

Estimates of annual survival, growth, and recruitment of a white-tailed ptarmigan population in Colorado over 43 years

Gregory T. Wann · Cameron L. Aldridge ·
Clait E. Braun

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Abstract Long-term datasets for high-elevation species are rare, and considerable uncertainty exists in understanding how high-elevation populations have responded to recent climate warming. We present estimates of demographic vital rates from a 43-year population study of white-tailed ptarmigan (*Lagopus leucura*), a species endemic to alpine habitats in western North America. We used capture-recapture models to estimate annual rates of apparent survival, population growth, and recruitment for breeding-age ptarmigan, and we fit winter weather covariates to models in an attempt to explain annual variation. There were no trends in survival over the study period but there was strong support for age and sex effects. The average rate of annual growth suggests a relatively stable breeding-age population ($\bar{\lambda} = 1.036$), but there was considerable variation between years for both population growth and recruitment rates. Winter weather covariates only explained a small amount of variation in female survival and were not an important predictor of male survival.

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G. T. Wann (✉) · C. L. Aldridge
Natural Resource Ecology Laboratory, Colorado State
University, 1231 East Drive, Fort Collins, CO 80523, USA
e-mail: greg.wann@colostate.edu

C. L. Aldridge
Department of Ecosystem Sciences and Natural Resource
Ecology Laboratory, Colorado State University, in Cooperation
with U.S. Geological Survey, Fort Collins Science Center, 2150
Centre Avenue Bldg. C, Fort Collins, CO 80526, USA

C. E. Braun
Grouse Inc., 5572 North Ventana Vista Road, Tucson,
AZ 85750, USA

Cumulative winter precipitation was found to have a quadratic effect on female survival, with survival being highest during years of average precipitation. Cumulative winter precipitation was positively correlated with population growth and recruitment rates, although this covariate only explained a small amount of annual variation in these rates and there was considerable uncertainty among the models tested. Our results provide evidence for an alpine-endemic population that has not experienced extirpation or drastic declines. However, more information is needed to understand risks and vulnerabilities of warming effects on juveniles as our analysis was confined to determination of vital rates for breeding-age birds.

Keywords Alpine · Colorado · Demography · *Lagopus leucura* · Weather

Introduction

Knowledge of long-term variation in demographic rates provide ecologists with an understanding of how populations have responded to past environmental change, and under what conditions they might be expected to decline or grow in size. Vertebrate populations have been affected by recent global changes in climate, including impacts to survival (Barbraud and Weimerskirch 2001; McMahon and Burton 2005) and fecundity (Sanz et al. 2003; Gaston et al. 2005; Both et al. 2006), the primary vital rates responsible for population growth. Alpine and arctic environments are the epitome of high latitude and elevation ecosystems, and their habitat characteristics are defined largely by cold temperatures (Diaz and Eischeid 2007). Climate warming is expected to reduce the extent of these systems through direct loss of habitat (Grace et al. 2002), changes in plant

community composition (Pauli et al. 1996; Theurillat and Guisan 2001), and loss of snow and ice (Haeberli and Beniston 1998; Hinzman et al. 2005). Thus, climate warming poses a threat to alpine and arctic ecosystems and there is evidence that their extent has already been reduced (Harsch et al. 2009), while continued loss is predicted (Guisan and Theurillat 2000; La Sorte and Jetz 2010).

Animal populations residing in alpine and arctic environments have received high interest in recent years (Berteaux et al. 2004; Chamberlain et al. 2012; Gilg et al. 2012). Survival mechanisms of birds endemic to alpine and arctic ecosystems are well studied and include behavioral, morphological, energetic, and physiological adaptations (Martin et al. 1993). Extremes in temperature, snow, and wind are abiotic conditions alpine and arctic birds must cope with to survive and reproduce, and seasonality provides additional reproductive challenges. Birds living in cold ecosystems have short breeding seasons and are at a reproductive disadvantage compared to birds breeding at lower elevations and latitudes due to re-nesting limitations during years with late snowmelt (Martin and Wiebe 2004). Most alpine and arctic birds overwinter at lower elevations and latitudes to avoid extreme winter conditions, but some remain in these habitats throughout the winter. For example, ptarmigan (*Lagopus* spp.) are well adapted to life in the cold and persist in alpine and arctic habitats year round, although short-distance migrations are common between the breeding and winter seasons (Irving et al. 1967; Hoffman and Braun 1975; Steen and Unander 1985; Martin et al. 2000).

Ptarmigan deal with challenging conditions throughout the winter period. Food availability during winter is generally limited and of low nutritional quality in arctic and alpine environments (Martin et al. 1993) and diets are commonly dominated by only a few plant species (e.g., May and Braun 1972; Thomas 1984). However, ptarmigan are well adapted to digesting winter forage (Moss 1974, 1983) and are capable of gaining mass in fall and winter (e.g., West and Meng 1968; Braun 1971). Mortality due to starvation or poor body condition has not been widely reported as a major factor affecting ptarmigan populations over winter. The major characteristic common to both alpine and arctic habitats during winter is snow. Snow is important to ptarmigan as it is used for roosting (Braun and Schmidt 1971; Stokken 1992) and can directly affect forage availability (Hakkarainen et al. 2007). It is also an important source of protection and concealment for ptarmigan. During winter months ptarmigan molt to a white basic plumage making individuals cryptic in snow-covered habitats, an adaptation to living in a strongly seasonal landscape (Piersma and Drent 2003). Snow conditions have generally not been tied directly to winter mortality of ptarmigan, but spring snow depth and timing of snow melt

can directly affect ptarmigan reproduction (Clarke and Johnson 1992; Martin and Wiebe 2004). Most demographic studies of ptarmigan focus on populations monitored during the breeding season, and there are few published studies examining the effects of winter weather or climate on ptarmigan demographic rates (but see Smith and Willebrand 1999; Wang et al. 2002a).

In this study we analyze demographic data from a 43-year study of white-tailed ptarmigan (*Lagopus leucura*), an alpine-endemic grouse species occurring in North America (Braun et al. 1993). White-tailed ptarmigan spend winters near or above tree line in Colorado where our population was studied. Males and females tend to segregate into different wintering areas after the breeding season (Hoffman and Braun 1977), a pattern that has also been observed in willow (*L. lagopus*) and rock (*L. muta*) ptarmigan (Weeden 1964; Gruys 1993; Schwab et al. 2005). We fit capture-recapture models to individual data to estimate annual survival, recruitment, and population growth. Sex and age-specific differences in survival have been well established in different ptarmigan species including white-tailed ptarmigan (e.g., Hoffman and Giesen 1983; Sandercock et al. 2005), and these effects were considered in our models. Differences in wintering locations between males and females also led us to consider that weather might affect sexes differently because wintering areas typically differ in topography and habitat characteristics. We chose winter weather covariates that we predicted would be biologically important to white-tailed ptarmigan demographic rates. Cumulative winter precipitation was predicted to positively affect survival because snow is important for snow roosting (Braun et al. 1976) and also provides concealment for ptarmigan. However, extreme amounts of winter snow might also cover willow (*Salix* spp.), the primary winter forage of white-tailed ptarmigan in Colorado, and we also considered a quadratic effect for this covariate. Average winter temperature was predicted to negatively affect ptarmigan demographic rates based on their previously described effects on population growth rates of white-tailed ptarmigan (Wang et al. 2002a). The mechanism behind this relationship is not known, but it may be due to temperature effects on snow quality. To examine this more closely we predicted the number of days in winter above freezing would negatively affect survival, because surface snow that melts and re-freezes can affect roost site suitability (Braun and Schmidt 1971). In rare cases ice on the surface of snow has even been known as a direct cause of mortality in some related grouse species (McGowan 1969). Finally, large-scale climate indices such as the North Atlantic Oscillation (NAO) can affect demographics of bird populations (Nott et al. 2002) and have been suggested as an important factor to consider in ecological studies (Stenseth et al. 2003). We tested the effects

of winter NAO index on all demographic rates. Delayed time effects in NAO were considered in growth and recruitment models because they can influence recruitment processes in ways not immediately apparent (Sandvik et al. 2012). We also examined correlations between the index and our winter weather covariates to consider larger scale links.

Methods

Study area

The Mt. Evans study area 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. The total study area consists of 9.2 km² of alpine habitat. Elevation ranges from 3,292 m to the summit of Mt. Evans at 4,347 m (Braun 1969). 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).

Field methods

White-tailed ptarmigan were studied at Mt. Evans from 1968 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 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 habitats that included areas adjacent to snowfields and moist meadows, both of which provide brood habitat, and ridgelines with rock cover which are used primarily by flocks of breeding-age birds.

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 (2 years of age or older). We made an attempt to capture all unmarked birds encountered in the study area using a noose attached to a telescoping pole

(Zwickel and Bendell 1967). Breeding-age birds received four colored bandettes in unique sequence that allowed identification without need for recapture during subsequent reobservations. We considered observations of marked birds from 1 May to 30 September which represented our sampling window. During some years birds were located in the winter months. Records outside the sampling period and area were not included in the analysis.

The Mt. Evans population experienced varying hunting pressure throughout our study. The implementation of a closed hunting area within 0.8 km of the road at Mt. Evans went into effect in 1994 and effectively ended the harvest of birds from our study population (C. 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 individuals. We treated harvested birds in our survival and recruitment models as being not released at last capture prior to known harvest. This was done in 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 by Braun (1969).

Weather 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, 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 climate conditions experienced at Mt. Evans, and comparisons with temperature data taken from a nearby SNOTEL station (site 936) available from 1998 to 2010 indicated a high correlation between the two sites ($r_p = 0.93$). We examined annual weather variables averaged, counted, or summed over the winter period, defined as occurring from 1 October through 31 March. Weather variables were recorded in millimeters for precipitation events and degrees Celsius for temperature events. Variables examined included the total cumulative sum of precipitation (CP), quadratic effects for CP (i.e., CP²), average minimum temperature (MinT), average maximum temperature (MaxT), and number of days with maximum temperature above freezing (warm days, WD). Ordinary least squares regressions were used to test for temporal trends in the weather variables. Additional models with additive (+ notation) and interactive (× notation) effects between

precipitation and temperature-based variables were also tested. We used the station-based NAO index for the winter period December through March provided by the University Corporation for Atmospheric Research (<https://climate.tedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>). Time lags of 1 and 2-years for the NAO (NAO-1 and NAO-2) were considered, in addition to a model without a time lag (NAO-0). Weather covariates and the NAO covariate were examined for correlations using Pearson correlation coefficients.

Analysis

Apparent survival

We constructed open-population mark-recapture models implemented in Program MARK to test potential differences in survival between sex and age classes (White and Burnham 1999). Encounter histories were constructed using 1's (detected by capture or reobservation) and 0's (not detected). Individuals killed by hunters and reported were coded by adding a duplicate encounter history with a negative 1 in the frequency column of the Program MARK input file. The Cormac–Jolly–Seber (CJS) model estimates apparent survival (ϕ) and probability of recapture (p) parameters. The survival parameter should be considered apparent survival because permanent emigration and mortality are confounded in the model. Models that included age (a), time (t), and sex (s) effects were developed for survival parameters. Models that included time (t) and sex (s) effects were developed for recapture parameters. Trend effects (T), including quadratic effects (TT), were considered for the survival parameters and were used to test for an increase or decline across the study period. A model set was developed 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 sex and time in the recapture parameter $\{\phi(a + s \times t), p(s + t)\}$. Our sample sizes were not sufficiently large to support a fully interactive and time dependent model as many of the parameters were non-estimable under the fully parameterized structure $\{\phi(a \times s \times t), p(s \times t)\}$. Thus, our global model was a reduced version of the fully interactive model but the most general our data could support. The total number of possible models to test was large, and we reduced the possible candidate set by first selecting the structure for the recapture parameter p . This was done by keeping ϕ in the time-dependent form $\{\phi(a + s \times t)\}$ and building increasingly parsimonious models with starting structure $\{p(s + t)\}$ for the recapture parameter. An information-theoretic approach was then used to select the most parsimonious model using the Akaike information

criterion adjusted for small sample size (AIC_c ; Burnham and Anderson 2002). The AIC_c -selected best structure for p was used to construct candidate models for apparent survival including the most general structure $\{\phi(a + s \times t)\}$ and reduced versions of this model. We used AIC_c to select the most parsimonious model from this candidate set.

The top-ranked candidate model from the survival analysis was used as the structural basis to fit weather covariates to survival. However, we analyzed males and females separately to simplify the design matrix in Program MARK and because we believed correlations between survival and weather could differ between sexes. All recapture parameters were modeled with the same structure found to be the most parsimonious in the previously described steps. Time (t) models were also maintained in the candidate model set for model comparisons. 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 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).

Population growth

We used Pradel's temporal symmetry model (Pradel 1996) implemented in Program MARK to estimate annual rates of population change (λ). Age effects cannot be included in Pradel models. Thus, we pooled data for yearling and adults, but maintained groups for males and females. The most parsimonious model structure from the survival analysis was used to structure ϕ and p . We fit models with additive sex effects $\{\lambda(s + t)\}$, interactive sex effects $\{\lambda(s \times t)\}$, and without sex effects $\{\lambda(t)\}$ to assess the best starting structure for λ using AIC_c , which was then used for random effects modeling. Several random effects models were examined, including models with the same covariates fit in the survival analysis, an intercept model with no change over time $\{\lambda(\text{Int})\}$, a linear time trend $\{\lambda(\text{T})\}$, and a quadratic time trend $\{\lambda(\text{TT})\}$. Based on the model receiving the highest support, we used the random effects module in Program MARK to estimate the average annual rate of population change in the population ($\bar{\lambda}$) (White et al. 2001). We calculated the amount of process variance explained by the top covariate model by taking the difference between the variance of the intercept model and covariate model and dividing by the variance of the intercept model. Losses on capture are not handled by the Pradel model in Program MARK, so parameter estimates from these models

included birds known to have been harvested. The years 1987–1998 included an expanded search effort for birds as a result of a radio-telemetry study that was being conducted during that time span. This resulted in some birds being marked or observed in areas that were not normally searched in other years and, as a result, these observations were eliminated from the data used to build Pradel models, because growth rates would reflect an expansion of the study area, not necessarily a true increase in population size.

Population recruitment

To estimate annual rates of population recruitment (f), we used the Link-Barker parameterization of the Jolly–Seber model (Link and Barker 2005) implemented in Program MARK. We chose this parameterization because the f parameter is not affected by losses on capture. Like the Pradel models, the Link–Barker Jolly–Seber models include φ and p parameters. The parameter f is interpreted as recruitment into the population from births or immigration, which cannot be differentiated. Thus, the f parameter represents a composite measure of recruitment from both the birth and immigration processes. Our approach to constructing and selecting models was identical to the methods used for population growth models and random effects. We had no reason to believe the f parameter estimates should be constrained within the $[0, 1]$ interval, and a log identity link was used to estimate all f parameters in the models.

Evaluating model fit

We evaluated goodness of fit for the survival analysis using the median \hat{c} procedure available in Program MARK on the most general model in our data set to estimate the variance inflation factor \hat{c} . This estimated value was then used to correct for over dispersion by adjusting the width of confidence intervals. The median \hat{c} procedure also was applied separately on male and female data used in the climate survival analysis for the general model $\{\varphi(a + t), p(t)\}$. The median \hat{c} procedure in Program MARK was not available for use on the Pradel temporal symmetry models at the time of analysis, and goodness of fit was assessed using Program RELEASE (Burnham et al. 1987) on the most general model $\{\varphi(s \times t), p(s \times t), \lambda(s \times t)\}$ to estimate \hat{c} . This was done by pooling degrees of freedom and Chi square values from Tests 2 and 3 which collectively make up the goodness-of-fit test for the fully time-dependent model. 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

Climate data

There were no temporal trends in winter weather covariates fit to capture-recapture models (regression slope coefficients overlapped 0 for all covariates tested). Means and standard deviations for covariates were as follows: CP (669.9, SD = 148.1), MinT (−13.4, SD = 1.6), MaxT (−6.73, SD = 1.2), and WD (25.0, SD = 11.1). None of the weather covariates correlated highly with the winter NAO index, and the highest correlation was between cumulative winter precipitation and NAO ($r_p = 0.35$).

Survival

We used 1,344 marked birds (602 females and 742 males) of breeding age in our population analysis of apparent survival at Mt. Evans from 1968 to 2010. The number of re-observations resulted in 1,036 additional records for a total of 2,380 observations. Results from the goodness-of-fit test indicated our most general model had low over dispersion, and all model AIC_c values and standard errors were adjusted using the estimated variance inflation factor from the median \hat{c} procedure ($\hat{c} = 1.12$).

Survival for the interval 1999–2000 was non-estimable due to a reduced search effort and sample size during these years. Apparent survival varied among sex and age classes, and the model that included an additive structure between sex, age, and time for the apparent survival parameter received nearly all support (>99 %) based on $QAIC_c$ weights (Table S1 in the Electronic Supplementary Material, ESM). Models that included trend effects received no model support (Table S1 in ESM). Annual estimates of apparent survival varied widely from 0.12 for adult females between the 1972–1973 seasons and 0.94 for yearling males between the 1971–1972 seasons (Table S2 in ESM; Fig. 1). Yearling males had the highest survival, followed by yearling females, adult males, and adult females (Table 1). The recapture probability averaged over all years was 0.67 (SE = 0.033) and did not differ by sex, but varied considerably by year from a low of 0.30 in 2010 and a high of 0.94 in 1984 (Table S3 in ESM).

Minor overdispersion was present in both estimates of \hat{c} for females and males ($\hat{c} = 1.36$ females, and $\hat{c} = 1.14$ males). Weather covariates fit to mark-recapture models indicated substantially higher support for those covariates fit to female data than male data (Table S4 in ESM). The top models receiving all support for the male group did not include weather effects but did include time dependence in both apparent survival and recapture parameters. In the male candidate set nearly all of the model weight (97 %) supported model $\{\varphi(a + t), p(t)\}$. In contrast, models that

Fig. 1 Annual rates of apparent survival and associated 95 % confidence intervals for white-tailed ptarmigan at Mt. Evans (Clear Creek County, Colorado, USA) from 1968 to 2010. Estimates are for adult males taken from the additive model $\{\varphi(a + s + t), p(t)\}$. All other age and sex classes had identical slopes for point estimates but differed by a constant intercept. Estimates are for the period between sampling occasions, and year corresponds to the sampling occasion at the beginning of the interval

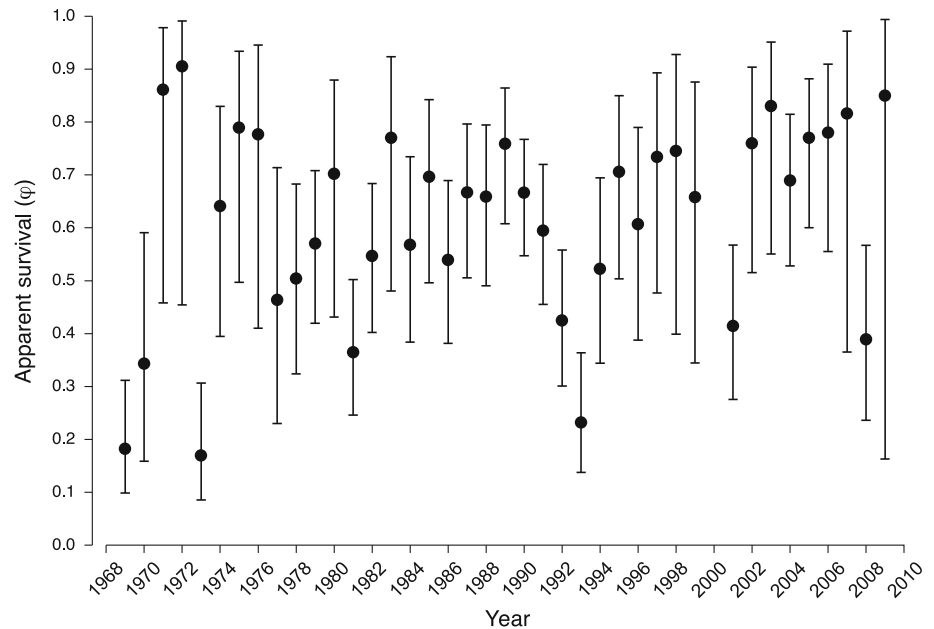


Table 1 Age and sex specific average estimates for annual survival of white-tailed ptarmigan at Mt. Evans (Clear Creek County, Colorado, USA) from 1968 to 2010

Sex and age	Survival	SE	Lower 95 % CI	Upper 95 % CI
Adult males	0.610	0.030	0.552	0.668
Yearling males	0.717	0.033	0.653	0.780
Adult females	0.502	0.032	0.439	0.564
Yearling females	0.612	0.035	0.543	0.680

Averages were taken from annual estimates produced from the model with the minimum QAIC_c value $\{\varphi(a + s + t), p(t)\}$ using the variance components feature in Program MARK

included weather effects for females accounted for 85 % of the AIC_c weights. Analysis of deviance results for the female data indicated the best covariate model $\{\varphi(a + CP2), p(t)\}$ explained 8.9 % of temporal survival variability (Table 2 and Table S4 in ESM). The best covariate model for males $\{\varphi(CP2 + WD), p(t)\}$ explained 10.1 % of temporal survival variability but did not receive any model support, and as a result we do not represent the ANODEV results for males in this paper. This covariate model for females had a quadratic relationship between cumulative precipitation and survival, with precipitation levels above and below the mean resulting in the lowest survival for female ptarmigan.

Population growth

The reduced sample size for the population growth analysis consisted of 1,298 individuals, and the total number of records including recaptures and reobservations was

reduced to 2,292. A goodness of fit test performed on the most general model indicated no evidence of overdispersion with an estimated $\hat{c} = 0.72$ ($\chi^2 = 142.88$, $df = 199$). Hence, no correction for overdispersion was used for Pradel models. The reduced model $\{\varphi(s + t), p(t), \lambda(t)\}$ received the highest AIC_c support and was used to develop random effects models for trend and covariate fitting. The first two growth rates and the last were non-estimable and not used for random effects models. There was little difference in support between the candidate random effects models, and all had ΔAIC_c values below 2 (Table 3 for top models; Table S5 in EMS for complete candidate model set). The model that received the highest support considered the effect of cumulative winter precipitation on population growth and showed a positive relationship which explained 2.9 % of annual process variance. The average annual rate of growth calculated from the intercept model indicated a relatively stationary population from 1970 to 2010 ($\bar{\lambda} = 1.036$, $SE = 0.034$; Fig. 2).

Population recruitment

The first two recruitment rates, the last, and the rate for the interval 2000–2001 were non-estimable and not used for random effects models. The reduced starting model $\{\varphi(s + t), p(t), f(t)\}$ received the highest AIC_c support and was used to develop random effects models for trend and covariate fitting. There was considerable uncertainty among candidate models and the top 8 models all had ΔAIC_c values below 2 (Table 3, Table S5 in EMS). The covariate model that included winter cumulative precipitation was top ranked and explained 5.8 % of annual

Table 2 Analysis of deviance results for covariate models applied to data from female white-tailed ptarmigan at Mt. Evans (Clear Creek County, Colorado) from 1968 to 2010

Model	ΔQAIC_c	Qw_i	K	$-2LK$	% Deviance explained
$\varphi(a + \text{CP2}), p(t)$	0.000	0.205	46	1800.764	8.89
$\varphi(a + \text{CP2} + \text{WD}), p(t)$	0.622	0.150	47	1798.626	11.33
$\varphi(a + \text{CP2} + \text{MinT}), p(t)$	2.187	0.069	47	1800.754	8.91
$\varphi(a + \text{CP2} + \text{MaxT}), p(t)$	2.194	0.068	47	1800.764	8.89
$\varphi(a + \text{NAO-0}), p(t)$	2.219	0.068	45	1806.760	2.03
$\varphi(a + \text{WD}), p(t)$	2.500	0.059	45	1807.142	1.64
$\varphi(a + \text{CP}), p(t)$	2.963	0.047	45	1807.771	0.92

Covariate models with ΔQAIC_c values less than 3 are presented, along with their associated weights (Qw_i), number of parameters (K), negative log-likelihood ($-2LK$), and percentage of variation explained by covariate. Effects that included age (a) were included in all candidate models. Covariates in table were cumulative winter precipitation with and without a quadratic effect (CP2 and CP, respectively), number of warm days (WD), average minimum and maximum winter temperature (MinT and MaxT, respectively), and the North Atlantic Oscillation index without time lag (NAO-0). All models were adjusted with a variance inflation factor ($\hat{c} = 1.36$)

process variance, followed by a covariate model that included the NAO index with a 2-year time lag which explained 8.5 % of annual process variance. The average annual recruitment rate calculated from the intercept model from 1970 to 2010 was 0.415 (SE = 0.019), but annual recruitment varied widely (Fig. 3).

Discussion

Our analysis of capture-recapture data for white-tailed ptarmigan presents the longest time series of data available for this species and allowed us to test for trend, weather and climate effects. This has rarely been done for alpine bird species as long-term datasets tend to be particularly uncommon for alpine ecosystems.

Survival

The Mt. Evans white-tailed ptarmigan population demonstrated highly variable demographic rates over the 43 years studied. Survival changed considerably from year to year, and there were no indications of any consistent trends or patterns in this vital rate. Our most parsimonious survival model was additive in structure with respect to age and sex of birds. This model indicated that birds of different age and sex co-vary in their annual survival patterns, although the rank of each age and sex class relative to the other does not change from year to year suggesting the existence of common factors influencing survival. Average survival rates for the Mt. Evans population and other populations where annual survival estimates have been reported are provided in Table S6 in ESM. Male white-tailed ptarmigan tend to have higher annual survival than females, although there is considerable variation among populations. In Colorado, males at Pikes Peak (Hoffman and Giesen 1983),

Niwot Ridge (May 1975), and Rocky Mountain National Park (RMNP; C. E. Braun, unpublished data) had higher survival than females. Males also had higher survival in the Yukon Ruby Ridge Mountains (Wilson and Martin 2011). In contrast, no survival differences between sexes were found at Glacier National Park in Montana (Choate 1963) or Vancouver Island in British Columbia (Hannon and Martin 2006). Subadults had higher annual survival rates than adults. Of the age-specific survival estimates available for white-tailed ptarmigan, female subadults had higher annual survival than adults in three out of five populations reported, including the Mt. Evans population (Table S6 in ESM). Most reports of age-specific survival are from Colorado, but estimates from a population in the Yukon were nearly identical (S. Wilson, unpublished data). Male subadults had higher annual survival than adults in half the studies reported, including the Mt. Evans population, although unpublished data from RMNP indicate subadult and adult males have similar annual survival rates. In the larger context of available studies, our result do not appear to differ greatly from reported annual survival rates for white-tailed ptarmigan in Colorado, but they are considerably higher than a population studied in the Yukon (Wilson and Martin 2011) and Montana (Benson 1999). It is difficult to gauge the importance of age effects for different populations of white-tailed ptarmigan as in many cases only sex-specific survival rates are reported. Age effects appear to be an important factor for Colorado populations, and we encourage future studies to estimate these effects whenever sample sizes allow as they are a critical component to consider when assessing population stability, as done in a population viability analysis (e.g., Morris and Doak 2002).

We attempted to explain annual variation in survival using winter weather covariates, in addition to age and sex effects initially tested. Winter covariates were found to

Table 3 Model selection results for random effects covariate models fit to white-tailed ptarmigan capture-recapture data from Mt. Evans (Clear Creek County, Colorado) from 1968 to 2010

Model	Trace G	ΔAIC_c	w_i	K	$-2LK$
Pradel (λ)					
$\varphi(s+t), p(t), \lambda(\text{CP})$	27.998	0.000	0.070	113.998	14977.337
$\varphi(s+t), p(t), \lambda(\text{Int})$	27.960	0.098	0.067	113.960	14977.518
$\varphi(s+t), p(t), \lambda(\text{NAO-1})$	27.605	0.178	0.064	113.605	14978.378
$\varphi(s+t), p(t), \lambda(\text{NAO-2})$	28.214	0.291	0.060	114.214	14977.154
$\varphi(s+t), p(t), \lambda(\text{T})$	28.212	0.445	0.056	114.212	14977.312
$\varphi(s+t), p(t), \lambda(\text{CP2})$	28.314	0.555	0.053	114.314	14977.197
$\varphi(s+t), p(t), \lambda(\text{CP} + \text{MinT})$	28.411	0.612	0.051	114.411	14977.042
$\varphi(s+t), p(t), \lambda(\text{CP} + \text{MaxT})$	28.419	0.638	0.051	114.419	14977.050
Link-Barker (f)					
$\varphi(s+t), p(t), f(\text{CP})$	20.068	0.000	0.131	101.068	15741.287
$\varphi(s+t), p(t), f(\text{NAO-2})$	19.889	0.131	0.123	101.889	15739.632
$\varphi(s+t), p(t), f(\text{Int})$	20.071	0.809	0.088	102.071	15739.915
$\varphi(s+t), p(t), f(\text{CP} + \text{MinT})$	20.935	1.306	0.068	102.935	15738.531
$\varphi(s+t), p(t), f(\text{CP2})$	20.813	1.307	0.068	102.813	15738.797
$\varphi(s+t), p(t), f(\text{CP} + \text{MaxT})$	20.929	1.368	0.066	102.929	15738.607
$\varphi(s+t), p(t), f(\text{CP} + \text{WD})$	20.743	1.435	0.064	102.743	15739.077
$\varphi(s+t), p(t), f(\text{CP} \times \text{WD})$	21.222	1.692	0.056	103.222	15738.291

The top 8 models from growth (λ) and recruitment (f) models are presented, along with their associated G matrix (Trace G), weights (w_i), number of parameters (K), and negative log-likelihood ($-2LK$). Effects included sex (s) and age (a) in survival and recapture probabilities, linear (T) trend, time (t), and constant (Int). Covariates tested included winter cumulative precipitation with linear and quadratic effects (CP and CP2, respectively), average minimum and maximum temperature (MinT and MaxT, respectively), days above freezing (WD), and the NAO index with no lag and 1 and 2-year lags (NAO-0, NAO-1, and NAO-2, respectively)

have only small effects on female survival. This conclusion stems from the low amounts of deviance explained by the covariates. In contrast, simple time variation and age were the best explanatory variables for males. This suggests that males and females in the Mt. Evans population may be affected differently by winter weather, although underlying ecological factors are unknown. Hoffman and Braun

(1975) studied white-tailed ptarmigan at Guanella Pass, a nearby winter use site that shares some seasonal movements of birds with Mt. Evans. The authors collected data on recoveries and reobservations of ptarmigan banded at Guanella Pass and found that distances moved between summer and winter sites were significantly greater for females than males (Braun et al. 1976). Males were also found to winter in areas dominated by willow above tree-line while females normally winter in areas with extensive stands of willow at or below treeline. Snow accumulation (snowpack) varies spatially in alpine and subalpine habitats due primarily to topographic characteristics, wind, and vegetation (Elder et al. 1991; Blöschl and Kirnbauer 1992; Hiemstra et al. 2002). Locations sheltered from wind tend to accumulate the greatest amounts of snow, and snow depth tends to decrease with increasing elevation in alpine habitats (Erickson et al. 2005). This suggests that habitat characteristics in terms of snow accumulation are likely to differ substantially between sites used by males and females.

Population growth

The overall mean rate of annual growth indicated the Mt. Evans population did not dramatically change over the study period. However, annual growth showed considerable variation, and a potential existence of a cyclic pattern in the annual rates of population change should be further studied (Fig. 2). Population cycles have been well established in the Tetraoninae, and causes of these cycles have been attributed to a wide variety of factors including density-dependence (Gardarsson 1988; Watson et al. 1998, 2000), climate (Lindström 1996; Watson et al. 2000), and even parasites (Watson and Shaw 1991; Hudson et al. 1998; Cattadori et al. 2005). In terms of the overall growth rate of the Mt. Evans population, our results contrast with those obtained for white-tailed ptarmigan at RMNP which were declining from 1975 to 1999 (Wang et al. 2002a), and also Mt. Evans and surrounding populations during the period 1989–1997 (Sandercock et al. 2005). In the former case, population declines were attributed to at least partially to warming winters. In the latter case, survival of breeding-age adults was found to be too low to support a stationary population when considered with age-specific estimates of fecundity. A population studied from 2004 to 2008 in the Yukon was also found to be in decline based on age-specific estimates of survival and fecundity (Wilson and Martin 2011).

Results from our analysis indicate a positive effect of cumulative winter precipitation on annual growth, but only 2.9 % of annual process variation in growth rates could be explained, and there was a lack of strong support for models that included trend effects. Thus, the winter

Fig. 2 Annual growth estimates and associated 95 % confidence intervals for white-tailed ptarmigan at Mt. Evans (Clear Creek County, Colorado, USA) from 1970 to 2010. Point estimates were obtained using a random effects intercept with a Pradel model $\{\varphi(s + t), p(t), \lambda(t)\}$. Estimates are for the period between sampling occasions, and year corresponds to the sampling occasion at the beginning of the interval

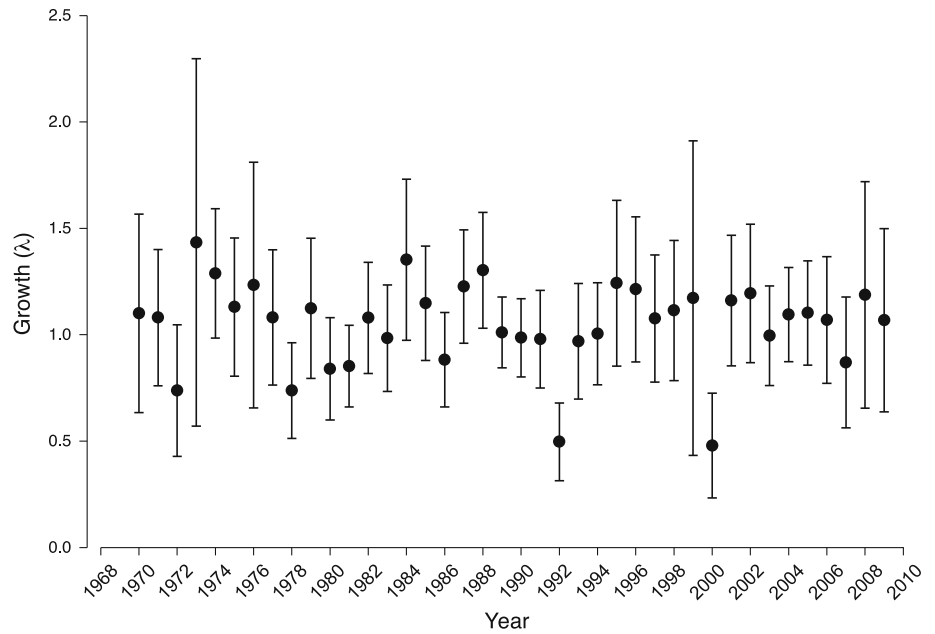
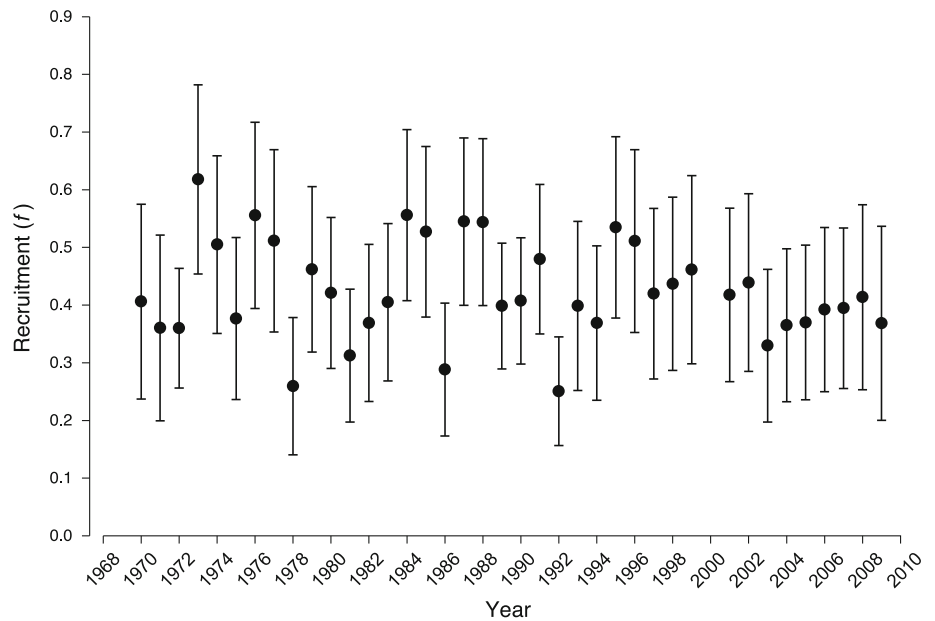


Fig. 3 Annual recruitment estimates and associated 95 % confidence intervals for white-tailed ptarmigan at Mt. Evans (Clear Creek County, Colorado, USA) from 1970 to 2010. Point estimates were obtained using a Link–Barker Jolly–Seber model $\{\varphi(s + t), p(t), f(t)\}$. Estimates are for the period between sampling occasions, and year corresponds to the sampling occasion at the beginning of the interval



covariates tested did not have a strong direct impact on growth of our population, and there was no evidence that breeding-age birds have declined at Mt. Evans. Results from our analysis appear to be in contrast to reports from previous work. It is important to state that our annual estimates of population growth from the Pradel model are representative of the age classes used in the analysis. In our study, breeding-age birds were those individuals surviving to their first breeding season (yearlings) and those that survived to their second breeding season and beyond (adults). It is possible to have a situation where breeding-age birds may have a positive growth trajectory even in the

presence of declining fecundity. In this case we would expect external recruits (i.e., immigrants) from surrounding populations to maintain the Mt. Evans population and perhaps even cause it to grow if reproductive success in surrounding areas is high. Indeed, previous work has shown that external recruits (discussed in the recruitment section) are critical to sustaining the Mt. Evans population (Martin et al. 2000). Demographic modeling also supports this conclusion (Sandercock et al. 2005). Given the open population structure of white-tailed ptarmigan, our results could be misleading as potential declines in fecundity cannot be ascertained based on analysis of breeding-age

birds alone. Thus, we acknowledge that considering reproductive performance of the Mt. Evans white-tailed ptarmigan population, particularly with respect to weather and climate, is important to gain an understanding of vulnerabilities the species may face during the breeding season.

Population recruitment

Direct estimates of reproduction were not made in our analysis and we instead estimated annual recruitment rates of breeding-age individuals into the Mt. Evans population. The Link–Barker Jolly–Seber model used to produce these estimates does not distinguish external and internal recruits, so these estimates do not necessarily represent the reproductive performance contribution to recruitment of the Mt. Evans population. Instead, they should be interpreted as estimates that represent both external (immigration) and internal (births from the population) processes. The recruitment parameter represents the number of individuals that enter the population between time t and $t + 1$ for each individual in the population at time t . Estimates of annual recruitment were highly variable, but no trends were detected. Winter cumulative precipitation and the NAO with a 2-year time lag both received the highest support and both correlated positively with recruitment.

Weather, climate, and demographic rates

There are relatively few studies that have tested winter weather or climate effects on vital rates of alpine and arctic species. In addition, most avian species breeding in alpine and arctic environments spend winter at much lower elevations and latitudes, and comparisons of weather effects on survival rates between these species and white-tailed ptarmigan are not particularly meaningful given their winter habitats and climates are substantially different. A 25-year study of white-tailed ptarmigan at RMNP examined winter climate on population growth rates (Wang et al. 2002a). Growth rates were negatively affected by high winter temperatures at RMNP and precipitation was not found to be an important driver. Weather did not correlate strongly with any of the demographic rates measured in our study, but in contrast to the aforementioned results the temperature covariates never ranked higher than winter cumulative precipitation in any of our models. Kéry et al. (2006) found that warm and wet winters enhanced both survival and fecundity of pink-footed geese (*Anser brachyrhynchus*) in Svalbard. The authors believed the positive relationship between survival and warm winters was likely due to increased food availability at wintering and staging areas. Thus, a direct effect of climate on survival was not suspected, but rather an indirect link between

climate and food availability. Winter food limitations have been suggested as a limiting factor for northern populations of black-capped chickadee (*Poecile atricapillus*) in Alberta (Desrochers et al. 1988) and willow tit (*Poecile montanus*) in Sweden (Jansson et al. 1981), but studies tying winter food limitations to survival in Tetraonidae are not well established. Winter food sources of Tetraonidae tend to be restricted to a few species which are generally abundant, such as willow (May and Braun 1972), spruce (*Picea* spp.; Ellison 1976), and birch (*Betula* spp.; Gasaway 1976). The mechanism linking winter cumulative precipitation and demographic vital rates in the Mt. Evans white-tailed ptarmigan population was not specifically tested and not particularly strong, but we tend to think the precipitation effect on survival was likely due to indirect effects and not a direct cause of mortality. For example, if low cumulative precipitation limits snow roost availability birds may be forced to expend more energy searching for roost sites, which in turn would be expected to deplete body condition and ultimately reduce survival. It is noteworthy that telemetry studies of Tetraonidae nearly always implicate predation events as the primary cause of natural mortality (e.g., Small et al. 1991; Caizergues and Ellison 1997; Connelly et al. 2000; Sandercock et al. 2011). Thus, it appears when winter weather is an important factor in mortality of breeding-age ptarmigan and grouse, it is probably due to indirect effects in most cases (but see McGowan 1969).

Large-scale climate is frequently cited as a highly important factor to consider when conducting demographic studies (e.g., Stenseth et al. 2003). Morrison and Hik (2007) found a positive effect of Pacific Decadal Oscillation (PDO) on collared pika (*Ochotona collaris*) adult survival, likely due to its effects on timing of spring snowmelt which occurred later during years with low PDO. In contrast to the pika study, Wang et al. (2002b) found that local climate had a bigger influence on white-tailed ptarmigan population dynamics at RMNP than large-scale climate measures. No relationships between NAO and local climate patterns relevant to white-tailed ptarmigan demographics have been identified, and we did not find strong correlations between winter weather covariates tested and winter NAO. One of our highest ranked recruitment models included the NAO index with a 2-year time lag (Table S5 in ESM). This model received equivalent support to the top ranked winter cumulative precipitation model. As noted in Sandvik et al. (2012), the importance of time lags in large-scale climate patterns on population dynamics depends on demographic characteristics of the population studied. For example, if climate is a strong driver of survival a time lag would not be expected in a large-scale process like NAO as the effect should occur within the season. In contrast, if climate affects reproduction then time lags are likely to be

important, because the effects of past climate will not be immediately apparent until individuals recruit into the population. We currently lack appropriate reproductive data to test if a mechanism exists capable of explaining the correlation between a 2-year NAO lag and recruitment, and the model uncertainty associated with the covariates tested can only lead us to speculate on this relationship.

There was a high amount of temporal variation in the demographic rates of our population. The low amount of variation explained by winter weather indicates the presence of other important factors which we did not consider or were unable to measure. Environmental stochasticity and density-dependent variation are factors that can affect temporal variation in demographic rates (e.g., Sæther 1997). With respect to environmental stochasticity, weather effects during the breeding season were not considered in this analysis, but average survival rates from the mid-May to mid-September period were very high for our population (0.96 for males and 0.93 for females; G. T. Wann, unpublished data). Thus, on average most mortality occurs during the non-breeding season in our population. Predation is another stochastic factor that we were unable to measure but one that undoubtedly plays a major role in seasonal survival. If predation pressure at wintering sites varies substantially from year to year it is a likely mechanism for unexplained annual variation found in our population's demographic rates. Prior to analysis we found that annual survival and growth did not correlate with spring densities at Mt. Evans. Although density-dependence may play a role in regulating some aspects of the population dynamics of the Mt. Evans population (e.g., annual reproductive rates), there is no evidence it was a major factor in the annual variation observed in survival, recruitment, or growth.

Conclusion

We are cautious to dismiss the importance of weather events in shaping demographic rates of white-tailed ptarmigan as they do appear to play a small role in annual variation in the rates we measured. Although the Mt. Evans populations appears to be resilient to annual variation in winter weather experienced in this study, the enormous variability in topography and conditions in alpine regions will probably lead to differences in how disparate populations respond to this variation. Long-term data from the Mt. Evans white-tailed ptarmigan population provided us with annual demographic estimates of survival, population change, and recruitment. Based on these estimates we conclude the following major points: (1) the Mt. Evans population did not dramatically decline or increase in size over the 43 years studied, (2) winter weather did not appear

to impact male annual survival, but winter weather did have a small effect on females which might be due to differences in dispersal or wintering strategies between sexes, and (3) winter weather explained a small amount of annual variation in population growth and recruitment. The Mt. Evans population does not appear to be in any immediate danger of decline or extinction, but high uncertainty still exists in our understanding of the environmental factors responsible for high annual variability in the demographic rates measured. Finally, white-tailed ptarmigan occur in an open population system (Martin et al. 2000), and if connectivity between neighboring populations ever becomes affected, the stability of populations could very well become jeopardized.

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