apparent survival estimates are for intervals between rows of year, and recapture probabilities are for each capture period.

	φ_t SAM		φ_t AM		φ_t SAF		φ_t AF		p_t All	
Year	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1968	0.182	0.054	0.259	0.070	0.124	0.040	0.182	0.055	1.000	0.000
1969	0.343	0.117	0.450	0.129	0.250	0.098	0.343	0.118	0.426	0.186
1970	0.861	0.122	0.907	0.086	0.797	0.164	0.861	0.122	0.423	0.115
1971	0.905	0.107	0.937	0.073	0.859	0.152	0.905	0.107	0.857	0.094
1972	0.169	0.056	0.242	0.075	0.115	0.041	0.169	0.057	1.000	0.000
1973	0.640	0.118	0.737	0.100	0.532	0.129	0.641	0.118	0.567	0.123
1974	0.789	0.113	0.854	0.086	0.704	0.142	0.789	0.115	0.557	0.109
1975	0.776	0.142	0.845	0.108	0.689	0.176	0.776	0.142	0.565	0.120
1976	0.464	0.135	0.576	0.138	0.355	0.123	0.464	0.139	0.492	0.147
1977	0.504	0.096	0.615	0.093	0.393	0.093	0.504	0.098	0.620	0.111
1978	0.570	0.076	0.675	0.071	0.458	0.077	0.570	0.078	0.767	0.087
1979	0.702	0.121	0.787	0.100	0.600	0.138	0.702	0.123	0.625	0.117
1980	0.365	0.067	0.474	0.075	0.268	0.058	0.365	0.070	0.930	0.070
1981	0.546	0.074	0.654	0.069	0.435	0.075	0.547	0.076	0.868	0.074
1982	0.770	0.116	0.840	0.090	0.681	0.143	0.770	0.119	0.580	0.108
1983	0.568	0.093	0.674	0.086	0.456	0.095	0.568	0.095	0.939	0.063
1984	0.696	0.091	0.783	0.076	0.594	0.103	0.697	0.092	0.817	0.098
1985	0.539	0.081	0.648	0.076	0.427	0.082	0.540	0.084	0.680	0.095
1986	0.666	0.076	0.758	0.066	0.560	0.085	0.667	0.080	0.793	0.078
1987	0.658	0.080	0.752	0.070	0.551	0.089	0.659	0.084	0.594	0.085
1988	0.758	0.066	0.831	0.052	0.667	0.081	0.759	0.067	0.849	0.059
1989	0.666	0.057	0.758	0.050	0.560	0.064	0.667	0.060	0.818	0.060
1990	0.594	0.069	0.697	0.067	0.483	0.071	0.595	0.075	0.757	0.083
1991	0.424	0.067	0.537	0.073	0.320	0.062	0.425	0.072	0.899	0.099
1992	0.232	0.058	0.322	0.073	0.161	0.046	0.232	0.060	0.717	0.140
1993	0.522	0.093	0.632	0.088	0.410	0.091	0.522	0.093	0.925	0.075
1994	0.705	0.091	0.790	0.075	0.604	0.104	0.706	0.092	0.816	0.100
1995	0.607	0.108	0.708	0.096	0.496	0.113	0.607	0.110	0.580	0.119
1996	0.734	0.110	0.812	0.088	0.637	0.131	0.734	0.113	0.578	0.102
1997	0.745	0.144	0.821	0.113	0.650	0.172	0.745	0.145	0.493	0.109
1998	0.657	0.149	0.751	0.126	0.550	0.163	0.658	0.150	0.089	0.043
1999	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.310	0.082
2000	0.414	0.077	0.526	0.083	0.311	0.069	0.415	0.080	0.630	0.100
2001	0.760	0.102	0.832	0.079	0.668	0.123	0.760	0.103	0.515	0.095
2002	0.830	0.100	0.885	0.073	0.757	0.130	0.830	0.101	0.595	0.091
2003	0.689	0.075	0.777	0.064	0.586	0.086	0.690	0.078	0.723	0.077
2004	0.770	0.072	0.840	0.057	0.681	0.090	0.770	0.075	0.741	0.073
2005	0.780	0.091	0.848	0.070	0.693	0.114	0.780	0.093	0.581	0.084
2006	0.816	0.156	0.874	0.117	0.739	0.200	0.816	0.159	0.466	0.106
2007	0.389	0.087	0.500	0.094	0.289	0.077	0.389	0.090	0.609	0.115
2008	0.849	0.220	0.899	0.157	0.782	0.292	0.850	0.219	0.364	0.107
2009	0.854	0.590	0.902	0.419	0.789	0.789	0.854	0.588	0.295	0.218

Table 3.6. Age and sex specific average estimates for annual survival of white-tailed ptarmigan at Mt. Evans, CO (1968-2010). Averages were taken for the entire span of data analyzed (1968-2010) from the model with the minimum AIC_c value $\{\phi(a+s+t)p(t)\}$. The variance components module in Program MARK was used to produce the average estimates and associated standard errors.

Sex and Age	Survival	SE	Lower 95% CI	Upper 95% CI
Adult males	0.6226	0.0307	0.5625	0.6828
Subadult males	0.7263	0.0325	0.6626	0.7900
Adult females	0.5228	0.0336	0.4570	0.5886
Subadult females	0.6282	0.0355	0.5585	0.6979

Table 3.7. Model selection results for weather covariates fit to female survival models for white-tailed ptarmigan at Mt. Evans, CO (1968-2010). Models are ranked by AIC_c adjusted for overdispersion ($QAIC_c$). Delta (Δ $QAIC_c$), model weights (Qw_i), and number of parameters are provided for each model. Beta coefficient estimates are provided for each variable in the apparent survival structure. All models were adjusted with a variance inflation factor ($\hat{c}$ = 1.36).

Model structure	$QAIC_c$	Δ $QAIC_c$	Qw_i	K	Coefficient Estimates				
					β_0	β_1	β_2	β_3	β_4
$\beta_0 + \beta_1$(AGE) + $\beta 2$(CP) + $\beta 3$(CP^2)	1420.450	0.000	0.232	46	-2.597	-0.423	0.010	0.000	-
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_3(CP^2) + β_4(WD)	1421.072	0.622	0.170	47	-3.047	-0.468	0.010	0.000	0.013
$\beta_0 + \beta_1$(AGE)	1421.824	1.374	0.117	44	0.474	-0.388	-	-	-
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_3(CP^2) + β_4(MinT)	1422.637	2.187	0.078	47	-2.690	-0.419	0.010	0.000	-0.006
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_3(CP^2) + β_4(MaxT)	1422.644	2.194	0.077	47	-2.596	-0.423	0.010	0.000	0.000
$\beta_0 + \beta_1$(AGE) + $\beta 2$(WD)	1422.950	2.500	0.067	45	0.238	-0.423	0.011	-	-
$\beta_0 + \beta_1$(AGE) + $\beta 2$(CP)	1423.413	2.963	0.053	45	0.122	-0.285	0.001	-	-
$\beta_0 + \beta_1$(AGE) + β_2(MaxT)	1423.992	3.542	0.039	45	0.539	-0.393	0.009	-	-
$\beta_0 + \beta_1$(AGE) + $\beta 2$(MinT)	1423.996	3.546	0.039	45	0.586	-0.393	0.008	-	-
β_0	1424.176	3.726	0.036	43	0.201	-	-	-	-
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_1(WD)	1424.427	3.977	0.032	46	-0.167	-0.422	0.001	0.011	-
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_3(MaxT)	1425.601	5.151	0.018	46	0.143	-0.387	0.001	0.003	-
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_3(MinT)	1425.602	5.152	0.018	46	0.099	-0.384	0.001	-0.002	-
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_3(WD) + β_4(CP*WD)	1426.611	6.161	0.011	47	-0.040	-0.423	0.000	0.006	0.000
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_3(MinT) + β_4(CP*MinT)	1427.417	6.967	0.007	47	2.076	-0.395	-0.003	0.137	0.000
$\beta_0 + \beta_1$(AGE) + β_2(CP) + β_3(MaxT) + β_4(CP*MaxT)	1427.531	7.081	0.007	47	1.119	-0.394	-0.001	0.133	0.000

Table 3.8. Analysis of deviance results for covariate models applied to female data from white-tailed ptarmigan at Mt. Evans, CO (1968-2010). Covariate models with Δ $QAIC_c$ values less than 4 are presented, along with their associated weights (Qw_i), number of parameters (*K*), percentage of variation explained by covariate, *F* statistic with associated degrees of freedom in the numerator and denominator (*dfn* and *dfd*), and *P* value. All models were adjusted with a variance inflation factor ($\hat{c}$ = 1.36).

Model	Δ $QAIC_c$	Qw_i	*K*	Variance explained (%)	$F_{(dfn,\ dfd)}$	*P*
$\{\varphi(a+CP^2),p(t)\}$	0.000	0.232	46	0.112	$F_{2,41}$=1.904	*P*=0.163
$\{\varphi(a+CP^2+WD),p(t)\}$	0.622	0.170	47	0.113	$F_{3,41}$=1.618	*P*=0.201
$\{\varphi(a+CP^2+MinT),p(t)\}$	2.187	0.078	47	0.089	$F_{3,41}$=1.238	*P*=0.309
$\{\varphi(a+CP^2+MaxT),p(t)\}$	2.194	0.077	47	0.089	$F_{3,41}$=0.373	*P*=0.310
$\{\varphi(a+WD),p(t)\}$	2.500	0.067	45	0.016	$F_{1,41}$=0.667	*P*=0.419
$\{\varphi(a+CP),p(t)\}$	2.963	0.053	45	0.009	$F_{1,41}$=0.373	*P*=0.545
$\{\varphi(a+MaxT),p(t)\}$	3.540	0.040	45	0.000	$F_{1,41}$=0.011	*P*=0.916
$\{\varphi(a+MinT),p(t)\}$	3.550	0.039	45	0.000	$F_{1,41}$=0.009	*P*=0.927
$\{\varphi(a+CP+WD),p(t)\}$	3.977	0.032	46	0.027	$F_{2,41}$=0.009	*P*=0.581

Table 3.9. Annual estimates of population growth (λ_t) and recruitment (f_t) from minimum AIC_c models $\{\varphi(t)p(t)\lambda(t)\}$ and $\{\varphi(s+t)p(s+t)f(s+t)\}$, respectively, for white-tailed ptarmigan at Mt. Evans, CO (1968-2010). Age models cannot be accommodated in Pradel models.

	λ_t All			f_t Males		f_t Females	
Year	Estimate	SE	Year	Estimate	SE	Estimate	SE
1968-1969	0.329	16.964	1968	0.029	0.094	0.036	0.117
1969-1970	2.551	1.289	1969	1.768	0.906	2.213	1.136
1970-1971	1.208	0.620	1970	0.433	0.483	0.542	0.605
1971-1972	1.264	0.264	1971	0.311	0.220	0.389	0.277
1972-1973	0.552	0.103	1972	0.390	0.103	0.488	0.131
1973-1974	1.949	0.443	1973	1.179	0.371	1.476	0.465
1974-1975	1.289	0.325	1974	0.477	0.250	0.597	0.312
1975-1976	1.009	0.262	1975	0.192	0.139	0.241	0.173
1976-1977	1.345	0.450	1976	0.921	0.349	1.153	0.440
1977-1978	1.153	0.347	1977	0.611	0.285	0.764	0.358
1978-1979	0.665	0.127	1978	0.108	0.088	0.135	0.109
1979-1980	1.173	0.217	1979	0.468	0.143	0.586	0.178
1980-1981	0.784	0.148	1980	0.388	0.112	0.486	0.141
1981-1982	0.850	0.114	1981	0.250	0.076	0.313	0.094
1982-1983	1.109	0.192	1982	0.313	0.117	0.392	0.147
1983-1984	0.964	0.175	1983	0.373	0.123	0.467	0.154
1984-1985	1.380	0.199	1984	0.656	0.157	0.821	0.198
1985-1986	1.202	0.206	1985	0.606	0.158	0.758	0.198
1986-1987	0.819	0.124	1986	0.181	0.085	0.227	0.106
1987-1988	1.282	0.195	1987	0.593	0.150	0.743	0.187
1988-1989	1.365	0.180	1988	0.588	0.148	0.736	0.186
1989-1990	0.990	0.096	1989	0.350	0.070	0.439	0.088
1990-1991	0.945	0.104	1990	0.378	0.073	0.474	0.092
1991-1992	1.001	0.145	1991	0.499	0.094	0.625	0.117
1992-1993	0.459	0.104	1992	0.212	0.063	0.265	0.079
1993-1994	0.965	0.197	1993	0.428	0.153	0.536	0.192
1994-1995	0.990	0.168	1994	0.302	0.110	0.378	0.138
1995-1996	1.281	0.309	1995	0.639	0.221	0.801	0.276
1996-1997	1.362	0.347	1996	0.586	0.246	0.733	0.308
1997-1998	1.047	0.262	1997	0.313	0.162	0.392	0.203
1998-1999	0.983	0.389	1998	0.354	0.288	0.443	0.360
1999-2000	1.662	0.573	1999	0.493	0.442	0.617	0.553
2000-2001	0.377	0.100	2000	0.019	0.062	0.024	0.078
2001-2002	1.151	0.231	2001	0.344	0.166	0.431	0.207
2002-2003	1.331	0.264	2002	0.466	0.194	0.584	0.244
2003-2004	0.934	0.152	2003	0.250	0.110	0.312	0.138
2004-2005	1.118	0.144	2004	0.326	0.103	0.408	0.130
2005-2006	1.140	0.176	2005	0.326	0.111	0.408	0.140
2006-2007	1.107	0.244	2006	0.358	0.142	0.448	0.179
2007-2008	0.775	0.195	2007	0.346	0.135	0.433	0.169
2008-2009	1.295	0.399	2008	0.372	0.221	0.466	0.276
2009-2010	0.734	12.452	2009	0.509	0.270	0.637	0.339

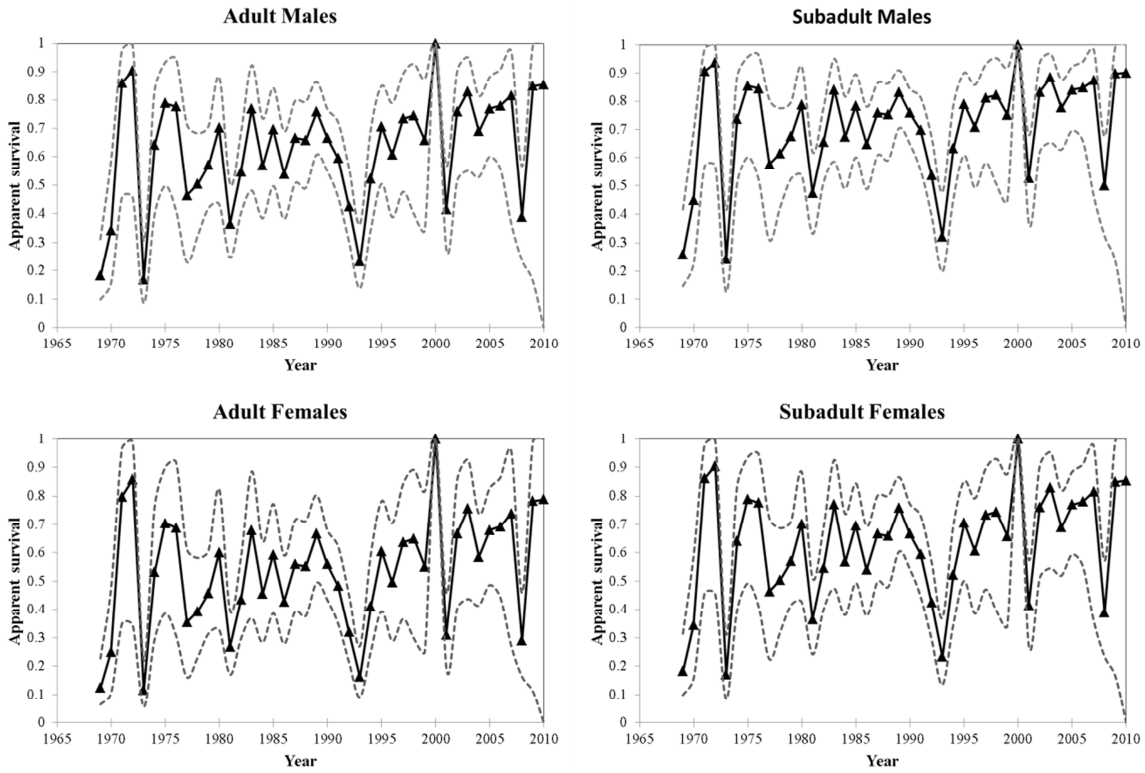

Figure 3.1. Apparent survival estimates for adult and subadult male and female white-tailed ptarmigan at Mt. Evans, Colorado, USA. Survival estimates (solid line) and associated 95% confidence intervals (dashed lines) were generated from the minimum AIC_c model $\{\varphi(a+s+t)p(t)\}$. Estimates differ only in their intercepts.

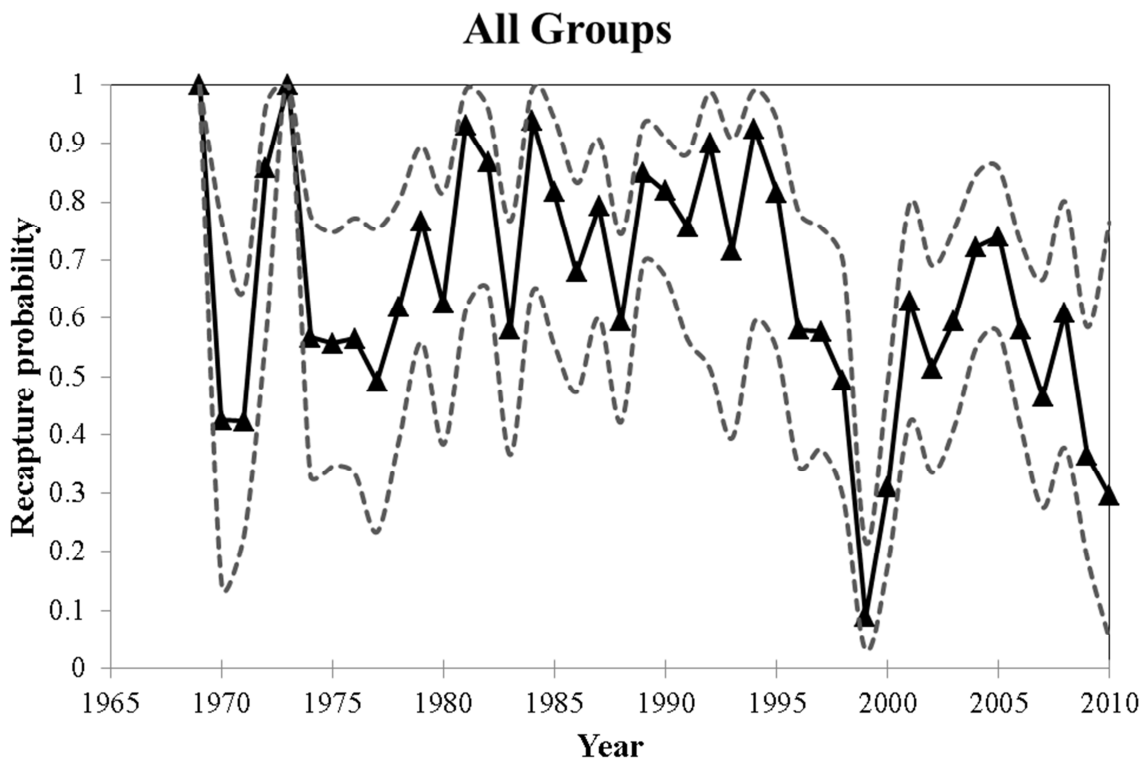

Figure 3.2. Probability of recapture/reobservation estimates for all age and sex groups of white-tailed ptarmigan at Mt. Evans, Colorado, USA. The recapture/reobservation probability estimates (solid line) and associated 95% confidence intervals (dashed lines) were generated from the minimum AIC_c model $\{\varphi(a+s+t)p(t)\}$.

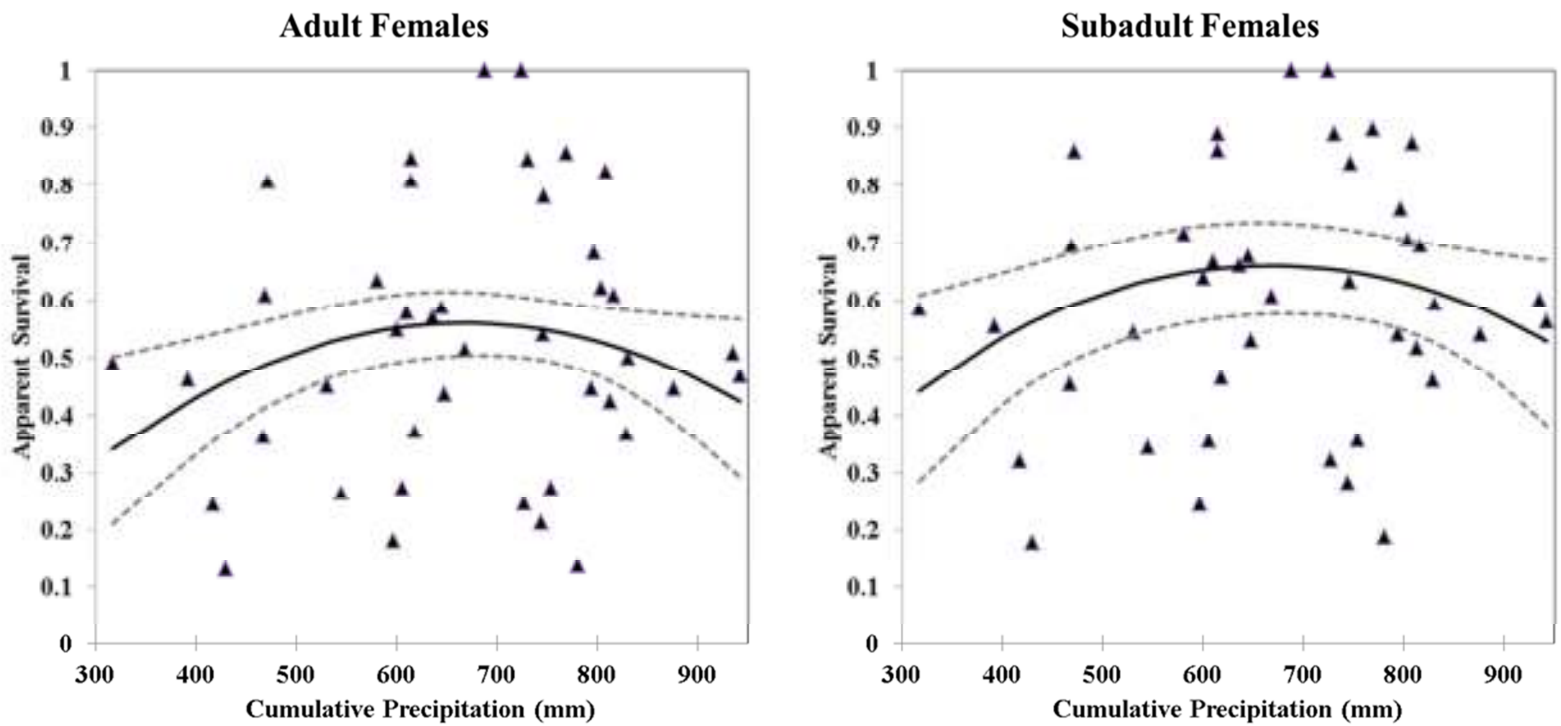

Figure 3.3. Apparent survival estimates as a function of cumulative precipitation for female white-tailed ptarmigan at Mt. Evans, Colorado, USA. The observed data points (triangles) were taken from the model $\{\varphi(a+t)p(t)\}$. The apparent survival estimates (solid line) and associated 95% confidence intervals (dashed lines) were produced from the model with the lowest AIC_c score $\{\varphi(a+CP^2)p(t)\}$.

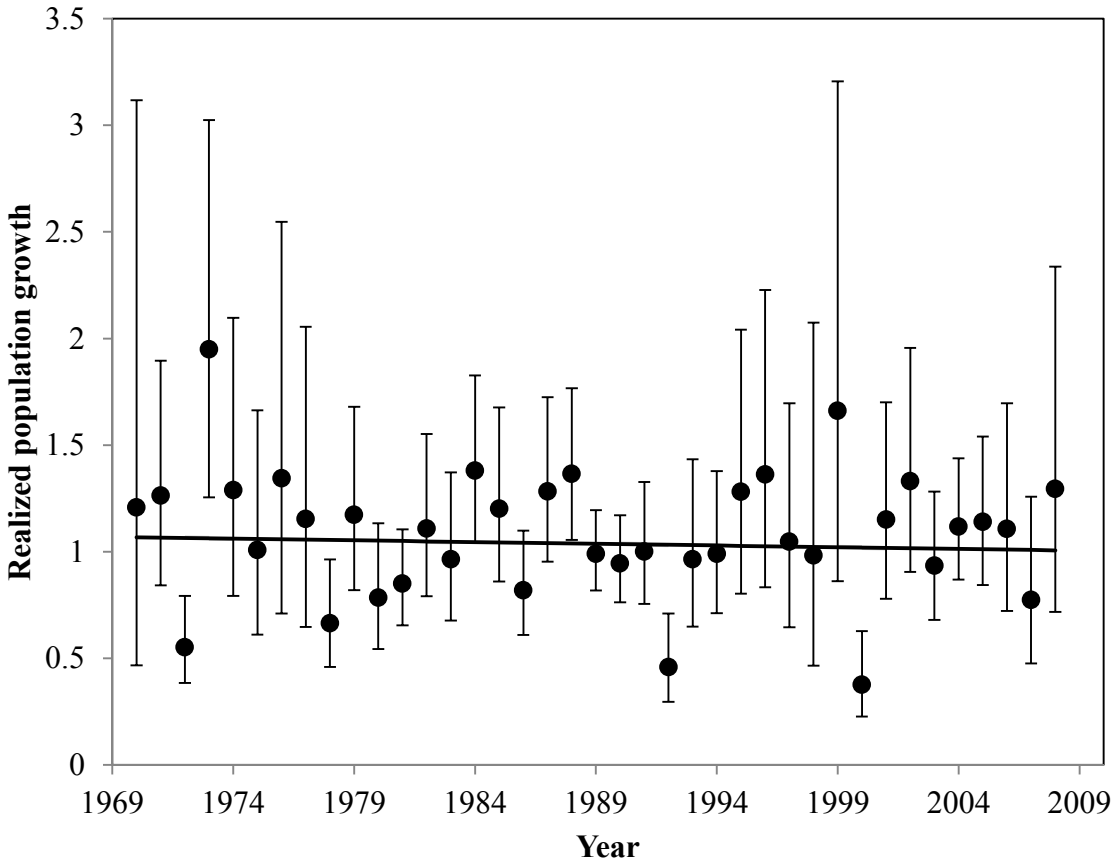

Figure 3.4. Annual rate of population change (λ_t) for white-tailed ptarmigan at Mt. Evans, Colorado, USA. Point estimates and associated 95% CI were generated from the model $\{\varphi(t)p(t)\lambda(t)\}$ for years 1971 to 2009. The trend line (T) was from the random effects model with the minimum AIC_c developed from the time dependent model $\{\varphi(t)p(t)\lambda(t)\}$.

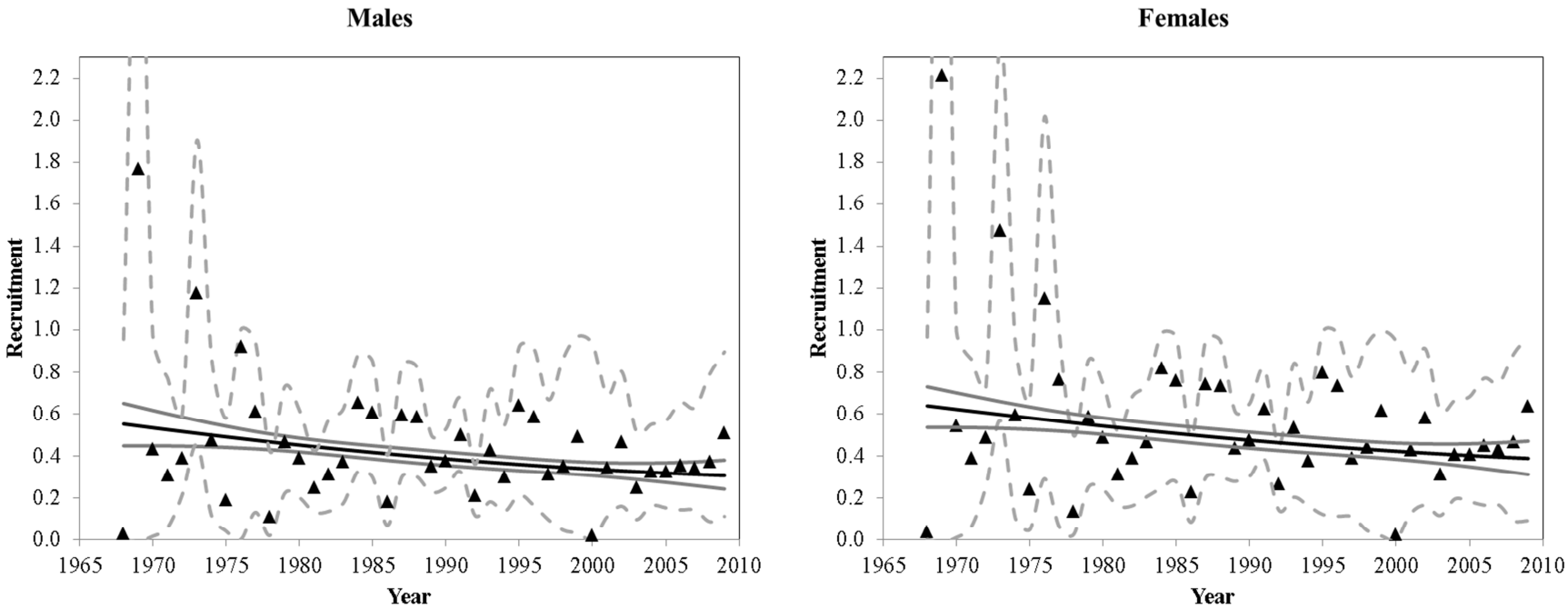

Figure 3.5. Annual recruitment of male and female white-tailed ptarmigan at Mt. Evans, Colorado, USA. Observed values (triangles) were from the additive model {φ(*s*+*t*)*p*(*s*+*t*)*f*(*s*+*t*)}, and the trend line (solid black line) was from the minimum AIC_c model {φ(*s*+*t*)p(*s*+*t*)*f*(*s*+*TT*)}. Associated 95% confidence intervals are also shown for the trend (dark gray line) and point estimates (dashed gray lines).

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CHAPTER 4: CONCLUSIONS

SUMMARY

The sensitivity of alpine habitats to warming effects will likely be a continued concern over coming decades. Alpine animals are at the extreme limits of environmental conditions experienced by terrestrial animals and will likely be confronted by limitations in dispersal abilities as the earth continues to warm. For example, species occurring in habitats at lower elevations have the opportunity to shift and disperse upwards as habitats change in response to warming (Lenoir et al. 2008, Habel et al. 2010). This is not an option for those species living above treeline, because dispersal upwards to more suitable habitat is clearly not possible. Much has been made of the threats that shifting treelines and habitats will have on alpine species, and this is undoubtedly true for the aforementioned reasons. However, it seems plausible that alpine endemic species may begin to respond (and potentially suffer) long before their habitat is physically lost to species invading from lower elevations. For example, yellow-bellied marmots in southern Colorado have already responded to spring warming by emerging from hibernation earlier (Ozgul et al. 2010). Earlier springs for marmots has led to individuals gaining mass (an improvement in body condition) and, as a result, survival and population abundance has dramatically risen in at least one population. Thus, a direct impact on the demographics of one alpine species has been shown to occur, and habitat loss was not the driving factor. Our white-tailed ptarmigan study population has also

responded to increases in spring temperature by advancing breeding phenology, but we did not find evidence that this was beneficial or detrimental to the population, even though reproductive success generally declined from the mid-1970s through 2008. This highlights the uncertainty in predicting the effects of climate warming in alpine habitats. However, our work has led to some insights which will help guide future research and inform management for the species.

In the second chapter we tested the effects of different post-hatch and seasonal weather variables on *a priori* predictions made for annual rates of reproduction of white-tailed ptarmigan. The results from the analysis largely supported our expectations of the predicted direction each climate variable would have on reproduction. Warm and dry seasons tended to negatively affect reproductive success, while wetter than normal seasons tended to be beneficial. However, post-hatch weather generally had a stronger effect on reproduction in white-tailed ptarmigan than seasonal conditions. While weather models successfully explained reproductive success, none of the models explained more than 20% of the variation in this demographic trait, suggesting there were processes that we were unable to model. The conclusions from this work are still concerning for white-tailed ptarmigan, however, as predictions of continued seasonal warming may cause alpine habitats to become dryer in upcoming years. The presence of snowfields and moist areas is critical for brood habitat, and loss of these areas with warming trends is expected to negatively impact reproduction in white-tailed ptarmigan.

In the third chapter we examined long-term trends in several demographic traits of breeding age white-tailed ptarmigan, and fit climate covariates to models in an attempt to explain annual variation in survival. Results from this work indicated females are more

sensitive to variation in climate than males. The causes for this difference are not well understood but are in part believed to be due to general differences in wintering locations used by males and females. For example, female white-tailed ptarmigan at Mt. Evans tend to move farther from breeding areas in the winter than males, and generally occur at lower elevations (Hoffman and Braun 1975). The best covariate in the models was cumulative winter precipitation, and survival of hens was negatively affected in years when precipitation was above and below the mean. The expectation was that birds would fare poorly when precipitation was low due to reductions in available roosting habitat. Low survival of female white-tailed ptarmigan during high precipitation years was surprising and the reasons behind this finding are unknown. Without being too speculative, it seems plausible that high precipitation years may affect resource availability if snowpack covers forage, but this has not been directly tested, and it is not known if this relationship holds in other ptarmigan populations. Predicted decreases in snowpack in Colorado are troubling given the negative relationship between survival and low winter precipitation for the species (Mote et al. 2005, Christensen et al. 2007). However, it should be noted that overall white-tailed ptarmigan at Mt. Evans appear to be fairly robust to conditions experienced during the winter periods, a promising finding given concerns over winter warming and potential effects on snowpack (Christensen et al. 2007).

RESEARCH NEEDS

Data collection for the white-tailed ptarmigan population analyzed began in the mid-1960s. The purpose of research for the species at the time was to examine the effects of hunting on white-tailed ptarmigan populations. The study was not designed to assess the

effects of climate on white-tailed ptarmigan populations. Thus, the analyses presented were retrospective and observational in nature, and inferences were limited by the availability of weather and climate data. Even with the limited amount of weather and climate data available, it was still clear that warming has had a detectable effect on white-tailed ptarmigan, particularly with respect to their breeding phenology. The declines in reproductive success measured from the mid-1970s through 2008 is thought to be partially due to warming seasons that may affect habitat quality. The largest piece of information likely to be of interest to land managers is a population viability analysis (PVA) for the species, given predicted climate conditions. Unfortunately we are limited in our ability to provide a meaningful PVA at this time due to limitations in forecasted climate data. Precipitation related covariates were found to be the best environmental predictors for both fecundity and survival, but predicting precipitation is difficult relative to temperature projections (Dennis S. Ojima, personal communication). This makes projecting future population trends for white-tailed ptarmigan particularly difficult.

A way forward will potentially involve the use of integrated population models (Schaub and Abadi 2011). Integrated population models are models that combine sources of demographic and count data into a single analysis through a joint likelihood. Demographic data may include mark-recapture data for estimates of survival, and counts of chicks for estimates of reproductive success. Latent (unobservable) states, such as immigration rates, can often be estimated from the combined analysis of multiple data sources. Data sources are linked through a population model, normally an age or stage structured matrix model (Caswell 2001), and demographic and count data are estimated through the joint likelihood that is estimated through maximum likelihood or sampling

from the joint posterior distribution using Markov Chain Monte Carlo (MCMC). A state-space model is used for the count data which partitions the variance into observation and process components. Environmental covariates can be fit to the fecundity and survival data, and downscaled climate models can be used to provide point estimates and measures of uncertainty around the estimates, given that the environmental outcome actually occurs. The model could be run over multiple different climate scenarios (i.e., high or low precipitation, high temperature, etc.) to obtain predictions over the next several years. Combining this type of analysis with additional datasets available for white-tailed ptarmigan is expected to increase our ability to make meaningful inferences on the likely stability of populations in the face of climate change. Using a modeling approach that accounts for uncertainty in the count process is the only way forecasting of populations can occur.

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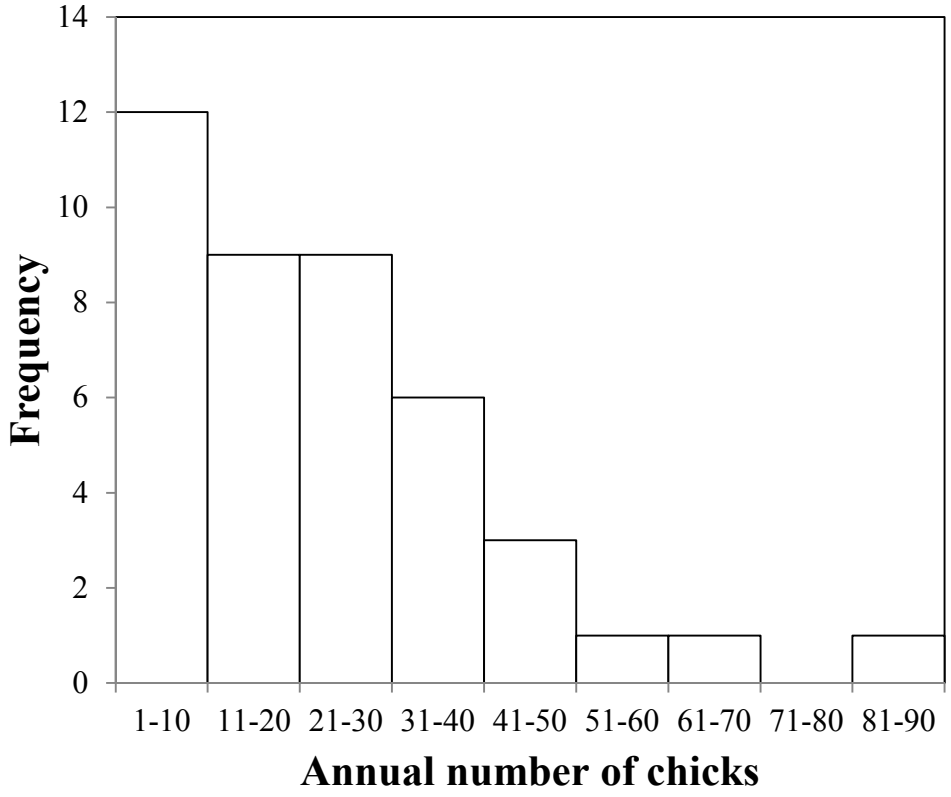
APPENDICES

Appendix A. Annual summaries for reproduction and phenology of white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado. Number of hens, chicks, and median date of hatch and associated standard error of the median are provided for each year in the study. Standard error of the median was not available for years 1984 and 2004 as number of broods could not be determined.

Year	Hens	Chicks	Median	SE Median	Year	Hens	Chicks	Median	SE Median
1968	16	2	203.0	-	1990	27	31	191.0	4.6
1969	10	6*	195.7	1.3	1991	20	10	192.0	4.9
1970	3	3	196.8	7.8	1992	23	28	190.1	6.0
1971	2	27*	200.0	4.2	1993	18	9	193.3	5.2
1972	20	70	186.0	0.7	1994	17	8	195.0	16.3
1973	11	16	198.0	0.8	1995	17	13	207.7	13.0
1974	18	33	183.0	3.8	1996	17	22	184.8	4.8
1975	12	8	192.5	12.3	1997	17	28	193.0	1.7
1976	8	11	188.3	2.4	1998	19	9	197.0	2.8
1977	21	46	189.5	2.3	1999	-	-	-	-
1978	33	86	191.5	2.7	2000	23	8	180.3	5.8
1979	19	41	195.5	2.3	2001	13	13	180.3	6.1
1980	22	60	201.7	1.5	2002	11	17	179.7	3.9
1981	18	28	186.0	2.3	2003	17	10	192.0	3.6
1982	8	8	192.0	3.8	2004	15	2	183.0	-
1983	9	13	199.5	-	2005	23	14	180.5	1.2
1984	18	34	193.0	2.7	2006	16	21	178.8	2.2
1985	17	25	185.8	2.5	2007	21	21	187.0	2.4
1986	20	17	191.0	2.8	2008	16	25	188.0	1.4
1987	10	16	189.0	3.8	2009	13	38	186.0	2.5
1988	16	31	185.7	2.2	2010	12	36	191.5	2.3
1989	27	44	190.8	3.0					

* Median date of hatch based on hunter returns of harvested chicks at Mt. Evans in late September.



Appendix B. Frequency histogram of annual number of white-tailed ptarmigan chicks at Mt. Evans in Clear Creek County, Colorado.

Appendix C. Relative support among post-hatch and seasonal weather variables used to predict reproductive success of white-tailed ptarmigan at Mt. Evans in Clear Creek County, Colorado. Also shown the number of parameters (K), delta AIC_c (ΔAIC_c), and AIC_c weights (w_i).

Model	-2(LL)	K	AIC_c	Δ AIC_c	w_i
Post-hatch					
Nrain	-144.37	3	295.44	0.00	0.52
PHIndex	-145.38	3	297.47	2.02	0.19
Tmin	-145.50	3	297.71	2.27	0.17
Tmax	-145.82	3	298.34	2.89	0.12
Seasonal					
GDD(2)	-145.46	3	297.62	0.00	0.40
Sind(3)	-145.56	3	297.83	0.21	0.36
CP(2)	-146.01	3	298.73	1.11	0.23

Appendix D. Model selection results for realized population growth (λ) and recruitment (*f*) models for white-tailed ptarmigan at Mt. Evans, CO (1968-2010). Realized population growth models were modeled using random effects.

Model	AIC_c	ΔAIC_c	w_i	K
λ models				
{φ(t)*p*(t)λ(T)}	15240.06	0.00	0.44	115.43
{φ(t)*p*(t)λ(TT)}	15240.30	0.23	0.39	115.69
{φ(t)*p*(t)λ(.)}	15241.98	1.92	0.17	116.20
f models				
{φ(s+t)*p*(s+t)*f*(s+TT)}	15230.65	0.00	0.87	89
{φ(s+t)*p*(s+t)*f*(s+T)}	15234.80	4.16	0.11	86
{φ(s+t)*p*(s+t)*f*(s+t)}	15238.57	7.93	0.02	128
{φ(t)*p*(t)*f*(t)}	15243.35	12.70	0.00	118
{φ(t)*p*(t)*f*(T)}	15244.72	14.07	0.00	86
{φ(s+t)*p*(s+t)*f*(s)}	15252.70	22.05	0.00	86
{φ(t)*p*(t)*f*(.)}	15266.35	35.70	0.00	83