Wildlife Research Report ADF&G/DWC/WRR–2021–2

Evaluation of the Effects of Weather on Ruffed Grouse Population Abundance in Interior, Alaska, 1993–2019

Cameron J. Carroll

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Alaska Department of Fish and Game Division of Wildlife Conservation

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Cover Photo: Photo of juvenile ruffed grouse (*Bonasa umbellus*). ©2016 ADF&G. Photo by Mike Taras.

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Abstract

Weather plays an important role in the population dynamics of many species of grouse and ptarmigan. Availability of snow during the winter, to reduce thermoregulatory costs and predation risk, is likely one of the most important variables determining overwinter survival; whereas warm and dry conditions during the brood rearing period are likely to have a large influence on reproductive success in tetraonid populations throughout their range. Understanding the effects of weather on grouse abundance indices will allow managers to better anticipate how changing climate conditions may influence long-term persistence of these populations. Using generalized linear mixed models (GLMMs) I evaluated the influence of 22 weather variables on ruffed grouse (*Bonasa umbellus*) abundance indices from Interior, Alaska, observed from 1993 to 2019. Model selection following Akaike's Information Criterion indicated there was strong model uncertainty in the candidate model set where 11 of the 12 models considered in the final analysis were included in the 95% confidence set. Marginal (0.06) and conditional R^2 estimates (0.17) indicated that the proportion of the variance in ruffed grouse abundance indices explained by the fixed effects alone as well as the combination of fixed and random effects in the model was low. Despite the models generally doing a poor job of explaining the annual variation in ruffed grouse abundance indices there was some evidence that precipitation during the first 10 days of the brood rearing period may influence ruffed grouse abundance indices negatively in Interior Alaska. Although year was used as a random effect in the model to account for between year variation in abundance indices, future work should directly incorporate density-dependence into models since many populations of ruffed grouse exhibit a population cycle.

Key words: abundance, *Bonasa umbellus*, drumming surveys, GLMMs, grouse, population indices, rain, snow, weather.

Introduction

It is well documented that weather plays an important role in influencing the population dynamics of tetraonids throughout the northern hemisphere. Poor weather conditions during critical periods of survival and development have been shown to have negative effects on population growth and abundance.

Tetraonids such as grouse and ptarmigan are physiologically and behaviorally adapted to cold environments. Physiological adaptions to cold weather include increased metabolic rates and decreased body temperatures (Thompson and Fritzell 1988a). Behavioral adaptations include bouts of heavy feeding or “crop packing” that allow grouse and ptarmigan to sustain long periods of inactivity during very cold days (Irving et al. 1967). Grouse will also select warmer micro-climates such as snow burrows and conifer trees for roosting (Edminster 1947, Bump et al. 1947). In areas where there is sufficient snow (approx. 200 mm) tetraonids often select snow roosts to reduce thermoregulatory costs (Gullion 1970, Thompson and Frizell 1988b, Shipley et al. 2019) and evade predators (Bergerud and Gratson 1988, Marjakangas 1990, Heinrich 2017). Temperatures in snow roosts can be 20–40°C warmer than the outside air temperature (Donaurov 1947, Marjakangas et al. 1984, Thompson and Fritzell 1988b). Despite these physiological and behavioral adaptations, winters with little snow (Spidso et al. 1997) or low temperatures and little snow (Zimmerman et al. 2008, Pomara and Zuckerberg 2017) have been associated with reduced survival and abundance of grouse. Snow depth is likely the critical factor as warm winters with little snow have also been related to reduced abundance of tetraonids (Loneux et al. 2003, Wang et al. 2002).

The brood-rearing period is also a critical time of year. Chick survival is often heavily dependent on weather encountered within the first few weeks of life. During the first 8 to 10 days of life, grouse and ptarmigan chicks are unable to thermoregulate (Boggs et al. 1977) and must rely on their hen to brood them. The negative effects of weather during this period can be felt both directly, with chicks dying of exposure, or indirectly, due to reduced foraging times and food intake. This can lead to starvation because of increased time spent being brooded by hens (Erikstad and Spidso 1982). Recent research using long term datasets (11 to 45 years) has provided evidence that cold weather (Ludwig et al. 2006) or cold and wet weather during the brood-rearing period are associated with reduced reproductive success due to low chick survival (Moss et al. 2001, Ludwig et al. 2006, Viterbi et al. 2015, Novoa et al. 2016, Wann et al. 2016).

Increasing temperatures due to climate change are expected to have variable effects on many tetraonid populations. In northern latitudes where continuous snow cover is present throughout much of the winter, increasing winter temperatures have resulted in more rain-on-snow events when precipitation normally falling as snow instead falls as rain (Zhang et al. 2012, Pan et al. 2018, Peeters et al. 2019). Projected increases in rain-on-snow events will likely negatively influence tetraonid populations in high latitudes by reducing food availability (Hansen et al. 2013) and eliminating snow roosting opportunities when thick crust layers form. In many areas increasing temperatures are altering snow season length, resulting in a contraction of the period of continuous snow cover (Brown and Robinson 2011). A delay in the onset of continuous snow cover had a negative effect on growth rates for a population of rock ptarmigan in the Alps (Imperio et al. 2013). Conversely, earlier snowmelt in Spring has been positively related to reproductive success in several populations of rock ptarmigan in the Alps (Novoa et al. 2008, Imperio et al. 2013, Novoa et al. 2016, Viterbi et al. 2015). This is presumably through increased reproductive success due to favorable pre-nesting foraging conditions for hens.

Yet, the effects of warming trends on tetraonid populations may not be consistent throughout their range. For example, in Finland black grouse (*Lyrurus tetrix*) chicks are hatching earlier because warmer temperatures in April have led to earlier nesting. However, temperatures during hatch in June have not noticeably increased. This has led to higher chick mortality as hatchlings must contend with lower post-hatch temperatures (Ludwig et al. 2006). Although other studies on Capercaillie (*Tetrao urogallus*), black grouse (Wegge and Rolstad 2017), and white-tailed ptarmigan (*Lagopus leucura*; Wann et al. 2016) found no mismatch in advancement of hatch and conditions experienced during the early post-hatch period. In fact, higher spring temperatures led to increased breeding and reproductive success in Capercaillie (Wegg and Rolstad 2017).

An increase in the frequency and intensity of precipitation events has been linked to increasing temperatures, with changes most prominent within mid-latitudes of the northern hemisphere (Hartmann et al. 2013). Precipitation at higher latitudes also appears to be increasing but there is more uncertainty associated with these trends in part due to issues with data coverage and data quality (Hartmann et al. 2013). Increases in precipitation in summer during the critical brood-rearing period could have substantial negative effects on tetraonid populations. A long-term climate trend of increasing rain in June is a least partially responsible for declines in numbers of Capercaillie and black grouse in Abernethy Forest, Scotland (Summers et al. 2010) due to reduced reproductive success (Summers et al. 2004).

Despite this growing body of research demonstrating the effect of weather and changing weather conditions on tetraonids throughout their range, little direct research is available from Alaska where the effects of warming are amplified (Serreze et al. 2009). There is very limited research aimed at evaluating the effects of weather or changing climate conditions on populations of ptarmigan in Alaska and none on grouse, likely because there are very few long-term datasets. To address that gap in knowledge I used a long-term dataset (1993–2019) of spring breeding counts of male ruffed grouse (*Bonasa umbellus*) from Interior Alaska to evaluate the effects of important weather variables on population abundance indices.

Study Area

The study site is located near the town of Anderson, Alaska (64°21′N, 149°11′W) within Game Management Unit 20A (GMU 20A; Fig. 1). The town of Anderson is approximately 129 road kilometers southwest of Fairbanks, Alaska. The geographic area is low-lying with an average elevation below 200 m. Fire and human disturbance have played a dominant role in creating a mix of early successional vegetation within the area. The dominant vegetation in the area consists largely of quaking aspen (*Populous tremuloides*) with willow (*Salix* spp.) predominant near riparian areas. In some areas where disturbance has not taken place in the last 20 years, black spruce (*Picea mariana*) and white spruce (*Picea glauca*) are beginning to replace quaking aspen as the predominate species. Alder (*Alnus* spp.) and paper birch (*Betula papyrifera*) are also present but in much smaller numbers. The climate in the area consists of moderately warm summers (8.4°C to 20.7°C), cold winters (−14.5°C to −25.2°C), and relatively low snowfall (0.05–0.20 m) compared to other regions in the state. Land ownership within the study area consists of U.S. military, municipal, and state lands.

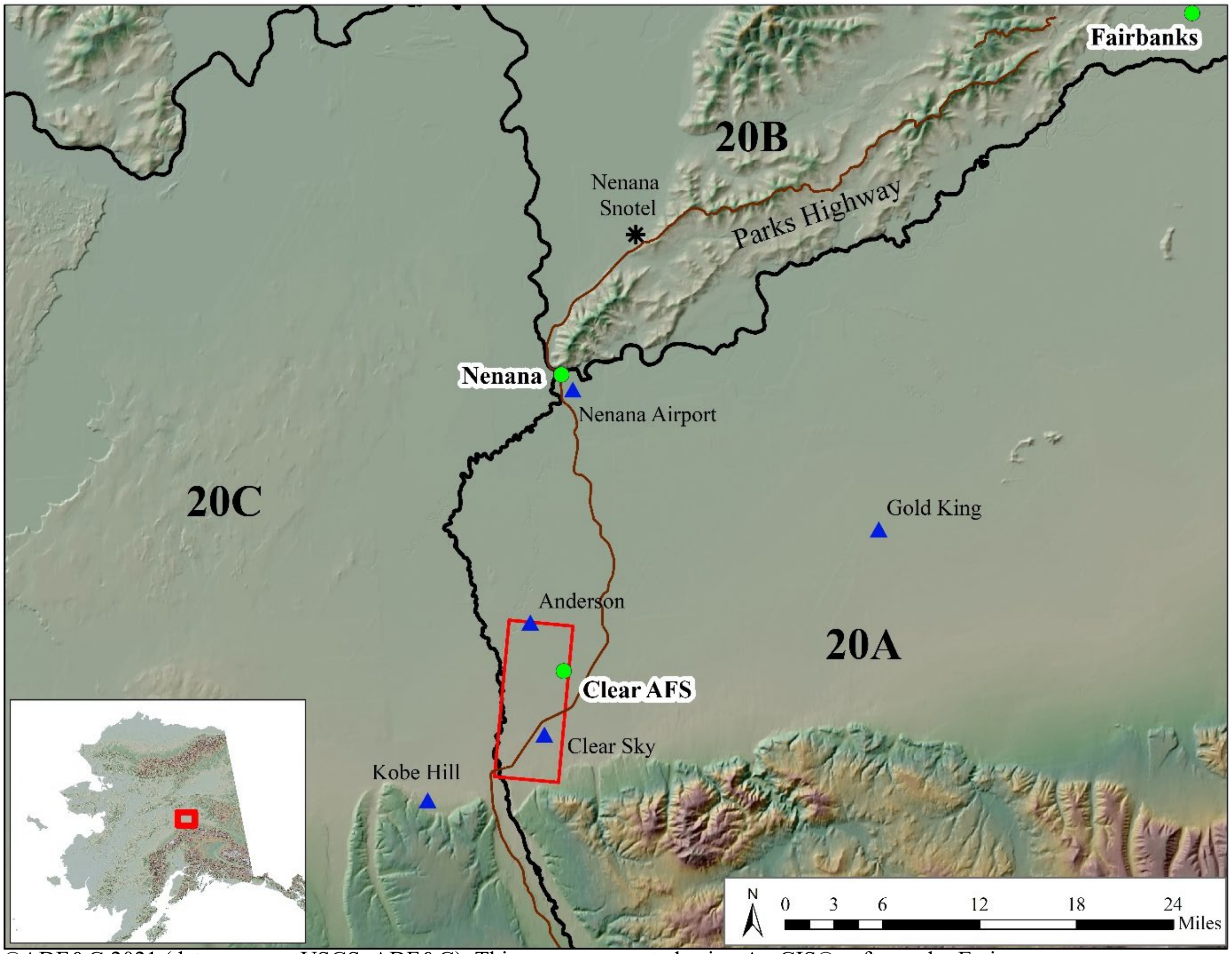

Figure 1. Map of region encompassing the study area (red rectangle), locations of National Oceanic and Atmospheric Administration (NOAA) weather stations (blue triangles), NOAA Snow Telemetry (SNOTEL) site (black asterisk), and nearby towns (green circles).

Methods

Ruffed Grouse Data

Ruffed grouse spring breeding survey data (i.e., male drumming data) were collected along 4 survey routes near Clear Space Force Station (SFS; formerly known as Clear Air Force Station) and the tow of Anderson, Alaska from 1993 to 2019 by Alaska Department of Fish and Game (ADF&G) staff and volunteers. Surveys were completed between late April and mid-May and in most years took place between 28 April and 5 May. In most years surveys were completed 4 times annually, twice in the morning, and twice in the evening in an effort to capture all active drumming grouse from the area; however, in 1998, surveys were conducted only once and in 2013 surveys were not conducted at all due to late spring snow or extremely cold temperatures. In several early years more than 4 surveys were conducted. Survey routes were established along secondary roads and all-terrain vehicle (ATV) trails and consist of 9–12 survey stops (listening posts) spaced approximately 0.8 km apart in an effort to avoid double counting. Observers counted the number of male drumming ruffed grouse heard within a 4-minute period of active listening at each listening post. Ruffed grouse seen or heard before or after the 4-minute period were not included in the count. The maximum number of drumming ruffed grouse heard along each survey route annually were used in the analysis. This estimate is an index of ruffed grouse abundance and is a metric often used to detect trends in ruffed grouse abundance throughout North America (Petraborg et al. 1953, Dorney et al. 1958).

WEATHER DATA

Twenty-two weather variables (Table 1) were initially considered for analysis, including daily minimum and average temperature, precipitation, and several snow characteristics which were limited to time periods known to be critical for grouse survival and reproduction.

Fourteen of the 22 weather variables considered for analysis were from the National Oceanic and Atmospheric Administration (NOAA) weather station located at the Nenana Municipal Airport (64°33′N, 149°4′W), approximately 30 kilometers to the north of the ruffed grouse survey area at a similar elevation. Daily spring and summer minimum temperatures (°C) were calculated using means for 3 critical 30-day-periods: pre-nesting (10 April–9 May), nesting (10 May–8 June), and brood-rearing (9 June–8 July). The number of days that were below freezing during the nesting period were also considered. Spring and summer precipitation were calculated using average daily precipitation and total precipitation (mm) during the brood rearing period. In addition, the number of rain days recorded in 3 successive 10-day periods (9–18 June, 19–28 June, and 29 June–8 July) during brood-rearing was calculated, as were the average daily minimum temperatures during the same successive 10-day-periods following methods used in Moss et al. (2001). All spring and summer weather variables were assumed to influence ruffed grouse population abundance indices in the subsequent year. Winter weather variables (1 October–31 March) included the number of days below −20°C and the number of days equal to or above 1.5°C. Winter weather variables were assumed to influence ruffed grouse population abundance indices in the current year (t). In addition to the 2 winter weather variables collected directly from the NOAA weather station at the Nenana Municipal Airport, I included 9 additional winter weather variables derived from a spatially explicit snow-evolution model (SnowModel; Liston and Elder 2006, appendices in Liston et al. 2020). SnowModel requires precipitation, wind speed and direction, air temperature, and relative humidity as data input. Winter weather data used as inputs to SnowModel were taken from 6 local meteorological stations as well as reanalysis data from NASA's Modern Era Retrospective analysis for Research and Applications, Version 2 (NASA 2019: MERRA-2; Gelaro et al. 2017). The meteorological stations used to provide data for SnowModel included 5 NOAA weather stations all located within 37 kilometers of the study site at Anderson (64°21′N, 149°11′W), Clear Sky Lodge (64°15′N, 149°11′W), Gold King (64°24′N, 148°28′W),

Table 1. Explanatory weather variables that were used in models. The current year is denoted as *t*, the previous year as *t*−1.

Variables	Description	Year
Temp	Average temperature (°C) during core snow period	*t*
DBT	Number of days less than −20°C during 1 October–31 March	*t*
DAT	Number of days ≥1.5°C during 1 October–31 March	*t*
CSP	Core snow period length (days)	*t*
MSD	Maximum snow depth (mm)	*t*
Snow	Number of days with at least 150 mm of snow	*t*
TS	Total annual snowfall (mm)	*t*
CR	Total amount of rain during core snow period	*t*
RSD	Number of days with rainfall ≥3 mm on snow depth ≥15 mm	*t*
Start	Start date of core snow period in day of the year (DOY)	*t*
End	End date of core snow period in day of the year (DOY)	*t*
P.Temp	Average daily minimum temperature (°C) during pre-nesting period (10 April–9 May)	*t*−1
N.Temp	Average daily minimum temperature (°C) during nesting period (10 May–8 June)	*t*−1
Br.Temp	Average daily minimum temperature (°C) during brood rearing period (9 June–8 July)	*t*−1
Br.DP	Average daily precipitation (mm) during brood rearing period (9 June–8 July)	*t*−1
Br.TP	Total precipitation (mm) during brood rearing period (9 June–8 July)	*t*−1
Br.Temp.1	Average daily minimum temperature (°C) during first 10 days of brood rearing period (9–18 June)	*t*−1
Br.Temp.2	Average daily minimum temperature (°C) during second 10 days of brood rearing period (19–28 June)	*t*−1
Br.Temp.3	Average daily minimum temperature (°C) during third 10 days of brood rearing period (29 June–8 July)	*t*−1
JP.1	Number of rain days (≥0.1 mm) during first 10 days of brood rearing period (9–18 June)	*t*−1
JP.2	Number of rain days (≥0.1 mm) during second 10 days of brood rearing period (19–28 June)	*t*−1
JP.3	Number of rain days (≥0.1 mm) during third 10 days of brood rearing period (29 June–8 July)	*t*−1

Kobe Hill (64°12′N, 149°26′W), the Nenana Municipal Airport (64°33′N, 149°4′W), and 1 SNOTEL station located near Nenana (64°41′N, 149°55′W). Winter weather variables derived from the model were as follows: average temperature (°C) during the core snow period (defined as the longest period with continuous snow cover), total annual snowfall (mm), maximum snow depth (mm), number of days with ≥150 mm of snow, total amount of rain during core snow period (mm), number of days with ≥3 mm of rain on snow depths of ≥150 mm, the length of the core snow period in days, the start date of the core snow period in day of the year (DOY), and the end of the core snow period in DOY. Based on work conducted by researchers on other tetraonids throughout their range as well as my knowledge of factors influencing ruffed grouse in Interior Alaska, I developed 11 hypotheses (Table 2) *a priori* to analysis, representing what I believed to be the most likely relationships between weather variables and population abundance indices of ruffed grouse in Alaska. Hypotheses considered in the analysis were limited to weather effects because I did not have sufficient data on predator numbers or other potentially important variables.

Table 2. *A priori* hypotheses and their predicted effect on population abundance indices of ruffed grouse in Interior Alaska.

Hypothesis	Predicted effect
Warmer winter weather or more days above certain temperature	+
Winters with deep snow conditions	+
Winters with long periods of extreme cold and little snow	−
Increased rain during winter	−
Low temperatures and more rain on snow events	−
Early spring snowmelt	+
Cold weather during pre-nesting	−
Cold weather during nesting	−
Cold weather during brood rearing	−
Wet conditions during brood rearing	−
Cold and wet weather during brood rearing	−

DATA ANALYSIS

I first summarized ruffed grouse population abundance indices for the last 27 years (1993–2019). Then I examined the data for long-term trends in weather variables using linear models. Lastly, I evaluated the effects of weather variables on ruffed grouse abundance indices using generalized linear mixed models (GLMMs) with a Poisson distribution and log link function. Year was included as a random effect to account for temporal autocorrelation between years and an offset term (log transformed) was included in all models to account for differences in effort by survey route because some routes had more listening posts than others. Explanatory (weather) variables included in the analysis were centered to improve model convergence. Years in which weather or relative abundance data were missing (1998, 2013) were excluded from the analysis. The response variable was the maximum number of ruffed grouse heard along each survey route each year. To rank each model's ability to fit the data, I used Akaike's Information Criterion (AIC; Akaike 1973). Models were compared using AIC_c, which is AIC corrected for small sample sizes (Burnham and Anderson 2002).

Data exploration indicated that there were collinearity issues between many of the weather variables. To avoid issues with collinearity and model uncertainty due to variables that are highly correlated, model selection proceeded in 2 steps. The first step included building a separate model for each of the 22 weather variables that also included year as a random effect. Only models that ranked higher than the null model (random effect of year only) and higher than models that included a similar weather variable were retained for the second and final step in the analysis. For example, if the variable TS (total snowfall) ranked higher than Snow (number of days ≥15 cm of snow) during the first step of model selection, then only the variable TS would be retained for the second step of analysis. If weather variables retained in the second step were highly correlated ($R > 0.50$; Zuur et al. 2009) with any other variables retained, then those variables were not included in the same model. In the final step of analysis, I included single variable models retained from the first step as well as both additive and interaction models based on biologically reasonable or previously supported hypotheses. I considered only models that contained 6 or fewer parameters due to sample size. For the highest ranked model in the candidate set, I estimated the proportion of variance explained by fixed effects (marginal R^2) and the proportion of variance explained by the entire model, which includes both fixed and random effects (conditional R^2) using the method described by Nakagawa et al. (2017).

All analyses were performed in the R software environment, version 4.0.2 (R Core Team 2020) and the glmer function (Poisson distribution with log link) found in R-package lme4 (Bates et al. 2015). The aictab function in the R-package AICcmodavg (Mazarolle 2019) was used to calculate AIC_c values for each candidate model and compute the 95% confidence set (Burnham and Anderson 2002), which can assist in interpreting model selection. Marginal and conditional R^2 values were estimated using the MuMIn package (Barton 2020).

Results

Ruffed Grouse Data

The ruffed grouse population near Clear SFS has gone through 3 clear population cycles since counts were initiated in 1993, with peaks documented in 1997, 2005, and 2017 (Fig. 2). Over that time the mean number of drumming males heard per survey route has ranged from a low of 0 males (mean of 0.0 males/stop for all survey routes combined) in 2010 to a high of 10 males (mean of 0.6 males/stop for all survey routes combined) in 1997.

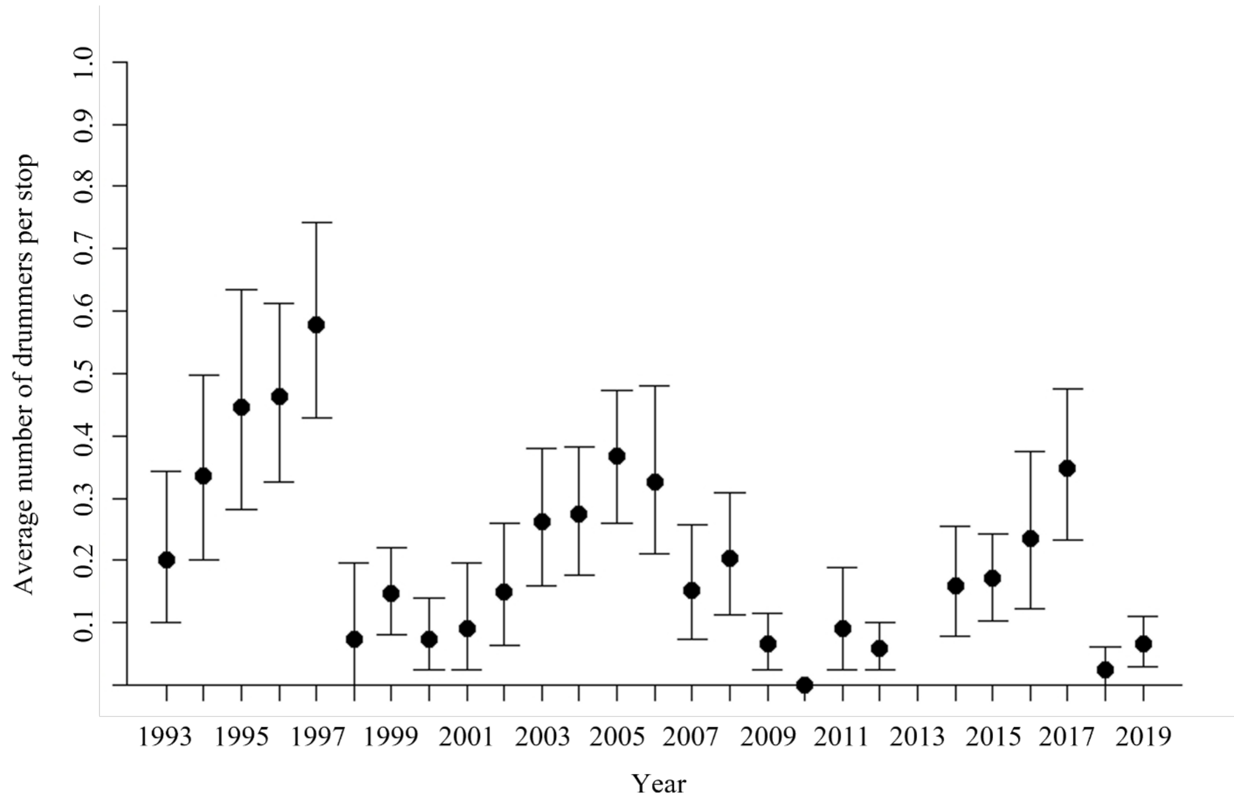

Figure 2. Estimates of the average number of male ruffed grouse heard per stop (listening post) across all 4 survey routes (with 95% confidence intervals estimated using the bootstrap method) near Clear Space Force Station (SFS) for 1993–2019.

TRENDS IN WEATHER FROM 1993–2019

Several of the weather variables used in analysis were found to have temporal trends over the period examined. The number of days with at least 150 mm of snow depth (Snow) showed a negative trend within the study area over the last 27 years (Fig. 3). Similarly, snowmelt has advanced with the end of the core snow period (End) also showing a negative trend over the same period (Fig. 4). Conversely, both the number of days equal to or above 1.5°C during the winter (DAT; Fig. 5) and the number of days with rain during the early part of the brood-rearing period (JP.1) showed positive trends over the same period (Fig. 6).

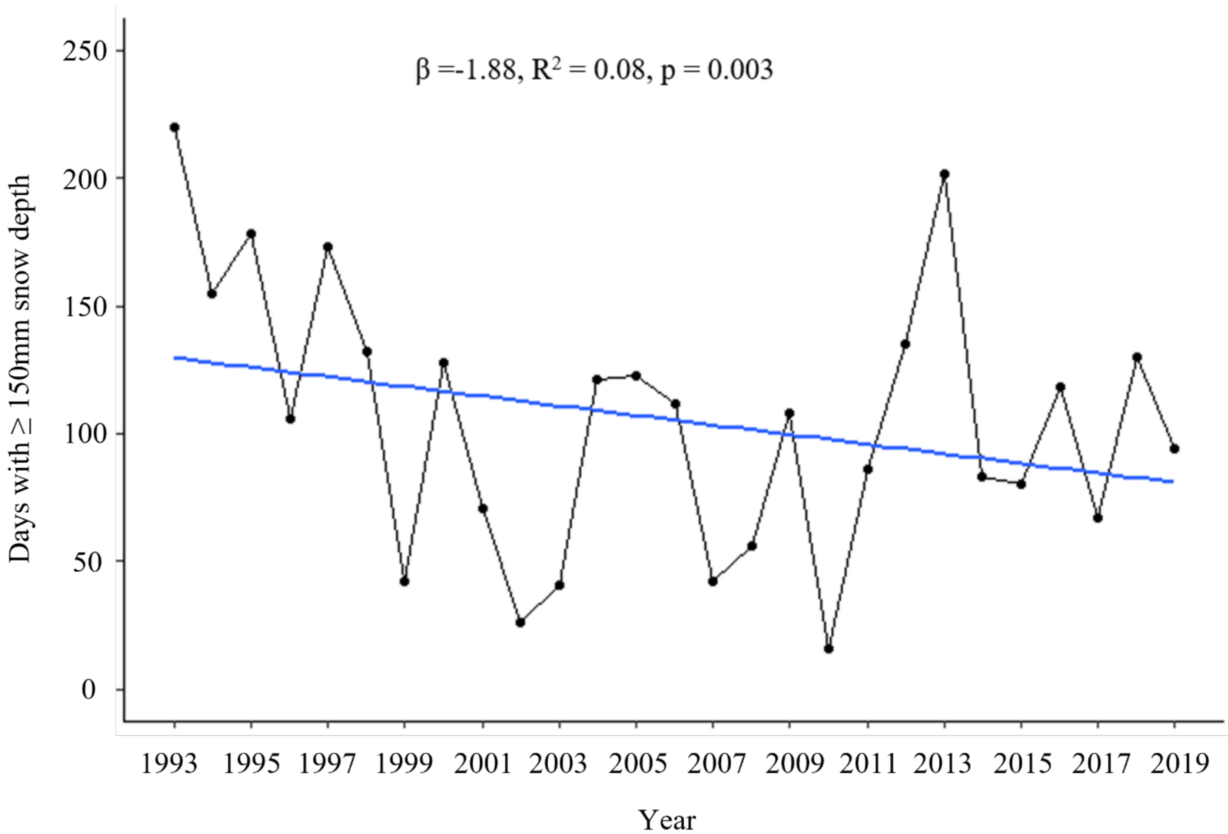

Figure 3. Trend in the number of days with at least 150 mm of snow depth during 1993–2019 estimated with a snow-evolution model (SnowModel) that used data from 5 National Oceanic and Atmospheric Administration (NOAA) weather stations, 1 snow telemetry (SNOTEL) station, and reanalysis data from NASA's Modern Era Retrospective analysis for Research and Applications (MERRA-2). The slope (β), coefficient of determination (R^2), and *P*-value (p) are also displayed.

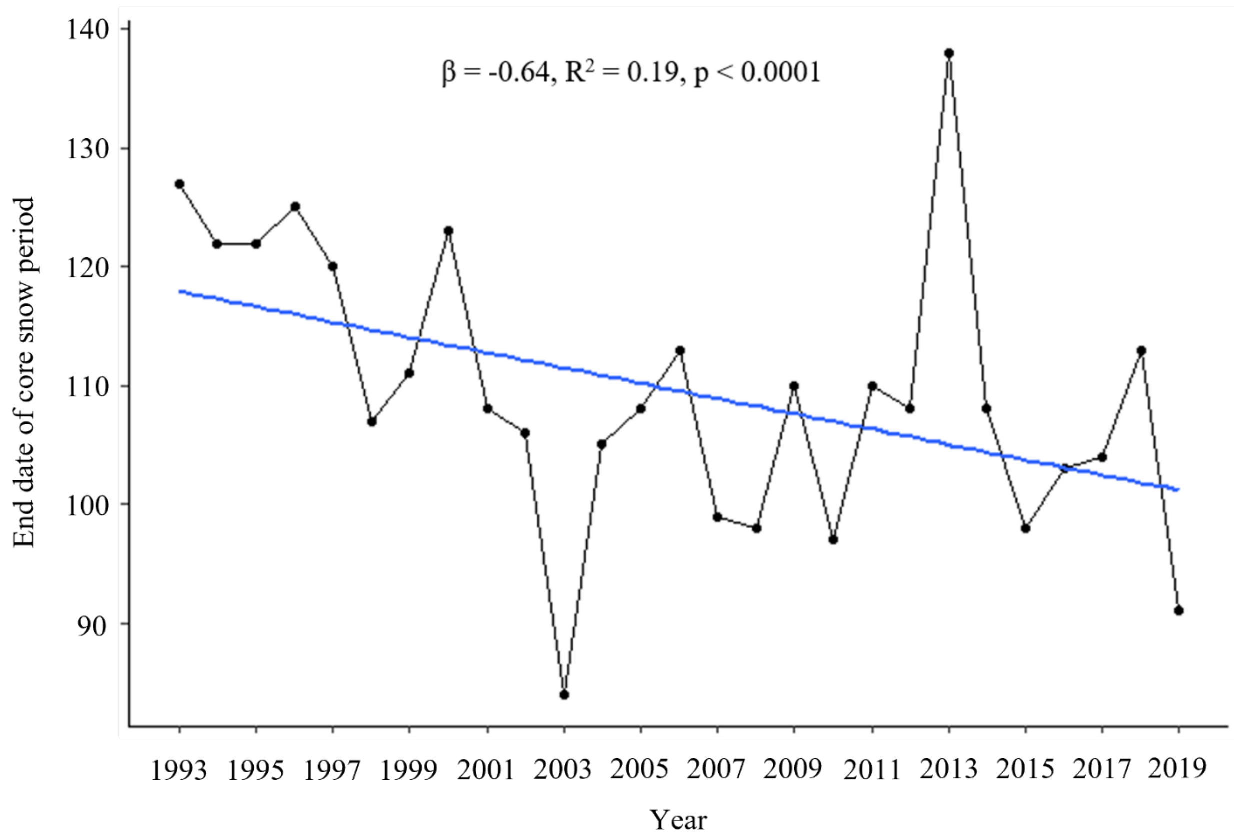

Figure 4. Trend in the end date of the core snow period in DOY (day of the year) during 1993–2019 estimated using a snow-evolution model (SnowModel) that used data from 5 National Oceanic and Atmospheric Administration (NOAA) weather stations, 1 Snow Telemetry (SNOTEL) station, and reanalysis data from National Aeronautics and Space Administration's (NASA) Modern-Era Retrospective Analysis for Research and Applications, Version 2 (MERRA-2). The slope (β), coefficient of determination (R^2), and *P*-value (p) are also displayed.

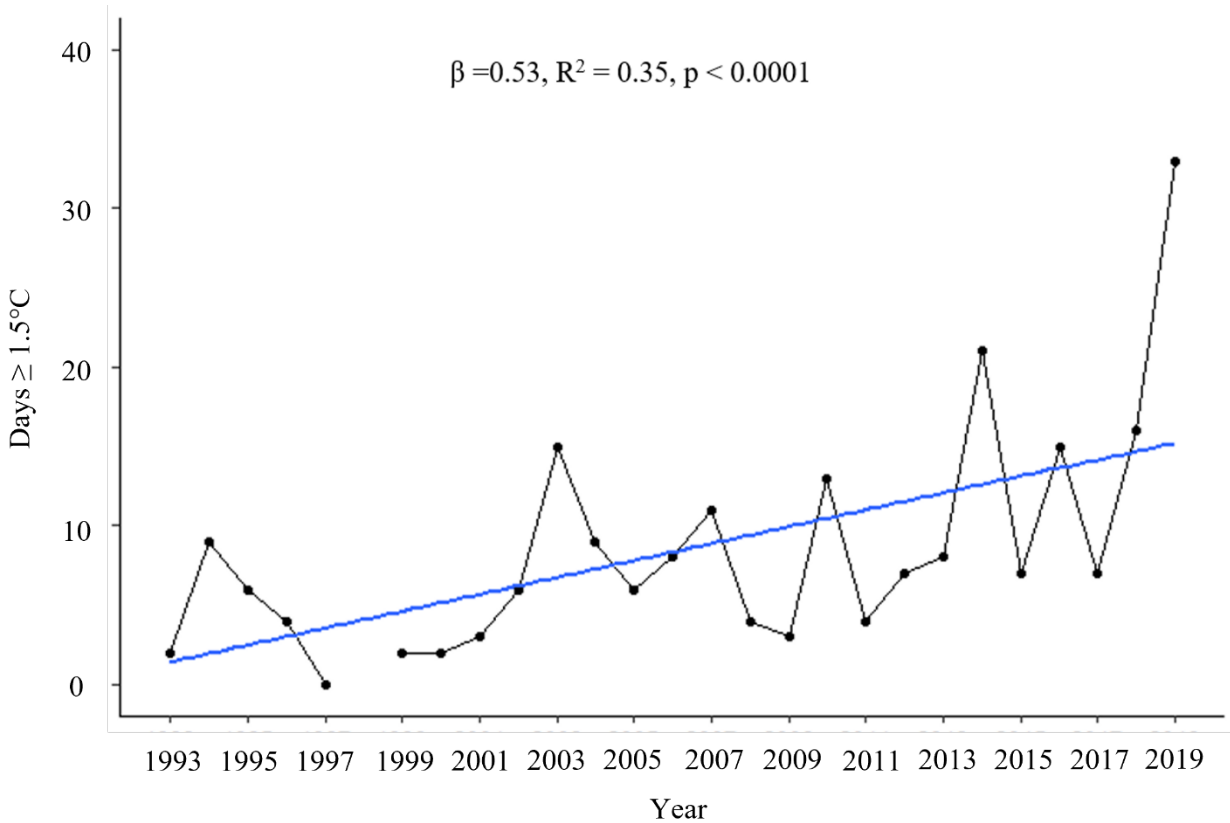

Figure 5. Trend in the number of days ≥1.5°C during winter (1 October–31 March). Data are from the meteorological weather station located in Nenana, Alaska. The slope (β), coefficient of determination (R^2), and *P*-value (p) are also displayed.

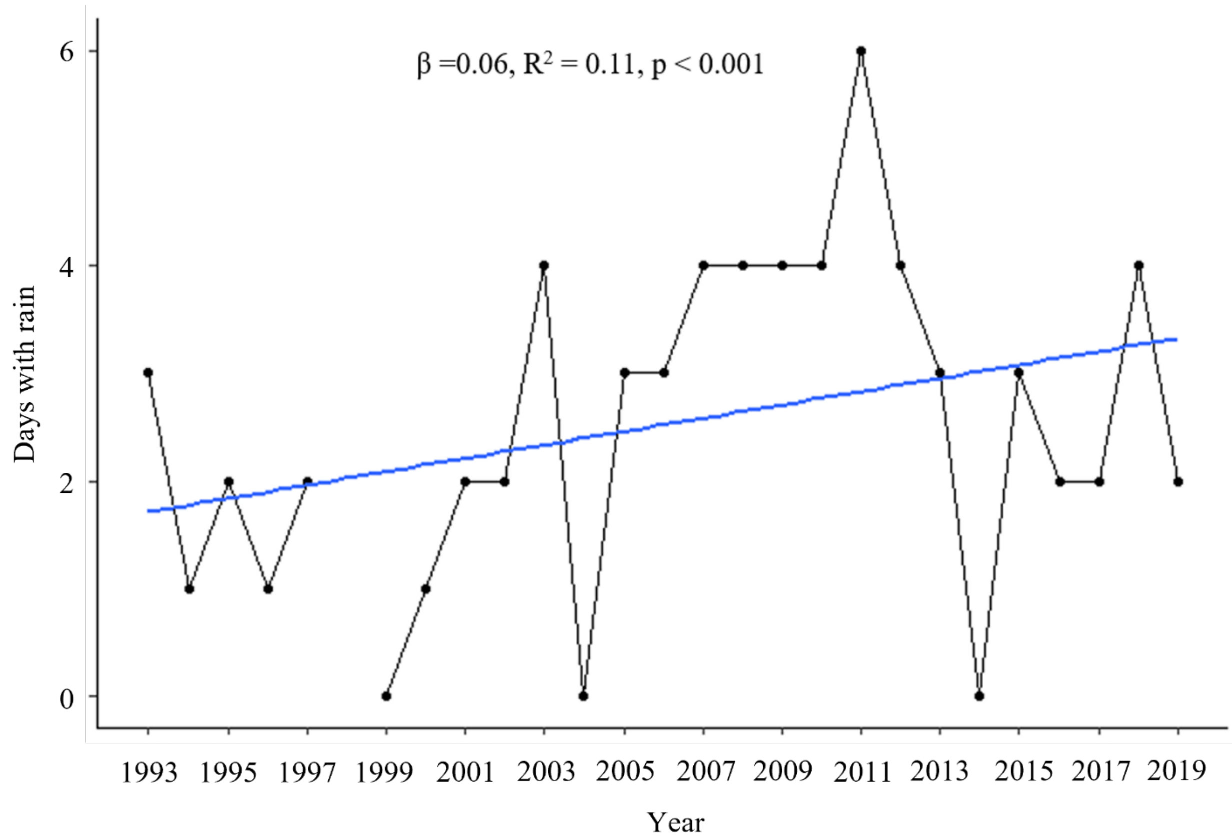

Figure 6. Trend in the number of rain days during the first 10 days of the brood-rearing period during 1993–2019. Data are from the meteorological weather station located in Nenana, Alaska. The slope (β), coefficient of determination (R^2), and *P*-value (p) are also displayed.

Effects of Weather on Ruffed Grouse

For the first step of model selection, 7 of the 22 models that included a single weather covariate ranked higher than the null model (Table 3). Three of those were highly correlated variables related to precipitation during the brood rearing period and 2 were highly correlated variables related to snow during the winter. Therefore, the highest ranked precipitation variable (JP.1) and the highest ranked snow variable (Snow), along with the variables DAT and End were retained for final analysis. The variables Snow and End were highly correlated and were therefore not included in the same model during the final step of analysis to avoid issues with collinearity.

Table 3. First step in model selection procedure for assessing relationships between weather and ruffed grouse population indices in Interior, Alaska, 1993–2019.

Model	K	AIC_c	ΔAIC_c	AIC_cWt	Cum.Wt	LL
JP.1 + (1|Year)	3	477.71	0.00	0.13	0.13	−235.73
Br.DP + (1|Year)	3	477.86	0.15	0.12	0.25	−235.81
Snow + (1|Year)	3	478.07	0.35	0.11	0.35	−235.91
TS + (1|Year)	3	478.69	0.97	0.08	0.43	−236.22
Br.TP + (1|Year)	3	478.89	1.18	0.07	0.50	−236.32
DAT + (1|Year)	3	479.38	1.67	0.06	0.56	−236.56
End + (1|Year)	3	479.57	1.85	0.05	0.61	−236.66
Null	2	479.63	1.91	0.05	0.66	−237.75

Note: Table only includes models with $\Delta AIC_c \leq 2$. Abbreviations and acronyms used in this table are defined as follows: K represents the number of parameters in the model; AIC is Akaike's Information Criterion (AIC; Akaike 1973); AICc is AIC corrected for small sample sizes (Burnham and Anderson 2002); Δ, the Greek letter delta, denotes change. In this case, the change in Akaike's Information Criterion with the top model having a value of 0 and all other values ranked relative to the top model; AICcWt represents the relative likelihood of a model; Cum.Wt is the cumulative weight of a specified model and those models ranked higher within a model set; LL is defined as the log likelihood; (1|Year) indicates that year is incorporated as a random effect in each model. The null model does not include any fixed effects (weather variables) but does include year as a random effect. Please refer to Table 1 for definitions of model variables listed under "Model".

There was high model selection uncertainty in the final step of analysis with the top 3 models having identical or near identical AIC_c values and Akaike weights (Table 4) with 11 of the 12 models falling within the 95% confidence set of models. Further, marginal and conditional R^2 estimates for the model containing the 3 explanatory variables JP.1, Snow, and DAT, were 0.06 and 0.17, respectively, indicating the proportion of the variance in ruffed grouse abundance indices explained by the fixed effects alone and the combination of fixed and random effects was low. That being said, there is some weak evidence that the weather variable JP.1, which is included in 4 out of the 5 models with ΔAIC_c values < 2 may influence ruffed grouse abundance indices negatively in Interior Alaska since the 95% confidence limits for the estimate of JP.1 did not overlap 0 (Table 5).

Table 4. Final model selection procedure for assessing relationships between weather and ruffed grouse population indices in Interior Alaska, 1993–2019.

Model	K	AIC_c	ΔAIC_c	AIC_cWt	Cum.Wt	LL
JP.1 + Snow + DAT + (1|Year)	5	476.69	0.00	0.17	0.17	−233.02
JP.1 + Snow + (1|Year)	4	476.69	0.00	0.17	0.34	−234.13
JP.1 + DAT + (1|Year)	4	476.71	0.02	0.17	0.50	−234.14
JP.1 + (1|Year)	3	477.71	1.03	0.10	0.60	−235.73
Snow + (1|Year)	3	478.07	1.38	0.08	0.69	−235.91
Snow + DAT + (1|Year)	4	478.72	2.03	0.06	0.75	−235.15
JP.1 + Snow × DAT + (1|Year)	6	478.86	2.18	0.06	0.80	−232.98
JP.1 + End + (1|Year)	4	478.98	2.30	0.05	0.86	−235.28
DAT + (1|Year)	3	479.38	2.69	0.04	0.90	−236.56
End + (1|Year)	3	479.57	2.88	0.04	0.94	−236.66
Null	2	479.63	2.94	0.04	0.98	−237.75
Snow × DAT + (1|Year)	5	480.90	4.22	0.02	1.00	−235.13

Note: Abbreviations and acronyms used in this table are defined as follows: K represents the number of parameters in the model; AIC is Akaike's Information Criterion (AIC; Akaike 1973); AICc is AIC corrected for small sample sizes (Burnham and Anderson 2002); Δ, the Greek letter delta, denotes change. In this case, the change in Akaike's Information Criterion with the top model having a value of 0 and all other values ranked relative to the top model; AICcWt represents the relative likelihood of a model; Cum.Wt is the cumulative weight of a specified model and those models ranked higher within a model set; LL is defined as the log likelihood; (1|Year) indicates that year is incorporated as a random effect in each model. The null model does not include any fixed effects (weather variables) but does include year as a random effect. Please refer to Table 1 for definitions of model variables listed under "Model".

Table 5. Parameter estimates and 95% confidence limits (CL) for the highest ranked model that included 3 weather variables.

Parameter	2.5% CL	Estimate	97.5% CL
(Intercept)	−1.27	−1.02	−0.78
JP.1	−0.51	−0.26	−0.01
Snow	−0.05	0.19	0.43
DAT	−0.46	−0.19	0.03

Note: Estimates were calculated using the bootstrap method. Please refer to Table 1 for definitions of model parameters listed under "Parameter".

Discussion

Weather variables considered in the analysis appeared to have little influence on ruffed grouse population indices from Interior Alaska from 1993 to 2019. There was some weak evidence that precipitation during the first 10 days of the brood-rearing period (JP.1) may negatively influence ruffed grouse abundance indices. This finding is consistent with other research that has found precipitation during the brood-rearing period to be negatively correlated with reproductive success in Capercaillie (Moss et al. 2001, Summers et al. 2004, Baines et al. 2016), rock ptarmigan (Novoa et al. 2008, Novoa et al. 2016) and white-tailed ptarmigan (Wann et al. 2016), and population growth rates in black grouse (Viterbi et al. 2015). However, at best, only 17% of the temporal variation in ruffed grouse abundance indices from Interior Alaska was explained by a model containing the weather covariate JP.1.

Weather trends indicate that winters have gotten warmer, and the arrival of spring has advanced in the last 25 years for the region encompassing the study area. It is possible that thresholds at which it would be possible to detect a strong effect of weather on ruffed grouse population abundance indices have not yet been reached in Interior Alaska. Advancement in the date of hatch has had varying effects on grouse and ptarmigan throughout their range, with negative effects seen in a population of black grouse (Ludwig et al. 2006), positive effects seen in a population of Capercaillie (Wegge and Rolstad 2017), and no quantifiable effects for a population of black grouse (Wegge and Rolstad 2017) and white-tailed ptarmigan (Wann et al. 2016). Although no data exist for ruffed grouse in Alaska, earlier snowmelt has resulted in advancement of nesting and hatching dates for rock ptarmigan. For example, hatching dates for a population of rock ptarmigan in Interior Alaska have advanced approximately 5 days from a mean hatch date of 21 June (range: 9 June to 5 July) during 1956 to 1970 (Shepherd and Weeden 1963, Ellison and Weeden 1965, Weeden 1965, Ellison and Weeden 1965, Ellison and Weeden 1966, Ellison and Weeden 1967, Ellison and Weeden 1968, McGowan and Weeden 1969, McGowan and Roseneau 1970, Weeden and Roseneau 1970) to 16 June (range: 12 June to 2 July) during 2016 to 2019 (C. Carroll, 2021 unpublished data; B. Wiltzen, Master's thesis, University of Alaska Fairbanks, *In prep*). However, it is unclear whether the advancement in nesting and hatching dates has had any effect on the rock ptarmigan population.

The large interannual variability in many of the weather variables may partly explain why no strong weather effects were found to influence ruffed grouse abundance indices in Interior Alaska. A stronger signal would most likely be observed if a string of "bad" years or "good" years were to occur. For example, 3 or 4 years of heavy rain during the first 10 days of the brood-rearing period would likely have an influence on population abundance indices due to several consecutive years of reduced chick survival resulting in poor recruitment. In addition, population abundance indices are likely less sensitive to the effects of weather than true estimates of abundance. Data from a similar study that used ruffed grouse population abundance indices from Minnesota found that the model with the most support was one that included an interaction between winter precipitation and mean minimum temperature with cold, snowless winters showing a negative association with ruffed grouse population indices (Zimmerman et al. 2008). However, the model only explained 17% of the temporal variation in ruffed grouse population abundance indices and the authors suggested future work should use robust estimators of ruffed grouse counts rather than indices. Repeat counts were conducted in most years for the Interior Alaska ruffed grouse population, making it possible to get yearly estimates of abundance using something akin to N-mixture models (Royle 2004). Future work should incorporate N-mixture models to get robust estimates of yearly abundance. In addition, other factors that likely influence the population dynamics of ruffed grouse in Interior Alaska should also be considered.

Predation is very likely a factor influencing ruffed grouse population dynamics in Alaska. Ruffed grouse populations in Interior Alaska follow an approximate 10-year population cycle, which is correlated with the snowshoe hare cycle, with ruffed grouse numbers declining 1–2 years prior to snowshoe hare numbers (Weeden 1965, Carroll and Merizon 2017). This is consistent with what has been documented in Alberta (Keith and Rusch 1989) and near Kluane Lake in southwestern Yukon (Martin et al. 2001) where declines in ruffed grouse numbers were associated with increased predation. In the Kluane region, long-term research has provided strong evidence that the snowshoe hare cycle is driven primarily by predators, including Canada lynx (*Lynx canadensi*s). The effect of high predation pressure acts both directly by increased mortality and indirectly through reduced reproduction by way of chronic stress due to constantly being pursued by predators (Krebs et al. 2017). Researchers suggested the decline in ruffed grouse numbers 1 to 2 years prior to the snowshoe hare decline was due to bycatch by predators when snowshoe hare numbers were still high (Martin et al. 2001).

Long-term data on the number of lynx harvested by trappers have been used to show the strong correlation and synchrony between snowshoe hare and lynx population cycles (Elton and Nicholson 1942, Keith 1963, Stenseth et al. 1997). Additional research has documented strong correlations between snowshoe hare numbers and abundance of other predators like coyotes, weasels, mink, goshawks, and great-horned owls (Boutin et al. 1995, Keith 1977, Keith and Cary 1991, O'Donoghue et al. 1997), many of which also prey on ruffed grouse and their nests. Thus, data on lynx harvested by trappers could be used as an index of general predator abundance and included in future work as a model variable to evaluate the importance of predation in influencing ruffed grouse population abundance indices or population abundance estimates.

Density-dependence is often a factor influencing cyclical populations and should be included in modeling efforts aimed at evaluating the effects of weather and other variables on population dynamics. Temporal autocorrelation structures can easily be incorporated into general linear models (GLMs) to account for density-dependent effects; however, this is not currently the case for mixed-effects models. Software implementation of autocorrelation structures is more limited in the R-package lme4. The R-package nlme does allow for the incorporation of an autocorrelation structure; however, it does not allow for the inclusion of an offset term, which was needed for this analysis. Although year was used as a random effect in the model to account for between-year variation in abundance indices, future work should directly incorporate density-dependence into models since many populations of ruffed grouse do exhibit a population cycle.

In summary, the ruffed grouse population near Anderson in Interior Alaska appears to be less sensitive to weather variables investigated here than many other populations of grouse and ptarmigan throughout their range. Nevertheless, changing environmental conditions are likely to have some influence on populations of grouse in Alaska. Continued research in Alaska on the effects of weather on grouse is critical as warming is projected to continue. Future work should 1) attempt to include additional variables known to affect populations of grouse, 2) use estimates of abundance rather than abundance indices, and 3) incorporate density-dependence into models.

Management Implications

This work was an important first step in evaluating the effects of weather variables on ruffed grouse population abundance indices in Interior Alaska. Weather alone does not explain annual changes in population abundance indices, although rainfall during the first 10 days of the brood-rearing period may have some influence on ruffed grouse abundance indices. It is very likely that there are weather thresholds that once met will begin to influence population abundance indices, but as of yet those thresholds do not appear to have been reached in Interior Alaska for the weather variables considered here. Since warming is projected to continue, it is important that managers continue to improve methods and extend long-term datasets in order to continue to evaluate the effects of weather and other factors on populations of grouse and ptarmigan.

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