Final Wildlife Research Report ADF&G/DWC/WRR-2018-1

Movement, Survival, and Nest Monitoring of Rock Ptarmigan in Game Management Unit 13B, 2013–2017

Richard A. Merizon, John P. Skinner, and Miles O. Spathelf

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Alaska Department of Fish and Game Division of Wildlife Conservation

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Cover Photo: Radiocollared male rock ptarmigan and hen along the Denali Highway, Alaska, May 2014. ©2014 ADF&G. Photo by Dale Rabe.

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Abstract

Ptarmigan hunting pressure in Game Management Unit (Unit) 13, Southcentral Alaska, is high, particularly where hunter accessibility is high along the Denali Highway in fall and winter. As a result, the Alaska Board of Game has considered several regulatory proposals since 2008 that address season dates and bag limits throughout Unit 13B. However, the Alaska Department of Fish and Game (ADF&G) has little information on potential effects of regulatory changes, spatial effects of harvest by humans, or population dynamics, particularly for rock ptarmigan (*Lagopus muta*) in Unit 13B. ADF&G studied rock ptarmigan movements, survival, and nesting behavior in Unit 13B between April 2013 and April 2017. We captured 102 adult and juvenile rock ptarmigan and fitted them with VHF radio necklace collars. Birds were relocated twice monthly between July and April. Females were closely monitored during nesting and brood rearing to document nest predation and chick recruitment. We found females (adults and juveniles) made the greatest movements primarily in the fall and spring whereas male movements tended to be less and within close proximity to their breeding territories throughout the year; most male movements were <5 km. Juvenile and adult female rock ptarmigan experienced higher mortality risk than adult males. Rock ptarmigan ≤3 km from a roadway experienced 28–286% higher risk of mortality than birds ≥3 km from a roadway. Overall mortality risk for juveniles, adult females, and adult males was greater and of similar magnitude in the spring (April–May) and fall hunting season (10 August–November) than during the summer (June–9 August) and winter (December–March) for birds ≤3 km from the highway, whereas fall risk for birds >3 km from roads was intermediate between spring risk and summer or winter risk. We monitored 13 rock ptarmigan nests throughout the nesting period with the use of motion-triggered cameras. Mean clutch size was 6.2 eggs, an average of 4.4 chicks departed the nest, and average brood size just prior to the start of hunting season was 2.4 chicks. Arctic ground squirrels (*Spermophilus parryii*) were found to be the dominant nest predator among all years. Our findings are consistent with previous research that has shown limited dispersal for ptarmigan and the tendency for harvest to be highly concentrated along roadways, with the implication that the breeding population in accessible areas could be depressed relative to remote areas.

Key words: harvest, hunting, *Lagopus*, mortality, movement, nesting, rock ptarmigan.

Introduction

Rock ptarmigan (*Lagopus muta*) and willow ptarmigan (*L. lagopus)* are important species in Alaska for subsistence and recreational hunters (Weeden 1965; McGowan 1973; Merizon and Carson 2013; Merizon et al. 2015). The 2 species remain among the most highly sought after upland bird species in Alaska (Merizon and Carson 2013; Merizon et al. 2015). Rock and willow ptarmigan occur throughout Alaska including alpine and tundra habitats. Rock ptarmigan also occur throughout the entire Aleutian Islands archipelago.

Despite their wide distribution and popularity among hunters, since the early 1970s, little has been done in Alaska to further understand rock and willow ptarmigan life history, movement, survival, population productivity, nesting ecology, or effects of various harvest strategies since Robert Weeden and Jerry McGowan's work in Interior Alaska (Weeden 1965; Weeden and

Watson 1967; Weeden 1968; McGowan 1975). However, others in Alaska have documented large-scale movements of specific ptarmigan populations throughout Alaska (Irving et al. 1967). Current knowledge on Alaskan rock and willow ptarmigan movement and vital rates has been gleaned from the work in the 1960s or from Canada, Scandinavia, Iceland, and Europe.

Rock and willow ptarmigan have been found to disperse long distance from natal areas occupied in the spring (Hörnell-Willebrand et al. 2014) despite strong breeding site fidelity (Schieck 1988). Dispersal among grouse has been documented to be largely sex-biased with females traveling greater distances than males (Schroeder 1986; Martin and Hannon 1987; Gruys 1993; Hörnell-Willebrand et al. 2014). Brøseth and Pedersen (2010) found no evidence to suggest hunting pressure affects dispersal patterns or the size of the area used by willow ptarmigan in Norway. Brøseth et al. (2005) also found that reductions in population density through harvesting does not seem to affect dispersal distances, thereby suggesting harvest may not be fully compensated by immigration despite higher densities in adjacent areas.

In the early 1970s, Alaska witnessed an economic surge with the development of the trans-Alaska oil pipeline. Alaska's population grew from approximately 260,000 in 1965 to approximately 420,000 in 1980 (State of Alaska 2015). The state continued to flourish through the 1980s and 1990s and with it so did the increased interest in hunting, fishing, and outdoor recreation. Most notably was the easy access for hunting and wintertime recreational opportunities near road accessible game management units like Unit 13 (Figure 1). Unit 13 is bounded on the west by the Parks Highway, on the east by the Richardson Highway, and bisected by the Glenn and Denali highways. It also has large urban centers to the south (Anchorage and the Matanuska-Susitna valley communities) and to the north (Fairbanks and Delta Junction). Much of Unit 13 affords easy off-road vehicle access throughout the year including all-terrain vehicles (ATV) and snowmobiles.

The popularity of hunting ptarmigan grew in Unit 13 particularly with the advent of improving off-road vehicle technology. As a result of the increasing popularity and accessibility of ptarmigan hunting in Unit 13, spring breeding, point-count surveys for rock and willow ptarmigan were initiated in 1992 as a means to index population abundance (Taylor 2013) by ADF&G-Division of Wildlife Conservation (DWC). These surveys were created and completed in Units 13E and 13B along the Denali Highway and near Isabel Pass on the Richardson Highway (Figure 1). These surveys documented a steady decline between 1999 and 2009 in the number of breeding male rock ptarmigan most notably within Unit 13B (Taylor 2013).

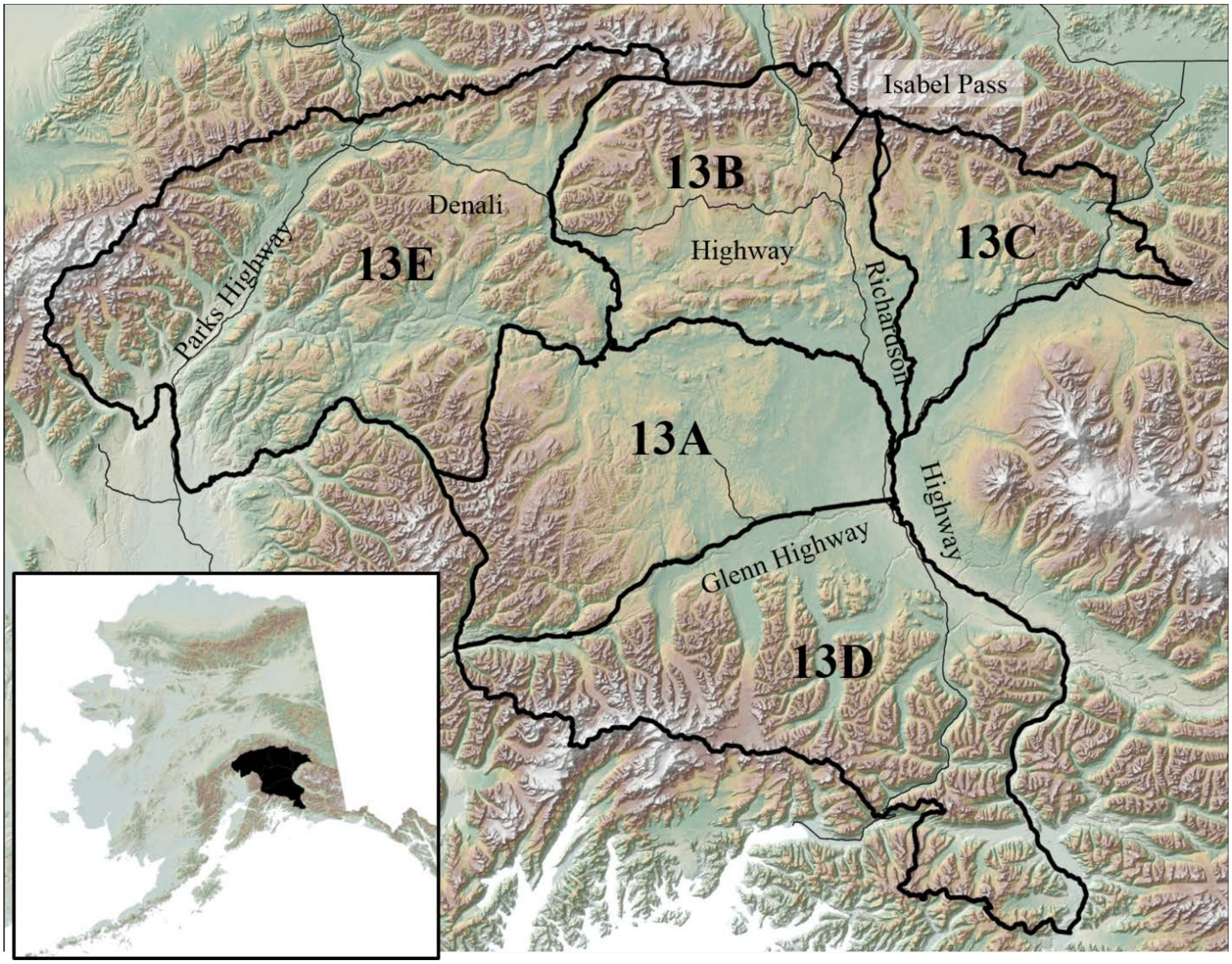

Figure 1. Game Management Unit 13, Southcentral Alaska.

Management concerns arose about what may be causing the declines including natural population cycles or harvest management and specifically liberal season dates and bag limits. Natural population cycles have been documented for various tetraonid populations in North America (McBurney 1989; Taylor 2013) and are often somewhat predictable over an 8–10 year period. However, Unit 13B rock ptarmigan exhibited a steady year over year decline for 10 consecutive years in the number of breeding males in the spring. Season dates have historically been liberal throughout Unit 13 (10 August–31 March) as were daily bag limits (10–20 ptarmigan/day). Contradictory evidence exists about the effects of season length and bag limits on ptarmigan populations both in Alaska and Norway. McGowan (1975) documented a 40% removal of the rock ptarmigan population in May from a small study area (7.5 km^2) in Interior Alaska did not affect the size of the breeding population the following year. However, counts of breeding males were only completed 1 year and this study occurred when off-road vehicle technology was much less advanced than over the past 10–15 years. Sandercock et al. (2011) recommended not exceeding a 15% reduction in the fall population to maintain a sustainable harvest provided annual chick production >2.5 per female. Beyond the 15% threshold was found to be additive mortality. They also recommended minimizing the additive mortality of winter harvest by closing seasons by early November or by reducing late season bag limits.

Hunter surveys are often used to gauge hunter effort and hunter success and provide a very rough index of wildlife abundance. In Alaska, small game hunter surveys were employed statewide in 2012 and 2014 (Merizon and Carson 2013; Merizon et al. 2015); however, harvest estimates were weak and did not accurately account for harvest in remote portions of the state, nor by specific units. Without nearly 100% harvest reporting compliance, even for small units, understanding the specific effects of harvest on ptarmigan populations will continue to be very challenging. However, trying to better estimate cause-specific mortality risk may provide insight into whether wintertime harvest may be compensatory or additive in Unit 13.

Increased hunter traffic utilizing improved off-road vehicle technology (Arlettaz et al. 2007; Patthey et al. 2008; Arlettaz et al. 2015) may be increasing the geographic extent of harvest. Over the past 40 years in Alaska, ptarmigan hunters have increased their access to areas that were once inaccessible through the use of improved off-road technology in both fall and winter. Currently, evaluating the effects of off-road technology on various ptarmigan populations across Alaska is very difficult.

Due to continued decline of rock ptarmigan in Unit 13B, in spring 2009 the Alaska Board of Game shortened the season duration by 4 months; from 10 August–31 March to 10 August–30 November (Taylor 2013). However, until this study was initiated in spring 2013, no effort had yet been attempted by DWC to take advantage of the unique opportunity to evaluate rock ptarmigan movement, vital rates, and closely examine a population with lower risk of harvest mortality when compared to other adjacent units (Units 13A, 13C, and 13E) with considerably longer seasons. Federal subsistence regulations still allowed a season closure of 31 March in Unit 13B despite the shorter season regulated by the state (30 November closure). However, overall rock ptarmigan harvest was anticipated to be low due to the restricted geographic extent of designated federal subsistence hunt areas and observed habitat use of rock ptarmigan through existing spring breeding surveys (Figure 2).

This study was designed to address 3 primary components of population management. One, annual movement patterns between seasons and demographic groups. Two, mortality rates between season, demographic groups, and in relation to distance from hunter-access corridors (i.e., roadways). Three, monitor nesting behavior and success. In order to achieve these objectives, rock ptarmigan were captured and fitted with a VHF radio necklace collar. Nesting behavior was evaluated through the use of motion-sensitive digital cameras and closely monitoring radiocollared females.

Study Area

This research was conducted in Unit 13B, which is largely undeveloped and is thus extremely popular for a wide variety of big game and small game hunting, fishing, hiking, and off-road vehicle access. The primary landowners within this study area are the State of Alaska, U.S. Bureau of Land Management, Ahtna Native Corporation, and small private inholdings.

This unit is 10,060 km^2 and is bisected by the Richardson Highway on the east and the Denali Highway from east to west through the middle of the unit and the upper Susitna River on the west (Figure 2). Unit 13B had a diverse suite of vegetation communities. Based on observed

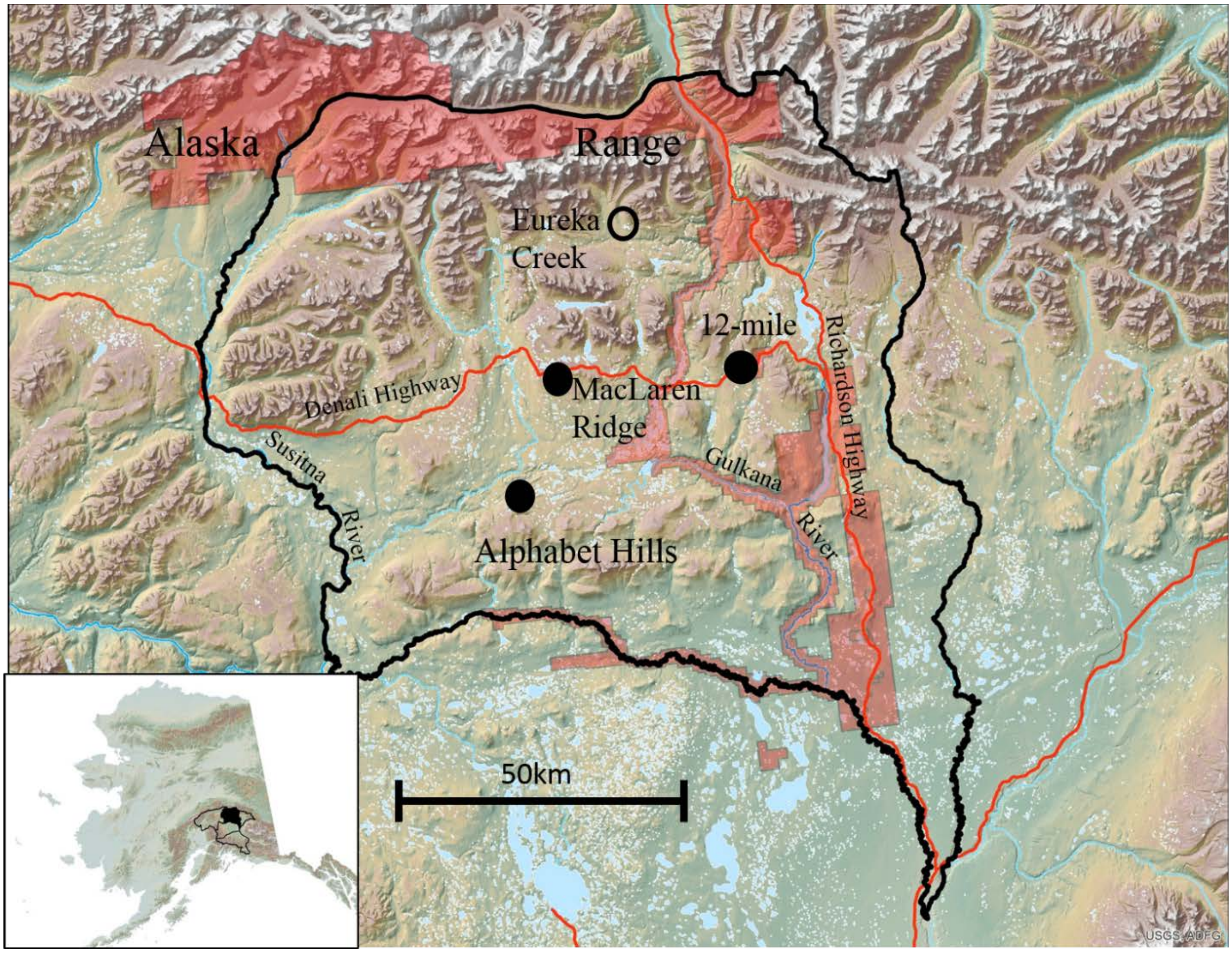

Figure 2. Map of Game Management Unit 13B, Southcentral Alaska, and the sites used to capture and radiocollar rock ptarmigan (solid circles). Eureka Creek was examined but not used as a capture location (open circle). Federal subsistence hunt areas are also shown (red shading).

habitat characteristics, the southern tip of the unit was largely composed of black spruce (*Picea mariana*) and resin birch (*Betula glandulosa*), numerous small lakes, and the Gulkana River. Much of the area adjacent to the Denali Highway (300–950 m) was composed of white spruce (*P. glauca*), resin birch, and willow (*Salix* spp.). The remainder of the unit including the foothills of the central Alaska Range and the Alphabet Hills (750–1,600 m) was composed of alpine vegetation communities including dwarf arctic birch (*B. nana*), crowberry (*Empetrum nigrum*), blueberry (*Vaccinium* spp.), alpine bearberry (*Arctous alpina*), bell heather (*Phyllodoce* spp.), and a variety of lichen species. Much of the alpine habitat that was occupied by rock ptarmigan also had boulder fields, scree slopes, or rock hilltops of various sizes interspersed with these high alpine vegetation communities. The climate was typical of the Alaska Range with cool summers (0–20°C), cold winters (−30 to 0°C), and moderate snowfall (2–4 m).

Ptarmigan were captured and collared at 3 primary sites within Unit 13B (Figure 2). One, an unnamed lake on the north side of the Alphabet Hills was 20 km from the nearest roadway. The alpine lake (1,035 m) was surrounded by resin birch stands to 1,060 m elevation with adjacent peaks and ridges ascending to 1,200 m. Two, 12-mile was a low angle ridge running from the Denali Highway (1,140 m) to a suite of hills 4 km north of the roadway ascending to 1,500 m. Surrounding habitat was composed of willow and dwarf arctic birch to rock scree, lichen, and crowberry at the highest elevations. Finally, MacLaren Ridge was an east-west oriented ridge immediately south of the Denali Highway east of the MacLaren River. Elevation ranged from 1,250 m to 1,440 m and had similar vegetation communities as 12-mile.

Methods

Capture and Radiocollaring

Male and female rock ptarmigan were captured during the spring breeding season (late April–May) and late summer to fall (early August through mid-October) annually between April 2013 and August 2016. Although efforts were made in the winter no birds were captured. No effort was made to capture birds during the nesting or brood rearing period (late May–late July; Weeden 1965; Potapov and Sale 2013).

Capture sites were chosen based on meeting the following 3 conditions. One, it could be reliably accessed by field crews every year regardless of spring snow melt conditions that were typical of the breeding season. Two, if it was remote, the site was near a lake that developed sufficient ice to allow safe access by aircraft with wheel-ski landing gear during spring melt. Three, it was within 2–5 km of known rock ptarmigan breeding habitat. During the course of this study only 3 sites, 12-mile, MacLaren Ridge, and Alphabet Hills (Figure 2), met all 3 requirements. On 26 and 27 April 2015 an attempt was made to capture and radiocollar rock ptarmigan near upper Eureka Creek (Figure 2; tributary of the Delta River). However, no rock ptarmigan were found and movement on the ground was restricted by deep snow (2–3 m) and subsequent capture efforts at that location were canceled.

Birds were captured using 4 techniques. First, during the breeding season, male rock ptarmigan were visually located defending their territories. Field crews moved into the territory and placed handmade noose carpets (Anderson and Hamerstrom 1967; McGowan and Simons 2005; Sutherland et al. 2010) in the middle of the territory adjacent to a mounted male rock ptarmigan decoy. Noose carpet panels were made of 5×10 cm weld-wire poultry fencing with 60–80 monofilament (2.5–3.5 kg test) nooses affixed with equal spacing on the panel. A Primos Alpha Dogg™ game caller was placed between 1 m and 3 m away from the decoy and was used to elicit a defensive response from the male rock ptarmigan using a prerecorded territorial male call (Peyton 1999; Taylor 1999; Carroll and Merizon 2014). The bird's toes would become entangled in the nooses upon approach to the decoy. Second, a Coda Enterprises™ shoulder-fired net gun was used to capture both males and females during the spring breeding season and during the fall. A .308 caliber blank was used to propel a 3.1 m×3.1 m net with 5 cm mesh attached to 4 steel, 5 cm projectiles. The effective range of this device was up to 9.5 m. Third, a fiberglass, B-n-M Black Widow™ 6.2 m telescoping noose pole was used to capture females during both the breeding season and fall capture periods (Braun et al. 2011). Birds were approached slowly and a rubber wire noose was fixed around the neck. Once captured a second crew member quickly approached the bird to alleviate the pressure of the noose and free the bird. Finally, in the fall, juveniles and uncollared adults were located by the previously collared member(s) of the same group and corralled into a 24 m×1.5 m black net by crews on foot. The net had 5 cm mesh and was strung using local woody vegetation. The net would be positioned at a 45° angle to the ground so that birds would travel under the net before becoming entangled in the loose portion of net adjacent to the ground (Silvy and Robel 1968). This technique was used with 2–3 field crew members to avoid birds having prolonged struggles in the net when multiple birds were captured in a single drive. All potential capture and marking methods were fully evaluated and compliant with Institutional Animal Care and Use Committee (IACUC) certification (2013-13).

To avoid prolonged handling periods all field crew members were trained in properly handling birds, data collection procedures, and efficiently applying radio collars. Once captured all birds were placed in a small cotton bag and weighed to the nearest gram. Age was determined based on pigmentation of the outer primary wing feathers (Bergerud et al. 1963); birds were classified as either hatch year (HY), second year (SY), or after second year (ASY). Sex was determined by external plumage characteristics. Finally, a VHF Advanced Telemetry Systems™ (ATS) 3950 radio collar (149.000–154.000 MHz) was fitted around the bird's neck. Collars transmitted at 35 beats per minute (bpm) while the bird remained active but switched to 70 bpm (mortality signal) when the bird became motionless for ≥6 hours. The collars weighed 12 g and were secured by a small aluminum crimp allowing for crop expansion. Birds were released at the point of capture. Capture time and location were recorded with a handheld Garmin™ Etrex GPS using WGS84 datum. Studies on red grouse (*L. l. scoticus*) or rock ptarmigan showed no evidence that radio necklace collars affected bird survival or movement patterns (Cotter and Gratto 1995; Thirgood et al. 1995). No tissue or blood samples were collected.

RELOCATION SURVEYS

Radiocollared rock ptarmigan were relocated using several different methods and schedules but the exact timing of surveys varied depending on weather and other logistics. All collared birds were relocated by ground telemetry within 24–48 hours of release to determine capture-related mortality or injury. An ATS R8000 or a Communications Specialist™ R1000 receiver and a single 4-element Yagi antenna were used for ground telemetry. Collared rock ptarmigan were included in the study only if they were relocated alive >48 hours after release. Females captured during the spring were relocated beginning in late May to determine nesting status via ground telemetry. If females were found incubating eggs an intensive period of nest monitoring began and they were monitored until they departed the nest for the final time. Beginning in mid- to late July all radiocollared rock ptarmigan were relocated twice monthly through April and monthly in May and June using aerial telemetry. Aerial relocation surveys were performed using a Piper PA-18 Super Cub equipped with an ATS R8000 receiver and a 4-element Yagi antenna mounted to each wing strut.

When relocated, a bird was classified as alive if its VHF radio pulse rate indicated activity or dead if one of the following conditions were met: 1) a mortality signal was heard with no return to an alive signal during subsequent surveys; 2) a signal was never again heard after having gone missing with <330 days of collar battery usage and during open hunting season; or 3) the bird was reported as harvested. ADF&G contact information was printed on the back of each radio necklace collar for hunters to report if they harvested a collared bird. Most collars transmitting a mortality signal within 8 km of a roadway were collected and a determination was made as to whether death was likely caused by harvest or nonharvest factors (e.g., predation, disease, exposure, etc.).

Movement and Distribution Analysis

Elevation (m) and aspect were recorded for each bird on each survey using Alaska National Elevation Dataset (U.S. Geological Survey 2017). For the movement and survival analysis, each relocation was categorized as one of the following seasons: spring (April–May); summer (June–9 August; the day before the hunting season); fall (10 August–November; the duration of the hunting season in Unit 13B); and winter (December–March). Directionality of rock ptarmigan movements were defined as north (337.5°–22.5°), northeast (22.5°–67.5°), east (67.5°–112.5°), southeast (112.5°–157.5°), south (157.5°–202.5°), southwest (202.5°–247.5°), west (247.5°–292.5°), and northwest (292.5°–337.5°). Movement rates and directions were analyzed with ArcGIS™ 10.3.1 Tracking Analyst extension (Esri, Redlands, California). A chi-square test was conducted to determine if there was a significant difference in directionality of movement between seasons.

Spatial distribution estimation of rock ptarmigan within Unit 13B were delineated using both recorded elevation values and kernel density estimation (KDE). Elevation-based distributions used observed location elevation values for rock ptarmigan and then applied those elevations ranges to a 5 m digital elevation model (U.S. Geological Survey 2017) of Unit 13B. KDEs were completed using point locations from radiotelemetry surveys. KDEs were computed using Geospatial Modeling Environment (Beyer 2015) with a 15 m grid and the plug-in bandwidth estimator (Bowman and Azzalini 1997).

Seasonal changes in elevation use by ptarmigan were estimated using a generalized additive mixed model (GAM). Elevation (response variable) was modeled against day of year (DOY), as a cyclic penalized cubic regression spline smoothed variable, and ptarmigan age-sex class, as a categorical variable, using package ‘mgcv’ (Wood 2006) in R (version 4.2.3). Random intercept and slope effects were included for bird identifier to account for correlated observations.

Survival Monitoring Analysis

Ground-based recovery attempts were made for all radio collars transmitting a mortality signal; however, due to limited staff time and project finances there was no effort made to collect collars ≥8 km from an access point. Once the collar was recovered, the site and collar were assessed for cause of mortality. Cause-specific mortality was difficult to determine if a collar could not be recovered within 1 day of the mortality event. The date a bird exited the study was either the date of harvest (if reported) or the date midway between the date last known alive and date considered dead or first determined to be missing. If a rock ptarmigan was missing under other circumstances not listed, it was considered alive on date of exit (i.e., right-censored).

Ptarmigan movement and survival were analyzed for each interval between survey dates (survey period) and the later date of each period was used to indicate the season as described under Methods | Movement and Distribution Analysis, this document. Furthermore, if the bird was found ≤3 km of a roadway (e.g., Denali or Richardson highway) during an open hunting season, it was considered to be in a “high access” area during the interval.

Environmental variables, including temperature and precipitation, were used to describe each survey period based on data from National Oceanic and Atmospheric Association weather stations. Temperature (C) was calculated as the average of daily average temperatures in Paxson, Alaska (62.945°N, −145.501°W) and precipitation (mm) was calculated as the average of daily average precipitation reported at Monahan Flat, Alaska (63.310°N, −147.650°W).

Survival functions were examined using the Kaplan-Meier estimators (Kaplan and Meier 1958) and risk factors associated with rock ptarmigan mortality were estimated using Cox proportional hazards (CoxPH) models with time-dependent covariates (Therneau and Grambsch 2010). Modeling was carried out using the "survival" R-package (Therneau 2015) in association with R-software (version 3.4.1; R Core Team 2016). The response variables for these models were produced from rock ptarmigan encounter histories that included DOY at the start and end of each survey period and the bird's fate (0 = alive, 1 = dead). Survey periods that extended across 2 years were split into 2 independent encounter histories with one censored on the last day of the year and the other beginning on the first day of the next year. A global CoxPH was constructed to associate survival outcome during each survey period with continuous predictor variables temperature and precipitation, categorical variables for age-sex (3-levels; male ≥1 yr, female ≥1 yr, and juvenile <1 yr), year (5-levels), and season (4-levels), and a dummy variable (0 or 1) indicating whether the bird was in "high access" during the interval. For model fitting, a robust sandwich variance estimator was used to account for multiple radio deployments on a single bird.

To determine which predictor variables were statistically important we used a best subsets approach (multi-model selection; Burnham and Anderson 2002) based on second order Akaike information criterion (AICc). We generated a set of candidate models which included "season" and subsets of all other predictor variables from the global model. These candidate models were then fit and ranked by AICc (lowest to highest). The top ranked model was considered to be the best suited candidate model for describing mortality risk although any candidates within 2 AICc units (Δ_{ic}) of the top model were also considered based on the fact that they would be considered statistically equivalent (Burnham and Anderson 2002).

The best suited candidate model was used to calculate relative risks and hazard ratios. Relative risk was calculated as the model estimated risk associated with any condition or group divided by the average risk in the population. Hazard ratios where calculated as the ratio of relative risks for any 2 groups. Hazard ratios are useful because they describe the increased (>1) or decreased (<1) relative risk of group A (numerator) compared to group B (denominator). Subtracting '1' from a hazard ratio and dividing by 100 provides an estimate of the percentage difference in mortality risk in group A compared to group B.

NEST MONITORING

Upon completion of spring capture efforts, females were relocated using ground-based radiotelemetry between 25 May and 10 June to determine nesting status. Beginning in 2014, once a female was located on a nest, a Reconyx^{TM} Hyperfire HC500 motion-sensitive digital camera was placed within 1–2 m of the nest mounted to a camouflaged aluminum t-post. Based on a literature search, this technology had not been used to monitor ptarmigan nests and nesting behavior. Digital images were stored on a 32GB removable memory card. Cameras were placed ≤10 cm above the immediately surrounding vegetation and often below surrounding vegetation. Adjacent vegetation was also used to further camouflage the camera and the post upon which it was mounted. Cameras were triggered either by motion or infrared heat differential within the frame. Cameras were programmed to take a 3 photo burst upon being triggered with a 1 second delay between bursts. Each photo included date, time, temperature, and moon phase. Camera angle was tested and tuned by examining images using a field laptop during deployment.

Nest site location data were recorded and included vegetation type and height at the nest, within 2 m of the nest, and within 10 m of the nest, elevation, aspect, and GPS location. Field crews attempted to keep each nest visit to within 4 minutes to minimize attention to the nest location and stress to the incubating female. Females were not flushed to determine number of eggs; instead, the number of eggshell fragments were recorded after the nest was abandoned. This provided a minimum count that was then checked against photos taken of the departing brood. Most females were reluctant to leave the nest when deploying or checking cameras. Cotter and Gratto (1995) found no difference between disturbed and undisturbed rock ptarmigan nests relative to predation, clutch size, and nesting success.

Field crews revisited each nest and camera every 7–10 days to replace memory cards and check on nesting status. Once nests were found vacant, overall condition of the nest was evaluated for harassment and the number of whole eggs and shells were counted to determine total clutch size and cameras were removed. Images were closely reviewed and daily behavior logs were created for each female including time and frequency of daily departure, time, frequency of nest harassment or predation, weather, and climatological patterns recorded by the photos, time and date of first chick observation, number of chicks departing the nest, and time and date of final brood departure from the nest.

Potopav and Sale (2013) documented a 21–24 day incubation period for ptarmigan which we used to estimate the date of incubation initiation from the hatch date that was documented from the cameras.

Throughout the remainder of the brood rearing period, broods were relocated 1–2 times by ground telemetry to determine scale of movement and chick survival. Broods were then relocated immediately prior (3–8 August) to the hunting season (10 August) to determine recruitment rates into the hunted population.

Results

Capture and Radiocollaring

A total of 102 rock ptarmigan (48 females, 53 males, and 1 unknown sex) were captured and fitted with a VHF radio collar between May 2013 and August 2016 (Table 1); a total of 27 at MacLaren Ridge, 15 in the Alphabet Hills, and 60 at 12-mile. Males were caught at a higher proportion in the spring than the fall (Table 1). This was largely the result of aggressive male breeding behavior.

Spring capture periods varied by year (22 May–10 June 2013, 7–17 May 2014, 3–21 May 2015, and 27 April–19 May 2016). Late-summer-fall capture periods also varied by year (10 October 2013, 7 August–17 September 2014, 4–24 August 2015, and 22–26 August 2016). Spring captures in 2013 were delayed due to late, deep snow (2–3 m), and cessation of breeding activity before 22 May. However, breeding activity between 2014 and 2016 appeared to coincide with long-term historical timing.

The shoulder-fired net gun was the most time efficient and successful capture method (47% of captures; n = 48) attempted in terms of times attempted versus number of rock ptarmigan captured (Table 2). However, drive netting proved to be very effective at capturing HY and adult rock ptarmigan in the late-summer-fall.

Average weight of adult females ($\bar{x}$ = 454 g; SE = 42 g) was not significantly different from adult males ($\bar{x}$ = 445 g, SE = 24 g; t-test, t = 0.242, P = 0.5). Breeding females were not significantly heavier in the spring ($\bar{x}$ = 465 g; SE = 41 g) than the fall ($\bar{x}$ = 432 g; SE = 38 g; t = 0.022, P = 0.05).

MOVEMENT

A total of 67 aerial relocation surveys were completed between 2013 and 2017 (Table 3). A variety of ground tracking was also performed to locate recently collared individuals or potentially nesting females. During the study, aerial surveys for radiocollared rock ptarmigan resulted in 502 relocations from 49 males, 279 relocations from 41 females, and 72 relocations from 12 juveniles. The lowest elevation recorded was 882 m and highest was 1,612 m.

Analysis of ptarmigan average daily movement on a logarithmic scale (ANOVA, F = 4.07, P = 0.01) showed that there was no marginal effect of sex (F = 1.72, P = 0.19) but a significant effect of season (F = 12.0, P<0.01) and an interactive effect of sex*season (F = 4.07, P = 0.01) on ptarmigan movement rates (log km/day). Using a Tukey HSD test, spring (P>0.01) and fall (P>0.01) females moved at significantly higher estimated daily rates (km/day) than summer females (Figure 3). Females tended to move away from breeding and brood rearing areas in the fall, be fairly sedentary during the winter and generally return to breeding areas in the spring (Figure 4). Also, fall males (P>0.05) moved at significantly higher estimated daily rates than summer males (Figure 5). Males tended to move much shorter distance than females regardless of season or age (Figure 6).

Maximum estimated daily movements occurred among adult (ASY) females in the spring (5.6 km) and fall (2.7 km; Figure 3). However, large movements were also documented for HY and SY females in the fall (1.4 km and 2.9 km respectively) and spring (3.3 km and 2.2 km respectively). Maximum estimated daily movement among males occurred during fall (2.9 km; Figure 5) but estimated daily movements >2 km were rare.

Overall, there was very little interchange of monitored breeding male or female rock ptarmigan between breeding populations at 12-mile, Alphabet Hills, and MacLaren Ridge. Individuals that were known breeding birds at one location tended to return to the same or similar location the following year. Ninety-six percent (n = 23) of all rock ptarmigan that had multi-year location information returned to the same location each spring for the duration of the study (7 females, 16 males).

Table 1. Demographic data for all rock ptarmigan captured and radiocollared during the study, Unit 13B, Southcentral Alaska, 2013–2017. Spring refers to all capture efforts in April and May; Fall refers to all capture efforts between August and October. HY = hatch year, SY = first breeding season, ASY = after second year (i.e., adult), and SY+ASY = all non-hatch year birds.

2013	Spring				Fall				
	SY		ASY		HY		SY+ASY		2013
Location	Male	Female	Male	Female	Male	Female	Male	Female	Total
12-Mile Ridge	2	1	3	1	0	0	0	1	8
MacLaren Ridge	0	0	1	0	0	0	0	0	1
Alphabet Hills	0	0	0	0	0	0	0	0	0
Total	2	1	4	1	0	0	0	1	9

2014	Spring				Fall				
	SY		ASY		HY		SY+ASY		2014
Location	Male	Female	Male	Female	Male	Female	Male	Female	Total
12-Mile Ridge	6	0	4	2	0	0	0	4	16
MacLaren Ridge	1	1	0	1	0	0	0	0	3
Alphabet Hills	2	0	4	0	0	0	0	0	6
Total	9	1	8	3	0	0	0	4	25

2015	Spring				Fall					
	SY		ASY		HY			SY+ASY		2015
Location	Male	Female	Male	Female	Male	Female	Unkwn	Male	Female	Total
12-Mile Ridge	2	4	4	4	0	0	1	0	1	16
MacLaren Ridge	0	0	3	2	2	2	0	1	2	12
Alphabet Hills	1	0	0	0	0	0	0	0	0	1
Total	3	4	7	6	2	2	1	1	3	29

2016	Spring				Fall				
	SY		ASY		HY		SY+ASY		2016
Location	Male	Female	Male	Female	Male	Female	Male	Female	Total
12-Mile Ridge	2	5	4	1	0	1	3	4	20
MacLaren Ridge	2	2	0	0	2	4	0	1	11
Alphabet Hills	0	0	4	4	0	0	0	0	8
Total	4	7	8	5	2	5	3	5	39

ALL YEARS	Spring				Fall					
	SY		ASY		HY			SY+ASY		
Location	Male	Female	Male	Female	Male	Female	Unkwn	Male	Female	Total
12-Mile Ridge	12	10	15	8	0	1	1	3	10	60
MacLaren Ridge	3	3	4	3	4	6	0	1	3	27
Alphabet Hills	3	0	8	4	0	0	0	0	0	15
Total	18	13	27	15	4	7	1	4	13	102

Table 2. Summary of successful rock ptarmigan capture methods for all years, Unit 13B, Southcentral Alaska, 2013–2017.

Method	Total	Percent
Net gun	48	47
Drive net	36	35
Noose carpet	10	10
Noose pole	8	8
Total	102	100

Table 3. Number of rock ptarmigan aerial surveys by month and year, Unit 13B, Southcentral Alaska, 2013–2017.

	Number of aerial surveys					
Month	2013[a]	2014	2015	2016	2017[b]	Total
January	NS[c]	1	2	2	2	7
February	NS[c]	NS[c]	2	1	2	5
March	NS[c]	NS[c]	2	2	1	5
April	NS[c]	NS[c]	2	1	2	5
May	NS[c]	2	1	NS[c]	NS[c]	3
June	1	NS[c]	NS[c]	1	NS[c]	2
July	1	1	1	1	NS[c]	4
August	1	1	2	2	NS[c]	6
September	2	2	2	2	NS[c]	8
October	1	2	2	2	NS[c]	7
November	2	2	2	2	NS[c]	8
December	1	2	2	2	NS[c]	7
Total	9	13	20	18	7	67

[a] Capture work began in May 2013 and aerial surveys began in June 2013.
[b] All aerial surveys were completed in April 2017.
[c] NS = no survey.

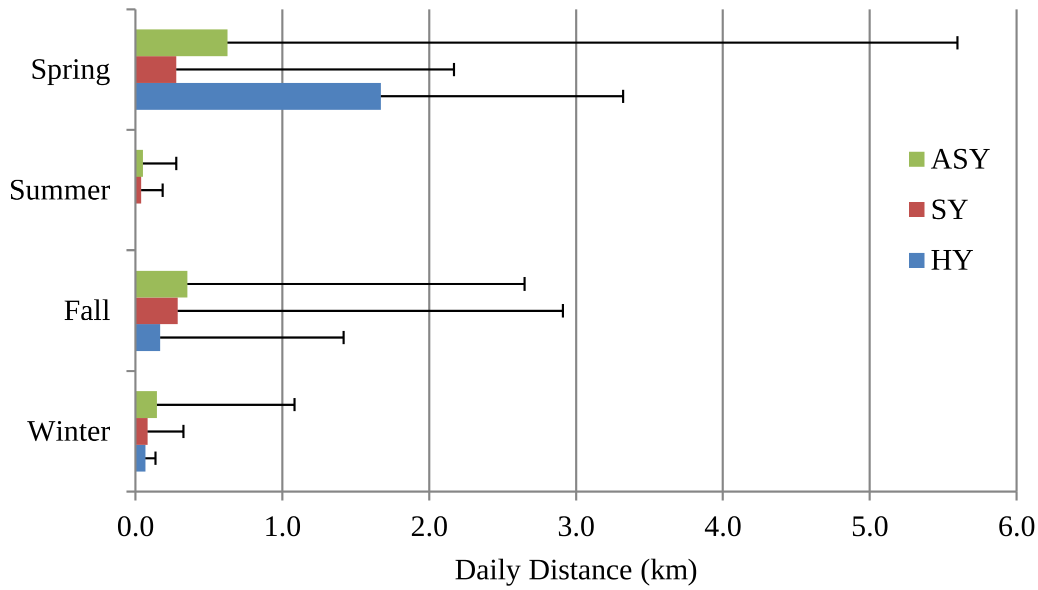

Figure 3. Daily average (columns) and maximum (lines) distance (km) traveled by female rock ptarmigan by season and age, Unit 13B, Southcentral Alaska, 2013–2017.

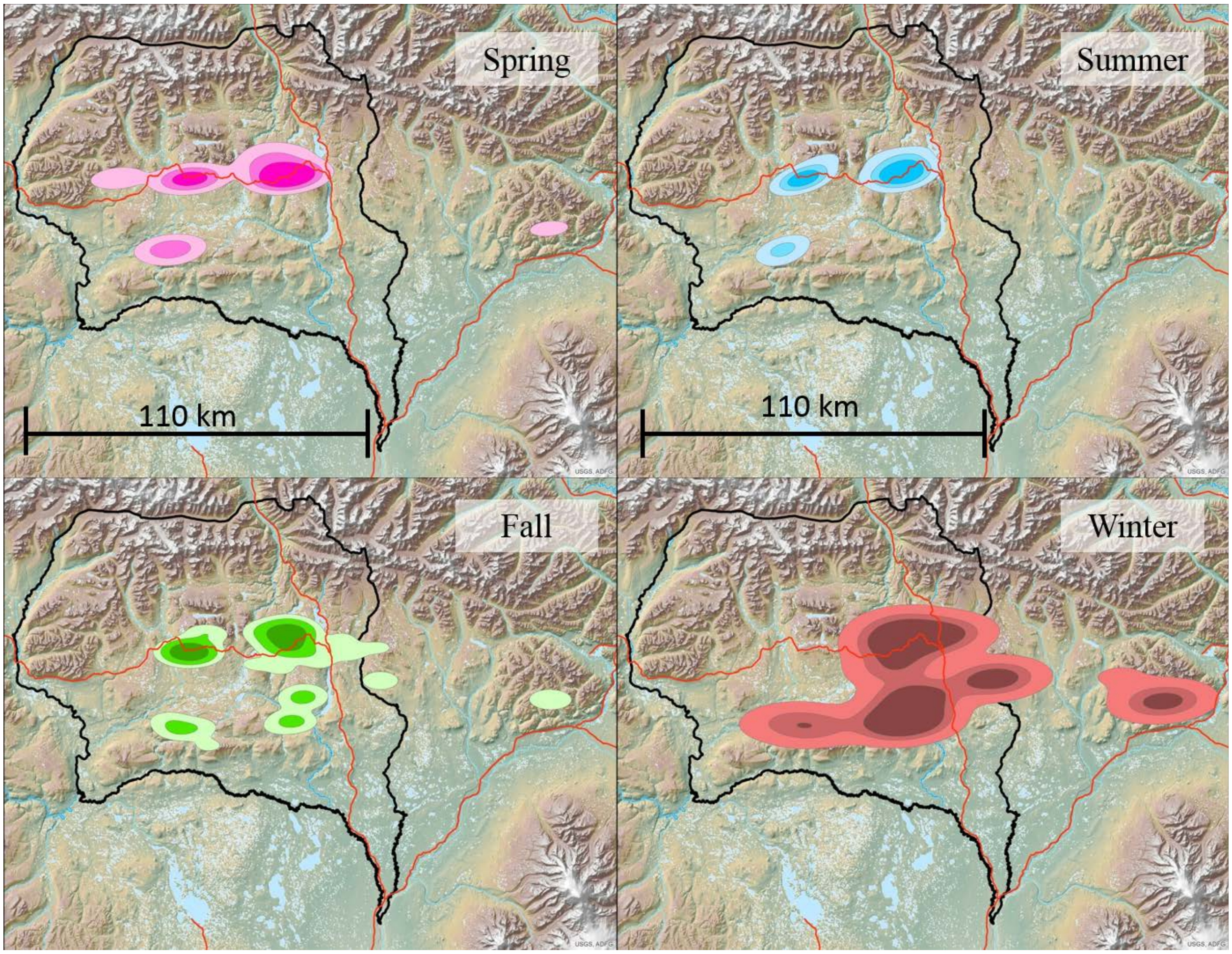

Figure 4. Female rock ptarmigan seasonal kernel density estimate movement maps using all relocation data by season with 50%, 75%, and 95% isopleth intervals, Unit 13B, Southcentral Alaska.

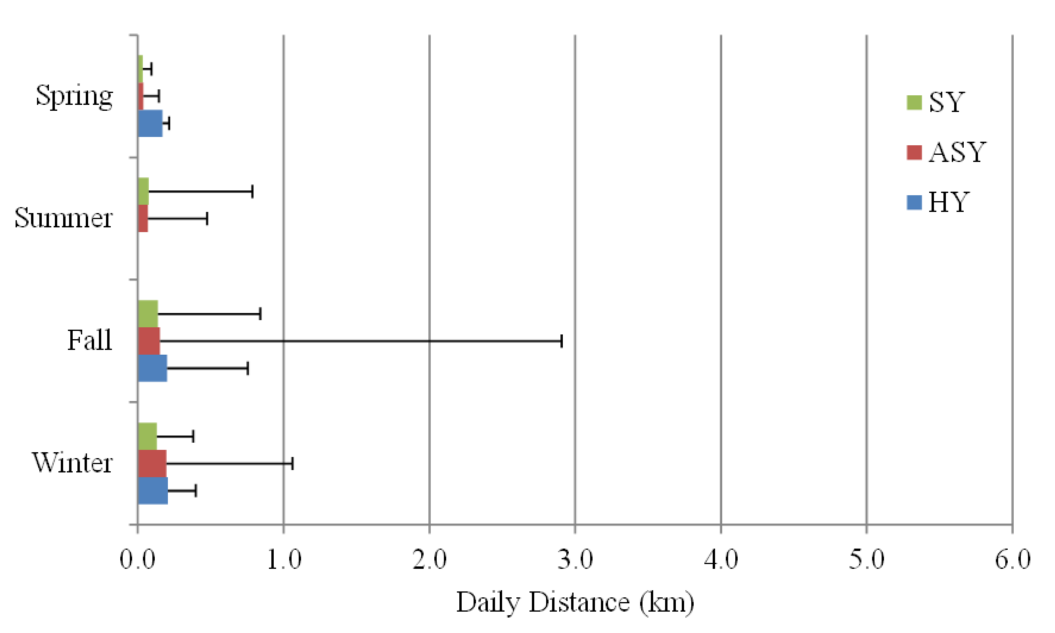

Figure 5. Daily average (columns) and maximum (lines) distance (km) traveled by male rock ptarmigan by season and age, Unit 13B, Southcentral Alaska, 2013–2017.

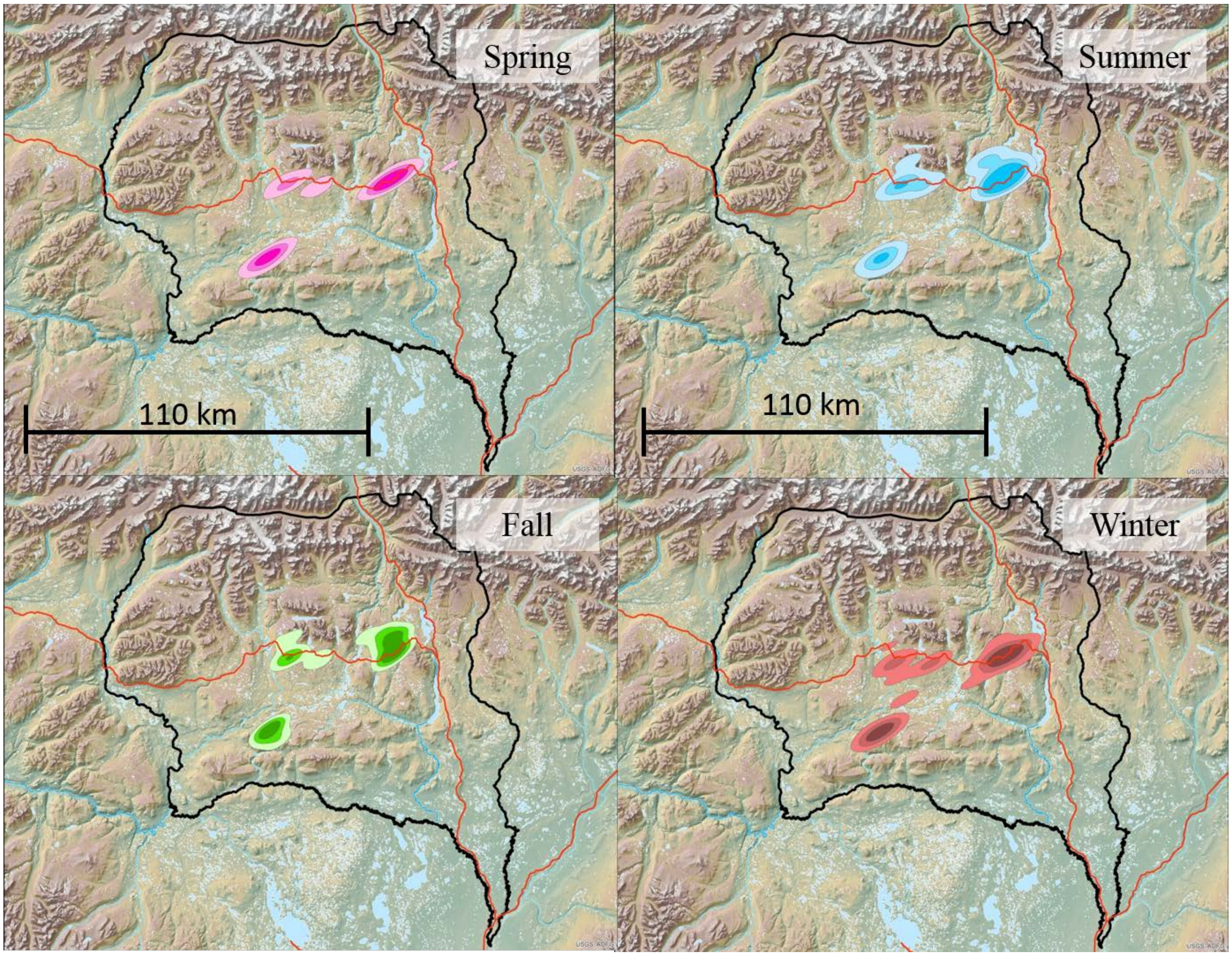

Figure 6. Male rock ptarmigan seasonal kernel density estimate movement maps using all relocation data by season with 50%, 75%, and 95% isopleth intervals, Unit 13B, Southcentral Alaska.

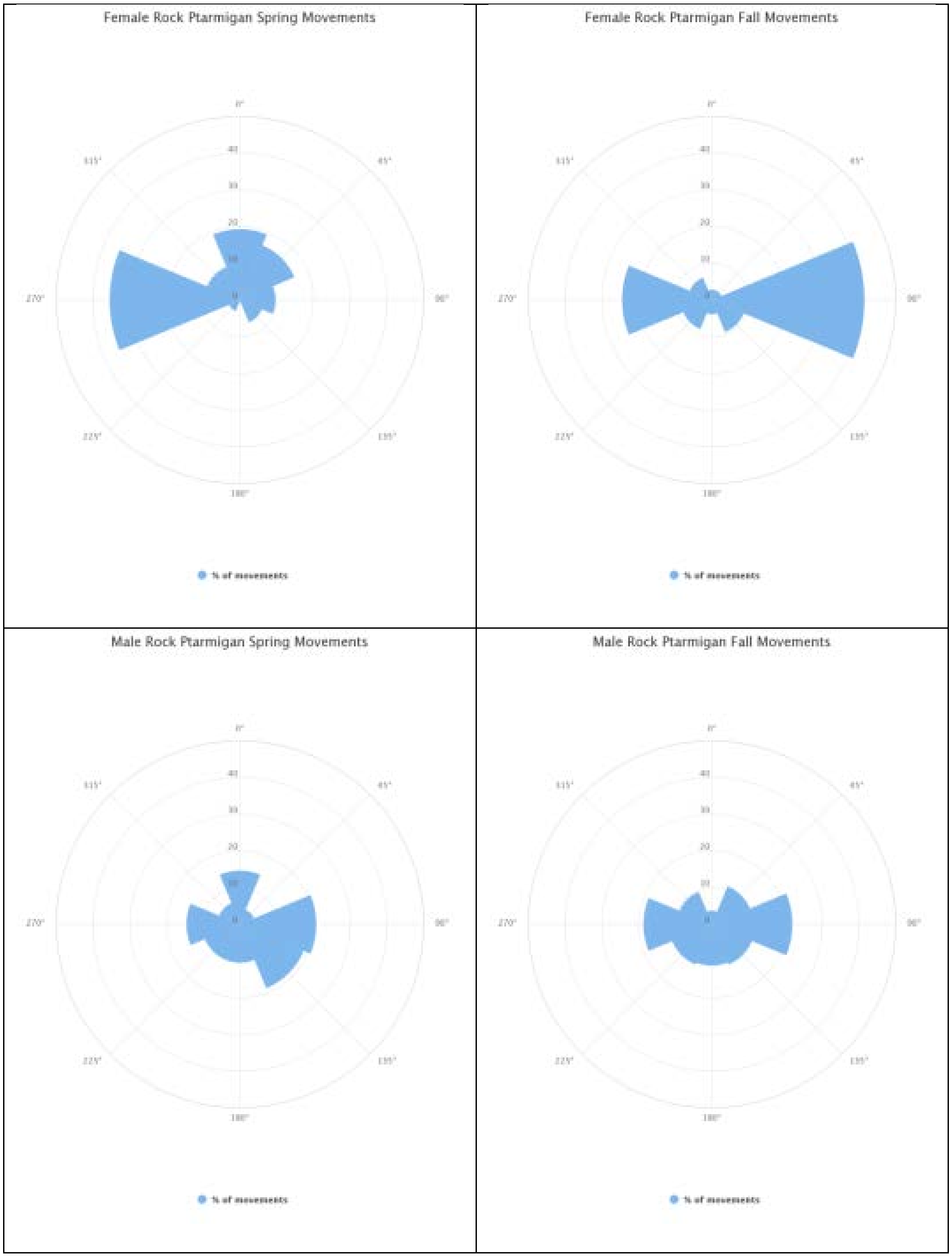

Figure 7. Movement directions of male and female rock ptarmigan. Blue cones signify the percentage of recorded movements in a specific direction based on travel direction between aerial surveys, Unit 13B, Southcentral Alaska.

Directionality of movements was oriented east-west for both males and females (Figure 7). Using a chi-squared test, males and females differed significantly from each other for spring (P = 0.032) and fall (P = 0.0025) but not summer (P = 0.65) and winter (P = 0.49). This movement behavior follows the potential habitat results calculated from observed elevation values. Higher elevations break up suitable habitat for rock ptarmigan into east-west bands in the study area and this appears to impact their spring and fall movements.

GAM residuals indicated that assumptions were adequately met and the model appeared to explain trends in elevation fairly well (adjusted R^2 = 0.55). The model intercept showed that the overall average elevation used by rock ptarmigan was 1,207 m (SE = 11.1 m, P = <0.001, Figure 8). Relative to females, juveniles used elevations 52 m higher (SE = 23.9 m, P = 0.03) and males used similar elevations (estimate, $\beta = -13.2$, SE = 14.7, P = 0.37). Elevation trends were the same for all age-sex classes with a strong non-linear shift in elevation use over day of year (estimated degrees of freedom = 4.7, F = 172.3, P<0.001, Figure 9). The model predicted that ptarmigan annually used the highest elevation (1,291 m; 95% CIE: 1,268–1,315 m) on 19 August and lowest elevation (1,108 m; 95% CIE: 1,083–1,134 m) on 26 January (Figure 10).

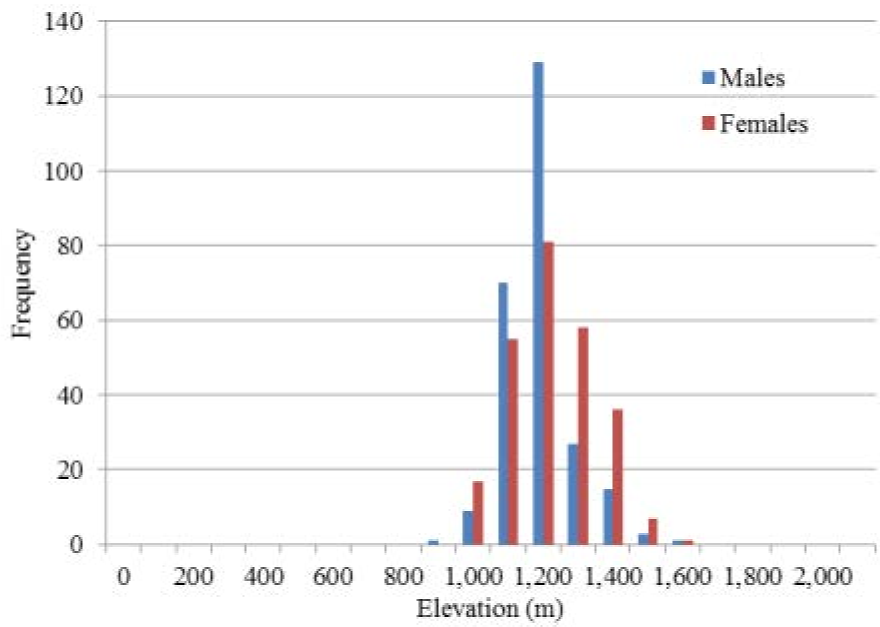

Figure 8. Elevational distribution of male and female rock ptarmigan using all known locations, Unit 13B, Southcentral Alaska, 2013–2017.

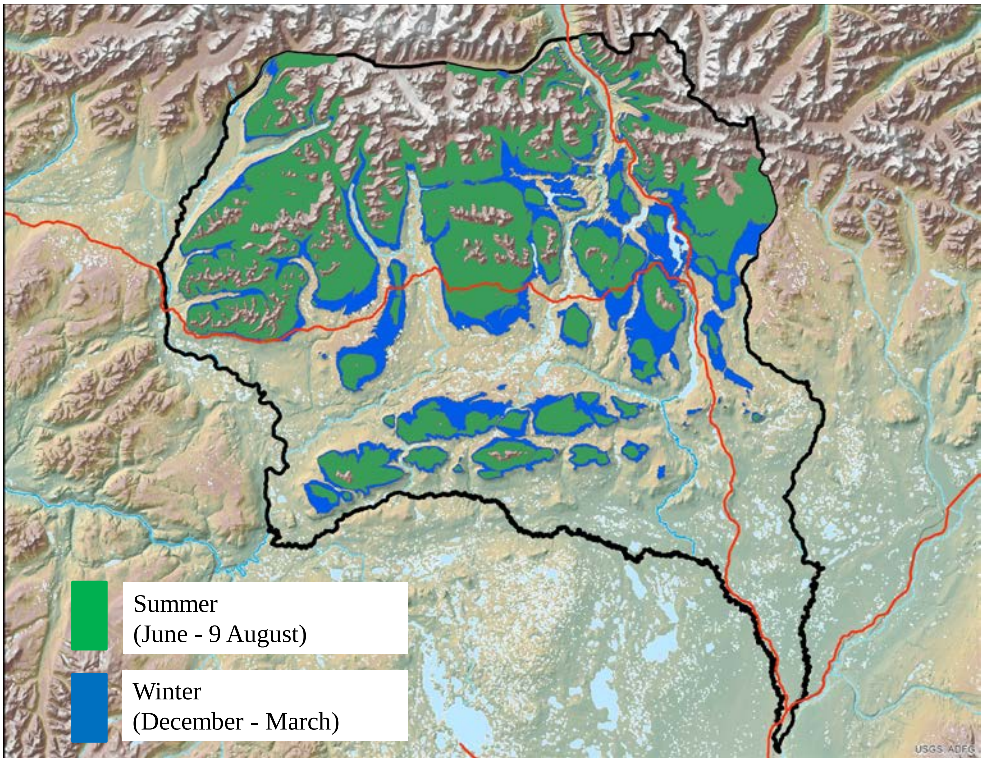

Figure 9. Modeled seasonal elevation use by rock ptarmigan using elevation records from all radiocollared individuals using the 90% isopleth interval, Unit 13B, Southcentral Alaska.

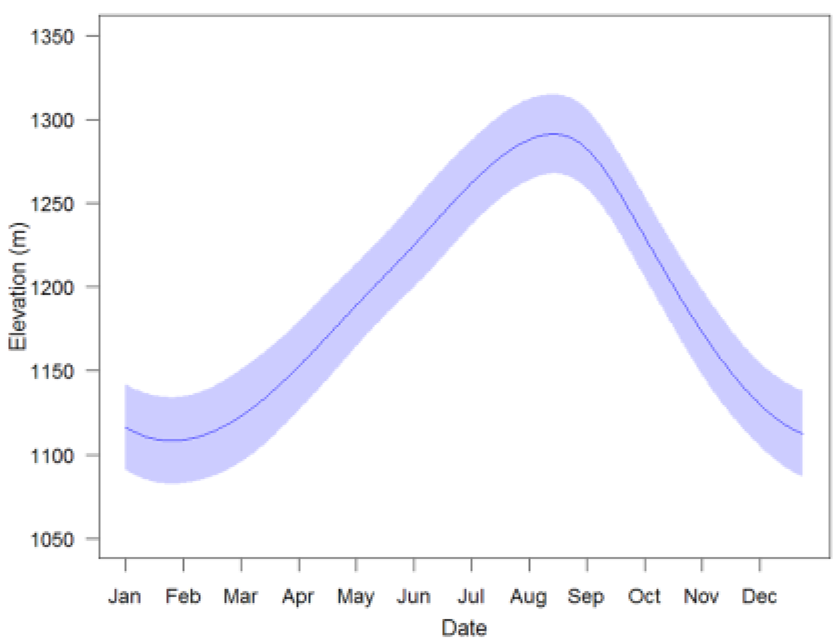

Figure 10. Yearly trend in elevation used by rock ptarmigan. Shown are model predicted elevations (m) of female rock ptarmigan over the course of a year (blue line) with 95% confidence interval estimates (CIE; blue bands), Unit 13B, Southcentral Alaska.

SURVIVAL

During the study, 87 mortality events occurred. For survival analyses, data for 2 birds were removed since 1 was suspected to have died as a result of capture and the other had missing data; no age-sex classification (Appendix A). During the study, average temperature varied considerably across seasons and generally precipitation was highest in the summer and fall seasons (Appendix B).

A total of 8 rock ptarmigan were positively confirmed to be hunter-harvested. Twenty-six (26) ptarmigan were last heard during the hunting season and the collars were not recovered. Likely causes of mortality for 15 of the 26 include unreported hunter harvest or reaching the collar battery life (330 d). However, 11 of the 26 were likely harvested by humans or they emigrated from the study area as they had not reached the 330 d battery life. Forty-two (42) rock ptarmigan collars were recovered and were categorized as one of the following causes of mortality based on the clues at the recovery site: 30 wildlife, 7 harvested by humans, 4 unknown, and 1 capture-related mortality. An additional 11 rock ptarmigan collars were not recovered but mortality was attributed to wildlife based on location and time of year. Finally, 15 additional rock ptarmigan were categorized as unknown cause of mortality. These collars were not recovered.

Based on Kaplan-Meier survival functions (Figure 11), median survival time was 131 d for males (95% CIE, 121 d–191 d), 78 d for females (95% CIE, 51 d–108 d), and 21 d for juveniles (95% CIE, 12 d–66 d). For the analysis of factors influencing mortality risk, 32 candidate CoxPH models were fit resulting in the top 4 models (Table 4). The top ranked model (#24) included season, sex and age class, precipitation, temperature, and high access as predictor variables; however, the second ranked model (#2), excluding temperature, was also supported (i.e., $\Delta_{ic} \leq 2$).

Model coefficients for model #24 (Table 5) suggested that mortality risk was fairly similar between juveniles and females (β = 0.36, SE = 0.49) with juveniles experiencing mortality risks from 0.1% lower to 9.6% higher than females (95% CIE of Table 6 minus 1.000 and expressed as a percentage). Males had a lower overall mortality risk (β = 0.68, SE = 0.25, Table 5) and hazard ratios showed males to have 0.1% to 9.0% lower mortality risk than females and 0.4% to 17.3% lower risk than juveniles (Table 6).

Across age and sex class and controlling for precipitation and temperature, mortality risk was higher in spring (April–May; estimated effect size, β = 0.45, SE = 0.48) and lower in summer (June–9 August; β = −0.56, SE = 0.46) and winter (December–March; β = −0.52, SE = 0.59) compared to fall (10 August–November). Although the errors in these seasonal estimates were fairly large, there was a clear pattern of higher relative mortality risk in spring compared to winter (Figure 12) when including the effects of differing average precipitation and temperature across seasons (Appendix B).

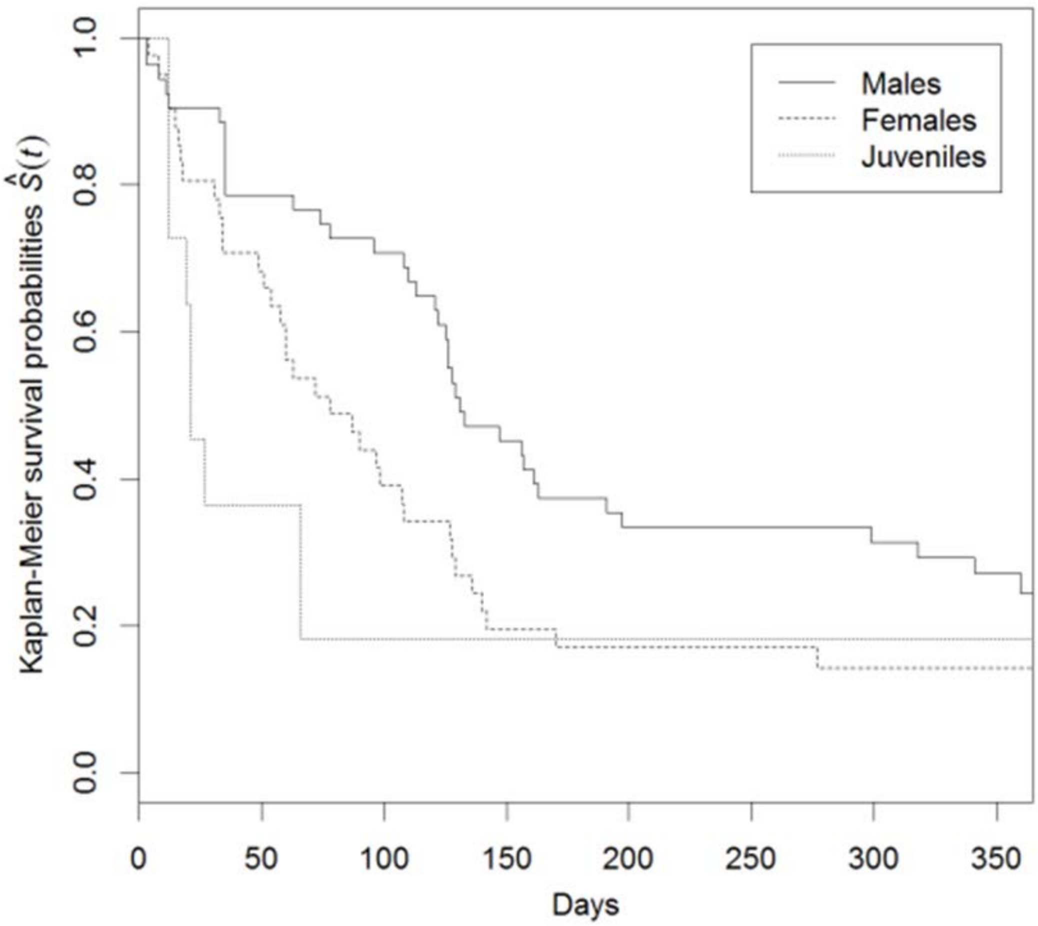

Figure 11. Kaplan-Meier survival functions for male (solid line), female (dashed), and juvenile (dotted) rock ptarmigan, Unit 13B, Southcentral Alaska.

Table 4. Model summary statistics for the 4 top ranked candidate models (of 32 candidates) estimating the effects of year, sex-age class (SxA), season (Sn), precipitation (Pr), temperature (Tp), and highway access (HA) on the mortality risk for rock ptarmigan, Unit 13B, Southcentral Alaska. Summary statistics shown are model parameters (K), log-likelihood [log($\mathcal{L}$)], second order Akaike information criterion (AICc), difference in AICc relative to lowest model (Δ_{ic}), and model weight (w_i).

Model	Variables	K	log($\mathcal{L}$)	AICc	Δ_{ic}	w_i
24	SxA + Sn + Pr + Tp + HA	8	−311.84	639.87	0	0.46
2	SxA + Sn + Pr + HA	7	−313.31	640.76	0.89	0.26
8	SxA + Sn + HA	6	−315.01	642.14	2.27	0.15
20	SxA + Sn + Tp + HA	7	−314.46	643.07	3.20	0.09

Table 5. Estimated coefficients, robust standard errors (SE), Z-scores, 2-tailed *P*-values, and 95% confidence interval estimates (CIE) for cox proportional hazard model #24 that was chosen to describe the mortality risk associated with *n* = 100 VHF radiotracked rock ptarmigan, Unit 13B, Southcentral Alaska.

	Coefficient	SE	z	Pr > | z |	95% CIE
Juveniles	0.363	0.494	0.74	0.46	−0.604, 1.331
Males	−0.675	0.247	−2.73	0.01	−1.159, −0.190
Spring	0.446	0.483	0.92	0.36	−0.500, 1.391
Summer	−0.556	0.457	−1.22	0.22	−1.451, 0.339
Winter	−0.520	0.590	−0.88	0.38	−1.677, 0.638
Precipitation (mm)	−0.271	0.114	−2.37	0.02	−0.495, −0.047
Temperature (°C)	0.046	0.024	1.95	0.05	0.001, 0.093
High access[a]	0.944	0.256	3.69	<0.01	0.443, 1.445

[a] Variable indicating if a rock ptarmigan was relocated ≤3 km of a highway during open hunting season.

Table 6. Relative rock ptarmigan mortality risk in association with highway access and age-sex class, Unit 13B, Southcentral Alaska. Shown are hazard ratios (HR) and 95% confidence interval estimates (CIE) that describe the increased (>1) or decreased (<1) mortality risk across groups.

Comparison	$\widehat{HR}$	95% CIE
Juvenile vs. Female	1.047	0.999, 1.096
Male vs. Female	0.955	0.910, 0.999
Male vs. Juvenile	0.911	0.827, 0.996
High vs. Low access	2.570	1.283, 3.858

Overall, mortality risk was negatively associated with precipitation (β = −0.27, SE = 0.11) while it was positively associated with temperature (β = 0.05, SE = 0.024, Figure 13). Independent of other factors including season, each 1 mm increase in average precipitation, which ranged from 0 mm to 7.6 mm across all survey periods, was associated with a 23.7% decrease in mortality risk. Furthermore, for each 1°C increase in temperature, which ranged from −22.2°C to 16.6°C, there was an associated 4.7% increase in mortality risk.

Rock ptarmigan residing in areas located ≤3 km of highways during hunting season (i.e., high access = 1) were found to experience an elevated mortality risk (β = 0.94, SE = 0.26, Table 5) compared to those located >3 km from highways. Birds considered to be in high access over a survey period, were estimated to experience 28–286% higher mortality than those farther from highways across all sex and age classes (Figure 14).

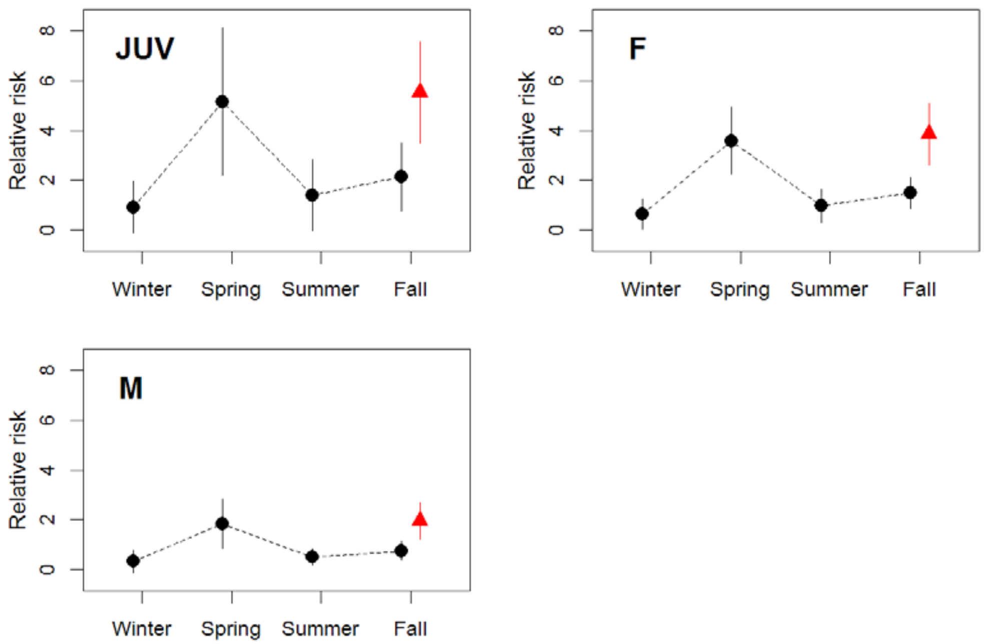

Figure 12. Relative risk of rock ptarmigan mortality (solid circles) and 95% confidence interval for estimates (vertical lines) for each season shown separately for juveniles of both sexes (top, left), adult females (top, right) and adult males (bottom, left), Unit 13B, Southcentral Alaska. Estimates are shown for when ptarmigan were in areas >3 km from highways and/or outside hunting season (black circles) and when they were considered to be in 'high access' areas in the fall (≤3 km from highway; red triangles).

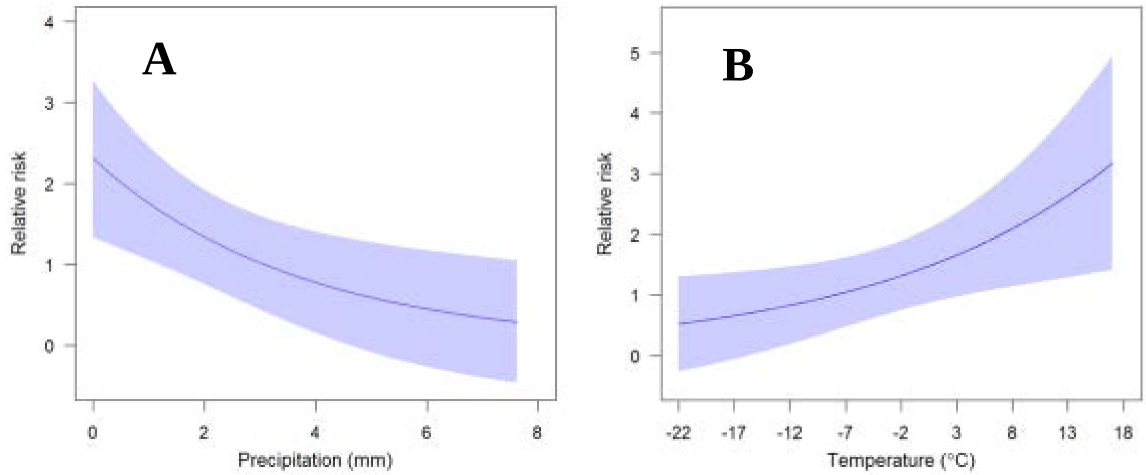

Figure 13. Relative risk estimates (blue curves) for rock ptarmigan mortality in association with increased precipitation (A) and temperature (B), Unit 13B, Southcentral Alaska. The 95% confidence intervals for relative risk estimates are shown as blue bands.

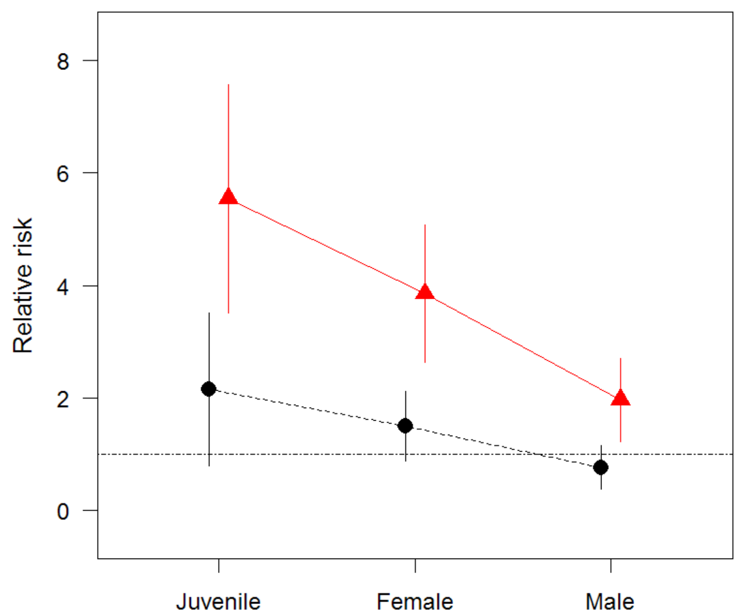

Figure 14. The estimated relative risk of mortality for rock ptarmigan during the fall season when located ≤3 km of a highway during hunting season (high-access; red triangles) and when at other locations or outside of hunting season (black circles), Unit 13B, Southcentral Alaska. The 95% confidence interval for estimates are shown as vertical lines.

NEST MONITORING

A total of 13 nests (7 at 12-mile, 6 at MacLaren Ridge) were identified and monitored for the full incubation period and the subsequent broods between spring 2014 and summer 2016 (4-2014, 6-2015, 3-2016). Ten (77%) nests were positioned in shrubs (9-willow, 1-resin birch). Nest shrub height ranged from 10 cm to 45 cm. The other 3 nests were positioned within graminoids, bell heather, and rock. The vegetation surrounding the nests (≤10 m) was composed of patchy willow shrubs and graminoids (9), rocks and bell heather (3), and patchy resin birch and crowberry (1). Nest site elevation at 12-mile was lower ($\bar{x}$ = 1,172 m, SE = 40 m) than MacLaren Ridge ($\bar{x}$ = 1,341 m, SE = 68 m).

Hatch date averaged 20 June (SE = 4.5 d) among all years and both sites (Table 7). Incubation initiation averaged 27–30 May (range: 22 May–10 June).

Females averaged a minimum of 3.2 trips (SE = 2.0 trips) away from the nest per day averaging 16 minutes (SE = 9 minutes) in duration. Time of nest departure throughout the 24-hour period was highly variable with equal numbers of trips among all times of the day.

Clutch size averaged 6.2 eggs (SE = 1.6 eggs) among all years and locations. The average minimum count for chicks departing the nest based on trail camera photos was 4.4 (SE = 3.1 chicks). Three of the 4 monitored females in 2014 abandoned their nest after incubation began presumably due to a short but intense snowfall (45 cm) on 18 June. One female was killed in early June after incubation began and therefore never hatched any chicks. Chick survival to 5 August (immediately prior to the start of the 10 August hunting season) averaged 2.4 chicks per brood (SE = 1.8 chicks).

Nesting females faced variable rates of nest harassment and nest depredation based on their location. Trail cameras at 12-mile documented no nest harassment or nest depredation based on photographs or visual nest monitoring. Four of the 6 (67%) monitored nests at MacLaren Ridge were harassed by arctic ground squirrels (*Spermophilus parryii*; Figure 15). At each of those nests, ground squirrels were photographed harassing the incubating female (≥25 times/day), stealing eggs (n = 8), and stealing live chicks (n = 2). One nest lost 4 eggs to ground squirrels. Long-tailed jaegers (*Stercorarius longicaudus*) were also photographed harassing a female returning to the nest as well as harassing a brood departing a nest. Other species documented by trail cameras in close proximity to nest locations with a female actively incubating included northern harriers (*Circus hudsonius*), caribou (*Rangifer tarandus*), and brown bears (*Ursus arctos*). Each year, at least one American tree sparrow (*Spizella arborea*) was photographed on the nest after the brood departed for the final time.

Table 7. Behavior of incubating female rock ptarmigan, hatch date and clutch size, Unit 13B, Southcentral Alaska, 2014–2016.

	2014	2015	2016	Total
Monitored Nests (n)	4	6	3	13
Daily Trips Away from Nest (n)				
Average	2.2	2.9	4.0	3.2
Minimum	1	1	1	
Maximum	4	19	6	
Trip Duration from Nest (min)				
Average	22	16	15	16
Minimum	10	4	1	
Maximum	75	50	41	
Eggs (n)				
Average	6.25	7.2	6.0	6.6
Minimum	5	3	5	
Maximum	7	9	7	
Hatch Date				
Average	6/18/15	6/21/15	6/19/16	6/20
Minimum	[a]	6/17/15	6/15/16	
Maximum	[a]	7/1/15	6/22/16	
Clutch Size				
Average	7.0	6.3	5.7	6.2
Minimum[a]	0	3	5	
Maximum	7	9	7	

[a] Three of the four monitored nests experienced nest abandonment.

Figure 15. Digital camera photograph of an arctic ground squirrel grabbing a live chick from an incubating female rock ptarmigan at MacLaren Ridge, Unit 13B, Southcentral Alaska, June 2016.

Discussion

Capture techniques used in this study had variable rates of success particularly as it relates to the time of year. The most successful techniques used seasonally specific behavioral traits of males and females. Males were most vulnerable to capture in the spring during the breeding season. Their aggressive springtime territorial behavior made them vulnerable to approach often within 5–10 m which is inside the effective range of the shoulder-fired net gun. Territorially defensive males were also vulnerable to a decoy “intruder” and noose carpets placed in close proximity (≤30 m) to a paired female. However, males were far more difficult to capture during the late summer and fall capture periods as they tended to readily flush upon approach, were very loosely connected to brood groups, or were in large flocks that were more prone to flushing.

Alternatively, females were most vulnerable to capture during the late summer and early fall capture periods. During this time period chicks and brooding females were generally reluctant to flush upon approach but instead often chose to run and maintain distance (10–50 m) from the capture team. This behavior made it advantageous for the drive net technique. Chicks and brooding females would readily run to the edge of the net by field personnel corralling the group. Chicks and accompanying hens would then attempt to maneuver under the portion of the net laying on the ground and become entangled. However, females were far more difficult to capture during the spring breeding season as they tended to flush upon approach.

In addition, females were often difficult to spot during the spring breeding season because of their cryptic behavior and plumage. Steen et al. (1992) found that female willow ptarmigan in Norway during the spring snowmelt compromised between food quality and optimal camouflage. As females transition between white winter plumage to brown summer plumage and as snow receded from the landscape, they spent increasingly more time away from snow patches in vegetated areas or bare ground in correlation to their plumage state. Field personnel for this study observed those exact behavior traits among rock ptarmigan each spring and often spotted females sitting adjacent to snow patches in bare, exposed ground.

Despite a small sample size (n = 13), female rock ptarmigan almost always placed their nests within a shrub (primarily willow) below the elevation at which they spent the majority of their summer rearing their brood. By early June each year leaf-out provided nearly complete concealment for incubating hens. Wilson and Martin (2008) also found rock ptarmigan in Yukon Territory, Canada selected for graminoid and woody shrub habitat for nesting. The documented encroachment of shrub communities into alpine ptarmigan habitats could impact these populations across the Alaska (Jackson et al. 2015). To what degree climate change will impact elevational use during the nesting period and nest site selection is difficult to anticipate. However, rock ptarmigan may be forced to move to higher elevations to locate similar nesting habitats as were documented in this study.

Weeden (1965) found similar timing of initiation of laying, incubation, and hatching within his study area near Eagle Summit in the 1960s and early 1970s (mile 104–110 Steese Highway northeast of Fairbanks). There was a high degree of synchrony between years and between the 2 studies. This is noteworthy due to the nearly 260 km and 45-year separation.

Although overall nest predation was low among monitored nests, arctic ground squirrels were the dominant nest predator in this study. Although arctic ground squirrels are known primarily as herbivores they have also been documented eating collared lemmings (*Dicrostonyx* spp.; Boonstra et al. 1990) and small adult passerines (DeSteno 2000). Until this study, they had never been documented eating both eggs and recently hatched chicks of rock ptarmigan. All of the observed nest harassment or nest depredation occurred at MacLaren Ridge where it appeared as though arctic ground squirrel density was higher than at 12-mile or Alphabet Hills. Long-tailed jaegers were also documented harassing monitored rock ptarmigan. Maher (1974) found *Lagopus* spp. (adult and chicks) in stomach contents of long-tailed jaegers in northern Alaska. At both 12-mile and MacLaren Ridge, long-tailed jaegers were seemingly abundant (2–6 nesting pairs within 1 km of each nest). In July 2014, a long-tailed jaeger was observed perched above a dead hen rock ptarmigan 3 days after her brood hatch date with no chicks nearby. Although there are many known ptarmigan predators within the study area, arctic ground squirrels and long-tailed jaegers were not believed to be significant predators of ptarmigan in Alaska. However this study documented both to be active predators of rock ptarmigan in Unit 13B.

This study documented the longer distance traveled on average by females than males particularly in the fall and spring. Fuglei et al. (2017) documented the same phenomenon among rock ptarmigan in Svalbard as did Frye and Merizon (*In prep*), Gruys (1993), Schieck (1988), and Hörnell-Willebrand et al. (2014) with willow ptarmigan. In those studies females tended to move greater distances than males and those movements also occurred in fall and spring. The smaller documented movements of males could be explained by competition among males for breeding locations outweighing the risk of moving to more favorable habitats during the winter. Schieck (1988) found a high level of breeding site fidelity among male willow ptarmigan. Although this study did not explicitly examine site fidelity, rock ptarmigan, particularly males were observed exhibiting a high level of breeding site fidelity.

Schieck (1988) also documented that regardless of breeding site fidelity, higher quality breeding habitats were consistently occupied by breeding pairs; whether individuals returned from previous years or new individuals occupied currently available territories. Through the course of spring breeding surveys (1997–2016) and this study, this phenomenon appears to be true for Unit 13B rock ptarmigan (Carroll and Merizon 2017). This would suggest that the ongoing spring breeding surveys across a large geographic scale have been an accurate index of breeding abundance and can therefore be an effective method of monitoring changes in breeding abundance at the scale of Unit 13B. The interchange of dispersal and immigration at greater spatial scales (e.g., Irving et al. 1967) is unknown for this unit.

Male rock ptarmigan in Unit 13B were shown to have higher overall survival (median survival = 31 d) than females (median survival = 78 d) and juveniles (median survival = 21 d) in this study. Weeden (1965) estimated annual rock ptarmigan mortality rates between 41% and 74% for adults and 60% and 77% for juveniles during his work in early 1960s near Eagle Summit. Potapov and Sale (2013) noted most rock ptarmigan annual mortality rates between 40–67%. Unfortunately, due to a small sample size, this study was unable to estimate annual mortality rates of rock ptarmigan to compare to these studies. However, based on raw estimates of the number collared to the number that survived 12 months it appears Unit 13B rock ptarmigan experience overall high annual mortality and were most likely on the high end of the published results from other studies.

Although we did not explicitly examine increased mortality risk due to camouflage mismatch, we documented several predation events over short periods during fall 2015 and 2016 when plumage and landscape colors were asynchronous. This is a subject that warrants additional examination particularly in light of climate change and the seemingly highly variable annual weather patterns in Alaska.

Unit 13B rock ptarmigan experience a lower risk of mortality, presumably mostly natural, throughout the winter (December–March). Despite the ptarmigan hunting season in Unit 13B closing on 30 November under State of Alaska regulations (5 AAC 85.065), federal subsistence (Office of Subsistence Management) regulations allow ptarmigan hunting between 10 August and 31 March in designated federal subsistence hunting areas (36 CFR Part 242; Figure 16). Federal subsistence ptarmigan hunting within Unit 13B between 1 December and 31 March likely had little impact on the results of this study particularly with regard to the highest risk of mortality within 3 km of a roadway. In addition the vast majority of radiocollared rock ptarmigan relocations and modeled habitat use were out of the federal subsistence hunt areas. Sandercock et al. (2011) also documented low natural winter mortality for willow ptarmigan in Norway suggesting most late season is additive. They suggest that harvest effects could be minimized by closing ptarmigan seasons by November. Therefore, it could be expected that rock ptarmigan in Unit 13B would have higher spring breeding abundance than rock ptarmigan in adjacent units with season closure dates in late March (e.g., Units 13A, 13C, 13D, and 13E). Carroll and Merizon (2017) documented lower spring breeding indices of willow ptarmigan in Unit 13E and higher indices in Unit 13B. Between 2014 and 2016 spring breeding abundance of willow ptarmigan was 27–85% higher in Unit 13B than Unit 13E. Spring breeding surveys for rock ptarmigan have only been completed in Unit 13B. Habitat and climatological factors are believed to be very similar across both Units 13B and 13E. Although this study cannot definitely document winter harvest mortality is additive, these data suggest that winter harvest mortality could contribute to lower overall spring breeding abundance.

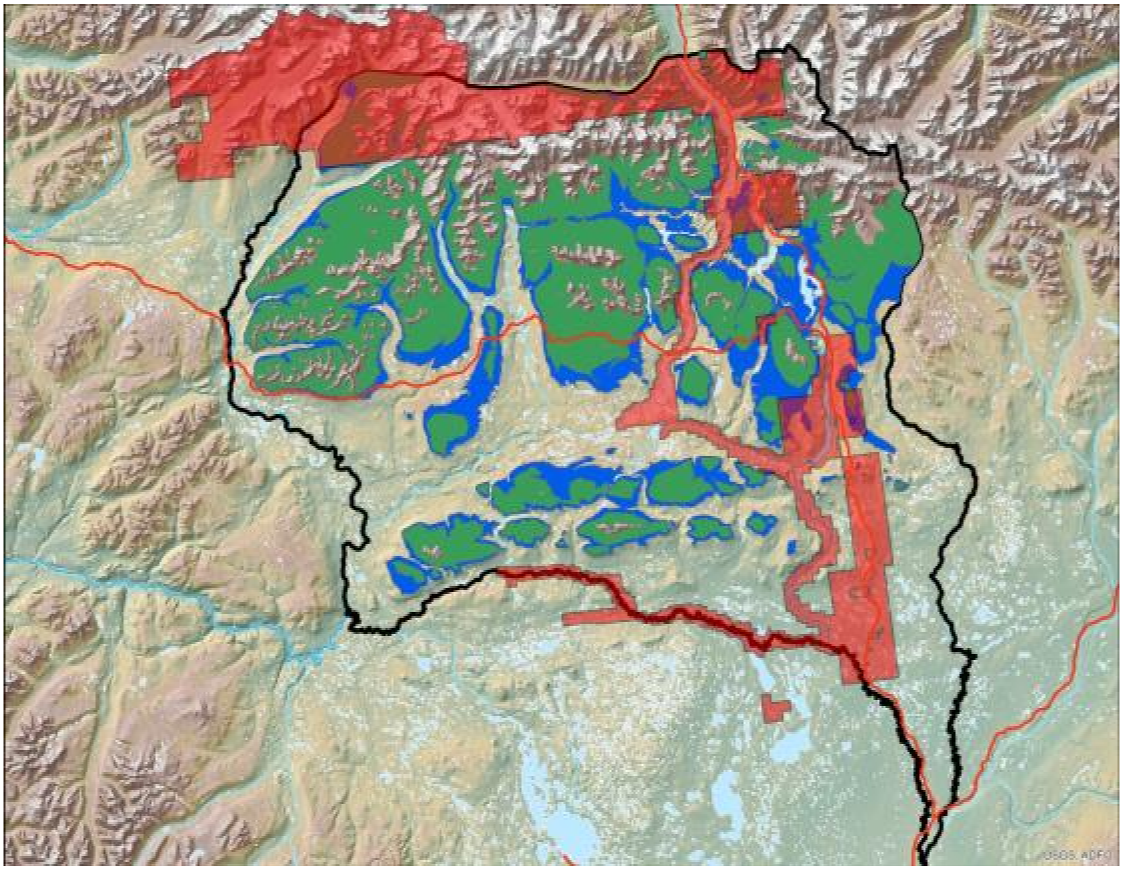

Figure 16. Unit 13, Southcentral Alaska, federal subsistence hunt areas (red shading) used by ptarmigan hunters through 31 March and the modeled seasonal elevation use by rock ptarmigan; green shading (May–August), blue shading (December–March).

We estimate from hunters statewide who voluntarily submitted wings from willow ptarmigan compose the majority of "ptarmigan" harvested in Unit 13 (91% including the 2011–2016 hunting seasons; Carroll and Merizon 2017). Fifty-eight percent (58%) of the hunter-harvested willow ptarmigan wings and 76% of the rock ptarmigan wings from Unit 13 were harvested between February and March (season closure date in Units 13A, 13C, 13D, and 13E is 31 March). The voluntary wing contributions that are used to estimate age ratio are not a systematic, robust estimate of harvest but do provide an index of annual hunting effort.

We estimated rock ptarmigan mortality risk as 2.6 times higher ≤3 km from roadways; a finding that supports the current understanding that the majority of ptarmigan hunting effort takes place near roadways or trail systems. Although the area of study was restricted, this is likely true across all lands within Unit 13.

Mortality rates and dispersal distances of juvenile and adult females appear to be a significant population parameter in explaining population dynamics among studied ptarmigan populations in

Scandinavia and Alaska (Willebrand and Hörnell 2001; Hörnell-Willebrand et al. 2014). Females are moving to areas in the fall and winter often distant from spring breeding locations. This may or may not expose them to increased hunting mortality risk during this period. This study did not explicitly examine breeding site fidelity among females (both adult and juvenile) however it did document several adult females returning to similar areas and with several females to the same male and territory. Juvenile females were more variable in their breeding locations. Therefore, if populations breeding adjacent to roadways are not being fully compensated from hunting pressure this could explain why spring breeding abundance indices for rock and willow ptarmigan are consistently higher in areas >3 km from roadways than from areas adjacent to roadways. This has also been observed by Frye and Merizon (*In prep*) examining willow ptarmigan in Unit 13. Therefore, the belief that birds from distant "refugia" are partially or fully replacing harvested birds near roadways, the basis for current State of Alaska ptarmigan hunting regulations, is not well supported (Paragi and Haggstrom 2005).

A shortcoming of this study was the inability to directly attribute harvest by humans to the higher risk of mortality adjacent to roadways. This is an issue that will require further study and evaluation. It is difficult to evaluate the effects of various harvest strategies on ptarmigan populations in Alaska. Either direct hunter contacts-interviews or strong hunter harvest reporting would be needed to properly evaluate these effects. Reporting of ptarmigan hunter harvest is believed to be low statewide based on several statewide small game hunter surveys (Merizon and Carson 2013; Merizon et al. 2015) and through this study. Without mandatory harvest reporting or greatly improved voluntary harvest reporting, making meaningful evaluations of management strategies are not possible using standard VHF radiotelemetry approaches. Future research should be focused on evaluating the effects of season duration and/or bag limits in small but intensely monitored locations. These management scenarios could then be altered to evaluate the subsequent effect.

Management Implications

Historically, ptarmigan in Alaska have been managed to maximize hunting opportunity (liberal season dates and bag limits) across the state since statehood (1959). Through this study we have been able to document rock ptarmigan are exposed to a higher risk of mortality adjacent to roadways. Through this study and other ptarmigan research across the northern hemisphere it has been demonstrated that increasing off-road technology and growing human populations could further expose ptarmigan to increased harvest pressure.

The state of Alaska has a rapidly evolving hunting public in terms of connectivity, technology, traditions, and the ability to access and exploit resources throughout the state. This study has begun to identify the importance of hunter access and various ptarmigan life history stages that will help inform discussions about managing rock and willow ptarmigan into the future in Alaska. Yet despite the advances, large portions of the state, even some areas within 20–30 km of a major roadway, remain remote and difficult to access. The concern about extirpating rock and willow ptarmigan throughout a unit are likely unfounded under the current management scheme, available technology, and human population. However, we found a significantly increased risk of mortality within 3 km of a roadway. Future roadway development, unregulated trail expansion, or further off-road vehicle technology improvement will likely result in higher harvest mortality and lower fall densities in areas that currently have limited or no motorized access for hunting.

Further research is needed in Alaska and elsewhere throughout the range of rock and willow ptarmigan to evaluate various management scenarios and the effects on population dynamics. As a result, in light of the existing research findings, a more conservative management approach may be warranted. Research is needed to understand the effects of bag limit size on harvest potential and season duration to understand the interaction of compensatory and additive mortality and the resulting impacts on spring breeding abundance.

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References Cited

Anderson, R. K., and F. Hamerstrom. 1967. Hen decoys aid in trapping cock prairie chickens with bownets and noose carpets. Journal of Wildlife Management 31(4):829–832.

Arlettaz, R., S. Nusslé, M. Baltic, P. Vogel, R. Palme, S. Jenni-Eiermann, P. Patthey, and M. Genoud. 2015. Disturbance of wildlife by outdoor winter recreation: Allostatic stress response and altered activity-energy budget. Ecological Applications 25(5):1197–1212. doi:10.1890/14-1141.1

Arlettaz, R., P. Patthey, M. Baltic, T. Leu, M. Schaub, R. Palme, and S. Jenni-Eiermann. 2007. Spreading free-riding snow sports represent a novel serious threat for wildlife. Proceedings of the Royal Society B 274:1219–1224. doi:10.1098/rspb.2006.0434

Bergerud, A. T., S. S. Peters, and R. McGrath. 1963. Determining sex and age of willow ptarmigan in Newfoundland. Journal of Wildlife Management 27(4):700–711.

Beyer, H. L. 2015. Geospatial modeling environment (Version 0.7.4.0). Spatial Ecology LLC. http://www.spatialecology.com/gme (Accessed 9 February 2018).

Boonstra, R., C. J. Krebs, and M. Kanter. 1990. Arctic ground squirrel predation on collared lemmings. Canadian Journal of Zoology 68(4):757–760.

Bowman, A. W., and A. Azzalini. 1997. Applied smoothing techniques for data analysis: The kernel approach with S-Plus illustrations. Oxford Statistical Science Series, University of Oxford, Oxford University Press, United Kingdom.

Braun, C. E., W. P. Taylor, S. E. Ebbert, R. S. A. Kaler, and B. K. Sandercock. 2011. Protocols for successful translocation of ptarmigan. Pages 339–348 [*In*] R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and Ptarmigan in a Changing World. The Peregrine Fund, Boise, Idaho. http://dx.doi.org/10.4080/gpcw.2011.0313 (Accessed 9 February 2018).

Brøseth, H., and H. C. Pedersen. 2010. Disturbance effects of hunting activity in a willow ptarmigan *Lagopus lagopus* population. Wildlife Biology 16(3):241–248. doi:10.2981/09-096

Brøseth, H., J. Tufto, H. C. Pedersen, H. Steen, and L. Kastdalen. 2005. Dispersal patterns in a harvested willow ptarmigan population. Journal of Applied Ecology 42(3):453–459. doi:10.1111/j.1365-2664.2005.01031.x

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.

Carroll, C. J., and R. A. Merizon. 2014. Status of grouse, ptarmigan, and hare in Alaska, 2014. Alaska Department of Fish and Game, Wildlife Management Report ADF&G/DWC/WMR-2014-1, Palmer.

Carroll, C. J., and R. A. Merizon. 2017. Status of grouse, ptarmigan, and hare in Alaska, 2015 and 2016. Alaska Department of Fish and Game, Wildlife Management Report ADF&G/DWC/WMR-2017-1, Juneau.

Cotter, R. C., and C. J. Gratto. 1995. Effects of nest and brood visits and radio transmitters on rock ptarmigan. Journal of Wildlife Management 59(1):93–98. doi:10.2307/3809120

DeSteno, F. M. 2000. Observations of red and ground squirrel predation on birds visiting a feeder. The Loon 72(4):247–248.

Frye, G. G., and R. A. Merizon. *In prep*. Population ecology or willow ptarmigan in Unit 13: Study Plan Section 10.17; Study Completion Report. Prepared for Alaska Energy Authority: Susitna-Watana Hydroelectric Project (FERC No. 14241).

Fuglei, E., M.-A. Blanchet, S. Unander, R. A. Ims, and Å. Ø. Pedersen. 2017. Hidden in the darkness of the Polar night: A first glimpse into winter migration of the Svalbard rock ptarmigan. Proceedings of 13th International Grouse Symposium, 4–7 September 2015, Reykjavik, Iceland. Wildlife Biology, Special Issue. doi:10.2981/wlb.00241

Gruys, R. C. 1993. Autumn and winter movements and sexual segregation of willow ptarmigan. Arctic 46(3):228–239. www.jstor.org/stable/40511410 (Accessed 13 February 2018).

Hörnell-Willebrand, M., T. Willebrand, and A. A. Smith. 2014. Seasonal movements and dispersal patterns: Implications for recruitment and management of willow ptarmigan (*Lagopus lagopus*). Journal of Wildlife Management 78(2):194–201. doi:10.1002/jwmg.650

Irving, L., G. C. West, L. J. Peyton, and S. Paneak. 1967. Migration of willow ptarmigan in arctic Alaska. Arctic 20(2):77–85.

Jackson, M. M., S. E. Gergel, and K. Martin. 2015. Effects of climate change on habitat availability and configuration for an endemic coastal alpine bird. PLoS ONE 10(11):e0142110. https://doi.org/10.1371/journal.pone.0142110 (Accessed 13 February 2018).

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53(282):457–481. http://www.jstor.org/stable/2281868 (Accessed 13 February 2018).

Maher, W. J. 1974. Ecology of pomarine, parasitic, and long-tailed jaegers in northern Alaska. Cooper Ornithological Society, Pacific Coast Avifauna No. 37.

Martin, K., and S. J. Hannon. 1987. Natal philopatry and recruitment of willow ptarmigan in north central and northwestern Canada. Oecologia 71(4):518–524.

McBurney, R. S. 1989. The grouse cycle. Pages 210–219 [*In*] S. Atwater and J. Schnell, editors. The Wildlife Series: Ruffed Grouse. Stackpole Books, Harrisburg, Pennsylvania.

McGowan, C. P., and T. R. Simons. 2005. A method for trapping breeding adult American Oystercatchers. Journal of Field Ornithology 76(1):46–49. https://doi.org/10.1648/0273-8570-76.1.46 (Accessed 13 February 2018).

McGowan, J. D. 1973. Effects of controlled spring hunting on rock ptarmigan. Alaska Department of Fish and Game, Division of Game, Research Final Report, Federal Aid in Wildlife Restoration Job 10.5R, Juneau.

McGowan, J. D. 1975. Effect of autumn and spring hunting on ptarmigan population trends. Journal of Wildlife Management 39(3):491–495.

Merizon, R. A., and S. J. Carson. 2013. Statewide small game hunter survey, 2012. Alaska Department of Fish and Game, Division of Wildlife Conservation, Wildlife Management Report ADF&G/DWC/WMR-2013-2, Anchorage.

Merizon, R. A., S. J. Carson, and L. S. Honig. 2015. Statewide small game hunter survey, 2014. Alaska Department of Fish and Game, Division of Wildlife Conservation, Wildlife Management Report ADF&G/DWC/WMR-2015-1, Palmer.

Paragi, T. F., and D. A. Haggstrom. 2005. Identifying and evaluating techniques for wildlife habitat enhancement in Interior Alaska. Alaska Department of Fish and Game. Division of Wildlife Conservation, Federal Aid Research Final Performance Report 1 July 2004–30 June 2005, Federal Aid in Wildlife Restoration Study 5.0, Juneau.

Patthey, P., S. Wirthner, N. Signorell, and R. Arlettaz. 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of Applied Ecology 45(6):1704–1711. doi:10.1111/j.1365-2664.2008.01547.x

Peyton, L. J. 1999. Bird songs of Alaska. Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York.

Potapov, R., and R. Sale. 2013. Chapter 7: Rock ptarmigan. Pages 252–274 [*In*] Grouse of the World. New Holland Publishers, London, United Kingdom.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/ (Accessed 13 February 2018).

Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Applied Ecology 80(1):244–258.

Schieck, J. 1988. Territory selection and site fidelity in willow ptarmigan: The importance of quality and familiarity with territory and partner. Dissertation, University of Alberta, Canada.

Schroeder, M. A. 1986. The fall phase of dispersal in juvenile spruce grouse. Canadian Journal of Zoology 64(1):16–20. https://doi.org/10.1139/z86-004 (Accessed 13 February 2018).

Silvy, N. J., and R. J. Robel. 1968. Mist nets and cannon nets compared for capturing prairie chickens on booming grounds. Journal of Wildlife Management 32(1):175–178. doi:10.2307/3798252

State of Alaska. 2015. Population estimates by borough, census area, and economic region. Department of Labor and Workforce Development, Research and Analysis. http://live.laborstats.alaska.gov/pop/index.cfm (Accessed 13 February 2018).

Steen, J. B., K. E. Erikstad, and K. Høidal. 1992. Cryptic behaviour in moulting hen willow ptarmigan *Lagopus l. lagopus* during snow melt. Ornis Scandinavica 23(1):101–104.

Sutherland, W. J., I. Newton, and R. E. Green. 2004. Bird ecology and conservation: A handbook of techniques. Techniques in Ecology and Conservation Series, University of Oxford, Oxford University Press, United Kingdom.

Taylor, W. P. 2000. Game Management Unit 13 ptarmigan population studies. Alaska Department of Fish and Game, Division of Wildlife Conservation, Final Research Performance Report 1 August 1997–30 June 1999, Federal Aid in Wildlife Restoration Study 10.70, Juneau.

Taylor, W. P. 2013. Status of upland game within Alaska's highway system: A comprehensive report focusing on 2007–2011. Alaska Department of Fish and Game, Wildlife Management Report ADF&G/DWC/WMR-2013-1, Palmer.

Therneau, T. M. 2015. A package for survival analysis in S. Version 2.38. https://cran.r-project.org/web/packages/survival/index.html (Accessed 13 February 2018).

Therneau, T. M., and P. M. Grambsch. 2010. Modeling survival data: Extending the Cox model, 2000 edition. Springer-Verlag, New York. doi:10.1007/978-1-4757-3294-8

Thirgood, S. J., S. M. Redpath, P. J. Hudson, M. M. Hurley, and N. J. Aebischer. 1995. Effects of necklace radio transmitters on survival and breeding success of red grouse *Lagopus lagopus scoticus*. Wildlife Biology 1:121–126.

U.S. Geological Survey. 2017. Alaska 5 meter digital elevation models (DEMS) – USGS National Map 3DEP Downloadable Data Collection. https://catalog.data.gov/dataset/lidar-point-cloud-usgs-national-map (Accessed 21 February 2018).

Weeden, R. B. 1965. Grouse and ptarmigan in Alaska: Their ecology and management. Alaska Department of Fish and Game, Division of Game, Research Project Report, Federal Aid in Wildlife Restoration Project W-6-R-5, Work Plan I, Juneau.

Weeden, R. B. 1968. Growth and survival of ptarmigan chicks. Alaska Department of Fish and Game, Division of Game, Work Segment Report 1 January 1968–31 December 1968, Federal Aid in Wildlife Restoration Job 7, Juneau.

Weeden, R. B., and A. Watson. 1967. Determining the age of rock ptarmigan in Alaska and Scotland. Journal of Wildlife Management 31(4):825–826.

Willebrand, T., and M. Hörnell. 2001. Understanding the effects of harvesting willow ptarmigan *Lagopus lagopus* in Sweden. Wildlife Biology 7(3):205–212.

Wilson, S., and K. Martin. 2008. Breeding habitat selection of sympatric white-tailed, rock, and willow ptarmigan in the southern Yukon Territory, Canada. Journal of Ornithology 149(4):629–637.

Wood, S. N. 2006. Generalized additive models: An introduction with R. Chapman & Hall/CRC Press.

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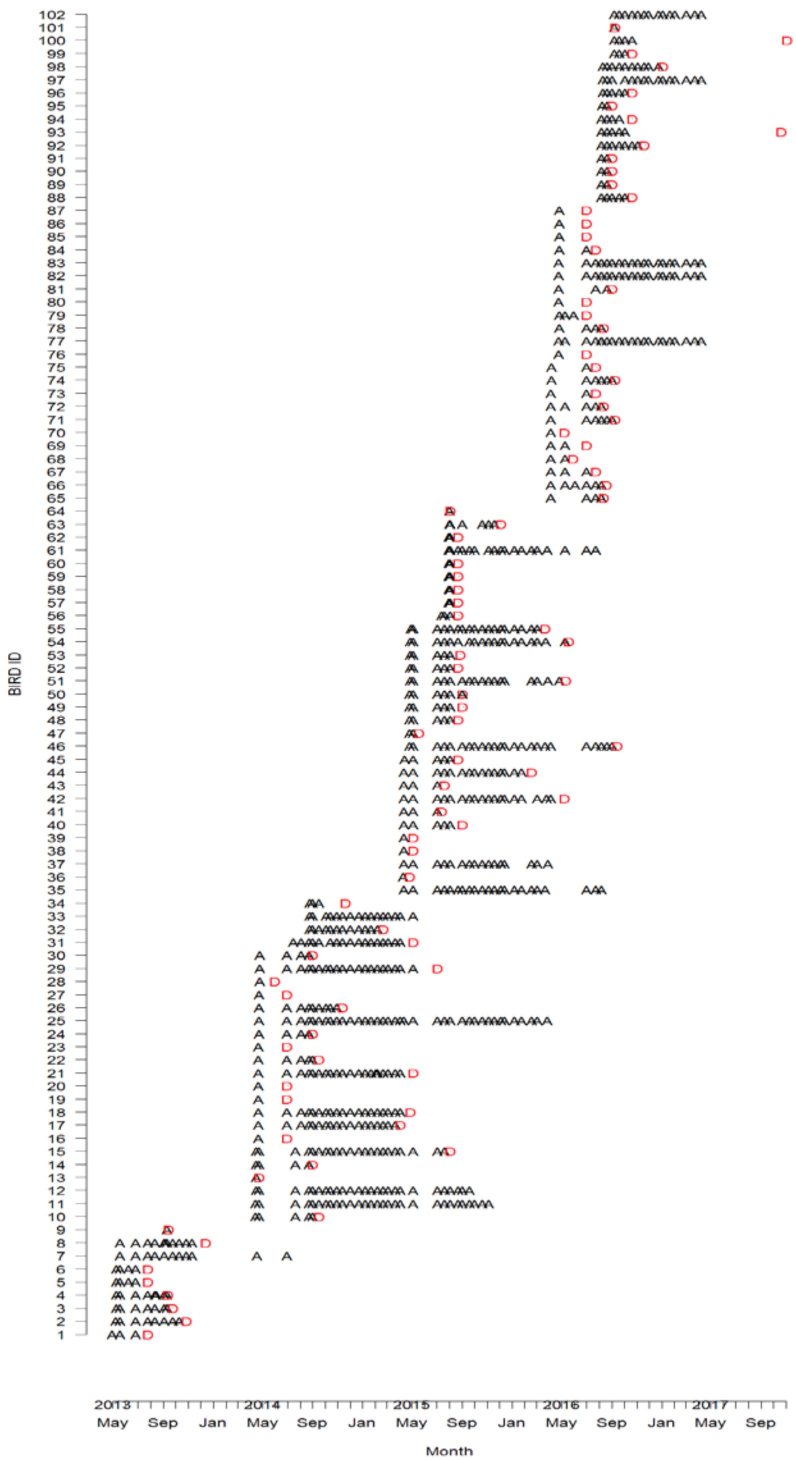
Appendix A. Survey schedule for 102 rock ptarmigan that were tracked using VHF radio collars, Unit 13B, Southcentral Alaska, 2013–2017. Each survey period is annotated to show if the bird was heard alive (A) or found to be dead (D). Blank space indicates that no signal was heard or that the bird was not in the study or actively monitored.



Appendix B. Seasonal daily average temperature measured at Paxson (Unit 13B) and precipitation measured at Monahan Flat (Unit 13E), Southcentral Alaska, 2013–2017.

Season	Dates	Average daily temperature (°C)	Average daily precipitation (mm)
Winter	1 Dec–31 Mar	−13.1	0.8
Spring	1 Apr–31 May	2.7	0.7
Summer	1 Jun–9 Aug	12.6	3.0
Fall	10 Aug–30 Nov	−0.8	2.2