FACTORS AFFECTING NEST AND BROOD SURVIVAL OF ROCK PTARMIGAN (*LAGOPUS MUTA*) IN INTERIOR ALASKA

by

Robert Wiltzen
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APPROVED:

Dr. Todd Brinkman, Committee Co-Chair
Dr. Mark Lindberg, Committee Co-Chair
Dr. Knut Kielland, Committee Member
Dr. Todd Brinkman, Chair, Wildlife Program
Department of Biology and Wildlife
Dr. Karsten Hueffer, Dean
College of Natural Science and Mathematics
Emeline Jones, Director
Graduate School

Abstract

Rock ptarmigan (*Lagopus muta*) are a circumpolar species endemic to high elevations and latitudes of North America and are common throughout Alaska. The *r*- selected life history of ptarmigan indicates that reproduction and specifically nest and brood survival is the most important component of population growth. However, factors affecting these population parameters have not been studied extensively or intensively, since there have only been three studies done in Alaska. Rock ptarmigan exhibit population fluctuations, which may be caused by changes in reproduction and survival due to predation and weather events. Warming climatic patterns and shifts in the range of their food resources may also be impacting rock ptarmigan populations. Previous research on rock ptarmigan in Alaska was completed five decades ago and methods of assessing their populations have improved. Therefore, a better understanding of factors affecting nest and brood survival is essential for understanding factors limiting population growth, particularly in a rapidly changing environment. In this study, we investigated whether variations in hen age, weather, timing of nest initiation, and nesting habitat affected nest and brood survival across two study sites. We focused this study on previously studied alpine populations of rock ptarmigan at Eagle Summit and Denali Highway sites in Interior Alaska from spring through summer in 2018 and 2019. Hens outfitted with transmitters were monitored weekly to determine the status of their nest or brood. We found canopy cover around the nest had the most effect on nest survival. Survival of nests with a closed canopy was more than five times higher than those with an open canopy at the Eagle Summit site and nearly two times higher at the Denali Highway site. Ptarmigan at Eagle Summit had higher brood survival than ptarmigan at the Denali Highway site. Our modeling indicated that survival of nests and broods was not affected by fluctuations in seasonal weather (e.g., minimum temperature and maximum precipitation). Establishing a basis for understanding temporal and spatial trends in population ecology is essential for effective management in a rapidly changing environment and these findings may improve the management of rock ptarmigan.

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Table of Contents

List of Figures

List of Tables

Chapter 1: Introduction and Literature Review

1.1 Population Status

In recent decades, animals found in high mountain habitats and at higher latitudes have increasingly been subjected to the effects of climate change (Booms et al., 2011; Heinemeyer et al., 2019; Jackson et al., 2015; Stewart et al., 2017). Specifically, these ecoregions are experiencing longer and wetter warm seasons and shorter cold seasons (Giorgi et al., 2016; Kotlarski et al., 2023; Napoli et al., 2019). As the climate warms, plant species generally found at lower latitudes expand their range both in terms of latitude and elevation (Gottfried et al., 2012; Seastedt & Oldfather, 2021). This vegetation expansion pushes some animal species in higher latitudinal areas to smaller "islands" of refugia (Gottfried et al., 2012). Animal studies on species endemic to alpine ecosystems indicate that these species are vulnerable to warming temperatures, which affects their distribution and population growth (Gottfried et al., 2012; Scridel, 2014; Stewart et al., 2017). These species have adapted to alpine systems and the relatively colder temperatures as compared to lower elevations and latitudes. Thus, their physiological limitations to temperature (Smith, 1974), and the changing structure or distribution of vegetation, may cause constraints on reproduction, dispersal, and survival. Consequently, this could constrain their ability to adapt to new environments (Dirnböck et al., 2003; Wilson & Nilsson, 2009).

Life history traits of a species dictates which fitness component; survival or reproduction is more important (McWilliam et al., 2022) for species viability. How species maximize fitness through differing rates of survival and reproduction (Stearns, 1983 & 2000) determine which species will maintain viable populations over evolutionary time. Populations that exhibit fast-growing (*r*-selected) traits commonly produce large litters or clutch sizes early and often while having a short lifespan. Slow-growing (k-selected) populations typically have low fecundity, small litters or clutch sizes, and long lifespans (Lebreton & Clobert, 1991; Promislow & Harvey, 1990). Fast-living species associated with higher reproductive productivities have potential trade-offs between survival and reproduction and are likely to be determined by how resources are allocated across facets of reproduction, including maternal and paternal allocation in terms of both the number and quality of offspring (Stearns, 1983).

Rock ptarmigan (*Lagopus muta*) are a circumpolar species found throughout the northern hemispheres (Montgomerie & Holder, 2020). They are considered an *r*-selected species that mostly occupy alpine regions, areas that are being disproportionately affected by climate change. In Alaska, rock ptarmigan inhabit the majority of the state including the Aleutian Islands and much of Southeast Alaska. They select habitat in higher elevations, on exposed rock faces, alpine ridges, scree slopes and rocky tundra with sparse vegetation (Merizon & Carroll, 2019; Montgomerie & Holder, 2020), and feed primarily on buds and catkins of dwarf-birch (*Betula spp.),* willows (*Salix spp*.), and occasionally, alder catkins (*Alnus spp.*) during winter and spring, various alpine forbs and insects during summer, and blueberry (*Vaccinium uliginosum*) and crowberry (*Empetrum nigrum*) in the fall (Weeden, 1969).

The alpine regions they occupy are changing relatively rapidly and there is concern about how rock ptarmigan are adapting to this change. Studies in Iceland (Nielsen & Pétursson, 1995) provide some evidence that rock ptarmigan abundance peaks once every 10 years, while a study in Alaska (Weeden, 1965) found six to nine-year cycles and did not find definitive evidence of these peaks occurring at known frequency. Many ptarmigan populations are known to fluctuate widely in numbers, and some cycle regularly as a response to specialized predators (Nielsen, 1999) and from variation in nest and brood survival (Watson et al., 1998). The amplitude and frequency of these cycles can vary from region to region and fluctuations may be exaggerated by climate change. These fluctuations and the factors influencing annual productivity have not been fully studied in Alaska. Variation in nest and brood survival in rock ptarmigan may be interacting with changes in alpine environments, warmer temperatures, phenological mismatches, and other climate induced fluctuations.

1.2 Nest Survival

Females are capable of breeding as juveniles (Montgomerie & Holder, 2020), which is a bird less than one-year-old. Females typically raise only a single brood in a breeding season. On occasion, they may renest if the nest is lost during egg laying or early incubation (Wiebe & Martin, 1998a). Ptarmigan make shallow scrapes in barren, often very exposed spots in dry, stony tundra, sometimes in natural depressions next to rocks (Wilson & Martin, 2012). These scrapes are the beginning stages of nest building. Nest areas are mostly in flat areas or natural depressions in the tundra and are lined with feathers, moss, lichens, and grasses from the immediate surroundings (Montgomerie & Holder, 2020). Some populations of white-tailed and rock ptarmigan select nest sites with higher lateral cover than other populations (Holder & Montgomerie, 1993; Wilson & Martin, 2012).

Nest site selection is a vital component for the survival of the adult and nest. Wiebe and Martin (1998b) found that greater amounts of overhead and lateral cover at nest sites led to higher nest survival in white-tailed ptarmigan, likely because concealed sites were detected less often by aerial predators. Similarly, in greater-sage grouse, taller vegetation was positively associated with higher nest success (Doherty et al., 2014). However, these sites are also riskier for incubating females, as there are fewer escape routes from ground predators. Thus, there are trade-offs with nest site selection (Wiebe & Martin, 1998b). These tradeoffs may be complicated by shrub expansion (Tape et al., 2010) into higher elevations and latitudes that could improve nest cover and survival, but these shrubs may outcompete preferred forage plants.

Nest initiation date is crucial for nest survival, as many species experience declining survival rates as the breeding season progresses due to deteriorating environmental conditions and diminishing food sources (García-González et al., 2016; Lepage et al., 1999; Martin, 1996). Early-nesting generally results in higher nest survival (Keever et al., 2022) and higher lifetime reproductive success of individual adults (Blums & Clark, 2004) as compared to late or delayed nesting. However, the benefits of early nesting may be negated by climate change, leading to mismatches between nesting timing and plant phenology. While increased vegetation cover later in the season can enhance nest concealment, predation risk may also rise as predators develop search images for nests (Sullivan & Dinsmore, 1990; Wiebe & Martin, 1998b). If predator saturation coincides with peak nest density, survival may be lowest midseason (Niemuth & Boyce, 1995; Wilson et al., 2007). Additionally, early-season snowmelt from warmer weather can influence nest initiation dates and indirectly affect predation rates and overall nest survival.

Nest survival can also vary across different habitat types. A study examining nest survival across different habitat types found that female Willow Ptarmigan (*Lagopus lagopus*) and White-tailed Ptarmigan (*Lagopus lecurus*) breeding at subalpine and alpine sites had smaller clutches and lower probabilities of nest survival, brood survival, and renesting than nests at low elevation arctic sites (Sandercock et al., 2005). While another study on prairie chickens (*Tympanuchus cupido*) found variations in nest survival between sites when vegetation cover, vegetation structure and avian predators were dissimilar (Hagen et al., 2009). Previous fieldwork on rock ptarmigan in Alaska and Japan found that lower nest survival was associated with wet, cool, and even snowy weather that occurred during incubation (Kobayashi & Nakamura, 2013; Merizon et al., 2018).

A study on rock ptarmigan diets found that the quality of food and protein content were correlated with the stage of when plants were consumed and dependent on snowmelt date. In years of early snowmelt, hens benefit from a longer period of high-quality food resources potentially leading to a higher breeding success (García-González et al., 2016).

Weather may affect reproductive success in avian species (Bolger et al., 2005; White, 2008). Warmer temperatures may be causing variations in breeding date and nest initiation date in ptarmigan hens. For many birds in the northern hemisphere, temperature is a key determinant of breeding date (Ludwig et al., 2006) as well as date of snowmelt (Wann et al., 2016). Individual characteristics such as hen age and previous reproductive experience also influence the timing of breeding (Wilson et al., 2007). Breeding is typically delayed by cold spring temperatures due to a reduction in potential lower food availability (Wilson & Martin, 2010) and increased thermoregulatory costs for adults (Wiebe and Martin 2000). If hens do not exhibit phenotypic plasticity to counter these warmer winter transitions to spring, then temperature could have strong implications for nest survival. Furthermore, previous fieldwork on rock ptarmigan in Alaska and Japan found that lower nest survival was associated with wet, cool, and even snowy weather that occurred during incubation (Kobayashi & Nakamura, 2013; Merizon et al., 2018).

Life history parameters can vary along altitudinal and latitudinal gradients within and between species and populations (Badyaev & Ghalambor, 2001; Sandercock et al., 2005; Wilson et al., 2012), although the specific environmental factors driving life history remain unclear (Hille & Cooper, 2015; McKinnon et al., 2010). Nest survival within a species can vary geographically and annually in relation to the abundance and richness of predator communities (Kurki et al., 1997; Wilson & Arcese, 2006). There may be temporal and spatial processes that are causing differences in nest survival (Hagen et al., 2009; Wilson et al., 2007) and changing weather conditions may also be adding to these effects.

1.3 Brood Survival

In ptarmigan species (*Lagopus sp.*), the recruitment of young birds into the breeding population can heavily influence population dynamics (Lack, 1966; Sæther, 2016; Sandercock et al., 2005). Several consecutive years of low recruitment can result in exponential declines in ptarmigan abundance, which has been found in central arctic populations in Canada (Cotter, 1999). The main causes of chick and brood mortality in ptarmigan are generally considered to be predation, unfavorable weather conditions, and chick or hen body condition (Erikstad, 1985; Ludwig et al., 2010). Ludwig (2010) for instance, found that the highest chick mortality rates occurred during the first 10-14 days after hatching due to predation and brood survival clearly increased with the extent shrub cover and warmer temperatures.

1.4 Factors Affecting Hen and Brood Survival

Hen body condition before laying may also affect nest survival due to the nutritional investments needed for developing a clutch of eggs (Houston et al., 1983; Stephens et al., 2009; Williams et al., 2017). The energetic costs of investing resources toward egg production with spring foraging may be detrimental to the females' overall body condition. This could, in turn, influence their reproductive success, which has been observed in tropical bird species (Milenkaya et al., 2015), waterfowl (Devink et al., 2008; Erikstad et al., 1993) and pheasants (Draycott et al., 1998). Similarly, since ptarmigan are income breeders, females that increase their mass before laying, may have more flexibility in how they allocate resources throughout the breeding period (Wiebe & Martin, 2000). Other studies of birds (Vézina & Salvante., 2010; Vézina & Williams., 2003) have shown that variation of individual reproductive investment prior to laying may influence reproductive success (egg size and quality) and production.

Age of the hen could influence brood survival because adult hens are better at foraging and avoiding predators than juvenile hens (Caizergues & Ellison, 2000). Adults may be better at foraging and avoiding predators and may have greater breeding experience than juveniles (Caizergues & Ellison, 2000). In many bird species, reproductive parameters vary dramatically with age (Sæther, 1990; Sandercock et al., 2005; Wiebe & Martin, 1998a). In addition, age-specific variations in reproductive parameters are crucial for more accurate modeling of population dynamics; the productivity of populations can be highly variable if reproductive success changes with age (Caizergues & Ellison, 2000). This age-specific reproductive variation may be exacerbated by climate change and as environmental factors could be selecting and favoring older hens that have different behaviors than younger hens (Grisham et al., 2013).

Similarly, early brood mortality rates in grouse are usually the highest during the first two weeks after hatching (Hannon & Martin, 2006; Ludwig et al., 2006). Weather may affect chick survival because ptarmigan chicks are precocial and incapable of thermoregulation during their first weeks of life and thus, they rely solely on the hens for warmth (Pedersen, 1979).

Much of what is known about the general ecology of rock ptarmigan is based on studies that took place 50 years ago or studies from outside of Alaska. Substantial advancements have been made in telemetry technology and analytical methods since previous work was conducted in Alaska, which, in part, prompted this research project. In 2018, the Alaska Department of Fish and Game (ADF&G) and the University of Alaska Fairbanks (UAF) initiated this study, which was a continuation of research at both the Eagle Summit (Carroll, 2018 [*unpublished data*]) and Denali Highway (Merizon et al., 2018) study sites (Figure 1.1) to examine the reproductive ecology of rock ptarmigan more comprehensively. The focus of this study is to investigate what factors had the greatest influence on nest and brood survival across these two study sites. Specifically, we examined how nest survival and brood survival were affected by hen age, weather (temperature and precipitation), nesting habitat, nest age, nest initiation date, brood age, site, and year.

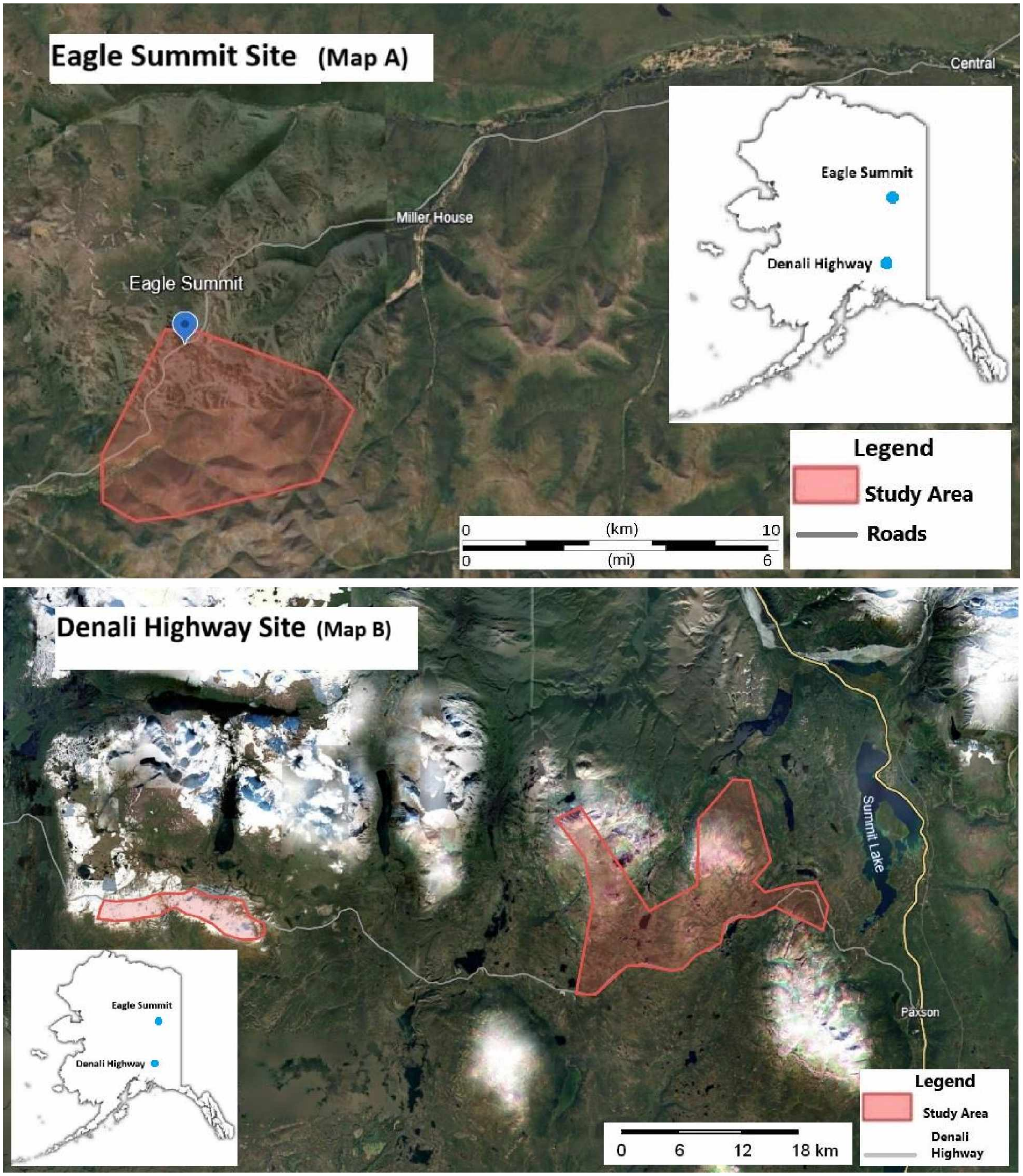

Figure 1.1. Locations of our two field sites for the rock ptarmigan study conducted during 2018 & 2019 in Interior Alaska: Eagle Summit site (Map A) and Denali Highway site (Map B).

Chapter 2: Methods

2.1 Study Sites

We selected field sites (Figure 1.1) adjacent to Eagle Summit (65.458, -145.425) and along the Denali Highway (63.070 -145.701) of Interior Alaska to facilitate comparisons to previous studies of rock ptarmigan by Weeden (Weeden 1965, Weeden &Theberge 1972) and Merizon et al. (2018). These sites have similar alpine and subalpine tundra habitats between 900 m and 1350 m in elevation. The alpine habitat vegetation consists mostly of perennial grasses, sedges, forbs, and low-growing shrubs with abundant lichens and mosses and rocky outcroppings (Billings, 1979).

2.2 Capture and Morphometrics

Female rock ptarmigan were captured during the breeding season in early May through July in 2018 and 2019 using a shoulder-fired net gun (Coda EnterprisesTM, Mesa, Arizona) and drive nets from Memphis Net & Twine (www.memphisnet.net, 1-1/2 in sq. mesh and 12-ft deep). After capture, a number of morphometric variables were recorded but only age was used in the analysis here. Hen age (juvenile or adult) was determined by examining the pigmentation patterns of the eighth and ninth primary feathers (Bergerud et al., 1963; Pyle 2008). Juvenile birds were defined as ≤ one- year-old, and adult birds were > one-year-old.

2.3 Monitoring

Juvenile and adult hens were fitted with necklace-style VHF radio transmitters from Advanced Telemetry Systems™ (ATS model A3950) in early May through July in 2018 and 2019. All transmitters weighed 12 g and did not exceed 3% of the individual's body mass, as suggested by Thirgood et al. (1995). These transmitters were programmed to transmit 30 beats per minute (bpm) while the bird remained alive. A period of six hours of inactivity would cause the transmitters to switch to 60 bpm, indicating a mortality. In 2019, there were 3 hens captured and fitted with Holohil transmitters (Model RI-2DM). These transmitters weighed 7.5 g and had a mortality switch that activated after 12 hours of inactivity. The Holohil transmitters had similar bpm programmed as the ATS transmitters for alive and dead birds.

Telemetry was accomplished by using a handheld ATS receiver (R1000) or ATS box receiver (R4000). We attempted to monitor radio marked hens from the ground daily from May to early August. On occasion, field personnel did not detect signals. The steep slopes and mountainous terrain did limit the collars' VHF signals, occasionally there were periods longer than the optimal four to five-day window between observations. If we did not detect the signal after four separate occasions on foot (over approximately 14 days), the bird was identified as missing. Each season, a pilot flew fixed-wing aircraft two to three times as a final attempt to locate missing birds. If we still did not detect a signal, we excluded these birds ($n = 5$) from the analysis to reduce possible bias in estimates of survival. Nest searching began in late May, birds that had active collar were radio tracked until nests were found. Additionally, in 2019 birds that were collared the previous year were radio tracked until nests were found. Nest locations were recorded using handheld GPS units (Garmin™ Rino 650t or Garmin™ 64st). The eggs were counted, and incubation stage was estimated using egg flotation methods derived from a study on greater prairie chickens (McNew et al., 2007).

Nests were visited on average every five days before hatch to determine nest fate (hatch success or failure) following protocols in Martin & Geupel (1993). These visits made up 'encounter histories' for each nest history to estimate daily survival during the 21-day incubation period (Weeden, 1965), which was based on: 1) when the nest was found, 2) when the nest was last seen alive, and 3) the last time the observer checked the nest or individual. Additionally, we added three days to the incubation period to account for exposure days to eggs laid before incubation, totaling 24 days of exposure. This strategy follows previous studies that suggest using the "laying-plus-incubation" concept for reducing bias and accounting for exposure when estimating cumulative nest survival (Blomberg et al., 2015).

Trail cameras (ReconyxTM Hyperfire HC500) were used for determining the exact hatch day of a subset of nests (only at the Denali Highway site) and to assist with developing estimated hatch dates for nests with unknown hatch dates. Eggs were floated at nests with known hatch date (monitored by trail cameras until date of hatch) and these float angles were used to estimate hatch dates for nests not monitored with trail cameras, but with data on float angles. Nest initiation dates were estimated by backdating 21 incubation days from the hatch date (Weeden, 1965). In our study, an additional 3 days were added to account for nest survival days before incubation. The duration of 3 days was appropriately used to standardize survival intervals for all nests. Cameras were placed within 2 meters from the nests to better estimate hatch date. In an effort to place these cameras without alluring predators to the nest by additional scents, field technicians wore nitrile gloves and prior to placing in the field the cameras were cleaned with alcohol wipes.

Encounter histories for brood survival were developed from attempts to track hens after hatch and count their chicks on average every five days. The total duration of brood tracking varied across broods because some hens were first captured with a brood. Most broods were tracked from hatch date until the week before ptarmigan hunting for each year of the study, which averaged 58 days.

2.4 Precipitation and Temperature Data

Weather data were obtained from the USDA SNOTEL weather stations at Eagle Summit, Alaska (65.4847, -145.4124) and Monahan Flat, Alaska (63.3001, -145.6501) for the Denali Highway site. The Eagle Summit study site is 0.5 km southeast from the Eagle Summit weather station and the Denali Highway study sites are 80 km southeast from the Monahan Flat weather station. The minimum daily temperature (°C) and maximum precipitation (mm) were used to examine if weather factors affected the daily survival rates (DSR) of nests and broods.

2.5 Measuring Relative Canopy Cover

Photographs were taken above each nest site (~1m) by standing over the nest to estimate the canopy cover. Canopy cover was categorized as closed by obstructing vegetation if shrub/ground cover was present in more than 50 % of the area within a 0.3 m radius from the center of the nest and at least 0.3 m in height. Open canopy nests were defined as having less than 50 % cover within 0.3 m from the center of the nest.

2.6 Statistical Analysis

Nest survival models were used to obtain maximum likelihood estimates of survival probabilities given a set of covariates thought to influence daily nest and brood survival. Assumptions of the daily nest–survival models described here are: (1) homogeneity of daily survival rates; (2) nest and brood fates are correctly determined; (3) nest and brood discovery and subsequent checks do not influence survival; (4) nest or brood fates are independent; (5) all visits to nests or broods are recorded; and (6) checks are conducted independently of nest or brood fate.

We constructed these models in program R v4.05 (R core team, 2021) using the *Rmark* package (Laake, 2013) as an interface for Program MARK (Cooch & White, 2019). We then fit a binomial nest survival model with a logit link function to estimate nest and brood survival using:

$$logit(\hat{p}) = \ln\left(\frac{\hat{p}}{1-\hat{p}}\right)$$

Because modeling was completed on a transformed scale (logit) for numerical optimization efficiency, back transformation was needed to obtain the desired estimates on the 0–1 scale. The output given from the software is of the following form:

$$logit(\hat{p}) = \beta_0 + \Sigma_{j=1}^{k}\beta_j x_{ji}$$

Back transforming these estimates into real scale (0,1) yields the following expression:

$$\hat{p} = \frac{exp\left(\beta_0 + \Sigma_{j=1}^{k}\beta_j x_{ji}\right)}{1 + exp\left(\beta_0 + \Sigma_{j=1}^{k}\beta_j x_{ji}\right)}$$

where x_{ji} is the value of the j^{th} covariate at time *i,* and $\hat{p}$ is the probability of survival.

Nest survival (NS_{ij}) is defined as the probability that a hen will hatch at least one egg in year *i* at site *j*. Brood survival (BS_{ij}) is defined as the probability that at least one chick in a brood will survive 58 days post-hatch in year *i* at site *j.*

Average daily nest survival probabilities were raised to a 24-day nest survival probability ($P(\text{daily survival})^{24}$) to evaluate the probability of a nest surviving to hatch. Similarly, average daily brood survival probabilities were raised to a 58-day brood survival probability ($P(\text{daily survival})^{58}$) to evaluate the probability of a brood surviving to fledging. We also estimated survival at a mid-point (29 days), shown in figure 3. Both survival probabilities then required the use of the delta method to estimate the standard error of the estimate (Powell, 2007), due to changing time scales from daily survival to the survival of the entire 24-day nesting period, or the 58-day brood period. Example of the delta method and 24-day nesting survival:

$$\left[\frac{\partial \hat{S}_{24}}{\partial \hat{S}_d}\right] = \left(\ddot{S}_d^{24}\right) = 24_d^{23}$$

And now accounting for the variance approximating 24 days:

$$v\hat{a}r\left(\hat{S}_{24}\right) = 24^2 * v\hat{a}r\left(\hat{S}_d\right) * \hat{S}_d^{46}$$

To test for covariate effects on the probability of nest survival, 22 a priori models (Table 2.1) were fit on nest survival (n = 114) that incorporated the following covariates: hen age, nest age, initiation date, canopy, Time (trend with calendar date), time (varies with calendar date), site, year, minimum temperature, maximum precipitation, and constant survival models. Similarly, 19 a priori models (Table 2.2) were fit on brood survival (n = 47) to test the effects from these covariates: hen age, brood age, Time, time, site, year, minimum temperature, maximum precipitation, and constant survival models. Both nest and brood model sets had combinations of single variable, additive, and interactive effects. The variations of these models were developed to examine biological theories, processes and observations.

Models were then ranked using Akaike's Information Criterion (AICc) corrected for small sample sizes where the model with the lowest AICc score was considered the best model to support the data and models within 2 AICc of the lowest scoring model competing models (Burnham & Anderson, 2002).

We examined the effects of canopy cover (canopy), hen age (HenAge), nest initiation date (Init) nest age (NestAge), minimum temperature (min_temp), maximum precipitation (max_precip), year (Year), site (Site), and time of season (Time = quadratic; time = linear). We used Akaike information criterion (AICc) to compare and select the model that best-explained variation in survival (Canopy * Site).

Table 2.1. Results from nest survival models for our rock ptarmigan study during 2018 and 2019 in Interior Alaska.

Model	npar	AICc	DeltaAICc	weight
S(Canopy * Site)	4	292.80	0.00	0.47
S(Canopy)	2	293.85	1.04	0.28
S(Canopy + min_temp)	3	295.85	3.05	0.10
S(Canopy * Year)	4	297.45	4.65	0.05
S(Canopy + Init + min_temp)	4	297.60	4.79	0.04
S(Canopy * HenAge)	4	297.83	5.03	0.04
S(max_precip)	2	299.89	7.08	0.01
S(Site)	2	301.20	8.40	0.01
S(Site + Time)	3	303.21	10.41	0.00
S(1)	1	304.46	11.66	0.00
S(HenAge + NestAge + Site)	4	304.68	11.88	0.00
S(HenAge + Site + Year)	4	305.00	12.19	0.00
S(NestAge)	2	306.28	13.47	0.00
S(min_temp)	2	306.39	13.59	0.00
S(HenAge)	2	306.41	13.61	0.00
S(Year)	2	306.44	13.63	0.00
S(Time)	2	306.46	13.65	0.00
S(HenAge * Site * Year)	8	309.49	16.69	0.00
S(HenAge * NestAge * Site)	8	310.95	18.14	0.00
S(Site + time)	49	368.82	76.01	0.00
S(time)	48	372.58	79.77	0.00
S(Site * time)	96	465.39	172.59	0.00

We examined the effects of hen age (HenAge), brood age (BroodAge), minimum temperature (min_temp), maximum precipitation (max_precip), year (Year), site (Site), and time of season (Time = quadratic; time = linear). We used Akaike information criterion (AICc) to compare and select the best fit model (HenAge*BroodAge * Site).

Table 2.2. Results from brood survival models for our rock ptarmigan study during 2018 and 2019 in Interior Alaska.

Model	npar	AICc	DeltaAICc	weight
S(HenAge * BroodAge * Site)	8	106.60	0.00	0.99
S(HenAge * Site * Year)	8	116.85	10.24	0.01
S(Time)	2	121.38	14.78	0.00
S(Site + Time)	3	122.45	15.85	0.00
S(BroodAge + Time)	3	123.08	16.47	0.00
S(BroodAge)	2	123.88	17.28	0.00
S(1)	1	124.87	18.26	0.00
S(min_temp)	2	125.48	18.88	0.00
S(max_precip)	2	125.49	18.89	0.00
S(Year)	2	125.99	19.39	0.00
S(max_precip + min_temp)	3	126.67	20.07	0.00
S(Site)	2	126.85	20.25	0.00
S(HenAge)	2	126.86	20.26	0.00
S(HenAge + BroodAge + Site)	4	127.80	21.20	0.00
S(max_precip * min_temp)	4	128.60	21.99	0.00
S(HenAge + Site + Year)	4	129.91	23.30	0.00
S(time)	57	214.73	108.13	0.00
S(Site + time)	58	216.03	109.43	0.00
S(BroodAge + time)	58	217.30	110.69	0.00

Chapter 3: Results

3.1 Sample Size

A total of 185 rock ptarmigan were captured over two field seasons (2018-2019) at our two study sites. Of the 185 captured, 170 were hens (juveniles = 80, adult = 90), which were collared, 6 were males, and 9 hens were capture mortalities. In 2018, 95 rock ptarmigan were captured: 53 at Eagle Summit (50 hens; 25 juveniles, 23 adults, 3 males, 2 hen capture mortalities) and 42 at Denali Highway (40 hens; 23 juveniles, 14 adults, 2 males, 3 hen capture mortalities). In 2019, 90 rock ptarmigan were captured: 54 at Eagle Summit (54 hens; 25 juveniles, 29 adults, 1 hen capture mortality) and 36 at Denali Highway (35 hens; 16 juveniles, 19 adults, 1 male, 3 hen capture mortalities). Of the 161 hens radio-tracked, 114 hens had nests (66 Eagle Summit; 48 Denali Highway) and 47 of these nests were recorded to have hatched; 22 at Eagle Summit and 25 at Denali Highway.

3.2 Precipitation

When examining the precipitation over the two field seasons, the Denali Highway site appeared to be the drier site having less summer precipitation on average (146 mm) compared to Eagle Summit (188 mm) (USDA, 2024). Average summer precipitation during our study period was consistent with the longer term (2010-2016) averages (Denali Highway = 210 mm, Eagle Summit = 230 mm).

3.3 Nest Initiation and Survival

The average nest initiation date (i.e., 24 days before hatch) between sites differed by 5 days in 2018 (May 27th at Eagle Summit (± 1.27*SE*) and June 1st at Denali Highway (±0.76*SE*), and 4 days in 2019 (May 26th at Eagle Summit (±0.94*SE*), and May 30th at Denali Highway (±0.98*SE*),). For both years, the hens at Eagle Summit initiated nests and hatched earlier than at Denali Highway. The average hatch dates differed by 2 – 5 days between sites for both years, with nests at Eagle Summit hatching on average on June 18th in 2018, and June 20th in 2019, at Denali Highway: June 20th in 2018, and June 25th in 2019. I found 26% (15/57) and 14% (9/65) of nests in closed canopies at the Denali Highway and Eagle Summit sites, respectfully.

The top three models for nest survival all included canopy cover (Table 2.1), and when combined, accounted for 0.85 of the model support. The top model with a canopy*site interaction had a model weight of 0.47. There was limited support (model weights ≤ 0.05) for models that did not include canopy cover; therefore, I based inference on the top model.

Survival to 24 days at both study sites was higher for nests with a closed canopy than those with open canopies (Figure 3.1). Because of the interaction with the site, survival of nests with a closed canopy was higher at Eagle Summit than at Denali Highway (0.71 ± 0.18*SE* with a 95% CI, 0.351, 1.063 and 0.56 ± 0.15*SE* with a 95% CI, 0.277, 0.849, respectively), but survival of a nest with an open canopy was lower at Eagle Summit than at Denali Highway (0.13 ± 0.04*SE* with a 95% CI, 0.049, 0.213 and 0.33 ± 0.10*SE* with a 95% CI, 0.277, 0.849, respectively). Therefore, the difference in survival rates between canopy types was greater at Eagle Summit than at Denali Highway (0.58 ± 0.18 *SE* and 0.23 ± 0.18 *SE*, respectively).

3.4 Brood Survival

The top model for brood survival (Figure 3.2), which included a three-way interaction of hen age, brood age, and site, received 0.99 of the model weights (Table 2.2). Of the 45 broods monitored at both sites (20 Eagle Summit; 25 Denali Highway), 28 survived to the end of the field season (12 Eagle Summit; 16 Denali Highway). Patterns of brood survival were complex because of the interactions and the sensitivity of our estimates to mortalities given our sample sizes. For example, the daily survival of broods with adult hens at Eagle Summit was 0.996 (95% CI, 0.96-1.0) at day 29, the middle point of the season, while survival rates at day 1 declined from 1.0 (95% CI, 0.94-1.0) to 0.97 (95% CI, 0.77-1.0) by day 58 (Figure 3.2). In contrast, the daily survival of broods with juvenile hens at Eagle Summit was 0.952 (95% CI, 0.88-1.0) at day 29, while survival rates at day 1 increased from 0.97 (95% CI, 0.5-1.0) on day 1 to 0.99 (95% CI, 0.78-1.0) on day 58 (Figure 3.2). The daily survival of broods with adult hens at Denali Highway was 0.991 (95% CI, 0.92-1.0) at day 29, while survival rates increased from 0.29 (95% CI, 0.0-1.0) on day 1 to 0.99 (95% CI, 0.77-1.0) by day 58 (Figure 3.2). However, the daily survival of broods with juvenile hens on the Denali Highway was 0.994 (95% CI, 0.97-1.0) at day 29 and decreased from 1.0 (0.88-1.0) on day 1 to 0.97 (0.77-1.0) by day 58 (Figure 3.2). Holding site and hen age constant, mean daily brood survival were highest immediately after hatching in adult hens from Eagle Summit and juvenile hens for the Denali Highway, gradually decreasing out to day 58 (Figure 3.2). While the mean daily brood survival of adult hens at Denali Highway and daily brood survival of juvenile hens from Eagle Summit were lowest immediately after hatching and increased out to day 58 (Figure 3.2).

The probability of a brood surviving from hatch to the end of the season over a duration of 58 days (June 11th to August 9th) at Eagle Summit was 0.464 ± 0.09*SE* when accompanied by an adult hen and 0.441 ± 0.09*SE* when the hen was a juvenile. The probability of a brood surviving 58 days (June 11th to August 9th) at Denali Highway was 0.443 ± 0.12*SE* when accompanied by an adult hen and 0.426 ± 0.13*SE* when the hen was a juvenile.

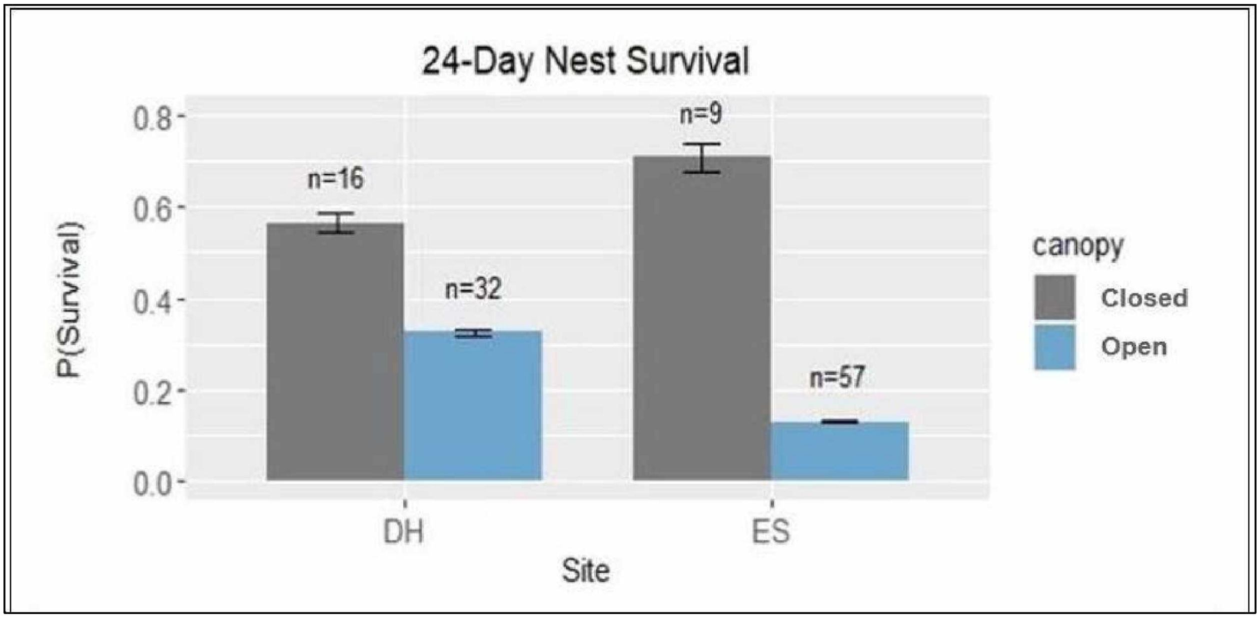

Figure 3.1. Probability of nest survival for two study sites Eagle Summit (ES) and Denali Highway (DH) over the entire nesting period of 2018 & 2019 (21 days for incubation plus three additional days of exposure prior to incubating) for open and closed canopy nests. Error bars indicate the standard error of the mean for each group.

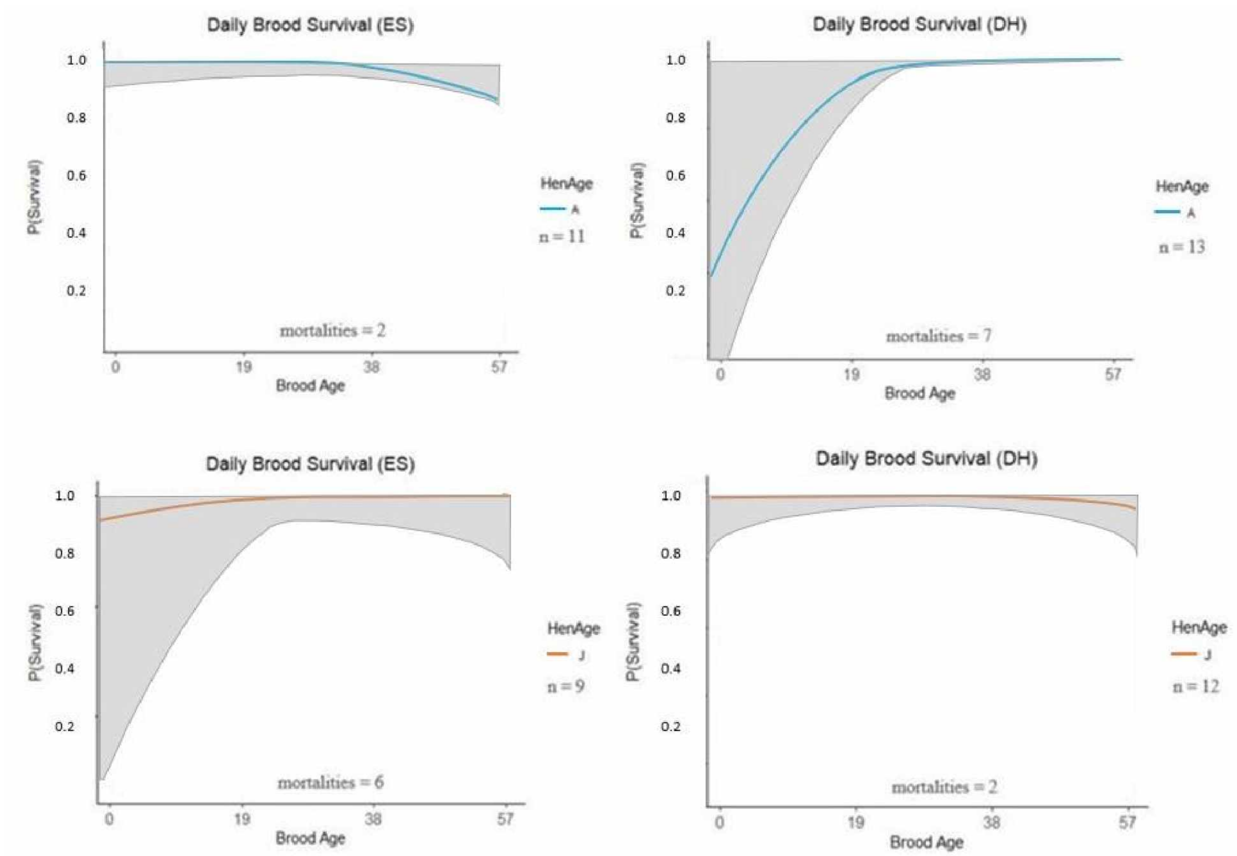

Figure 3.2. Daily brood survival estimates and numbers of total brood mortalities at our two study sites Eagle Summit (ES) and Denali Highway (DH) for adult (A) and juvenile (J) hens. Estimates above are for our top model for brood survival which included (hen age*, brood age*, site). The shaded lines represent the 95% confidence intervals around the survival estimates (blue/orange). Sample sizes of each group are listed as n.

Chapter 4: Discussion

4.1 Study Comparisons

We estimated nest and brood survival, considering a number of variables thought to influence each, for two populations of rock ptarmigan in Interior Alaska. With previous assessments of population dynamics of rock ptarmigan being nearly five decades old (McGowan, 1975; Weeden, 1972), our findings provide relatively novel information on survival because previous studies were based on apparent nest and brood survival (Weeden 1965), which are positively biased estimates that do not account for undetected loss. The most recent relevant study conducted on rock ptarmigan may not be directly comparable (Merizon et al. 2018) because they did not directly follow broods throughout the season, and therefore could not estimate brood survival, and sample sizes were lower. Therefore, our research expands on knowledge of a relatively understudied species important to hunting and higher-elevation ecosystems in Interior Alaska.

4.2 Nest survival

We found that nesting habitat (measured by canopy cover) and site were important explanatory variables for nest survival. Survival of nests with closed canopy was about five times higher than nests with an open canopy at the Eagle Summit site and nearly two times higher at the Denali Highway site. Closed canopy nests at the Denali Highway site (N=16) had lower nest survival ($0.60 \pm 0.12 SE$) than Eagle Summit (N=9) ($0.78 \pm 0.09 SE$). Additionally, hens at the Denali Highway site were observed in closed nests more frequently ($0.31 \pm 0.06 SE$) compared to hens at the Eagle Summit site ($0.13 \pm 0.04 SE$; Figure 2). The differences in survival between sites and canopy types, may simply be because of differences in habitat quality, thus affecting suitable nest sites and survival (Wilson & Martin, 2008). We did not estimate availability of habitat types or habitat quality at each site. However, in general, we observed less shrub cover at the Eagle Summit site which could have been related to hens nesting in proportionally fewer locations with shrub cover at Eagle Summit (14% nesting in closed cover) as compared to the Denali Highway site (26% nesting in closed cover). Habitat features considered important during nest selection would also be attributes that maximize nest survival. For example, hens that are avoiding areas with greater canopy cover may inadvertently choose areas that do not provide the necessary vegetation height needed to conceal nests from predators and thus leading to increased predation rates and decreased survival. Hens at the Denali Highway site are selecting nest sites with more closed habitat than at Eagle Summit. Ptarmigan using nesting sites with greater amounts of shrub cover may have higher nest survival because of predator avoidance as found in rock and willow ptarmigan (Kobayashi, 2013; Wiebe & Martin, 1998b) and concealment from avian predators that Sawa et al. (2011) found in rock ptarmigan, and refugia from the warmer temperatures of sites with little or no canopy cover in ptarmigan (Tape et al., 2010).

Our results regarding age affecting nest survival are consistent with two earlier studies of ptarmigan at Chilkat Pass, British Columbia (Hannon & Smith, 1984) and throughout Colorado (Robb et al., 1992; Wiebe & Martin, 1998a). All three studies found no evidence of the effects of hen characteristics on nest survival. Although, older females tend to breed earlier, produce larger clutches, and are more likely to re-nest following failure (Wiebe & Martin, 1998a). Hen age may be less important for nest survival compared to other variables, because while incubating and mostly sedentary, these hen characteristics may be more important later on with brood survival when the hen is more active. Other variables such as predator avoidance strategies, nest location, vegetation characteristics, and predator density may have a greater influence on nest survival. Although nest survival might be influenced by the physical characteristics of the hen, how the hen reacts to predators may be more influential. Aggressive behavior towards predators and deceptive nest defense found in various ground nesters (Smith & Edwards, 2018) and factors aligned nest site selection and vegetation characteristics as found in sage grouse (Doherty et al., 2014; Watters et al., 2002) and ptarmigan (Kobayashi, 2013; Wiebe & Martin, 1998b) may be more important for nest survival because of the ability to deter predators or remain undetected by predators. Sawa et al. (2011) found that rock ptarmigan were selecting nest sites in shrubs but vegetation height was lower at nest sites than random sites, suggesting that ptarmigan were selecting for sites with cover that were open enough to detect predators.

Although study sites were similar in topography and elevation, Eagle Summit and Denali Highway sites had different weather patterns during this two-year study. Over two seasons equaling 228 total days, Denali Highway had fewer recorded precipitation days (32) and 23% less precipitation (146 mm) compared to Eagle Summit, which had 42 days of precipitation and 188 mm of precipitation. Weather variables such as precipitation and temperature are commonly found to affect success of nests (Kobayashi & Nakamura, 2013). However, we found these variables did not explain nest survival in this study likely because above-average precipitation was uncommon during our study. Nests may be more resilient to cold temperatures and precipitation than we expected. For example, extreme cold or wet weather conditions can make it more difficult for eggs to hatch and chicks to survive. However, ptarmigan are well adapted to their arctic and alpine environments and are able to withstand a wide range of weather conditions.

Nest timing might affect nest survival because as the season progresses, vegetation grows and improves nest concealment (Wiebe & Martin 1998b) from predators. However, we did not find any effect from initiation date, nest age, or calendar date on nest survival. Therefore, these variables associated with time did not change vulnerability to nest predation. Factors other than nest timing such as predation are the main cause of poor nest survival in birds (Martin 1995; Ricklefs 1969). The predation risk to a nest can be affected by nest location and incubation behavior, which may be more important factors than nest timing leading to the overall nest survival (Conway & Martin 2000; Smith et al. 2007, 2012). The quality of parental care provided by the hen can also impact nest survival. Factors such as the hen's ability to defend the nest from predators can influence nest success regardless of nest timing (Meyer et al. 2020; Smith et al. 2007, 2012).

4.3 Brood survival

We found that the interactions among hen age, site, and brood age influenced brood survival. As the brood ages, the daily survival rate for broods with adult hens at Denali Highway and juvenile hens at Eagle Summit increased at different rates; broods accompanied by adults had initially low survival, but by day 29 had a higher rate than those accompanied by juveniles (Figure 3.2). Similarly, brood age interacted with site because increases in brood survival with age were earlier in the season for the Eagle Summit site. This indicates highest survival was for broods with an adult hen at Eagle Summit, the lowest was for broods with an adult hen at Denali Highway.

Broods that were accompanied by adult hens at both sites had a higher probability of survival (Denali Highway 0.443 ± 0.12*SE* and Eagle Summit 0.464 ± 0.09*SE)* compared to broods with juvenile hens (Denali Highway 0.426 ± 0.13*SE* and Eagle Summit 0.441 ± 0.09*SE)* over the duration of the brood rearing period. Between sites, Eagle Summit had higher brood survival for both age classes of hens. However, site only accounted for approximately a 1.7% higher probability of survival for broods with adult hens and approximately a 2.3% higher probability with juvenile hens parenting the brood. Therefore, site was not an important ecological factor for explaining survival rates. However, the three-way interaction showed that there are different dynamics at each site (Figure 3.2). Specifically, older broods accompanying older hens at Eagle Summit had higher average survival rates compared to all other combinations of hen age and site. Broods that were parented by adult hens at Eagle Summit had similar brood survival rates throughout the season compared to broods that were parented by juvenile hens at Denali Highway. There were also similarities when comparing broods parented by juvenile hens at Eagle Summit to broods parented by adults at Denali Highway. Although the Denali Highway site had largely different brood survival rates early in the season (0.29) than Eagle Summit (0.97) and by day 28 had a lower survival rate (0.991) than Eagle Summit (0.952).

Differences in brood survival due to the age of the hen could be attributed to adult hens being better at foraging, avoiding predators, and having greater breeding experience than juvenile hens (Caizergues & Ellison, 2000). Differences in brood survival with effects of brood age could also be explained by the fact that precocial young often experience high mortality prior to achieving the ability to thermoregulate and fly (Cowell et al., 2007). Thus, this could cause brood survival to increase as the brood ages (Cowell et al. 2007). Differences in brood survival among sites may also be attributed to differences in predation rates from varying predator densities and species. Given our top model (Figure 3.2), the three-way interaction (Hen Age * Brood Age * Site), there were slight variations to brood survival when each one of the variables were examined. I believe this caused an interaction effect and was the reason why this model was ranked the highest. This interaction occurred because the impact of brood survival is influenced by hen age, and brood survival may only increase as hen age increases. While also, brood survival is influenced by brood age, and each additional day increase the brood survival increases.

Similar to weather effects on nest survival, we did not find clear evidence of minimum temperature or maximum precipitation affecting brood survival for our study. There may not have been a weather effect on survival because extensive variations in weather conditions did not occur during this study and ptarmigan have exhibited resiliency to normal weather fluctuations because they are adapted to arctic and alpine environments. We did not observe any failures of young broods that were attributed to precipitation or weather events. Since we did not mark the chicks, we were not able to assess chick survival.

Moreover, precipitation and how it can influence survival may be better investigated on the finer scale of individual chick survival than what we observed with brood survival. Rock ptarmigan chicks may be less resilient to weather factors than we found in our study since other related ptarmigan studies found that younger broods were more susceptible to weather (Hannon & Martin, 2006; Kobayashi & Nakamura, 2013; Ludwig et al., 2006; Novoa et al. 2008; Pedersen, 1979; Wann et al., 2016).

Trade-offs between investments in laying date, clutch size, and incubation may exist (Wiebe & Marten, 2000). We were unable to collect consistent and comparable estimates of hen body mass. Therefore, we excluded these measurements from our analysis. We suggest, however, that future research address the effects of hen body mass on nest and brood success. Hen age and hen mass may play an important role in overall survival of a clutch, and eventually brood survival. Other studies of birds (Vézina & Salvante, 2010; Vézina & Williams, 2003) have shown that variation of individual reproductive investment prior to laying may influence reproductive success (chick quality) and production further in the season.

In our study we did not find any effects from hen age on survival on nests but did find effects from hen age on brood survival in the interaction model (hen age * brood age * site). This discrepancy could be due to natural variation of individual hen traits in the factors that influence survival (Individual quality, survival, body condition, nest initiation date). Additionally, heterogeneity in individual quality in resource acquisition, which has been reported among individuals~~,~~ could also be masking resource-based tradeoffs (Vedder & Bouwhuis, 2018). Therefore, it is possible that other variables may be more important predictors of survival in our study.

4.4 Censoring

A common issue with survival studies is that mortality can be confounded with permanent emigration. For instance, an individual thought to have died may have emigrated from the survey area. A common approach to dealing with missing animals is to censor them from the study after the last known location (right censoring). This issue with right censoring can cause a bias in survival estimates (Decesare et al., 2016). In our study, we right censored a small portion, 0.03% (n=5) of the marked hen sample. Therefore, we don't believe censoring affected our findings. Other bias in vital rate estimation can also happen when failing to meet a variety of assumptions during the sampling and monitoring stages, such as transmitters do not affect the animals being monitored, and that marked animals are representative of the population (Decesare et al., 2016).

4.5 Conclusions

Overall, our study suggests that canopy cover is an important factor affecting nest survival in these two populations of rock ptarmigan. Based on model selection criteria the relative effects of hen age, brood age, and site on brood survival were much lower than the effect canopy cover had on nest survival. Our nest survival models identified more significant factors for survival, as evidenced by the canopy covariates being consistently ranked higher than the null model. In contrast, when examining brood survival, the top interaction model's individual covariates generally ranked below the null model, indicating that these covariates were less effective in explaining survival dynamics than nest survival covariates.

With site effects we found that nest survival was higher at Eagle Summit (0.423 ± *SE* 0.009), than at Denali Highway (0.416 ± *SE* 0.001) in 2018, and then in 2019 switched with nest survival being lower at Eagle Summit (0.275 ± *SE* 0.005) than at Denali Highway (0.625 ± *SE* 0.009). We speculate that low survivability and switching of survival rates between sites and years could be because predators were associating the presence of technicians visiting nests with an increased likelihood of finding nests, which ultimately may have increased predator presence and had a negative impact on nest survival. In our study there may be a multitude of factors affecting nest survival, but what I believe is the best explanation are predator-prey dynamics, and predator densities and how they affect ptarmigan behavior and habitat use, which can further impact their survival and reproductive success.

Factors that may have caused variability in survival, such as predation rates, could have changed between sample years but were unaccounted for in our analyses. Research on similar ground-nesting species has shown that local and landscape scale habitat features influenced nesting habitat selection (Jackson et al., 2015) and corresponding nest survival rates. In our study, closed canopy nests had greater survival because the foliage most likely reduced predators' ability to detect nests.

Through our field observations, predator communities and densities varied among sites and seemed to greatly influence nest and brood survival in our study. Furthermore, the effects of nest predation are the most important limiting factor to nest survival (Wilson et al., 2007). Golden eagles (*Aquila chrysaetos),* which commonly prey on ptarmigan (Nyström et al., 2006), are known to nest at both the Denali Highway and Eagle Summit site, although they were seen more frequently at the Denali Highway site. This might explain some differences in nest survival between sites. Red foxes (*Vulpes vulpes)* were observed at both sites and seemed more abundant at the Eagle Summit site, but we do not have data to confirm actual predator densities. Arctic ground squirrels, which have been shown to prey on the eggs of nesting ptarmigan (Merizon et al., 2018), were only observed at the Denali Highway site.

More avian predators may have been associated with open-canopy nest predation at Eagle Summit than Denali Highway. However, identifying which predator was responsible for nest predations was difficult, except for a small proportion of nests preyed on by ground squirrels and foxes. We interpreted the evidence of nest predation from eight VHF transmitters found in or near fox dens and trail cameras near nest sites, while only four VHF transmitters were found in or adjacent to golden eagle nests.

Other possibilities affecting survival in population studies are staggered entries into the sample population (Kendall, 1999; Pollock, 1991; Winterstein et al., 2001). Juvenile hens that return to the study as 2nd year birds (adults) may affect the precision of nest and brood survival estimates for the 2nd year of the study because more adults potentially laying a clutch and surviving to a brood. In this case, the estimate of survival in the 2nd year will be more precise than the 1st year of the study. However, the limited number of hens returning to the study site, that transitioned between age-class and nested was minimal (n=1), and likely had little effect on our study.

This research was needed to increase the currently limited data on ptarmigan populations in Alaska and to provide baseline data for the assessment of future ptarmigan populations. Alpine species and ecosystems will likely continue to experience drastic effects of local and landscape-scale changes due to climate change (Gottfried et al., 2012). The survival of animals in an alpine community requires a combination of behavioral, morphological, energetic, and physiological traits (Martin & Wiebe 2004), which, as managers, we will need further understanding of these complex systems for future generations of ptarmigan to proliferate.

4.6 Future Work

The relationships with predation, rising temperatures, shifting seasonality, and changing landscapes, and their effects on nest and brood survival, will likely be a key component to be examined in future research of ptarmigan and alpine endemic species, as well as extending the length of the study to capture temporal dynamics of populations as they change.

Specifically, changes in alpine and northern environments may be affecting production and survival of rock ptarmigan in a few ways. A diverse group of birds and mammals rely on molting from summer dark to their winter white coat annually to increase crypsis against the snow (Zimova et al., 2018) and as snow cover retention declines from climate change, color molting species become increasingly mismatched with their background (Mills et al., 2013). The changing of daylength is the primary driver of molt changing across taxa, however, temperature can further affect the phenology of those molts each year (Zimova et al., 2020). The ability for ptarmigan to change their plumage seasonally may increase camouflage mismatches within their environment, and could potentially mean higher predation rates, as found in snowshoe hares (Zimova et al., 2020).

Additionally, the short duration of this study, spanning two field seasons made it difficult to monitor variations in these two populations effectively and to provide strong inference to variables affecting nest and brood survival. Our study may have only captured a small window of the temporal dynamics which can change substantially as populations naturally fluctuate. The duration of other studies on ptarmigan exceeds two years; being between five to 12 years (Cotter et al., 1999; Kobayashi et al., 2013; Novoa et al. 2008; Wilson et al., 2007). Future work should strive to do a minimum of five years of data collection to potentially capture natural population trends and cycles.

Table 4.1. Comparison of open and closed nest numbers that survived (at least one egg hatched) by site (Denali Highway and Eagle Summit), and hen age during our 2018 and 2019 rock ptarmigan study.

Raw Data of Nests by Site

Site	Eagle Summit		Denali Highway		Both Sites		
Age Class	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Totals
Closed Nests	5	4	9	7	14	11	25
Survived	4	3	7	2	11	5	16
Open Nests	29	28	12	20	41	48	89
Survived	8	6	6	8	14	14	28

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