

Southern White-tailed Ptarmigan Interim Monitoring Report

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COVER PHOTOS

Main Left:

Female southern white-tailed ptarmigan on a nest (S. Rocksund)

Side (top to bottom):

Female southern white-tailed ptarmigan with chick (credit S. Rocksund)

Southern white-tailed ptarmigan chick (credit G. Detweiler)

Male southern white-tailed ptarmigan molting into nuptial plumage (credit S. Conner)

Male southern white-tailed ptarmigan (credit. D. Sapena)

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TABLE OF CONTENTS

SUMMARY	1
INTRODUCTION	1
METHODS	2
Occupancy	2
Sex and Age Ratios	5
Statistical Methods	5
RESULTS	7
Occupancy	7
Weather Variables and Occupancy	11
Patterns in Detection Probability	11
Sex and Age Ratios	12
DISCUSSION	12
Occupancy	12
Sex Ratios	14
Chick Occupancy and Age Ratios	15
Other Considerations	16
Caveats	17
Implications for Conservation and Management	18
FUTURE AND ONGOING EFFORTS	18
ACKNOWLEDGMENTS	19
LITERATURE CITED	19

LIST OF FIGURES

Figure 1. Southern white-tailed ptarmigan summer and fall predicted range model with plot locations sampled for occupancy surveys in 2011, 2021, and 2022.	4
Figure 2. Breeding season (May-July) minimum temperatures on plots surveyed for southern white-tailed ptarmigan occupancy in 2011, 2021, and 2022.	6
Figure 3. Breeding season (May-July) maximum temperatures on plots surveyed for southern white-tailed ptarmigan occupancy in 2011, 2021, and 2022.	6
Figure 4. Winter season (January-April) minimum temperatures on plots surveyed for southern white-tailed ptarmigan occupancy in 2011, 2021, and 2022.	7
Figure 5. Winter season (January-April) maximum temperatures on plots surveyed for southern white-tailed ptarmigan occupancy in 2011, 2021, and 2022.	7
Figure 6. Breeding season (May-July) precipitation on plots surveyed for southern white-tailed ptarmigan in 2011, 2021, and 2022.	7
Figure 7. Winter season (January-April) precipitation on plots surveyed for southern white-tailed ptarmigan in 2011, 2021, and 2022.	7
Figure 8. Results of a posteriori analysis examining the effects of minimum temperature during the breeding season on female and chick southern white-tailed ptarmigan occupancy at the plot-level in 2011, 2021, and 2022. Monthly temperature variables were averages of daily temperatures from May-July.	12

LIST OF TABLES

Table 1. Models fit for plot-level occupancy analysis for all ptarmigan combined. $\Delta AICc$ is the difference between the referenced model and the low-AICc model, w_i is the model weight, and k is the number of parameters in the model.	8
Table 2. Estimates from the logit and sin scales for the top two models of the plot-level analysis for all ptarmigan combined.	8
Table 3. Models fit for occupancy at the quadrat-level for all ptarmigan combined. $\Delta AICc$ is the difference between the referenced model and the low-AICc model, w_i is the model weight, and k is the number of parameters in the model.	9
Table 4. Estimates from the logit and sin scales for the top three models of the quadrat-level analysis for all ptarmigan.	11
Table 5. Models fit for occupancy for the plot- and quadrat-level for males, females, and chicks. $\Delta AICc$ is the difference between the referenced model and the low-AICc model and k is the number of parameters in the model. Female plot results are not included as models did not provide meaningful estimates.	10
Table 6. Quadrat-level occupancy rates for chicks-only, with lower (LCI) and upper (UCI) confidence intervals, for each year and strata.	11

SUMMARY

We investigated occupancy rates for the southern white-tailed ptarmigan (*Lagopus leucura altipetens*) in 2011, 2021, and 2022 in northern, central, and southern Colorado. Estimates of occupancy for males increased from 2011–2022. Conversely, female and chick occupancy declined from 2011 to 2021. Female occupancy rates were not statistically different from 2021 to 2022. Chick occupancy almost doubled from 2021 to 2022, however, it did not reach the 2011 occupancy values. Chick occupancy declined the most in the southern portion of the state, San Juan Mountains, and remained low in 2022. We also estimated sex and age class ratios and found similar patterns with male to female adult sex ratios becoming more skewed in favor of males from 2011–2022. Like chick occupancy, the ratio of chicks per hen declined dramatically from 2011–2021 and then increased in 2022, but not to original values recorded in 2011.

A posteriori analysis of weather variables for female-only and chick-only analyses found that both female and chick occupancy decreased as minimum temperatures in the breeding season increased. Male occupancy appeared to be unaffected by weather conditions. Lower female occupancy associated with increased minimum breeding temperatures may be due to reproductive costs associated with uniparental care. In this species, the female is solely responsible for incubating and raising broods, and thus may encounter physiological challenges such as hyperthermia, reduced body condition, and dehydration with increases in temperature. Females may also experience intensified exposure to predation in an attempt to find cooler microclimates for self-maintenance. An increase in the distortion of adult sex ratios in a monogamous species reliant on adult female survival to maintain viable populations, may indicate potential negative effects to the population.

Low chick occupancy and number of chicks per hen measured across the state in 2021 is concerning. Demographic rescue is thought to be important in maintaining population viability for the southern white-tailed ptarmigan, thus low reproductive output could affect emigration (i.e., dispersal) from source to sink populations. The area of most concern was the southern population where chick occupancy remained depressed even in 2022. The lower number of chicks counted and estimates of occupancy may be a result of fewer females nesting during an abnormally hot, dry breeding season and lower nest success for females that did nest. During brood rearing, the lack of summer moisture and warmer

conditions may have caused the desiccation of vegetation affecting foraging opportunities. Loss of persistent snowfields caused by higher temperatures could have resulted in chicks and hens traveling greater distances to find cool microclimates and mesic vegetation potentially exposing them to increased predation rates.

Our surveys also documented additional threats of potential concern for southern white-tailed ptarmigan, including an increase in human recreation and numerous large wildfires in surrounding forested areas that produced heavy smoke at high elevations. Because of the accelerated changes apparent in the alpine, it is imperative to continue to monitor the southern white-tailed ptarmigan population and incorporate conservation measures to reduce threats, especially for females, to help preserve this alpine dependent species.

INTRODUCTION

Avian species that inhabit high elevation mountainous habitats have adapted to survive within a wide range of demanding environmental conditions including extended periods of freezing temperatures, abundant snowfall, high winds, intense solar radiation, low partial pressure O₂, and short growing seasons (Martin 2014). Because of this, alpine avian specialists have developed physiological, morphological, and behavioral adaptations to improve their ability to survive and thrive in these extreme environments (Chamberlain et al. 2023). Unfortunately, temperatures are increasing at high elevations (Grimm et al. 2013), and the cold-adapted strategies of alpine obligates may prove to be a detriment in a warming world (Flousek et al. 2015). Overall, it has been thought that climate change will have a greater negative impact on birds inhabiting colder, high elevation habitats than species associated with warmer, lower elevation sites (Chamberlain et al. 2023).

One species that has been identified as a species of concern that occupies high elevation alpine habitats is the white-tailed ptarmigan (WTPT; *Lagopus leucura*). This species lives year-round in the alpine and subalpine life zones and has developed numerous adaptive strategies for this harsh environment (Martin et al. 2020). First, breeding in the alpine means WTPT have less time to produce and raise a clutch of chicks, and the timing for which they can breed varies from year-to-year based on amount and depth of snow cover on breeding territories (Clarke and Johnson 1992, Martin et al. 2009). Because of this, evolution has led to plasticity in breeding phenology and life history traits that favor adult survival, especially female survival, over high reproductive output

(Morton 1976, 2002, Martin and Wiebe 2004, Sandercock et al. 2005a, 2005b, Bears et al. 2009, Martin et al. 2009, Lu et al. 2010, Martin 2014, Wann 2017). Second, they use a strategy of molting feathers across three discrete molts (Pyle 2007) enabling them to blend into their environment during all seasons, rendering them almost invisible to predators. Because of this camouflage, WTPT spend a majority of the time walking rather than flying and seem almost tame as they forage on alpine plants near rocky slopes. The WTPT's cryptic plumage and sedentary behavior allows them to conserve energy so they can tolerate extreme cold in winter, avoid overheating in summer, and successfully occupy hypoxic high elevation alpine habitats (Martin et al. 2020). Finally, WTPT survive the long winter by burrowing under the snow to stay warm, subsisting on willow buds and twigs, and growing feathers on their tarsi and feet for insulation and to function as snowshoes (Hoffman 2006, Martin et al. 2020).

The WTPT was petitioned to be listed as threatened under the Endangered Species Act (ESA) in 2010. The U.S. Fish and Wildlife Service (USFWS) determined on 5 June 2012 that substantial biological information existed to warrant a 12-month status review for two of the five recognized subspecies of WTPT: the Mt. Rainier WTPT (*L. l. rainierensis*) that occurs in Washington State and the southern WTPT (*L. l. altipetens*) which occurs primarily in Colorado with a small, peripheral population in New Mexico (Langin et al. 2018, USFWS 2012). Concern for the southern WTPT was based on predicted climate change that could directly affect adult survival by impacting the health and distribution of alpine and subalpine willow (*Salix spp.*) that are important forage for the species; changing temperatures in winter that could impact snow quality limiting roost site availability; alterations in summer monsoonal moisture patterns potentially impacting vegetation availability; increasing mean daily temperatures at breeding areas affecting nest success and chick survival; and increases in the stochasticity and severity of spring storms that could affect vulnerable chicks and nesting hens (Martin 2001, Hoffman 2006, Center for Biological Diversity 2010, Seglund et al. 2018). The southern WTPT has been identified as a Species of Greatest Conservation need in Colorado's State Wildlife Action Plan (SWAP; 2015). The SWAP cites domestic sheep grazing in the alpine, increases in recreation, and climate change as the main threats to the species.

In response to the 2010 petition, Colorado Parks and Wildlife (CPW) initiated a seven-year research project to help inform the USFWS 12-month status review (Seglund

et al. 2018). This project incorporated a number of metrics to determine distribution, abundance, seasonal survival, site fidelity, reproductive success, and genetic structure. CPW's research found that the southern WTPT was a resilient species occupying all suitable habitats in the alpine, with stable populations in Colorado that contained high genetic diversity, and low predicted extinction risk into the future. Based largely on the results of CPW's findings, the USFWS determined by means of a thorough Species Status Assessment, that the southern WTPT was not warranted for listing in 2020 (USFWS 2020). Conversely, the Mt. Rainier WTPT was proposed for listing as threatened due to changing habitat conditions caused by climate change, specifically rising temperatures, that were modeled to have direct negative impacts on birds and populations (USFWS 2021).

Though southern WTPT populations appeared to be healthy, CPW has continued to monitor the statewide population to assess changes in distribution and to evaluate demographic parameters as environmental changes become more pronounced and recreation in the alpine increases. To develop a baseline distribution and inventory of the species, we first conducted statewide occupancy surveys (Mackenzie and Royle 2005) in 2011 with subsequent surveys completed in 2021 and 2022. We evaluated changes in male and female occupancy across the state and calculated adult sex ratios based on birds encountered during surveys. Understanding adult sex ratios with regards to species mating systems is vital for understanding potential impacts to population growth, extinction, and demography (Lee et al. 2011). We also estimated occupancy rates of chicks, and the ratio of the number of chicks to hens across all survey years. We included weather variables as covariates to assess potential impacts of climate change on occupancy rates for both sexes and chicks. Using this integrated monitoring approach, we improved our understanding of the status of the southern WTPT population in Colorado. Understanding population trends and distributional changes for this species are critical for conservation and management.

METHODS

Occupancy

To obtain a baseline distribution, the primary parameter of interest for our monitoring program was the proportion of occupied plots and quadrats by males, females, and chicks, within the modeled predicted summer and fall range of the southern WTPT. The predicted summer and fall range model was developed using the following criteria: all areas > 3292 m in elevation with Colorado GAP vegetation types that

included Mixed Tundra, Meadow Tundra, Prostrate Shrub Tundra, Bare Ground Tundra, Exposed Rock, Shrub Dominated Wetland/Riparian, and Graminoid/Forb Dominated Wetland. A random sample of 60 plots for sampling statewide was derived from overlaying a grid of 5.3 x 4.6 km plots across the predicted range model. Due to the extreme topography and heterogeneous habitats in the alpine, only plots that contained a minimum of 50% suitable habitat within their boundaries were selected for sampling (Figure 1). The sampling frame was divided geographically into three strata with 20 plots per stratum; sites north of Interstate 70 (north), sites between Interstate 70 and Highway 50 (central), and sites south of Highway 50 (south).

In 2021 and 2022, we surveyed the same plots selected in 2011 with the exception of seven plots that were surveyed in Rocky Mountain National Park in 2011, but not surveyed in 2021 nor 2022 (Seglund 2011; Figure 1). In 2022, we added four survey plots (selection criteria was the same as for the original 60 plots) not surveyed in 2011 or 2021; two in the La Plata Mountains, one in the Mount Zirkel Wilderness, and one in the southern San Juan Mountains, to cover all potential mountain ranges where southern WTPT may occur (Figure 1). The addition of these peripheral sites will be important for future monitoring as they may be the first areas where populations decline or become extirpated because of limited connectivity to other suitable habitats.

In 2021 and 2022, the larger plots were subdivided into four quadrats (2.65 km x 2.3 km). The reason for using quadrats in addition to our original plot-level sampling was because almost all plots were occupied in 2011, indicating our plot size was too large. Therefore, smaller quadrats may be more reflective of southern WTPT use of the landscape while at the same time allowing for comparisons in occupancy rates from 2011–2022. In 2021 and 2022, surveys were conducted in two to three quadrats of each original plot to evaluate occupancy at the plot-level and the quadrat-level. Quadrats that had positive detections of southern WTPT in 2011 were all revisited, with an additional quadrat sampled that was not previously surveyed or where southern WTPT were not detected in 2011. We determined which quadrats were visited in 2011 based on survey track locations collected on GPS units by surveyors and by UTM locations of where southern WTPT were detected.

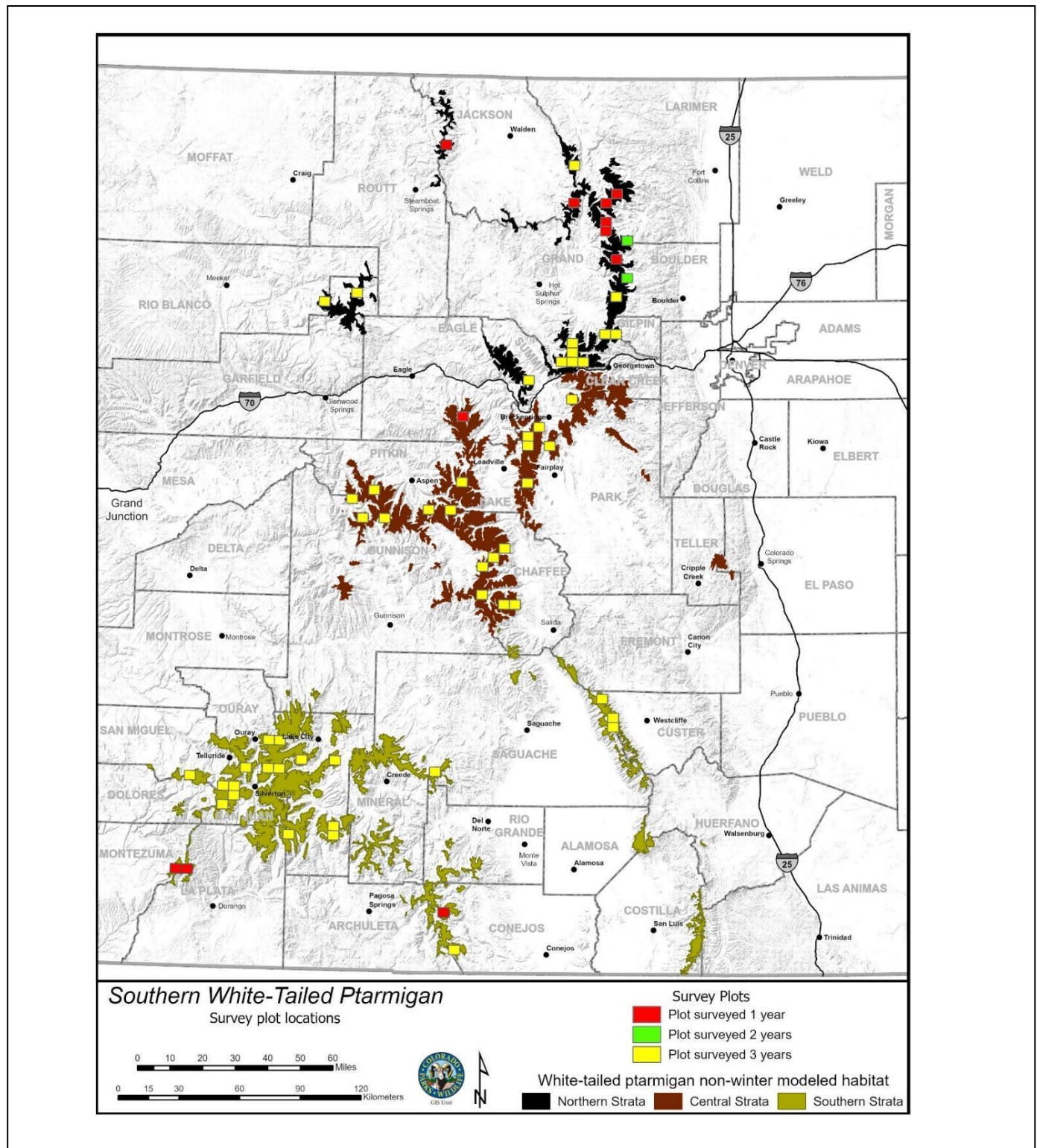
Two surveys were completed at each plot and quadrat on different dates with different surveyors to estimate the detection probability for southern WTPT.

Each survey effort was conducted by a pair of surveyors to locate birds. Surveyors consisted of trained technicians that were hired solely to conduct surveys for southern WTPT and CPW Area Biologists that were trained to do occupancy surveys, but also had many other job duties and thus completed only several surveys throughout a season. Surveyors walked approximately 100 m apart while surveying in suitable habitat. Suitable habitat was considered alpine areas above treeline (Hoffman 2006). The most important vegetation features used by southern WTPT are presence of willows, boulder, talus and scree fields, moist alpine meadows, dry alpine tundra, and snow fields (Choate 1963, Braun and Rogers 1971, Hoffman 2006). Willows are important because they serve as the primary food source from late fall to early summer. Rocky areas and dry alpine tundra lying near snow fields and other moist areas become the most commonly used sites from mid-summer to early fall for brood rearing. Adult males and unsuccessful breeding females use high rocky windswept ridges, steep slopes, and sparsely vegetated chutes in late summer and fall.

Surveys began 30 minutes before sunrise with no ending time designated. A survey of a quadrat was considered complete once all suitable habitat within a quadrat had been surveyed or a positive detection of a southern WTPT occurred. Because surveyors were required to identify sex and age of birds, a positive detection of a southern WTPT was defined as a visual of a bird. Positive detections did not include vocalizations, scat, or feathers found on the plot or quadrat. Surveys within a plot or quadrat could occur over a 2-day period if the survey was interrupted by weather. Surveys were conducted in most weather conditions with the exception of thunderstorms, heavy rain, or hail storms. To control for survey effort, observers could not spend more than three hours surveying a quadrat or 12-hours surveying a plot. The average time to survey a quadrat by the two person crews was 2.07 hours across all years. The maximum time spent on a plot to locate birds was 9.48 hours and the minimum time was 10 minutes.

Broadcast calls of male territorial vocalizations and young chicks begging were used to increase detection rates for this cryptic species (Braun and Rogers 1971). Broadcast calls were played on a FoxPro NX3 unit (FoxPro Inc. Lewiston, PA). Surveyors broadcast the calls from a high point in all directions to ensure birds could adequately hear the recording, especially in windy conditions. Surveyors waited approximately 20-30 seconds for a response. If no response occurred after two male broadcast calls, the chick begging call was played for about 10 seconds. If no response occurred with either

Figure 1. Southern white-tailed ptarmigan summer and fall predicted range model with plot locations sampled for occupancy surveys in 2011, 2021, and 2022.



call, surveyors would continue with their search. Surveyors walked slowly through suitable habitat looking and listening for birds, periodically playing broadcast calls to elicit responses. Surveyors avoided excess disturbance to birds by limiting the number of broadcast calls they used. All surveyors watched for potential predators in the area and immediately stopped broadcast calls if any type of predator was detected (this included ravens – *Corvus corax*). Surveys continued once the predator left the area.

When a southern WTPT was detected, a UTM coordinate was collected where each bird was first seen, not where the bird flew to when responding to a broadcast call. Information on time to detection, surrounding vegetation, presence of rocks, talus, and snowfields within 10 m of detections were recorded as well as evidence of human disturbance within 100 m. Human disturbances recorded included presence of hiking trails, dirt and paved roads, mining operations, or other human recreational activities such as camping.

Sex and age ratios

If a bird responded to a broadcast call, the surveyor tried to obtain a visual of the southern WTPT. Once a visual was obtained, the area was searched to get a full count of all birds present and to identify sex and age classes (chicks/adults). If a male was detected during the breeding season, he was followed to determine if he was paired with a female. Male WTPT are territorial and will respond to broadcast calls with their own territorial call. Sometimes they will call while flying and/or running in the direction of the broadcast call, and at other times they may call but remain at their location. Males that are paired with a female often will not fly far from their mate and if they do, they will immediately return to her location. If a male bird flew into the call and immediately returned to his original location, he was observed from a safe distance to locate his female. In contrast, single unmated males will often fly into the broadcast call and not return to their original location. For any territorial male detected, the surveyor hiked to where the bird was heard/seen and searched the area to locate a female. Normally beginning in mid-July, males and unsuccessful breeding females will start to flock up. Many times only one bird will respond to a broadcast call even though there are many more at a location. Surveyors adequately searched an area where a bird was detected to try and ensure all adults were counted and recorded.

Broadcast calls of chicks assisted with the detection of females with chicks or females with recently failed reproductive attempts (Braun and Rogers 1971). Females

will respond to chick distress calls by clucking, making themselves visible by coming into the open, jumping onto a boulder, or by running or flying to the call source. If surveyors detected a female that responded to a chick begging call, they observed the female from a distance to get a count of chicks and to age them. Surveyors waited until the brood and female resumed foraging activities to obtain a count. It was imperative that surveyors waited sufficient time to see all chicks get up and move off as sometimes chicks can be quite a distance from the hen and very well camouflaged. If the brood was accidentally flushed, counts included chicks flying or running.

Statistical Methods

Occupancy

We used the occupancy module in Program MARK (White and Burnham 1999) to estimate the probability that plots and quadrats were occupied by southern WTPT in 2011, 2021, and 2022. We hypothesized that occupancy might change over year, over the three strata, and that technicians trained specifically to find southern WTPT would have a higher detection probability than CPW Area Biologists occasionally helping with surveys. Mixed groups of surveyors that included both a technician and a CPW Area Biologist were considered as a technician for analysis. We also hypothesized that detection probability may change by year. The global model contained a strata*year interaction term for occupancy and a technician type*year term for detection.

We fit all subsets of the global model (total of 25 models) and used Akaike's Information Criterion (AIC_c) adjusted for small sample size (Akaike 1973, Hurvich and Tsai 1989) to find the model that best explained the data. Because some values of occupancy were near 1.00, we used the sin link to obtain better estimates near 1.00. However, the use of the sin link for design matrices with more than one variable informing occupancy can lead to unrealistic results, so we used this technique only when a single variable informed occupancy. If the model had more than a single variable, we used a logit link. The link used did not affect the AIC_c value.

We ran separate analyses for plots and quadrats. We collected data on 59 plots in 2011 (n= 20 north, 19 central, 20 south), 51 plots in 2021 (n=12 north, 19 central, 20 south), and 57 plots in 2022 (n=14 north, 20 central, 23 south). Within plots we collected data on 97 quadrats in 2011 (n=31 north, 31 central, 35 south), 98 quadrats in 2021 (n=23 north, 39 central, 36 south), and 115 quadrats in 2022 (n=28 north, 44 central, 43 south). We ran plot-level and quadrat-level analyses for all southern WTPT detected, males-only, females-only, and chicks-only. We

used the low AIC_c-model detection from the all ptarmigan analysis because it contained the most data and thus, we surmised the best fit for the covariates in detection. For occupancy in the age-based and sex-based analyses, we investigated whether occupancy varied by strata and year, and fit all subsets (a total of five models each for the males-only, females-only, and chicks-only analyses). For some analyses with occupancy estimates 0.989 or greater, program MARK returned unrealistically large confidence intervals. We used the programming environment R (R Core Team 2023) to generate one million samples from a beta distribution based upon the point estimate and standard error estimated by program MARK; the 2.5% and 97.5% quantiles of these distributions were then used as corrected CIs.

A posteriori analysis of weather variables on occupancy

We ran an *a posteriori* analysis examining the effects of precipitation and temperature variables on occupancy. We included weather variables from PRISM 800 m gridded climate data (<https://prism.oregonstate.edu/>). We included three variables; minimum temperature, maximum temperature, and precipitation for months January through April (winter period; wtmin, wtmax, and wprecip) and May through July (breeding period; btmin, btmax, and bprecip) (Figures 2-7). Monthly temperature variables were averages of daily temperatures, and monthly precipitation was the total precipitation summed within the respective winter and breeding periods.

Temperature values were correlated so we only included one temperature variable in each model. We began with an additive precipitation + temperature model for occupancy, then fit each variable separately and compared with the best model from the *a priori* analysis. For all models we used the technician type term for detection as informed by the *a priori* analysis (see below). We repeated this for all ptarmigan, males-only, females-only, and chicks-only at the plot-level. We did not assess weather variables at the quadrat-level because data were only available at the resolution of the plot.

Sex and age ratios

To determine sex and age ratios, we treated quadrats for southern WTPT in the same manner that has been developed by CPW for sex and age surveys for mule deer (*Odocoileus hemionus*). The Horwitz–Thompson (1952) estimator for a proportion (r_{HT}) used is based on equations from Bowden et al. (1984). As an example, we estimated the proportion of males (m) to females (f) in each quadrat (i) with each proportion weighted (w) by the number of animals observed in that quadrat as:

$$\hat{r}_{HT} = \sum_{i=1}^N \left[w_i \frac{m_i}{m_i + f_i} \right] = \sum_{i=1}^N \left[\frac{m_i + f_i}{\sum_{k=1}^N (m_k + f_k)} \frac{m_i}{m_i + f_i} \right] = \frac{\sum_{i=1}^N m_i}{\sum_{k=1}^N (m_k + f_k)} = r$$

The variance of this estimate is:

$$\hat{\text{var}}[\hat{r}_{HT}] = \left[\sum_{i=1}^n \frac{(1 - \pi_i)}{\pi_i^2} r_i^2 + \sum_{i=1}^n \sum_{\substack{j=1 \\ j \neq i}}^n \frac{(\pi_{ij} - \pi_i \pi_j)}{\pi_i \pi_j \pi_{ij}} \frac{r_i r_j}{\pi_{ij}} \right]$$

where the $\pi_i \propto 1/w_i$.

Results are presented in the format of number of males per 100 females and number of chicks per 100 females. The Delta method (Doob 1935) was used to convert the variance of the proportion to variance of females per 100 males and chicks per 100 females.

Figure 2. Breeding season (May–July) minimum temperatures on plots surveyed for southern white-tailed ptarmigan occupancy in 2011, 2021, and 2022.

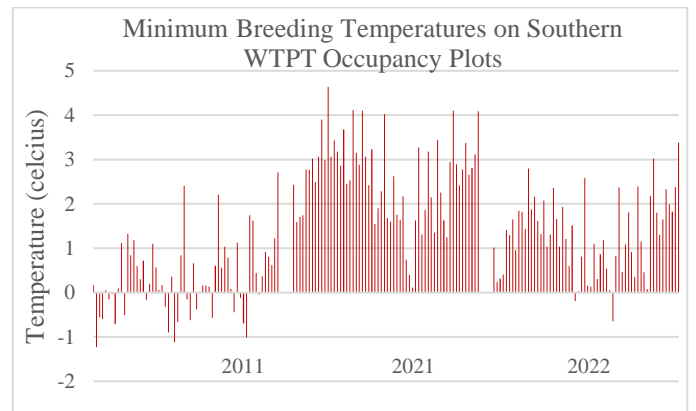


Figure 3. Breeding season (May–July) maximum temperatures on plots surveyed for southern white-tailed ptarmigan occupancy in 2011, 2021, and 2022.

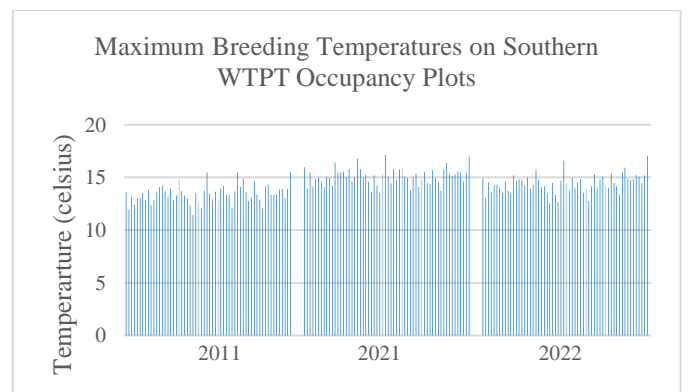


Figure 4. Winter season (January-April) minimum temperatures on plots surveyed for southern white-tailed ptarmigan occupancy in 2011, 2021, and 2022.

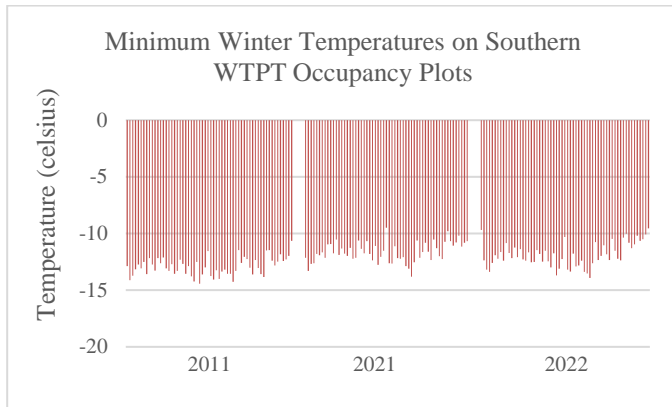


Figure 5. Winter season (January-April) maximum temperatures on plots surveyed for southern white-tailed ptarmigan occupancy in 2011, 2021, and 2022.

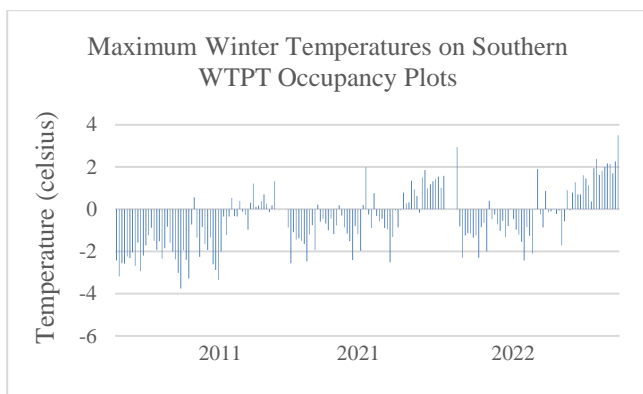


Figure 6. Breeding season (May-July) precipitation on plots surveyed for southern white-tailed ptarmigan in 2011, 2021, and 2022.

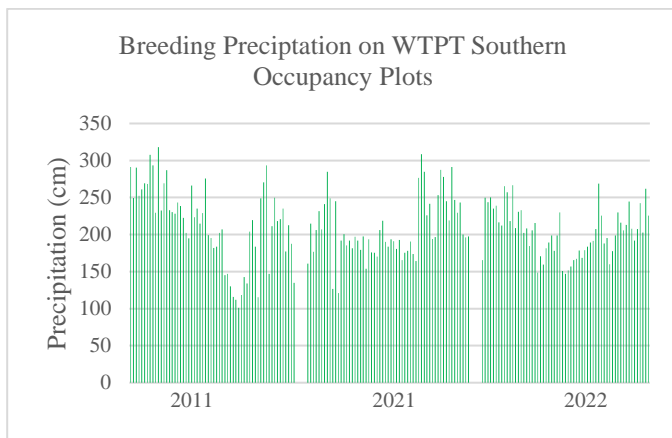
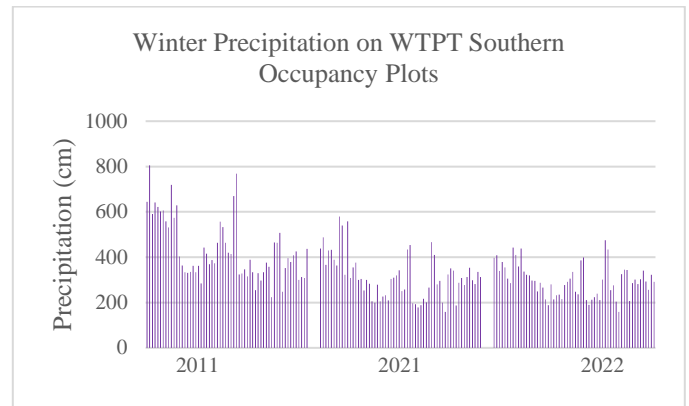


Figure 7. Winter season (January-April) precipitation on plots surveyed for southern white-tailed ptarmigan in 2011, 2021, and 2022.



RESULTS

Occupancy

All ptarmigan

Models with the technician*year interaction would not converge to estimates for either the plot-level or quadrat-level analyses using all ptarmigan. In the plot-level analysis, of the 20 models that converged, the low-AIC_c model included a technician effect on detection probability and no effects of year or stratum on occupancy, and no other models were within 2.00 AIC_c units of the top model (Table 1). Overall occupancy was estimated as 0.985 (95% Confidence Interval (CI): 0.903–0.998). Technicians had a higher detection probability than CPW Area Biologists for both models (Table 2). Occupancy estimates from the top model for detection probability were 0.607 (95% CI: 0.450–0.745) for groups with only CPW Area Biologists, and 0.945 (95% CI: 0.901–0.970) for groups that contained technicians. No other models were within 2.00 AIC_c units of the top model (Table 1). The logit and sin scale estimates are presented in Table 2.

For the quadrat-level analysis, three models were competitive (Table 3), all with an effect of technician on detection probability. The low-AIC_c model contained an effect of year on occupancy. The 2nd-ranked model was 0.39 AIC_c units higher than the best ranked model and contained no effects of year or stratum on occupancy (i.e., pooled effects across all factors). The 3rd-ranked model was 0.97 AIC_c units higher than the low-AIC_c model and contained an effect of stratum on occupancy. All other models were > 2.00 AIC_c units higher than the best-ranked model.

Table 1. Models fit for plot-level occupancy analysis for all ptarmigan combined. ΔAIC_c is the difference between the referenced model and the low-AICc model, w_i is the model weight, and k is the number of parameters in the model.

Model	ΔAIC_c	w_i	k
Detection (technician) Occupancy (.)	0.00	0.49	3
Detection (technician) Occupancy (strata)	2.01	0.18	5
Detection (technician + year) Occupancy (.)	2.88	0.12	5
Detection (technician) Occupancy (year)	3.59	0.08	7
Detection (technician) Occupancy (strata + year)	3.79	0.07	5
Detection (technician + year) Occupancy (strata)	5.06	0.03	7
Detection (technician + year) Occupancy (year)	6.99	0.01	7
Detection (technician + year) Occupancy (strata + year)	7.65	0.01	9
Detection (technician) Occupancy (strata * year)	10.61	0.00	11
Detection (technician + year) Occupancy (strata * year)	14.85	0.00	13
Detection (year) Occupancy (.)	24.91	0.00	4
Detection (year) Occupancy (strata)	26.81	0.00	6
Detection (.) Occupancy (.)	28.07	0.00	2
Detection (year) Occupancy (year)	28.61	0.00	6
Detection (year) Occupancy (strata + year)	28.97	0.00	8
Detection (.) Occupancy (strata)	30.35	0.00	4
Detection (.) Occupancy (strata + year)	31.72	0.00	6
Detection (.) Occupancy (year)	31.92	0.00	4
Detection (year) Occupancy (strata * year)	37.14	0.00	12
Detection (.) Occupancy (strata * year)	39.39	0.00	10

Table 2. Estimates from the logit and sin scales for the top two models of the plot-level analysis for all ptarmigan combined.

Parameter	Link	Estimate	SE	95%LCL	95% UCL
Detection intercept	logit	0.44	0.32	-0.20	1.07
Detection technician	logit	2.40	0.44	1.54	3.27
Occupancy intercept	sin	1.32	0.12	1.09	1.56

Table 3. Models fit for occupancy at the quadrat-level for all ptarmigan combined. ΔAIC_c is the difference between the referenced model and the low- AIC_c model, w_i is the model weight, and k is the number of parameters in the model.

Model	ΔAIC_c	w_i	k
Detection (technician) Occupancy (year)	0.00	0.28	5
Detection (technician) Occupancy (.)	0.39	0.23	3
Detection (technician) Occupancy (strata)	0.97	0.17	5
Detection (technician + year) Occupancy (strata)	2.23	0.09	7
Detection (technician + year) Occupancy (year)	2.68	0.07	7
Detection (technician + year) Occupancy (.)	2.74	0.07	5
Detection (technician) Occupancy (strata + year)	3.39	0.05	7
Detection (technician + year) Occupancy (strata + year)	6.09	0.01	9
Detection (technician) Occupancy (strata * year)	7.04	0.01	11
Detection (technician + year) Occupancy (strata * year)	9.33	0.00	13
Detection (year) Occupancy (strata)	24.97	0.00	6
Detection (.) Occupancy (year)	26.35	0.00	4
Detection (year) Occupancy (.)	26.69	0.00	4
Detection (.) Occupancy (strata + year)	28.45	0.00	6
Detection (year) Occupancy (strata + year)	28.80	0.00	8
Detection (year) Occupancy (year)	28.84	0.00	6
Detection (.) Occupancy (.)	30.05	0.00	2
Detection (.) Occupancy (strata)	30.30	0.00	4
Detection (.) Occupancy (strata * year)	31.53	0.00	10
Detection (year) Occupancy (strata * year)	33.14	0.00	12

Much like the plot-level analysis, technicians had a higher detection probability than CPW Area Biologists in all of the top models. In the best-ranked model, the quadrat-level occupancy rate was 0.893 (95% CI: 0.759–0.956) in 2011, 1.00 (95% CI: undefined) in 2021, and 0.970 (95% CI: 0.862–0.994) in 2022. Quadrat-level detection probability was 0.504 (95% CI: 0.368–0.639) for groups with only CPW Area Biologists, and 0.859 (95% CI: 0.815–0.895) for groups that contained technicians. For the top three models based on the quadrat-level analysis, we present logit and sin scale estimates in Table 4.

In the 2nd-ranked model, quadrat-level occupancy rates were 0.962 (95% CI: 0.883–0.988) pooled across all years and strata. The 3rd-ranked model produced occupancy estimates of 1.00 (95% CI: undefined) in the north, 0.988 (95% CI: 0.379–1.00) in the central, and 0.922 (95% CI: 0.811–0.970) in the south.

Males

Of the five models we ran in the plot-level analysis to assess male occupancy, the low- AIC_c model contained an effect of year on occupancy. No other models were within 2.00 AIC_c units of the top model (Table 5). Occupancy estimates from the top model were 0.701

(95% CI: 0.555–0.816) in 2011, 1.00 (95% CI: undefined) in 2021, and 0.996 (95% CI: 0.953–0.998) in 2022.

For the quadrat-level male occupancy analysis, the low- AIC_c model contained an effect of year on occupancy, and like the plot-level analysis, no other models were within 2.00 AIC_c units of the top model (Table 5). In the best-ranked model, quadrat-level occupancy estimates were 0.600 (95% CI: 0.472–0.717) in 2011, 1.00 (95% CI: undefined) in 2021, and 0.980 (95% CI: 0.738–0.999) in 2022.

Females

The plot-level female occupancy analysis failed to produce meaningful estimates. The real scale estimates for the null model were 1.00 for occupancy across all years and strata indicating a lack of convergence for this data set.

The quadrat-level female occupancy analysis did produce meaningful results with two models being competitive (Table 5). The low- AIC_c model contained an effect of year on occupancy. The quadrat-level occupancy estimates were 0.918 (95% CI: 0.349–0.996) in 2011, 0.688 (95% CI: 0.445–0.858) in 2021, and 0.714 (95% CI: 0.509–0.857) in 2022. The 2nd-ranked model was 0.50

Table 4. Estimates from the logit and sin scales for the top three models of the quadrat-level analysis for all ptarmigan.

ΔAIC_c	Parameter	Link	Estimate	SE	95%LCL	95% UCL
0.00	Detection intercept	logit	0.02	0.28	-0.54	0.57
	Detection technician	logit	1.80	0.32	1.17	2.42
	Occupancy intercept	sin	0.90	0.15	0.60	1.20
	Occupancy 2021	sin	0.67	0.64	-0.58	1.92
	Occupancy 2022	sin	0.32	0.20	-0.07	0.72
0.39	Detection intercept	logit	-0.04	0.28	-0.60	0.52
	Detection technician	logit	1.83	0.31	1.21	2.44
	Occupancy intercept	sin	1.18	0.12	0.95	1.41
0.97	Detection intercept	logit	-0.06	0.27	-0.60	0.47
	Detection technician	logit	1.82	0.31	1.21	2.43
	Occupancy intercept	sin	1.57	0.70	0.20	2.94
	Occupancy middle	sin	-0.22	0.75	-1.69	1.26
	Occupancy south	sin	-0.57	0.71	-1.97	0.83

Table 5. Models fit for occupancy for the plot- and quadrat-level for males, females, and chicks. ΔAIC_c is the difference between the referenced model and the low-AICc model and k is the number of parameters in the model. Female plot results are not included as models did not provide meaningful estimates.

Analysis	Model	ΔAIC_c	k
Male Plot	Detection (technician) Occupancy (year)	0.00	5
	Detection (technician) Occupancy (strata + year)	2.38	7
	Detection (technician) Occupancy (strata * year)	10.25	11
	Detection (technician) Occupancy (.)	19.91	3
	Detection (technician) Occupancy (strata)	23.48	5
Male Quadrat	Detection (technician) Occupancy (year)	0.00	5
	Detection (technician) Occupancy (strata + year)	2.75	7
	Detection (technician) Occupancy (strata * year)	7.04	11
	Detection (technician) Occupancy (.)	36.82	3
	Detection (technician) Occupancy (strata)	39.23	5
Female Quadrat	Detection (technician) Occupancy (year)	0.00	5
	Detection (technician) Occupancy (.)	0.50	3
	Detection (technician) Occupancy (strata + year)	2.43	7
	Detection (technician) Occupancy (strata)	2.70	5
	Detection (technician) Occupancy (strata * year)	9.52	11
Chick Plot	Detection (technician) Occupancy (year)	0.00	5
	Detection (technician) Occupancy (strata + year)	0.74	7
	Detection (technician) Occupancy (strata * year)	4.52	11
	Detection (technician) Occupancy (.)	8.12	3
	Detection (technician) Occupancy (strata)	9.22	5
Chick Quadrat	Detection (technician) Occupancy (strata + year)	0.00	7
	Detection (technician) Occupancy (year)	1.53	5
	Detection (technician) Occupancy (strata * year)	4.57	11
	Detection (technician) Occupancy (.)	13.75	3
	Detection (technician) Occupancy (strata)	13.98	5

AIC_c units higher than the best ranked model and contained no effects on occupancy.

Chicks

The low-AIC_c model for the plot-level chick occupancy analysis contained an effect of year on occupancy (Table 5). Plot-level occupancy estimates from the top model were 1.00 (CI undefined) in 2011, 0.387 (95% CI: 0.186–0.636) in 2021, and 0.727 (95% CI: 0.407–0.912) in 2022. The 2nd-ranked model was within 2.00 AIC_c units of the top model. This model included an additive effect of strata and year on occupancy and was 0.74 AIC_c units from the top model (Table 5).

For the quadrat-level analysis, two models were competitive (Table 5). The low-AIC_c model contained an effect of year and strata on occupancy with the central stratum generally having the highest estimates followed by the north then south (Table 6). The yearly occupancy pattern was similar to females with 2011 being the highest year, followed by a decrease in 2021 and an increase in 2022 but not to 2011 levels (Table 6). The 2nd-ranked model was 1.53 AIC_c units higher than the best ranked model and contained an effect of year only on occupancy.

Table 6. Quadrat-level occupancy rates for chicks-only, with lower (LCI) and upper (UCI) confidence intervals, for each year and strata.

Year	Strata	Occupancy	LCI – UCI
2011	North	0.997	0.972 – 1.000
2021	North	0.417	0.133 – 0.769
2022	North	0.670	0.342 – 0.889
2011	Central	0.997	0.983 – 1.000
2021	Central	0.510	0.220 – 0.793
2022	Central	0.748	0.363 – 0.939
2011	South	0.989	0.887 – 1.000
2021	South	0.174	0.058 – 0.418
2022	South	0.375	0.157 – 0.658

Weather variables and occupancy

All ptarmigan

For all ptarmigan, the term wprecip² returned values for which occupancy exponentially grew with increased winter precipitation or did not decrease until levels of unrealistically high values of winter precipitation, thus we did not consider winter precipitation further. No models had a lower AIC_c than the best model from the *a priori analysis* that did not include weather variables. The nearest model contained an effect of wtmax on occupancy, but it was 0.98 AIC_c units higher and the 95%

CI for wtmax broadly overlapped 0 (logit scale estimate - 0.59, 95% CI: -1.83–0.65).

Males

For the males-only analysis, all the models with weather variables were at least ~16.5 AIC_c units higher than the best *a priori* model, thus we did not investigate them further.

Females

For the female-only analysis, the addition of weather variables as covariates resulted in models that converged, unlike the models including only strata and year. The model containing breeding temperature was the low AIC_c model for this analysis. The logit scale estimate for btmin was -2.39 (95% CI: -5.41–0.63) indicating that female occupancy decreased as btmin increased (Figure 8). The nearest model was 1.53 AIC_c units higher and included terms for btmin and bprecip with precipitation during the breeding season having a positive effect on occupancy, however, the 95% CI broadly overlapped 0 (logit scale estimate 0.03, 95% CI: -0.05–0.12).

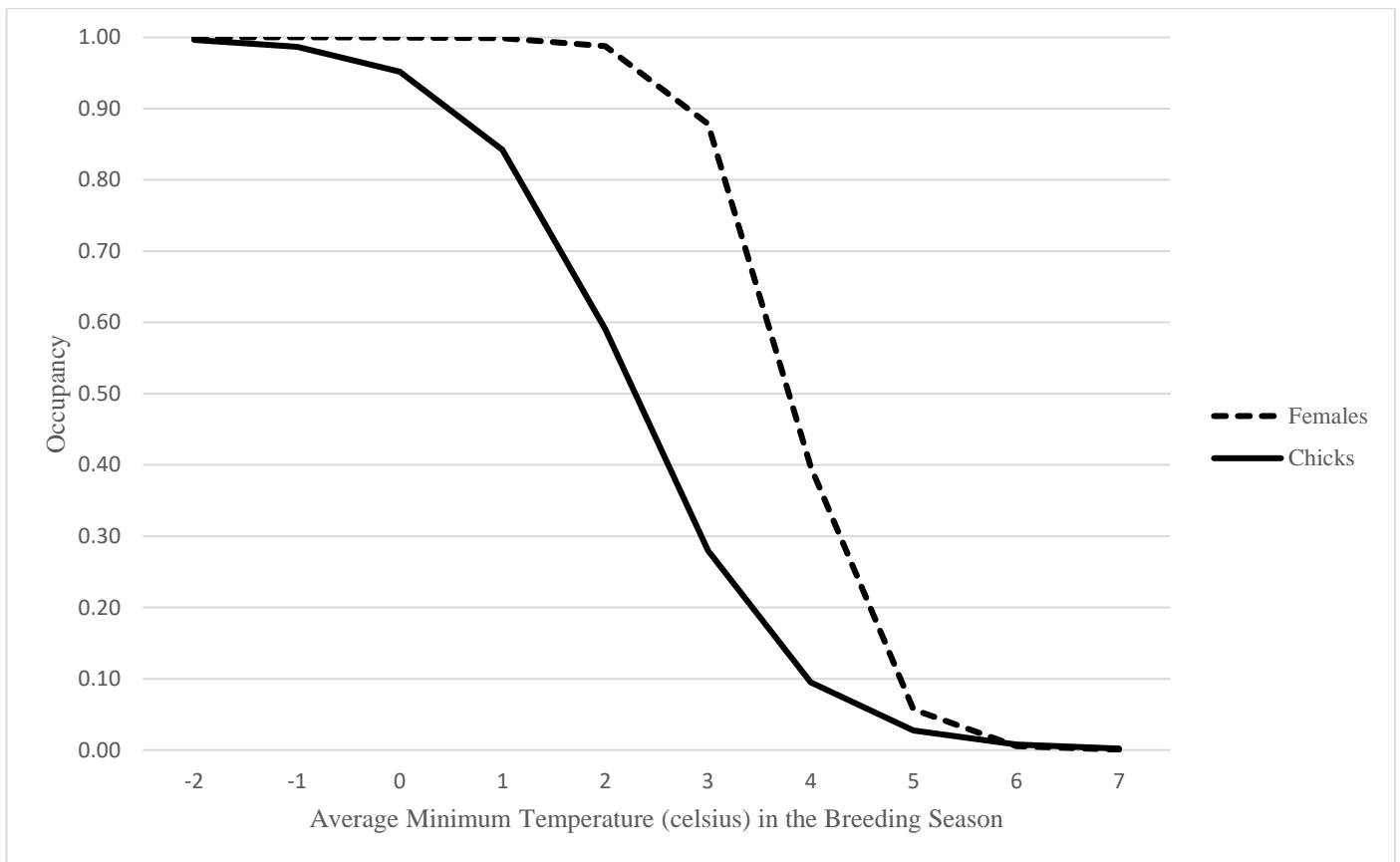
Chicks

Similar to females, the chick-only analysis suggested that btmin was the variable best explaining variation in occupancy (Figure 8). The model containing only btmin was 8.25 AIC_c units lower than the best model from the *a priori* analysis and showed that as btmin increased, occupancy by chicks decreased (logit scale estimate -1.31, 95% CI: -2.113 – -0.49). The next best model was 1.78 AIC_c units higher and additionally contained a positive effect of bprecip (logit scale estimate: 0.01, 95% CI: -0.02–0.03).

Patterns in Detection Probability

The majority of surveyors for occupancy surveys across all years were technicians rather than CPW Area Biologists and therefore, differences in detectability across sex and age classes were most pronounced for technicians. Detection probability by technicians for occupancy of males at the plot-level was 0.871 (95% CI: 0.813–0.912), for females was 0.543 (95% CI: 0.471–0.613) and for chicks was 0.392 (95% CI: 0.296–0.497). Quadrat-level detection probabilities were less than those for plots, as expected because of the smaller scale. Area CPW Biologist detection probabilities were significantly lower than technicians for males (95% CI on logit scale 1.59–2.38), or functionally equivalent for females (95% CI -0.80 – 0.64) and chicks (95% CI -0.57 – 0.93).

Figure 8. Results of a posteriori analysis examining the effects of minimum temperature during the breeding season on female and chick southern white-tailed ptarmigan occupancy at the plot-level in 2011, 2021, and 2022. Monthly temperature variables were averages of daily temperatures from May-July.



Sex and Age Ratios

We estimated sex ratios of 128.9 males per 100 females (95% CI: 83.4–199.4) in 2011, 245.9 males per 100 females (95% CI: 190.9–306.7) in 2021, and 306.3 males per 100 females (95% CI: 248.7–377.3) in 2022. We estimated age ratios of 206.6 chicks per 100 females (95% CI: 159.8–267.1) in 2011, 45.9 chicks per 100 females (95% CI: 26.1–80.7) in 2021, and 150.6 chicks per 100 females (95% CI: 106.9–212.2) in 2022.

DISCUSSION

Occupancy

The original plot size (5.3 x 4.6 km) used in 2011 was refined for the 2021–2022 surveys by dividing each plot into four equal quadrats (2.65 km x 2.3 km). Southern WTPT move only short distances in the breeding and early fall season (Seglund et al. 2018), but live in areas with complex topography. The complexity of their environment requires a larger sampling unit than one based solely on their home range size because not all areas within a given sample cell are suitable. In 2011, we also

surveyed smaller plots (200 m x 200 m) within the larger plots, but our results suggested that occupancy rates were extremely low and therefore not suitable for monitoring trends (Seglund 2011). Our current quadrat-level sampling should be more informative relative to potential changes in abundance than the plot-level analysis due to the scale being closer to the movement patterns of the species of interest (Ellis et al. 2014). However, weather variables were only measured at the plot-level, i.e., we did not measure quadrat-to-quadrat variation in weather variables due to limitations in resolution. Therefore, we recommend continued use of the same plots and quadrats we have identified and surveyed to assess occupancy and potential variables affecting changes in occupancy rates.

We think it is imperative to have a well-trained crew to conduct occupancy surveys based on the lower detection probabilities for CPW Area Biologists than technicians. Detecting southern WTPT in the field, even with the aid of broadcast calls, can be tricky with their cryptic nature. It

requires extensive experience conducting surveys to become proficient. The hiking required to access southern WTPT habitat is difficult and requires extremely fit individuals with excellent orienteering skills. The surveys are also time consuming and require extensive travel. Therefore, we recommend the use of a dedicated crew to conduct surveys to ensure results are more reliable and comparable.

All ptarmigan

Our estimates of occupancy rates for southern WTPT showed little variation among years sampled at the plot-level. The quadrat-level occupancy rate also varied little among years, from 0.893 in 2011, to 1.00 in 2021, and 0.970 in 2022. However, focusing on occupancy results for all southern WTPT pooled across sex and age may be misleading. Our results showed that male WTPT have a higher detection probability than both females and chicks as they are territorial and readily respond to male broadcast calls throughout the summer and fall. Also, because WTPT have a male-biased sex-ratio (Braun et al. 1993), relying solely on an all ptarmigan analysis could provide a misinterpretation of the population trajectory (Donald 2007, Amrhein et al. 2007). Thus, examining the occupancy rate for each sex and cohort provides a better assessment of the demographic status and dynamics of the population and should continue to be incorporated in future survey efforts.

Males

Our surveys found occupancy rates by male southern WTPT increased from 2011 to 2021–2022 for both plots and quadrats. For models run, no covariates were found to be good predictors of male occupancy, including weather variables. Male southern WTPT are known to have higher survival rates than females (Braun and Rogers 1971, Wann 2017). This higher survival is most likely due to males traveling shorter distances to wintering areas (Hoffman and Braun 1975, Seglund et al. 2018) and because breeding is less costly for males than it is for females. Southern WTPT are seasonally monogamous, with males arriving to set up breeding territories prior to females (Schmidt 1969, Braun 1984, Hoffman 2006). Males are very vocal during territorial establishment and will actively defend territories from other males. May and early June is the time period when male mortality is highest due to their lack of attention to predators and conspicuous behavior during territorial disputes (Schmidt 1969, Braun and Roger 1971, Hoffman 2006). Once paired with a female, the male stays close to the hen while she incubates and remains

vigilant for predators and other males in the area (Wiebe and Martin 1997, Martin 2014). After the eggs hatch, the male normally leaves the female to flock up with other males and unsuccessful breeding females (Braun and Rogers 1971). Males do not engage in parental care of the brood (Martin et al. 2020). Thus, males have lower incidence of predation during the nesting and brood rearing seasons and may be able to withstand variation in extreme weather conditions due to their freedom of mobility to access microrefugia. Our findings are in line with other research that has found that female monogamous gamebirds are the more sensitive sex to climate extremes (Latham 1947).

Females

Our surveys measured a decline in quadrat-level occupancy by females from 2011 to 2021–2022, with 2021 and 2022 statistically similar in estimated occupancy rates. While models incorporating the effects of year and strata failed to converge for the plot-level analysis, models containing weather variables showed a negative effect of higher minimum temperatures during the breeding season. CPW research from 2013–2017 (Seglund et al. 2018) found that annual survival of female southern WTPT was lowest during years with below normal snowpack and drier and warmer breeding conditions. This research also found that the birds in the south maintained higher annual survival with less variability as compared to birds occupying study sites in the north and central strata. Though the mechanism for this lower survival was not identified, increasing temperatures during the breeding season may negatively impact female southern WTPT because they are physiologically well adapted for heat retention in both the summer and winter, making overheating a risk in high ambient temperatures and intense solar radiation (Johnson 1968, Martin et al. 2020). To deal with high temperatures, birds behaviorally adapt by selecting cool microsites, including those with water, snow, or shade (Wiebe and Martin 1997, Visinoni et al. 2015, Oswald et al. 2019). Visinoni et al. (2015) found that rock ptarmigan (*L. muta*) selected topographic sites in summer that were cooler than random sites. They found the greatest microclimate differences between random and used sites were most apparent during the hottest part of the day and on rainless days. Alpine habitats in Colorado have normally maintained a buffer from high temperatures in summer due to afternoon thunderstorms that cool the environment (https://climate.colostate.edu/climate_long.html) and help maintain verdant vegetation. Thus southern WTPT have been thought to be less dependent on

engaging in behaviors to avoid hyperthermia than has been observed in other areas e.g., following retreating snowfields in Montana (Johnson 1968, Choate 1960, Benson and Cummins 2011). However, with warmer summers and reduced summer moisture, breeding southern WTPT females may be facing new challenges in terms of resource availability, access to cool microsites, and increased susceptibility to predation.

Southern WTPT females have been measured to have the lowest survival during the early breeding and nesting period (Seglund et al. 2018). Females are the most vulnerable during nesting because the hen is solely responsible for incubating eggs, and for ensuring she meets her energetic demands for self-maintenance (Wiebe and Martin 1997, Sandercock 2005a, Coe et al. 2015, Carroll et al. 2018). To keep eggs protected and to potentially minimize predation risks, females maintain a passive nest defense with a constant incubation strategy (Wiebe and Martin 1997). The female normally only leaves her nest unattended to feed during crepuscular hours (Giesen and Braun 1979). Changes in a hen's normal recess activity are thought to be the result of the microclimate condition at the nest and/or due to her body condition (Wiebe and Martin 1997). Because females on nests are restricted in their movements, incubating hens can experience the greatest heat stress (Choate 1960). Therefore, if a southern WTPT female selected a nest that did not provide suitable protection from high temperatures and exposure to intense solar radiation, they could experience thermoregulatory problems such as hyperthermia and dehydration (Oswald et al. 2019, Strinella et al. 2020). To alleviate heat stress, females may take more frequent recesses from incubation to cool themselves. Hotter temperatures also speed up the melting of snowfields which are not only important spots to provide cool microrefugia for snow bathing, but to provide moisture for mesic vegetation at their melting edges for foraging, especially in summers with reduced precipitation. With more dispersed snowfields, females may need to travel greater distances to find microsites to cool themselves and to locate food resources. Therefore, females may not only be taking more frequent incubating recesses, but potentially longer ones as well. For Rockjumpers (*Chaetops frenatus*), another avian alpine specialist, microsite use for cooling during the hottest part of the day came at a cost in the form of reduced foraging opportunities (Oswald et al. 2019). Thus, because southern WTPT are susceptible to overheating during incubation due to their cold-adapted strategies, increasing

temperatures in alpine habitats could reduce their survival through physiological processes and a reduction in self-maintenance (Wiebe and Martin 1997, Strinella et al. 2020). Additional research is needed to evaluate the effect of nesting on female survival and nest success as temperatures increase in alpine habitats. This research could incorporate the use of temperature data loggers in nests of radio-collared females to help monitor nest recesses.

Sex ratios

An increase in male to female sex ratio is an indicator of potential population declines for a monogamous species (Hannon and Martin 1992). The frequency and causes for variation in adult sex ratios is not well understood, but it has been suggested that adult sex ratios become more skewed towards males in threatened species than in species with robust populations (Donald 2007). Previous work has found that distortion in sex ratios results more from changes in survival than fecundity (Braun et al. 1993, Donald 2007). Wann (2017) reported sex ratios of banded southern WTPT at Mt. Evans and Rocky Mountain National Park from 1966–2016, regardless of age, to be 52 males to 48 females. Larison (2001) found the ratio of subadult males to subadult females to be a bit lower (48:52) but much higher for adults (62:38). Seglund et al. (2018) found subadult ratios to be around 50:50 and 66:34 male to female ratios for adults. In our 2011 surveys, we found the ratio of males to females to be almost equal, however in 2021 we estimated the ratio to be 67:33 in favor of males and by 2022, the ratio was 75:25 in favor of males. A reduction in female survival and an increasing distortion of the sex ratio could lead to negative population trends (Pearce-Higgins et al. 2015). Adult female survival has been found to be the most important vital rate affecting southern WTPT population growth and maintenance (Martin et al. 1993, Wiebe and Martin 1998a, Sandercock et al. 2005a, 2005b, Martin and Wilson 2011, Wann 2017) thus, a potential decline in the number of females is concerning and may warrant an increase in conservation efforts focusing on females. These efforts could include limiting the number of females that can be harvested annually and reducing recreational impacts at important wintering areas and at breeding areas where females are known to nest.

During the 2021 and 2022 surveys, numerous observations of males engaged in intense territorial defense were recorded. Males appeared more aggressive in 2021–2022 than during mark-resight surveys conducted from 2013–2016 (Seglund et al. 2018). These previous surveys described males

chasing one another in flight, making territorial calls, and then returning to mates; only two males were documented to be unpaired during this four-year survey effort. Conversely in both 2021 and 2022, we documented more extreme aggressive male interactions and a greater number of males were observed to be unmated. Research has found that up to 26% of WTPT males may be unmated during a breeding season whereas unmated females are extremely rare (Martin et al. 2020). Greater numbers of males could equate to females selecting superior mates within prime territories and potentially improving fecundity. However, studies have shown that male aggressiveness intensifies with an exacerbated male-biased sex ratio (Gilmartin and Eberhardt 1995, Taylor et al. 2001, Liker et al. 2014). These studies have shown that increased competition for mates accentuates the tendency for males to mob females causing a higher incidence of nest disturbance by unmated males and amplifying the stress level of females resulting in overall lower reproductive output. Continued monitoring and research is needed to determine the effect of male-skewed sex ratios in the southern WTPT population and to determine if adult sex ratios will normalize under current and future predicted climate conditions.

Chick occupancy and age ratios

For both plot- and quadrat-level analyses, chick occupancy declined from 2011 to 2021 and improved in 2022, but not to 2011 levels. Unlike female occupancy, chick occupancy almost doubled from 2021 to 2022. In addition to a year effect, the quadrat-level analysis suggested differences across strata with both the north and central strata improving chick occupancy in 2022, while the southern stratum maintained low chick occupancy. Chick per hen estimates followed the occupancy pattern with a high number of chicks in 2011, a low number of chicks in 2021, and a rebound in chicks in 2022, but not to the 2011 numbers. Similar to females, higher temperatures during the breeding season were correlated with reduced plot-level occupancy rates for chicks.

Several studies have investigated factors affecting WTPT fecundity, and in contrast to our current findings, they found dry conditions, and warmer springs increased nest and brood success (Novoa et al. 2008, Wilson and Martin 2010, Wann et al. 2016). Greater reproductive output during warm, dry years is thought to partly be due to a higher number of re-nesting attempts, with those attempts producing 25% more offspring (Wilson and

Martin 2010). Warmer springs may also allow for abundant food resources during nesting as there is more snow-free ground (Moss et al. 2008). For rock ptarmigan, early snowmelt lead to more available plants for forage, with higher digestible protein content improving nest success (García-González et al. 2016). The higher quality forage allowed females to enter the nesting season in better condition and spend less time off nests to obtain food resources, resulting in reduced predation during incubation.

Though previous research appears to find that warm and dry conditions may not be detrimental to ptarmigan production, we measured lower chick occupancy rates during an exceptionally dry summer and low snowpack year and improved chick occupancy during a summer with more normal monsoonal moisture. Since the first occupancy surveys were conducted in 2011, the Colorado Rocky Mountains have experienced variable snowpack. Snowpack in 2011, 2014, 2015, 2016, 2017, 2019, and 2020 was normal to above normal across much of the state. Conversely, 2012, 2013, 2018, 2021, and 2022 had snowpack below the median average with both 2012 and 2018 near the minimum amount of snow water equivalent recorded (<https://nrcs.usda.gov/wps/portal/wcc/home/quicklinks/states/colorado/products>). In addition to variable snowpack, temperatures in alpine habitats during every month of the year have been consistently rising since 1986, with the greatest warming occurring in the southwest part of the state (<https://coloradoencyclopedia.org/article/colorado-climate>). Based on weather data collected during our alpine surveys, summer monsoonal moisture was also extremely limited from 2018–2021.

Increasing temperatures during the breeding season could affect the thermal tolerance of embryos as hyperthermia has been found to be more detrimental to embryo development than cold stress (Webb 1987). Selection of a ground nest site for a southern WTPT is not only important for camouflage to avoid being easily spotted by predators, but also to provide an adequate microsite to mediate weather conditions and provide an appropriate temperature spectrum for egg development (Choate 1960, Deeming and Mainwaring 2015). WTPT most commonly position nests near boulders, under the edge of willows, and on open vegetated ground (Wiebe and Martin 1998b, Seglund et al. 2018). Additionally, because of the extreme weather in alpine habitats, nests are placed at locations to provide protection from wind, precipitation, and for

thermoregulation (Giesen et al. 1980, Wiebe and Martin 1998b). With increasing temperatures in alpine habitats and lack of monsoonal moisture, traditional nest placement may no longer provide the suitable microclimate needed for hatching.

Temperature data loggers placed in nests of WTPT found temperature profiles to vary from -2°C at night to over 45°C during the warmest part of the day (Wiebe and Martin 1997). Temperature increases could affect embryo development not only during incubation, but also during laying because WTPT do not start incubating until a clutch is complete (Giesen et al. 1980). On average a female lays 0.8 (\pm 0.2 SD) eggs per day (Martin et al. 1993, Wiebe and Martin 1995, Hoffman 2006) with an average clutch size of 5–6 eggs (Seglund et al. 2018). Reyna and Burggren (2017) found that a 5°C increase in pre-incubation temperature reduced hatching rate by approximately 50% for bobwhite quail (*Colinus virginianus*) eggs, possibly resulting in a negative effect on bobwhite quail populations caused by climate change.

In addition to concerns about hatching viable eggs, lower chick numbers and occupancy during hot years may be explained by potential nest abandonment or reduction of nesting attempts by females. Female WTPT become reluctant to reduce self-care below a certain threshold to engage in continued incubation (Wiebe and Martin 1997). Bolger et al. (2005) found that very few females among four nesting passerines attempted to nest during an extremely dry, hot year. If a female did select to nest, as discussed previously, she may have needed to take more and longer incubation recesses during the day to cool herself increasing potential predation risk of a nest and potential damaging effects to embryos (Webb 1987, Zerba and Morton 1983). Zerba and Morton (1983) found that white-crowned sparrows (*Zonotrichia leucophrys oriantha*) nesting at high elevation sites protected eggs from overheating by not leaving nests when solar radiation was at its highest. They also found that ground nest temperatures were significantly higher than nests placed in trees or shrubs. Thus, timing of incubation recesses in alpine habitats may be critical for protecting eggs from overheating and destroying embryos. In addition, Wiebe & Martin (1997) documented predation of WTPT nests associated with recess activity. Smith et al. (2012) found for shorebirds that the time spent off of a nest, either by taking more recesses or longer recesses, was positively correlated with higher predation risk of a nest.

For nests that do produce chicks during hot, dry summers, there may be less food available as plants became desiccated, insects are not as abundant, or a phenological mismatch may occur affecting chick survival (Wann et al. 2019). Snowfields for cooling and providing food resources for broods and hens can become more dispersed causing the family group to travel greater distances and potentially exposing them to higher predation risks. Increased temperatures may also result in hens and chicks spending the majority of the day cooling themselves at a detriment to their survival by foraging less and causing a reduction in body condition (Oswald et al. 2019).

Collective research has found that WTPT have low reproductive output with the southern WTPT laying the smallest average clutch size (Braun et al. 1993, Martin et al. 2020) of any North American Tetraonidae with the exception of the spruce grouse (*Falciapennis canadensis*; Johnsgard 1973, Schroeder et al. 2018). In poor reproduction years, recruitment from outside sources may be required to maintain viable local populations. In other words, sites with low fecundity due to high predation or unfavorable weather conditions can be rescued by immigration from sites that had superior annual fecundity. Despite the extensive alpine habitat in Colorado, which has allowed for connectivity among populations to promote both immigration and emigration, the southern portion of southern WTPT occupied habitat is isolated from the rest of the range as measured by fine scale genetic differences (Seglund et al. 2018). Thus, poor reproduction both across the state and in more isolated locations could limit demographic rescue resulting in some local populations declining. Continued increases in temperature caused by climate change warrant concern for some portions of the southern WTPT range especially in southwestern Colorado, where we measured the lowest chick occupancy in 2021 and 2022 and which is an area predicted to warm more quickly in future years. Additional research is needed to assess effects of increasing breeding temperatures on nest success and chick survival.

Other considerations

Several large wildfires created very smoky conditions during our surveys in 2021. Smoke in the alpine made it impossible for surveyors to complete field work due to unhealthy air quality, and many surveys were rescheduled. Though information about the effect of smoke on bird health is not well studied, the physiology of the avian respiratory system that enables birds to fly in oxygen-limited

environments at high altitudes could also make them more susceptible to poor air quality (Scott 2011). Air quality during surveys was not affected by wildfire smoke in either 2011 or 2022 when chick numbers were higher. Wildfires are predicted to burn bigger, hotter, and more frequently with four of the five largest wildfires in Colorado occurring in 2018 and 2020 (<https://dfpc.colorado.gov/sections/wildfire-information-center/historical-wildfire-information>). A better understanding of the effects of smoke and air quality on the immune system, movements, foraging behavior, and overall survival of southern WTPT may be needed.

An increase in human recreation is also likely to impact alpine habitats with 2021 having the highest recorded participation rate in outdoor activities ever recorded (U.S. Bureau of Economic Analysis 2022, Outdoorfoundation.org 2022). In Colorado, ninety-two percent of residents say that they participate in outdoor recreation and with the state's population growing, we would expect further increases in public land use (CPW 2020). Outdoor recreation encompasses a wide variety of activities that can negatively affect wildlife. A literature review completed by Steven et al. (2011) on non-motorized recreation, found that it had negative effects on various bird species including reduced fecundity and changes in behavior and physiology.

Recreational activities in winter can create challenges for a cold-adapted species already coping with extreme conditions. Arlettaz et al. (2015) found that black grouse (*Lyrurus tetrix*) in the European Alps experienced chronic stress and increased energy expenditures in response to winter recreation activities. Snowmobiles, snowbikes, and recreational skiing can have negative effects on the southern WTPT in winter including flushing of the species from preferred feeding, roosting or loafing areas, and causing them to expend extra energy when reserves may be low due to extreme temperatures and snow cover (Hoffman 2006, Martin 2014). Additional negative effects associated with high rates of mechanical snowmachine use include compaction of snow and crushing of willows affecting winter food resources and depletion of winter snow roost availability (Hoffman 2006).

Summer recreation can negatively affect southern WTPT particularly if they are disrupted during breeding activities. We have documented dogs off leashes harassing breeding birds and have documented a dog killing a chick. Human traffic near nests can also frighten females off nests exposing the

hens and eggs to increased predation risk or elevated temperatures that can affect embryos. Human disturbance causing common eiders (*Somateria mollissima*) to flush off nests resulted in higher predation risks than for birds that took natural recesses (Stein and Ims 2015). We have also documented negative effects to alpine vegetation caused by increases in recreational users such as incised trails and roads that captured and trapped water from rain and snowmelt leading to improper flow patterns that accelerated erosion, and caused dewatering and desiccation of meadows, wetlands, fens, and willow carrs. We have also documented an increase in trash and trampling of sensitive flora in the alpine.

Caveats

Our estimates of age and sex ratios did not include differences in sightability among years or age classes. Sightability could have varied for females across years as females with chicks will more readily respond to broadcast calls resulting in higher detection for females with chicks or for females that recently lost chicks. In years with low chick production detecting females could have been more difficult, however, we believe our estimates for sex ratios are valid for the following reasons. In 2021 and 2022, we made a concerted effort to locate females as we had already noticed fewer females and more aggressive males on the landscape during our earlier brown-capped rosy-finch (*Leucosticte australis*) surveys (Seglund and Runge 2021). Also, females are readily detected during the courtship season prior to nesting when surveyors can detect a male and then follow it to its mate. During the breeding season we recorded many more unpaired males in 2021 and 2022, despite increased efforts to locate females.

Sightability for chicks should not have varied greatly among survey years. We have confidence in our general estimates of age ratio because for the 2011 estimate of age ratio to be within the 95% CI for 2021, detection probability in 2011 would have needed to be almost 3.5x higher than 2021. Given that more CPW Area Biologists were conducting surveys in 2011 and that occupancy results showed that CPW Area Biologists had a lower detection probability for male occupancy and functionally equivalent to technicians for chicks and females, it seems unlikely that detection in 2011 would be 3–4 times higher than 2021. Similarly, for the 2021 estimate to be within the 2022 95% CI for age ratio, detection probability would have needed to be 2.3x higher in 2022 than 2021. Thus, we are confident that

age ratios significantly decreased from 2011 to 2021 and increased in 2022.

Implications for Conservation and Management

Understanding how avian species will respond to climate change, especially species like the southern WTPT which is a cold-adapted species of alpine habitats, can be challenging. Recent findings point to avian population trends being influenced more by temperature than precipitation, suggesting that warming may play the biggest role in demographic changes (Pearce-Higgins et al. 2015). The southern WTPT is known to have high annual variation in fecundity based on snowpack, spring, and summer conditions. To maintain populations, this variation is thought to be buffered with high adult survival especially by females (Martin and Wiebe 2004, Sandercock et al. 2005a, 2005b, Bears et al. 2009, Martin et al. 2009, Martin 2014, Wann 2017). Therefore, any long-term threats that increase the mortality of females would have the greatest potential negative effect on populations. We found that female occupancy declined between 2011 and 2021–2022, and we also measured an increased distortion in adult sex ratios in favor of males. Our findings are consistent with the idea that declines in female and chick occupancy were influenced most strongly by environmental changes producing drier and warmer conditions during the breeding season. Therefore, conservation measures should be undertaken to reduce threats to adult female survival and improve chick production. These measures could include better assessment of current hunting pressure and a reduction of hunting (e.g., lower bag limits for numbers of females and chicks that can be harvested) in alpine areas that are easily accessible. Domestic sheep grazing during drought years in the alpine can exacerbate the loss of important forage opportunities for chicks and hens and these impacts may become intensified with climate change. Land management agencies should ensure that sheep grazing is included in an adaptive management approach to protect alpine habitats from further degradation as a consequence of warmer springs, earlier snow melt, and higher summer temperatures. In addition, implementing conservation measures to mitigate the impacts of human recreation in alpine habitats could buffer southern WTPT populations from negative effects. These measures could include repairing overused trails and roads that trap natural runoff, reducing the amount of trash and food items left by recreationists that can attract predators, increasing dog control measures, and providing protection of important southern WTPT wintering and breeding areas.

Though the southern WTPT is thought to be a resilient species that can tolerate extreme weather, our surveys indicate potential problems. Colorado provides the species with abundant suitable habitat, but managers need to be aware of the synergistic threats of environmental and human factors that could push the southern WTPT into limited spaces and increase stressors that reduce population viability. Monitoring of this species should therefore be a priority for CPW to determine if female occupancy rates continue to decline, to assess if sex ratios remained skewed to overwhelmingly favor males, and to evaluate reproductive output, especially in the southern part of the range. Intensive research from 2013–2017 found that populations of southern WTPT were stable and contained high genetic diversity (Seglund et al. 2018), and nest success measured in Colorado during these years was higher than previously reported for WTPT (Wann et al. in press). Environmental conditions, however, are changing rapidly and our current findings advise a more cautious approach to understanding and conserving this alpine species.

FUTURE AND ONGOING EFFORTS

1. CPW plans to conduct southern WTPT occupancy surveys in 2024 to see if current trends are still apparent. We will survey the same plots and quadrats as in the previous occupancy survey efforts using the same protocol.
2. Current resource selection and human resource use modeling are being conducted by a PhD student (Nicholas Parker) at Colorado State University incorporating CPW radio-telemetry data and occupancy locations of southern WTPT statewide.
3. CPW has formed an internal working group to assess hunting impacts on the species and to evaluate timing of hunting and bag limits.
4. Future research could focus on the development of spatial models to assess the alpine areas in Colorado most susceptible to climate change. In those areas, it would be helpful to understand potential changes to female and chick southern WTPT survival, expanding upon the findings of Seglund et al. 2018. Incorporation of temperature data loggers in nests would help determine how increasing temperatures affect nesting behavior and success. Study sites could

be paired to examine dispersal rates among subpopulations of ptarmigan.

5. Additional research could focus on collecting fecal samples from chicks and hens for use in a cortisol metabolite analysis to assess stress levels of breeding birds that may become elevated because of warmer breeding temperatures and increased recreational impacts.

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