CARRY-OVER EFFECTS IN PARTIALLY MIGRATORY GREATER SAGE-GROUSE, SOUTHWEST MONTANA

by

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DEDICATION

This thesis is dedicated to the people who strive to protect and enhance wild places so people seven generations from now have the same opportunities to enjoy nature and wildlife that we have today.

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VITA, AMERICAN INDIAN HERITAGE

The Centennial Valley and northeastern Snake River Plain were the seasonal hunting and fishing grounds for many indigenous groups with a few groups occupying the area year-round. These groups include: Niitsítpiis-stahkoii (Blackfoot), Bana kwut (Bannock), Tukaduka (Mountain Shoshone, Sheepeaters), Agaiduka (Lemhi Shoshone, Salmoneaters), Bohogue (Fort Hall Shoshone, Sage Butte People), Nimiipuu (Nez Perce). There were likely many other groups that used the area over the past 10,000 years but written information on indigenous history of the area is sparse. I acknowledge that indigenous peoples were stewards of this land for thousands of years, and I honor their continued connections and stewardship to this land

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

Table Page

LIST OF FIGURES

ABSTRACT

Migration is a common natural phenomenon and an important life history strategy for many animal species. Migration allows individuals to accommodate changing environmental conditions, with the potential to increase survival or future reproduction. Many migratory species are subject to carry-over effects, where conditions experienced during one season or life stage influence subsequent life stages. Previous research has largely focused on evaluating the influence of carry-over effects on long-distance migrants, but less is known about these influences on shorter-distance migrants. During research in southwest Montana and southeast Idaho, we used VHF radio collars, red blood cells, stable isotopes, and morphometric information to understand the influence of carry-over effects on Greater Sage-grouse. In this population, some individuals migrate only short distances, while others may not migrate at all. We evaluated the influence of 1) different migration strategies and breeding locations on the body condition of females before breeding and 2) how variation in pre-breeding body condition influenced subsequent reproduction. We found non-migratory individuals were in better pre-breeding body condition than migrants during years with less winter precipitation. Similarly, individuals who experienced less precipitation during the breeding season also had higher pre-breeding body condition. Pre-breeding body condition positively influenced offspring weight early in the breeding season, but this relationship was less apparent later in the season. Our data suggest carry-over effects occur in this population of sage-grouse, but the magnitude of these effects was largely dependent on environmental conditions and timing of breeding. With increasing evidence of carry-over effects in sage-grouse populations, managers should broaden their conservation strategies to account for all life stages. Protecting a variety of winter habitat both near and distant from breeding areas will ensure the persistence and reproductive contribution of individuals with different migration strategies. Furthermore, protecting all known sage-grouse leks provides variation within a single population which allows for flexibility to respond in changing environments. Maintaining or enhancing landscape-level habitat heterogeneity supports variable life-history strategies and is critical for sage-grouse conservation.

CHAPTER ONE

INTRODUCTION TO THESIS

Migration, or the seasonal movement of animals from one area to another is an important life history strategy for many species (Hobson & Norris, 2008). These seasonal movements allow animals to respond to changes in environmental conditions, with the potential to increase survival or future reproduction (Shaw, 2016). Migration provides benefits to many species, but these seasonal movements also incur costs such as high energy expenditure and increased exposure to predation (Chapman, Brönmark, Nilsson, & Hansson, 2011). In contrast, non-migratory individuals can conserve energy and reduce the uncertainty associated with migration, but may experience harsher environmental conditions (Lundberg, 1988). Given the costs and benefits of migration some populations are partially migratory – where some individuals migrate and others remain sedentary. Each migration strategy influences foraging opportunities, energetic demands, and survival, with future consequences on fitness.

Survival and reproductive success of animals often are driven by many factors experienced throughout the annual life cycle, especially body condition immediately before the breeding period (Holmes, Marra, & Sherry, 1996; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2003; Sherry & Holmes, 1996; Webster, Marra, Haig, Bensch, & Holmes, 2002). Several mechanisms can influence pre-breeding body condition, including age, previous reproductive investment, and habitat quality an animal experienced in the past (Inger et al., 2010; Marra, Hobson, & Holmes, 1998). Adults are typically in better pre-breeding body condition than juveniles due to differences in foraging ability, experience, and intraspecific competition. Animals that successfully reproduce may have lower pre-breeding body condition the following year, due to energetic demands associated with reproduction (Inger et al., 2010). Individuals that utilize high-quality habitat during winter have better pre-breeding body condition than individuals with limited access to high-quality food resources (Norris et al., 2003). Given that pre-breeding body condition often results from earlier influences, this metric can be used to assess potential carry-over effects on future survival and reproduction.

Greater-sage grouse (*Centrocercus urophasianus*, hereafter sage-grouse) – a species of concern in the western U.S. and Canada – have migratory, non-migratory, and partially migratory populations (Connelly, Hagen, & Schroeder, 2011). Sage-grouse populations have declined 45-80% range-wide (Aldridge & Brigham, 2003; Braun, 1998; Connelly & Braun, 1997; Connelly, Schroeder, Sands, & Braun, 2000a), and as much as 92% in some areas (Carpenter, Aldridge, & Boyce, 2010). Because of these declines, sage-grouse are listed as an endangered species in Canada, have been proposed for listing under the Endangered Species Act in the United States (U.S. Fish and Wildlife Service, 2013). To conserve remaining populations, managers have focused on protecting core regions for sage-grouse; these areas have been identified largely based on data collected around breeding areas (Fedy & Aldridge, 2011). However, areas distant from breeding areas, such as overwintering areas, could influence the annual life cycle considerably through carry-over effects, similar to other migratory species (Marra et al., 1998; Norris et al., 2003).

We investigated the presence of carry-over effects in a partially migratory population of sage-grouse. Carry-over effects are well documented in long-distance migrants such as waterfowl (Chapman et al., 2011; Devries, Brook, Howerter, & Anderson, 2008; Gladbach, Gladbach, & Quillfeldt, 2010). However, less is known about how carry-over effects influence species with different migration strategies or other avian taxa such as Galliformes. In Chapter two, we explored the role of migration strategy on pre-breeding body condition of female sage-grouse. Chapter three assesses the influences of pre-breeding body condition on reproductive metrics. Specifically, we examined the relationship between pre-breeding body condition on 1) breeding propensity, 2) timing of nest initiation, 3) clutch size, and 4) offspring weight. Understanding the influence of migration strategy on pre-breeding body condition and carry-over effects on subsequent reproduction could provide valuable insights to managers trying to conserve remaining sage-grouse populations.

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CHAPTER TWO

EFFECTS OF MIGRATION STRATEGY ON PRE-BREEDING BODY CONDITION IN GREATER SAGE-GROUSE

Contribution of Authors and Co-Authors

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Contributions: Assisted in implementing the study, collected and analyzed the data, wrote the manuscript

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Effects of migration strategy on pre-breeding body condition in Greater Sage-grouse

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Abstract

1. Migration is a behavioral adaptation that allows animals to respond to changes in environmental conditions. Some populations are partially migratory, with individuals that have different migration strategies. Each migration strategy – whether an individual migrates and how far – influences survival and reproduction.
2. Body condition immediately before breeding is especially important for an individual's fitness, where females with better pre-breeding body condition often have increased reproductive performance. Factors driving pre-breeding body condition are well documented for migratory and non-migratory populations, but we know less about partially migratory populations.
3. We explored the influence of migration strategy on pre-breeding body condition of sage-grouse from a partially migratory population. We captured female sage-grouse on leks in Montana between 2014 and 2019 and telemetered and tracked 270 of these females year-round. We used data collected from individuals captured on leks, combined with stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to identify overwintering areas (and therefore migration strategy).
4. Migration strategy had little influence on pre-breeding body condition, except for when non-migratory individuals experienced more favorable conditions. Specifically, when less precipitation fell during winter, non-migratory individuals were in better pre-breeding body condition.

5. We found that precipitation at and around the lek during breeding season had a stronger influence on pre-breeding body condition than migratory strategy. Higher precipitation levels at leks during the breeding season was associated with lower body condition.
6. Non-migratory sage-grouse may have an advantage during winters with favorable conditions, if they also breed at leks that receive less precipitation. Variation in migration strategy in conjunction with numerous leks that have different environmental conditions create a situation where at least some individual sage-grouse have sufficient pre-breeding body condition for future reproductive activities.
7. *Synthesis and applications.* Partially migratory populations may be more resistant to environmental changes caused by climate change, extreme weather events, and disturbance. Although environmental changes may reduce or eliminate habitat in one area, the partially migratory behavior would allow at least some individuals to contribute to the population. Our work emphasizes the need to protect a wide diversity of breeding and wintering habitat for sage-grouse that support a variety of migration strategies and lekking locations.

Keywords

Partial migration, body condition, carry over effects, seasonal habitat, stable isotopes

Introduction

Migration allows animals to respond to changes in environmental conditions (Robinson et al., 2009). When conditions change, migrating animals may be able to increase foraging opportunities, reduce stress, and increase survival or reproduction (Shaw, 2016). For animals who live in areas with highly variable conditions, migrating to less variable environments provides an important behavioral adaptation that may better balance tradeoffs to increase fitness (Lundberg, 1988; Senner, Morbey, & Sandercock, 2020).

Although migration can provide benefits, these movements also incur costs. Migration may require high energy expenditure and increase exposure to predation (Chapman et al., 2011). Further, arriving individuals may encounter competition in overwintering areas and experience some degree of uncertainty about the conditions (Alerstam, Hedenström, & Åkesson, 2003). In contrast, individuals that do not migrate can conserve energy and reduce the uncertainty associated with migration, but may be subjected to harsher environmental conditions (Lundberg, 1988). Given the costs and benefits of migration, some individuals within a population may have different migration strategies, leading to populations that are partially migratory – where individuals share breeding areas, but differ in where they spend the winter (Chapman et al., 2011). Each migration strategy – whether an individual migrates, how far, and the conditions they experience –influences nutrient acquisition and energy requirements, with consequences for future survival and reproduction.

Body condition, or an animal’s fat reserves, can have significant impacts on fitness; individuals with better body condition have better chances of survival and higher fitness than individuals with less reserves (Blums, Nichols, Hines, Lindberg, & Mednis, 2005; T. E. Martin, 1987). For many species, body condition immediately before the breeding period is especially important, in that females with better pre-breeding body condition often have increased reproductive performance, with subsequent effects on the population (Holmes et al., 1996; Norris et al., 2003; Webster et al., 2002). Understanding what drives variation in pre-breeding body condition is critical when managing species that rely on stored fat reserves for reproduction.

Several factors can influence pre-breeding body condition, including age, previous reproductive investment, and habitat quality an animal experienced in the recent past (Inger et al., 2010; Marra et al., 1998). Adults typically have higher pre-breeding body condition than juveniles due to differences in foraging ability, experience, and position in the social hierarchy (Forslund & Part, 1995). Animals that successfully reproduce may have lower pre-breeding body condition the following year, due to energetic demands associated with parental care (Inger et al., 2010). Individuals that occupy high-quality habitat during winter have better pre-breeding body condition than individuals with less access to high-quality food resources (Norris et al., 2003). Given that pre-breeding body condition often results from earlier influences, this state can be used to assess potential carry-over effects on future survival and reproduction.

Factors driving pre-breeding body condition and consequences on reproduction are well documented for both migratory and non-migratory populations (Chapman et al., 2011; Devries et al., 2008; Gladbach et al., 2010). However, less is known about how variation in migration strategies within a partially migratory population could produce differences in pre-breeding body condition and future reproduction. For example, Greater-sage grouse (*Centrocercus urophasianus)* have migratory, non-migratory, and partially migratory populations, largely differing based on the elevation and topography of occupied areas. Populations in relatively low-elevation areas can be non-migratory (Wallestad & Pyrah, 1974), whereas populations that occupy higher-elevation mountain valleys with large elevational gradients often are completely or partially migratory (Connelly, Browers, & Gates, 1988). Sage-grouse tend to migrate when snow-cover reduces forage availability, and often have fidelity to known wintering areas (Connelly et al., 1988).

We explored the influence of migration strategy on pre-breeding body condition of sage-grouse from a partially migratory population. We used data collected from individuals captured on leks in southwestern Montana, combined with stable isotopes $\delta^{13}C$ and $\delta^{15}N$ to identify overwintering areas, and therefore, migration strategy. We hypothesized migration strategy would influence pre-breeding body condition because of differences in energetic demands and uncertainty in weather and resource availability between migratory and non-migratory individuals. In our study area, migratory individuals leave a high-elevation mountain valley (often snow-covered) and overwinter in a relatively low-elevation sagebrush plain (typically snow-free) or in sagebrush foothills between the two areas (mostly snow-free). Migratory individuals typically experience more favorable winter conditions with better access to forage and warmer temperatures than their non-migratory counterparts. However, the uncertainty, risks, and energetic demand of migration may outweigh the benefits of spending the winter in an area with more favorable conditions. Similarly, non-migratory individuals experience harsher winter conditions with less available forage, but do not experience the uncertainty, risks, and energetic demands of migration. If different migration strategies (and therefore different overwintering areas) lead to differences in pre-breeding body condition and subsequent reproduction, a subset of birds could disproportionately contribute to population growth and stability. Understanding the influence of migration strategy on pre-breeding body condition could provide valuable insights to managers trying to conserve remaining sage-grouse populations.

Materials and Methods

Study Area

Our study area encompasses approximately 6,500 km^2 in southwestern Montana and southeastern Idaho. The Montana portion of the study area has variable topography and lies north of the Continental Divide, whereas the Idaho portion is relatively flat and located primarily within the Snake River Plain, south of the Continental Divide. The northern portion of the study area occurs at higher elevations (mean = 2200 m), has lower mean annual temperature (2.65° C), higher mean annual precipitation (51 cm), and more persistent widespread snowpack during the winter months (PRISM climate group 2021), compared to areas farther south. The southern portion of the study area occurs at lower elevations (mean = 1709 m), has higher mean annual temperature (5.12° C), lower mean annual precipitation (34 cm), and is largely snow-free during winter months (PRISM Climate Group 2021). Montana provides lekking, brood-rearing, and winter habitat and Idaho provides overwintering habitat for some individuals. Most of the study area is public land administered by several different agencies including Bureau of Land Management, Department of Natural Resources and Conservation, Montana Fish, Wildlife and Parks, U.S. Fish and Wildlife Service, and U.S. Forest Service.

Sagebrush is the dominant vegetation type across the study area, represented by four different species: threetip sagebrush (*Artemisia tripartite*), low sagebrush (*Artemisia arbuscula*), black sagebrush (*Artemisia nova*), and big sagebrush (*Artemisia tridentate*) (LANDFIRE 2012). Big sagebrush can be further subdivided into four subspecies: basin big sagebrush (*Artemisia tridentata* spp. *tridentata*), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), and subalpine big sagebrush (*Artemisia tridentata* ssp. *spiciformis*). We will use “sage-types” to refer to species and subspecies of sagebrush, to alleviate any confusion. The occurrence of different sage-types is driven by temperature and soil moisture (Schlaepfer, Lauenroth, & Bradford, 2012), which differ along an elevational gradient (Lambrecht, Shattuck, & Loik, 2007). The northern portion of the study area is dominated mainly by mountain big sagebrush (Arno & Gruell, 1983; Lesica, Cooper, & Kudray, 2007) and the southern portion is dominated by Wyoming big sagebrush (Anderson & Holte, 1981).

Adult Captures and Tracking

To assess the influence of migration strategy on body condition, we captured, telemetered, and tracked female sage-grouse throughout the year from 2014 to 2019. Females were captured during the spring breeding season (March 20 – April 30) using spotlighting techniques on or near established leks (Giesen, Schoenberg, & Braun, 1982). Upon capture, we measured body mass, head length, tarsus length, and wing length. Head and tarsus measurements were taken using a digital caliper, and wing length was recorded using a rigid wing rule; all measurements were completed on the right side of the bird. We also confirmed sex and determined age (AHY: after hatch year, ASY: after second year) using feather characteristics and body mass (Braun & Schroeder, 2015). We then fitted females with VHF radio-telemetry transmitters (A4000 avian necklace transmitters, Advanced Telemetry Systems, Isanti, MN) and leg bands (size #14 aluminum leg bands, National Band and Tag, Newport, KY) on the right tarsus. All field procedures adhered to approved protocols (Montana State University IACUC protocol: 2015-30 and 2019-88) and scientific collecting permits (2014-40, 2015-023, 2016-049, 2017-043-W, 2018-003-W, and 2019-078-W).

We tracked individuals continuously throughout the year with ground and aerial radio-telemetry methods. Ground-tracking efforts were completed by snowmobile (winter) or ATV (summer), to get as close to individuals as roads allowed, then proceeding to circle or triangulate on foot. We used Communication Specialist receivers (R-1000 Telemetry Receiver, Orange, CA) with a 3-element YAGI antenna (165.000-167.999 MHz, Wildlife Materials, Murphysboro, IL) to obtain locations of individuals. Aerial tracking was completed using a Piper Super Cub fitted with two horizontally mounted YAGI antennae, one on each wing. Although we had individuals telemetered, tracking them throughout the winter proved to be challenging due to erratic and long-distance movements. We were unable to obtain winter locations on many individuals, so we explored the use of stable isotopes to determine migration strategy.

Body Condition Index

Univariate metrics, such as body mass, do not adequately characterize avian body condition (Freeman & Jackson, 1990), so we used body mass, after correcting for structural measurements, as a body condition index (BCI). This is a common method in avian studies and has been used to determine body condition in sage-grouse (Blomberg, Sedinger, Gibson, Coates, & Casazza, 2014; Sedinger, Flint, & Lindberg, 1995). We began computing BCI with a principal component analysis based on three body measurements: body weight, head length, and wing length, with the *prcomp* and *predict* functions in the base package of Program R (R Core Team 2018). We then extracted values for the first principal component (PC1) for each individual and regressed these values (explanatory) and the individual bird weights (response).

Lastly, we added the residuals from the simple linear regression to the mean bird weight, to get the final BCI value (Devries et al., 2008; Warren, Cutting, & Koons, 2013).

Isotopic Sampling and Analysis

As a first step in characterizing migration strategy, we quantified stable isotope concentrations in red blood cells, as these values reflect the animal's diet in the past 1-2 months (Hobson & Clark, 1992; Ogden, Hobson, & Lank, 2004). We collected blood samples from telemetered individuals using a 3 mL syringe with a 23-gauge needle. Blood samples were centrifuged within 12 hours of capture and blood constituents (plasma and red blood cells) were stored frozen in separate vials.

We also quantified stable isotope concentrations in sagebrush, to characterize food available to sage-grouse; sage-grouse eat sagebrush almost exclusively (> 99%) during the winter months (Patterson, 1952). We collected sagebrush leaves throughout southwestern Montana and southeastern Idaho in early March 2017 from sites used by wintering individuals, as well as from random locations. We selected random locations by first delineating the sampling area using a Landfire sagebrush data layer (www.landfire.gov) and stratifying based on precipitation and temperature PRISM data (30-year annual mean) to maximize isotopic variation (Wunder & Norris, 2008). We collected 3 samples from each sage-type that occurred within 300 m of each used or random point. Sagebrush leaves were collected from multiple stems on the same plant and immediately placed into a cryogenic vial (1.5 mL, Thermo Fisher Scientific, Waltham, MA), labeled, and capped with parafilm (Bemis Company Inc., Neenah, WI). We wore latex gloves while collecting leaves to prevent skin oils from contacting the samples and immediately froze collected samples using dry ice.

We freeze-dried blood and sagebrush samples, crushed them into small pieces, and rinsed them in a 2:1 chloroform to methanol solution. We encapsulated 0.6 mg (± 0.1 mg) of the samples in tin cups (3x5 mm, Costech Analytical Technologies Inc, Valencia, CA). Samples were analyzed for stable-carbon ($\delta^{13}C$) and stable-nitrogen ($\delta^{15}N$) isotopes using continuous-flow isotope-ratio mass spectrometry at the University of New Mexico Stable Isotope Laboratory. Isotope values were reported in parts per thousand (‰) relative to in-lab organic protein standards. Analytical error was 0.1‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$ based on 200 replicate within-run measurements.

Isoscape and Migration Strategy

Patterns of environmental isotopic variation can be mapped to create an isotopic landscape ("isoscape") and used to track animal migration (Bowen & West, 2008). Once created for a specific geographic range, an isoscape can be used to correlate isotope values of animal tissues to the place of nutrient assimilation, revealing an individual's location during a specific time (Bowen and West 2008). Stable hydrogen ($\delta^{2}H$) is often used for tracking animal migration with isoscapes because it has predictable gradients across large areas. We attempted to use $\delta^{2}H$ to track migration but lacked sufficient spatial autocorrelation and we suspect this was caused by the variable terrain within our study area. We instead used $\delta^{13}C$ and $\delta^{15}N$ which provided sufficient spatial autocorrelation to track migration. Although $\delta^{2}H$ iscoscapes are an effective method to track animal migration at large scales, it may not work as well as other stable isotopes for small-scale migration due to micro-habitat variability.

We created interpolated surfaces for both $\delta^{13}C$ and $\delta^{15}N$ from sagebrush isotope values using kriging methods in ArcGIS (version 10.6.1). Interpolated surfaces of the sagebrush samples were adjusted to be the same trophic level as sage-grouse, given that isotope values change among trophic levels (i.e., from sagebrush to red blood cells); we extracted values from the interpolated surfaces at sage-grouse use locations and compared them to the RBC values of individuals at those locations. After adjusting the interpolated surfaces of both δ^{13}C and δ^{15}N, we used them simultaneously to predict overwintering orgin

To characterize migration strategy, we compared red blood cell values of unknown individuals to the adjusted isoscape to create predicted probability surfaces of where that individual likely overwintered. We used a 2:1 odds-ratio approach (Campbell, Fitzpatrick, Vander Zanden, & Nelson, 2020) and assigned each bird a migration strategy: non-migratory (birds that remained in Montana), migratory (birds that migrated to Idaho), or shorter-distance migration (birds that migrated to the Montana-Idaho border), by calculating the proportion of cells in either state. Individuals that had 70% of the cells in one state were categorized as overwintering in that state; we categorized others as border individuals We tested assignment accuracy by comparing predicted probability maps from known-origin individuals to location data derived from telemetry. Assignment accuracy was 80% percent accurate at a 2:1 odds ratio threshold. Future work using δ^{13}C and δ^{15}N to track shorter-distance migration could be improved by removing non-habitat from the assignment surfaces, or by restricting assignment to known habitat types.

Precipitation

To investigate any potential association between precipitation and sage-grouse body condition, we used weather data from PRISM climate group (PRISM Climate Group 2021). Weather data were derived from 4-km^2 cells near the lekking and overwintering areas during the estimated time of use (lekking areas: March 20 – April 1, overwintering areas: December 1 – March 19, PRISM Climate Group 2021).

Statistical Analyses

To evaluate the relationship between body condition index (BCI) and migration strategy, we developed linear regression models with BCI as the response variable. For each analysis, we created a global model and implemented backwards variable selection to sequentially remove variables that did not explain sufficient variation ($P > 0.10$). Given our initial questions, we retained migration strategy as an explanatory variable in all models.

Complete Data Model

We created a model using the complete dataset (2014-2019) to evaluate the relationship between BCI and migration strategy; this additive global model included four total covariates (migration strategy, age, year, lek). We included age to account for known differences in body condition between age classes (juvenile vs. adult) (Beck & Braun, 1978; Remington & Braun, 1988). Annual variation in precipitation and temperature can influence sage-grouse populations (Blomberg, Sedinger, Atamian, & Nonne, 2012; Moynahan, Lindberg, & Thomas, 2006), so we included year to account for differences in environmental conditions that might influence female body condition. We also included lek location to account for any differences in body condition resulting from environmental conditions or habitat quality immediately preceding capture (Barnett & Crawford, 1994).

Subset Data Model

We were interested in exploring evidence for an interaction between year and migration strategy, but the complete dataset lacked birds to represent all possible combinations (e.g., 2014 and 2015, Table 2.1). As such, we created a separate model with a subset of the data (2016-2019). We included the Year*Migration strategy interaction in this global model, in addition to the covariates described above (migration strategy, age, year, lek).

Post Hoc Model

In the analyses above, we used lek as a proxy to account for influences on BCI during the time period immediately before capture. However, we also were interested in further exploring this “lek” effect, to understand the potential roles of environmental conditions experienced at the lek. We created additional additive models using the complete dataset (2014-2019), with precipitation or temperature instead of lek. Precipitation and temperature were correlated ($R = -0.64$), so we employed the backward selection procedure for two separate global models, one including precipitation and one including temperature, in addition to migration strategy and age. We did not include year in these models, given annual variation in the precipitation and temperature data.

Results

We telemetered 270 female sage-grouse during the spring lekking seasons (March-May) between 2014 and 2019. Most of the sage-grouse captured in the Centennial Valley wintered near the Idaho-Montana border (130, shorter-distance migration), followed by Idaho (93, migratory) and Montana (47, non-migratory), but the number of females using each migration strategy varied by year (Table 2.1). We telemetered between 30 and 56 individuals each year, with an average of 45 individuals per year (Table 2.1).

Complete Data Model

We failed to detect differences in BCI based on migration strategy or by year (Table 2.2). However, body condition did vary by age and lek. Body condition of adult females was 2.5% higher than juveniles (predicted BCI: adults = 1468.9, 95% CI: 1457.4–1479.2, juveniles = 1433.2, 1422.4–1443.9). Body condition also tended to increase from west to east; BCI of females in the westernmost leks was 4.8% higher than the easternmost leks (westernmost lek BCI = 1482.7, 1460.4–1505.0, easternmost lek BCI = 1414.7, 1380.4–1449.0, Figure 2.2).

Subset Data Model

When we had sufficient data to explore the potential interaction between migration strategy and year (n = 179 females, Table 2.2), we found that female body condition was similar for all migration strategies and years, except for birds that overwintered in Montana during 2018 and 2019 (Figure 2.1); only one individual wintered in Montana during 2019, suggesting that the main difference occurred in 2018. Females that did not migrate and remained in Montana during these years had a higher predicted BCI by 6.6% (BCI = 1550.5, 1496.5–1604.5) and 4.3% (1517.3, 1400.3–1634.3) than the median predicted value for all areas and years (1454.5, 1435.1–1473.7), after accounting for age and lek (Figure 2.1). As with the complete data set, adult females had a higher predicted BCI than juveniles (1.4% higher, adult BCI = 1463.6, 1451.3–1476.0, juvenile = 1442.5, 1428.8–1456.2) and body condition generally declined from the westernmost to the easternmost leks, after accounting for other factors (Table 2.2).

Post Hoc Model

When we explored the lek effect further, using precipitation and temperature values at the lek during the breeding season instead of the category, precipitation was retained in the final model (P = 0.096); temperature explained slightly less variation (P = 0.104). We found that birds in areas with lower mean daily precipitation had higher body condition values. Females captured at the driest lek (0.56 mm precipitation/day) had a BCI 1.4% higher (BCI = 1460.8, 1447.2–1474.4) than females captured at the wettest lek (3.20 mm/day, BCI = 1440.0, 1424.5–1455.4).

Discussion

Migration strategy had little influence on pre-breeding body condition, except for periods when non-migratory individuals experienced more favorable conditions during the winter. Montana consistently receives more precipitation than the Montana-Idaho border and Idaho, but the median winter precipitation in Montana was lowest in 2018 and 2019 (Figure 2.3, PRISM Climate Group 2021). During years with lower winter precipitation, non-migratory individuals were in better pre-breeding body condition than migratory individuals. When winter conditions were favorable (i.e., less snow-cover), the costs of migration seemed to exceed the benefits because non-migrating individuals were able to maintain body condition without expending unnecessary energy or increasing risk.

We instead found that environmental conditions experienced at and around the lek during breeding season had a stronger influence on pre-breeding body condition than migratory strategy. Higher precipitation levels at leks during the breeding season were associated with lower body condition. The proportion of individuals exhibiting each migration strategy were similar among leks, so distance between the wintering area and the lek is an unlikely source of this variation. Changes in pre-breeding body condition therefore are likely occurring around the leks between March 20 and whenever the individual was captured. The negative relationship between pre-breeding body condition and precipitation is likely a result of most of the precipitation falling in the form of snow (USDA Natural Resources Conservation Service, 2022).

Individuals that attend leks with less precipitation and lower snow cover likely have better access to higher quality forage (i.e., forbs) due to advanced vegetation phenology, whereas individuals that attend leks with more snow likely are relying on lower-quality foods (i.e., sagebrush) to meet dietary demands (Barnett & Crawford, 1994). Energetic demands for thermoregulation also could play a role in the observed differences in pre-breeding body condition and precipitation due to evaporative cooling.

Our data suggest that it is advantageous for female sage-grouse to lek at sites with lower precipitation levels because these individuals have more fat reserves to support later reproductive activities. Non-migratory individuals may have an advantage during years with less winter precipitation, if they also breed at leks that receive less precipitation. Similarly, the realized benefits of not migrating during dry winters may be counteracted by breeding at leks that receive high amounts of precipitation. In many areas, lack of precipitation is a limiting factor for sage-grouse because there is less high-quality food available (Blomberg, Gibson, Atamian, & Sedinger, 2017). In that sense, our study system is somewhat unique given high elevation and precipitation, where too much precipitation may have detrimental effects for sage-grouse. However, as the frequency and duration of drought periods increase with climate change, leks that currently receive low levels of precipitation may pass below a threshold where precipitation is insufficient to provide this advantage. If these leks become too dry to support better body condition, the cooler, wetter leks, where females currently have the lowest body condition, may play a key role in sustaining sage-grouse populations in the future

Partially migratory populations may be more resistant to environmental changes caused by climate change, drought, extreme weather events, and disturbance—especially if carry-over effects are present. Carry-over effects influence sage-grouse such that individuals with high pre-breeding body condition that breed early in the season produce the largest offspring (Chapter 3) that are more likely to reproduce successfully (Blomberg et al., 2014). As drought becomes more common, non-migratory individuals wintering in Montana may disproportionally contribute to the population, whereas migratory individuals may be the main contributors during years with more winter precipitation. Large-scale disturbances, such as wildfire, may reduce or eliminate habitat in one area, but the partially migratory behavior would allow at least some individuals to successfully reproduce and sustain the population. Sage-grouse conservation has largely been focused on protecting areas around leks, which works well for many sage-grouse populations, but may fall short for migratory and partially migratory populations. Our work emphasizes the need to conserve a wide diversity of breeding and wintering habitat for sage-grouse that can support a variety of migration strategies and lekking locations. Landscape-scale habitat heterogeneity within the sagebrush community is critical to conserving remaining sage-grouse populations. Given the conservation status of sage-grouse future work should further evaluate the role of carry-over effects in sage-grouse. Further investigation into the ultimate drivers of carry-over-effects in sage grouse would provide valuable insights for managers when conserving sage-grouse populations.

Authors' contributions

Kyle Cutting and Bok Sowell conceived the ideas and designed methodology; Kyle Cutting and James Waxe collected the data; James Waxe, Hannah Vander Zanden and Andrea Litt analyzed the data; James Waxe and Andrea Litt led the writing of the manuscript.

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Tables and Figures

Table 2.1. Estimated migration strategy of 270 female sage-grouse, captured in southwest Montana, 2014-2019. We assigned individuals to different migration strategies by comparing stable isotopes values ($\delta^{13}C$ and $\delta^{15}N$) in red blood cells to a rescaled isoscape based on sagebrush leaves.

Migration Strategy	2014	2015	2016	2017	2018	2019	Total
Montana	0	30	2	9	5	1	47
Border	1	25	32	29	30	13	130
Idaho	35	0	22	10	10	16	93

Table 2.2. Covariates in the global and final models examining the relationship between migration strategy and body condition (BCI) of female sage-grouse. The complete data and post hoc models included 270 individuals that bred on leks in southwest Montana, 2014-2019. The subset data model included 179 individuals that bred on leks in southwest Montana, 2016-2019. We used a backward variable selection procedure, sequentially removing terms that did not explain sufficient variation (*P* > 0.10, from Type II F-tests). Given our initial questions, we retained migration strategy as an explanatory variable in all models. Covariates included in the final models are listed in bold.

Model	Variable	*F*	*P*
Complete Data	**Migration Strategy**	**0.40** (2, 262)	**0.6720**
	Age	**21.82** (1, 262)	**< 0.0001**
	Lek	**5.83** (4, 262)	**0.0002**
	Year	0.48 (2, 262)	0.9581
Subset Data	**Migration Strategy**	**2.58 (2, 162)**	**0.0789**
	Age	**5.10 (1, 162)**	**0.0252**
	Lek	**5.85 (4, 162)**	**0.0002**
	Year	**0.24 (3, 162)**	**0.8667**
	Migration Strategy*Year	**1.82 (6, 162)**	**0.0992**
Post Hoc	**Migration Strategy**	**0.63 (2, 265)**	**0.5317**
	Age	**18.98 (1, 165)**	**< 0.0001**
	Precipitation	**2.78 (1, 165)**	**0.0964**

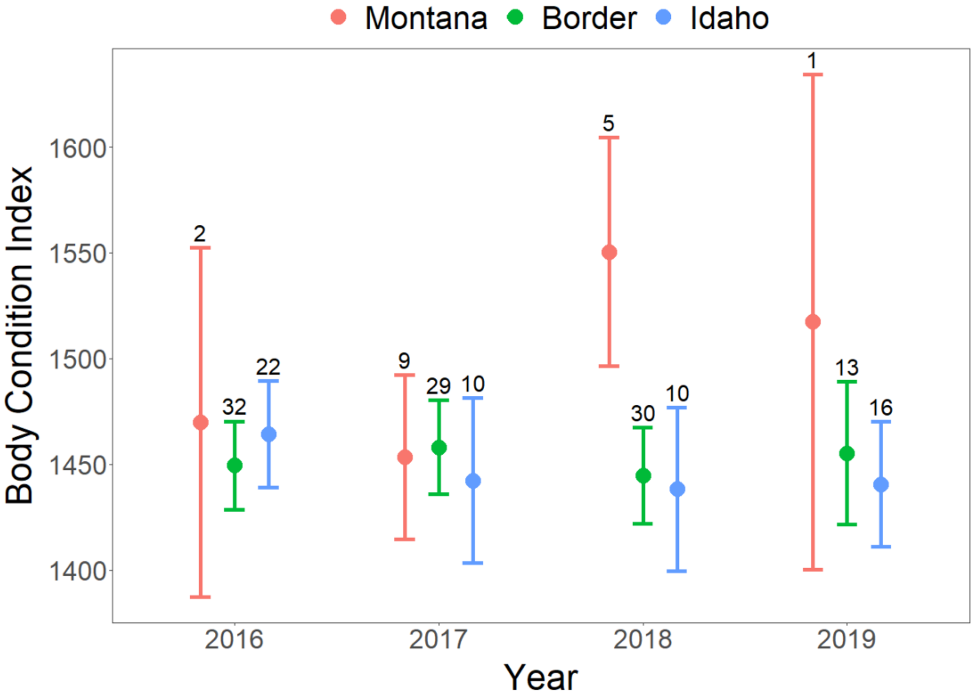

Figure 2.1. Variation in pre-breeding body condition index (and 95% CIs with sample sizes) of female sage-grouse by year and migration strategy: Montana (non-migratory), Montana-Idaho border (shorter-distance migration), and Idaho (migratory), based on the final model (Table 2.2) for 179 individuals that bred on leks in southwest Montana, 2016-2019. Body Condition Index is an individual's mass corrected for structural size and is used as a proxy for fat reserves.

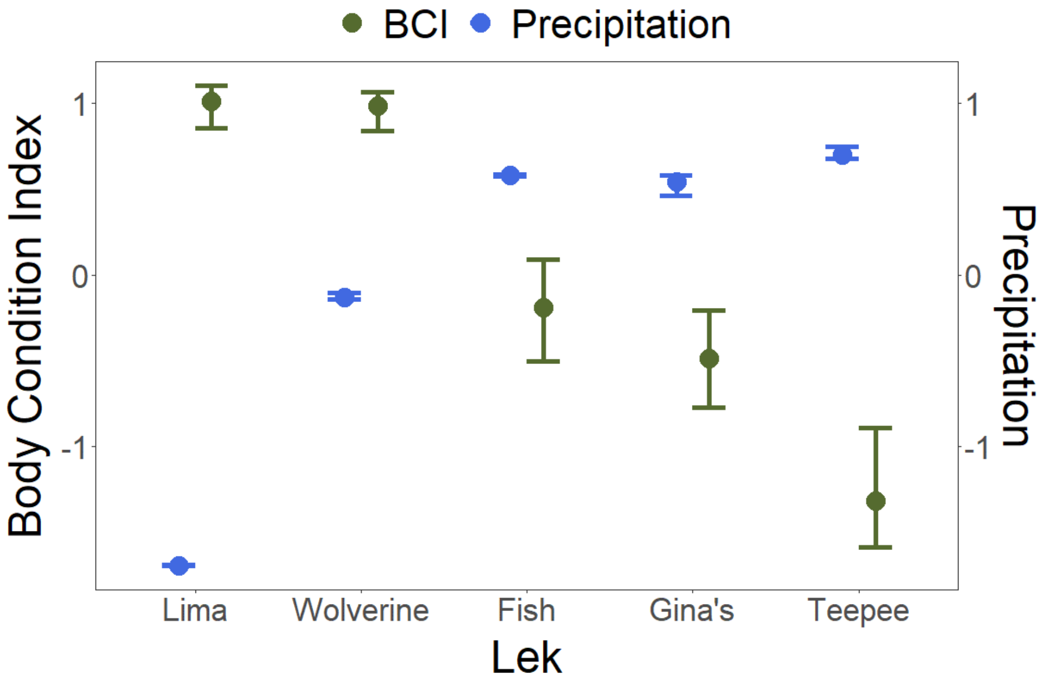

Figure 2.2. Variation in pre-breeding body condition index (and 95% CIs) of female sage-grouse by lek based on the final model (Table 2.2), 270 individuals, southwest Montana, 2014-2019. Leks are ordered from west to east. We also include mean precipitation values during breeding season (March 20 – May 1) for each lek. Body Condition Index is an individual’s mass corrected for structural size and is a proxy for fat reserves.

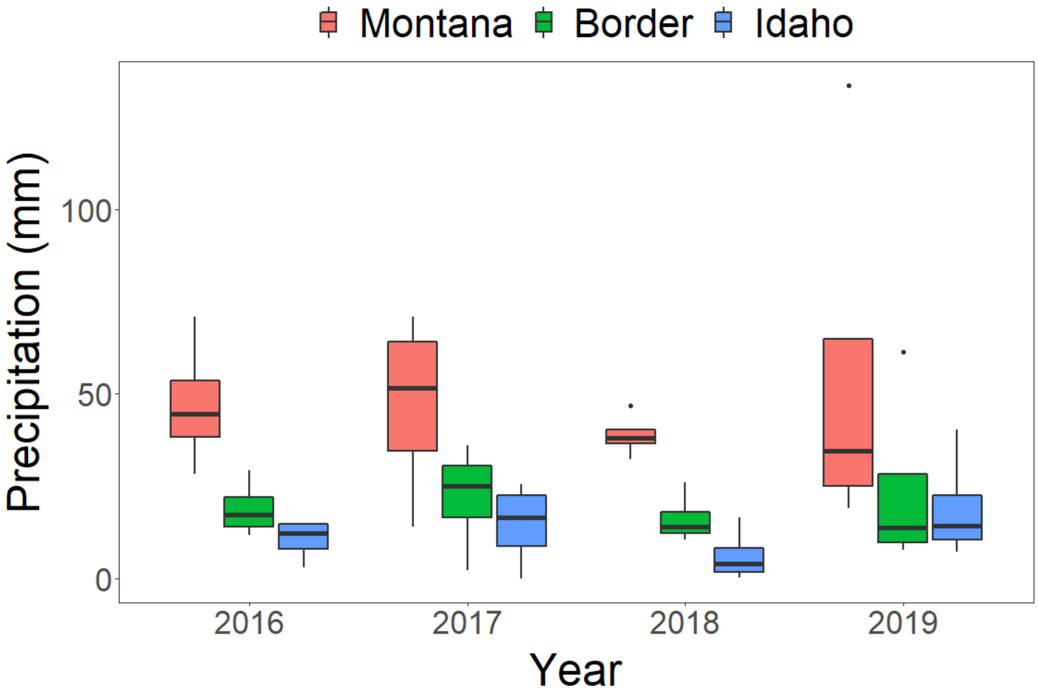

Figure 2.3. Monthly precipitation values during winter (December 1-March 20) for three sage-grouse overwintering areas (representing different migration strategies): Montana (non-migratory), Montana-Idaho border (shorter-distance migration), and Idaho (migratory), southwest Montana and southeast Idaho, 2016-2019. Box and whisker plots display the median precipitation value (center black bar), interquartile range (box), minimum and maximum values (whiskers), and outliers (dots).

CHAPTER THREE

CARRY-OVER EFFECTS ON REPRODUCTIVE METRICS OF GREATER SAGE-GROUSE IN SOUTHWEST MONTANA

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: James A. Waxe

Contributions: Assisted in implementing the study, collected and analyzed the data, wrote the manuscript

Co-Author: Andrea R. Litt

Contributions: Assisted with data analysis, extensive review of the manuscript

Co-Author: Kyle A. Cutting

Contributions: Conceived initial study idea, secured funding, designed the study, assisted with data collection, reviewed the manuscript

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Contributions: Conceived initial study idea, secured funding, assisted with study design, reviewed the manuscript

Manuscript Information

James A. Waxe, Andrea R. Litt, Kyle A. Cutting, Bok Sowell

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__X_ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-reviewed journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

Wiley on behalf of the British Ecological Society

Carry-over effects on reproductive metrics of Greater Sage-grouse in southwest Montana

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Abstract

1. Many species are subject to carry-over effects, where habitat quality experienced long before breeding may influence subsequent performance and overall fitness of an individual. In avian species, pre-breeding body condition can influence reproductive metrics including: breeding propensity, timing of nest initiation, clutch size, and offspring quality. Although the effects of pre-breeding body condition on reproduction have been well-studied in waterfowl, we know little about carry-over effects for gallinaceous birds.
2. During research in the Centennial Valley in southwestern Montana, we tracked 237 female Sage-grouse for 5 years and monitored nesting activity and broods until 30 days of age.
3. We found that pre-breeding body condition of females influenced chick weight and this relationship depended on when chicks hatched. For nests that hatched early in the season, females in the best body condition produced the heaviest chicks; this relationship was less obvious in the middle of the season and reversed late in the season.
4. Given that so many individuals nested (91%), we were unable to evaluate the influence of body condition on breeding propensity. We did not observe differences in timing of nest initiation or clutch size based on variation in pre-breeding body condition. Timing of nest initiation and clutch size varied among years, and clutch size also varied throughout the nesting season and by nesting attempt.
5. Our results indicate pre-breeding body condition is important for producing high-quality (heavier) sage-grouse offspring early in the breeding season, but becomes less important as the breeding season progresses. We suggest conditions female sage-grouse experience

during winter can influence chick weights, which provides evidence of a carry-over effect.

6. *Synthesis and applications.* Carry-over effects have large consequences for species that rely heavily on endogenous reserves for reproduction, where individuals with insufficient fat reserves have reduced reproductive performance. The importance of carry-over effects on species such as sage-grouse that rely on a combination of endogenous and exogenous reserves is less obvious but could have population-level effects. Although conservation of this species has focused on breeding grounds, our data suggest that the quality of wintering habitat also could influence the annual life cycle considerably via carry-over effects.

Keywords

Body condition, chick weight, cross-seasonal effects, offspring quality, short-distant migration

Introduction

Migration, or the seasonal movement of animals from one region to another, is a fundamental aspect of the ecology and evolution of many species (Hobson & Norris, 2008). Population dynamics of migratory species often are controlled by a combination of factors experienced throughout the annual life cycle (Sherry & Holmes, 1996). Conditions experienced during one season or life stage can influence subsequent life stages; such influences are referred to as carry-over effects (Harrison, Blount, Inger, Norris, & Bearhop, 2011). Carry-over effects can have a strong influence on the dynamics of migratory populations (Norris et al., 2003; Sherry & Holmes, 1996; Webster et al., 2002), including many avian species (Harrison et al., 2011).

For many avian species, pre-breeding body condition can influence subsequent reproduction efforts and survival (Blums et al., 2005; Devries et al., 2008; T. E. Martin, 1987; Nilsson, 1994). Pre-breeding body condition, namely fat reserves, could be influenced by several factors, including quality of wintering habitat (Marra et al., 1998), age, and previous reproductive investment (Inger et al., 2010). Fat reserves are critical for meeting the energetic requirements of egg laying and incubation for avian species that reproduce immediately after spring migration (Alisauskas & Ankney, 1992; Devries et al., 2008). For North American ducks, females that arrive at the breeding ground in good pre-breeding body condition (i.e., with ample fat reserves) have higher breeding propensity (Alisauskas & Ankney, 1992), initiate nests earlier (Dubovsky & Kaminski, 1994), produce larger clutches (Krapu, 1981) and are more likely to renest (Arnold et al., 2002). Although the effects of pre-breeding body condition on reproduction have been well-studied in long distance migrants like waterfowl, we know little about these effects on shorter distance migrants such as gallinaceous birds. The relationship between female body condition and offspring weight at hatch also remains an information gap in avian species; the few studies focused on this relationship suggest a positive association between body condition and chick weight (Erikstad, Asheim, Fauchald, Dahlhaug, & Tveraa, 1997; Tveraa, Sæther, Aanes, & Erikstad, 1998).

Greater Sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are sagebrush-obligate, gallinaceous birds (Connelly, Schroeder, Sands, & Braun, 2000b) endemic to North America (Knick & Connelly, 2011). During the spring breeding season, sage-grouse congregate and exhibit elaborate courtship displays in areas called leks (U.S. Fish and Wildlife Service, 2013). Sage-grouse have migratory populations (Connelly et al., 1988) with seasonal movements of up to 240 km between overwintering and lekking grounds (Smith, 2012). Populations of this species have declined 45-80% range-wide (Aldridge & Brigham, 2003; Braun, 1998; Connelly & Braun, 1997; Connelly et al., 2000a), and as much as 92% in some areas (Carpenter et al., 2010). Sage-grouse currently occupy an estimated 56% of the historical range (Connelly, Knick, Schroeder, & Stiver, 2004). Because of these declines, sage-grouse are listed as an endangered species in Canada, have been proposed for listing in the United States (U.S. Fish and Wildlife Service, 2013), and are a species of concern in the western U.S. and Canada (Knick & Connelly, 2011).

To conserve remaining populations, federal and state agencies have focused on protecting core regions for sage-grouse; these protected areas have been identified largely based on data collected at leks (Fedy & Aldridge, 2011). However, areas distant from leks, such as wintering grounds, could influence the annual life cycle considerably through carry-over effects, similar to other migratory species (Marra et al., 1998; Norris et al., 2003). Understanding the role of carry-over effects on pre-breeding body condition and subsequent reproduction could provide valuable information to guide conservation of this species and important insights that could apply to other gallinaceous birds.

We explored the role of carry-over effects on sage-grouse reproduction, specifically, the relationship between pre-breeding body condition and reproductive metrics. We examined the influence of body condition on 1) breeding propensity, 2) timing of nest initiation, 3) clutch size and 4) offspring weight. We predicted that females in better body condition would have higher breeding propensity, initiate nests earlier, have larger clutches, and have heavier offspring, as seen with other avian species (Alisauskas & Ankney, 1992; Dubovsky & Kaminski, 1994; Goudie & Jones, 2005; Krapu, 1981; Pattenden & Boag, 1989).

Materials and Methods

Study Area

Our study area encompassed a large portion of southwest Montana and southeast Idaho, covering approximately 6,500 km^2. Human population density is low throughout the study area (3.4 people/km^2, U.S. Census Bureau); recreation and agriculture are the primary land uses. Most of the study area is comprised of public land administered by several different agencies including Bureau of Land Management, Department of Natural Resources and Conservation, Montana Fish, Wildlife and Parks, U.S. Fish and Wildlife Service, and U.S. Forest Service. The northern portion of the study area provides lekking and brood-rearing habitat for sage-grouse and includes Red Rock Lakes National Wildlife Refuge. The southern portion of the study area provides habitat during winter and includes Camas National Wildlife Refuge, the U.S. Sheep Experiment Station, and Idaho National Engineering Laboratory.

The northern portion of the study area located in Montana occurs at higher elevations (mean = 2200 m), has lower mean annual temperature (2.65° C), higher mean annual precipitation (51 cm), and more persistent widespread snowpack during the winter months (PRISM climate group 2015), compared to areas farther south. The southern portion of the study area located in Idaho occurs at lower elevations (mean = 1709 m), has higher mean annual temperature (5.12° C), lower mean annual precipitation (34 cm), and is largely snow-free during winter months (PRISM Climate Group 2018).

Sagebrush is the dominant land cover type across the study area, represented by four different species: threetip sagebrush (*Artemisia tripartite*), low sagebrush (*Artemisia arbuscula*), black sagebrush (*Artemisia nova*), and big sagebrush (*Artemisia tridentate*) (LANDFIRE 2012). Big sagebrush can be subdivided into four subspecies: basin big sagebrush (*Artemisia tridentata* spp. *tridentata*), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), and subalpine big sagebrush (*Artemisia tridentata* ssp. *spiciformis*). We will use “sage-types” to refer to species and subspecies of sagebrush, to alleviate any confusion. The occurrence of different sage-types is driven by temperature and soil moisture (Schlaepfer et al., 2012), which differ along an elevational gradient (Lambrecht et al., 2007). In our study area, low sagebrush, black sagebrush, and basin big sagebrush occur at lowest elevations, threetip sagebrush and Wyoming big sagebrush occur at low to mid elevations, and mountain and subalpine big sagebrush occur at the highest elevations. The northern portion of the study area is dominated mainly by mountain big sagebrush (Arno & Gruell, 1983; Lesica et al., 2007) and the southern portion is dominated by Wyoming big sagebrush (Anderson & Holte, 1981).

Adult Captures and Associated Data

To assess the influence of pre-breeding body condition and reproduction, we captured, telemetered, and tracked female sage-grouse during the breeding season. During the spring lekking seasons (March-May) from 2014-2018, we captured 241 adult female sage-grouse using spotlighting techniques on or near established leks (Giesen et al., 1982). Upon capture, we measured body mass, head length, tarsus length, and wing length. Head and tarsus measurements were taken using a digital caliper, and wing length was recorded using a rigid wing rule; all measurements were completed on the right side of the bird. We also confirmed sex and determined age (AHY: after hatch year, ASY: after second year) using feather characteristics and body mass (Braun & Schroeder, 2015). We then fitted all 241 females with VHF radio-telemetry transmitters (A4000 avian necklace transmitters, Advanced Telemetry Systems, Isanti, MN) and leg bands (size #14 aluminum leg bands, National Band and Tag, Newport, KY) on the right tarsus. All field procedures adhered to approved protocols (Montana State University IACUC protocol: 2015-30) and scientific collecting permits (2014-40, 2015-023, 2016-049, 2017-043-W, 2018-003-W).

Tracking

We tracked individuals continuously throughout the breeding season with ground-based radio-telemetry methods. Ground-tracking efforts consisted of using ATVs to get as close to individuals as roads allowed, and then proceeding to circle or triangulate on foot. We used Communication Specialist receivers (R-1000 Telemetry Receiver, Orange, CA) with a 3-element

Yagi antenna (165.000-167.999 MHz, Wildlife Materials, Murphysboro, IL) to obtain locations of individuals. We circled females at a radius of 5 to 50 m to obtain a precise location without flushing the individual.

During the breeding season, we circled individuals 2-4 times per week to determine nest initiation (Coates, 2007). We assumed individuals were incubating a nest if they were in the same location on two sequential observations (Coates, 2007). We monitored these birds and nests daily until nest fate. Nest monitoring was completed by establishing a listening point 30 m from the nest; checks entailed going to the listening point and ensuring the signal was coming from the specified bearing (Gregg, Dunbar, & Crawford, 2007). Once an individual's signal was no longer originating in the direction of the specified bearing, we approached the nest to determine nest fate, categorized as abandoned, failed, or successful. Nests were categorized as abandoned if the female was absent from the nest for 10 days and eggs were intact with no evidence of depredation and categorized as failed if there was evidence of depredation. At least one egg hatched in successful nests.

Brood Captures and Associated Data

After a nest hatched successfully, we captured broods at 3 days of age. We captured broods during the pre-dawn hours (≈45 min before sunrise) to reduce the probability of predation and to ensure that chicks were not exposed to cold temperatures for prolonged periods. Female sage-grouse play a key role in thermoregulation of chicks, covering them at night (Patterson, 1952; Wallestad, 1975), which enabled us to locate broods via telemetry. We located individuals and slowly walked towards the signal until the female was visible and proceeded to flush her off the brood (Gregg et al., 2007). As the female flushed, we picked up the chicks by hand (Gregg et al., 2007). Immediately following capture, chicks were marked with a uniquely numbered metal tag (#1 fish fingerling tags, National Band and Tag, Newport, KY), placed on the leading edge of the patagium of the right wing. We then weighed them on a small digital scale. After data collection, chicks were released together in a tight group under a sagebrush near the capture location.

Precipitation Data

To investigate any potential association between precipitation and sage-grouse reproduction, we used weather data from PRISM climate group (PRISM Climate Group 2018). We extracted precipitation data for the duration of the breeding season (March – June) for 4 separate 4-km^2 cells across the study area. Cell values were then averaged across the study area to obtain a single precipitation value for each breeding season.

Body Condition Index

Univariate metrics, such as body mass, do not adequately characterize avian body condition (Freeman & Jackson, 1990), so we used body mass, after correcting for structural measurements, as a body condition index (BCI). This method is common in avian studies and has been used to determine body condition in sage-grouse (Blomberg et al., 2014; Sedinger et al., 1995). We began computing BCI by using a principal component analysis based on three body measurements: body weight, head length, and wing length, with the *prcomp* and *predict* functions in the base package of Program R (R Core Team 2018). We then extracted values for the first principal component (PC1) for each individual and regressed individual bird weights (response) and the PC1 values (explanatory). Lastly, we added the residuals from the simple linear regression to the mean bird weight, to get the final BCI value (Devries et al., 2008; Warren et al., 2013).

Statistical Analyses

To evaluate the relationship between pre-breeding body condition (BCI) and reproduction, we developed a separate model for each response variable of interest: breeding propensity, initiation of incubation, clutch size, and chick weight. We carefully considered additional covariates that might influence each response variable, based on previous research, which we describe in sections below. For all models, we included female age (AHY or ASY) to account for age-related differences (Forslund & Part, 1995) and year to account for annual variation not captured by other covariates (e.g., variation in temperature, precipitation and vegetation phenology). We also explored possible interactions between body condition and other covariates, and a quadratic effect of body condition. We collected multiple years of data for some females, but only included reproductive data for the year the female was captured. We fit linear mixed models and included a random effect for individual females, to account for potential similarities among chicks hatched from the same nest. Given that individual females could only have one successful brood in a given year, we placed the random effect on the female, instead of on individual broods. We created a full model for each response variable of interest (*lmerTest*, R Core Team 2018), then used a backward variable selection procedure, sequentially removing terms that did not explain sufficient variation ($P > 0.10$). Given our interest in BCI, we always retained that explanatory variable. We extracted model effects using the *effects* package (Fox, 2003; Fox & Weisberg, 2019), so we could visualize and quantify effect sizes. All covariates were set to the mean value when visualizing effect sizes.

Pre-breeding body condition and breeding propensity

Although we were initially interested in exploring the influence of body condition on breeding propensity, 91% of our tracked individuals laid at least one nest (187 of 206 individuals). Given that so many individuals nested, we were unable to evaluate the influence of body condition on breeding propensity.

Pre-breeding body condition and initiation of incubation

We were unable to accurately determine nest initiation dates for unsuccessful nests, so could not examine the influence of body condition on nest initiation (Gregg, 2006; Moynahan, Lindberg, Rotella, & Thomas, 2007). Instead, we explored the relationship between body condition and initiation of incubation, calculated as the mid-point date between when we first observed the female on the nest and the last time she was located away from the nest (Schroeder, 1997). In addition to the covariates described above (female age, year, BCI, BCI^2, BCI*female age, BCI*year), we included sage-type and BCI*sage-type in this global model to account for variation in nest initiation dates associated with elevational differences in snowmelt dates, temperature, and precipitation.

Pre-breeding body condition and clutch size

Clutch sizes typically decline throughout the breeding season (Klomp 1970) and with multiple nesting attempts (N. W. Kaczor, 2008). To better explore the influence of BCI on clutch size, we included nest initiation and nest number (as well as BCI*nest initiation and BCI*nest number) in this global model, in addition to the covariates described above (female age, year, BCI, BCI^2, BCI*female age, BCI*year). Only successful nests were included in this model, as we were unable to determine full clutch sizes for abandoned and depredated nests. As a result, we could include nest initiation (and not initiation of incubation) in this model. We censored one nest that contained a single egg from the dataset due to potential partial predation (Coates, 2007).

Pre-breeding body condition and chick weight

Chick weight tends to decrease with increasing clutch size (Godfray, Partridge, & Harvey, 1991), and clutch size declines throughout the breeding season (Klomp, 1970). We included hatch date to account for variation in chick weights due to seasonal declines in clutch sizes and variation in environmental conditions, in addition to the covariates described above (female age, year, BCI, BCI^2, BCI*female age, BCI*year). We also included nest number to account for variation in clutch size between first and second nesting attempts (N. W. Kaczor, 2008), which could result in differences in chick weights (Godfray et al., 1991). Sage-type was included to account for elevational differences in environmental conditions (i.e., precipitation, vegetative cover) that chicks encountered during the time between hatching and capture. We also included a heat loading index for each nest location (created with ArcGIS, Evans et al. 2014) to account for variation in temperature encountered during incubation and between hatching and capture. This model only included chicks that were exactly 3 days old, born to females captured that year.

Results

Pre-breeding body condition and initiation of incubation

Sage-grouse hens initiated incubation on May 15, on average (135th day of the year, SE = 0.85 days, *n* = 174 nests), but timing ranged from April 9 to June 13. Females in the lowest and highest body condition initiated incubation the earliest, suggesting a curvilinear relationship (Table 3.1, Figure 3.1). However, the influence of body condition on initiation of incubation also depended on the year (Table 3.1); females in high body condition began incubation earliest during some years, and the latest during other years (Figure 3.1). We did not detect effects of female age or sage-type (or interactions between body condition and these covariates, Table 3.1).

Pre-breeding body condition and clutch size

Clutch size averaged 7.0 eggs (95% CI: 6.7 - 7.4, *n* = 75 successful nests) and ranged from 3 to 10 eggs. We found little evidence that female body condition influenced clutch size, but clutch size did vary during the nesting season, among years, and based on nesting attempt (Table 3.2). Clutch size decreased by 0.08 eggs/day over the nesting season (-0.10 to -0.05); nests that hatched early in the season (during the first quintile) contained 9.2 eggs (8.4 - 9.9), compared to only 4.5 eggs (3.6 - 5.4) for nests that hatched at the end of the season (during the last quintile, Table 3.2, Figure 3.2). Mean clutch size also varied among years (range of annual means = 6.4 - 7.8 eggs, Figure 3.3A). Finally, mean clutch size increased from 6.9 (6.5-7.2) to 7.8 (7.1-8.6) eggs between the 1st and 2nd nesting attempts (Table 3.2). We did not detect a difference in clutch size based on female age (Table 3.2).

Pre-breeding body condition and chick weight

Female body condition influenced chick weight, but this relationship depended on when chicks hatched (BCI*hatch date, *n* = 33 females and 205 chicks, Table 3.3). For nests that hatched early in the season, females in the best body condition (highest BCI) produced the heaviest chicks (Figure 3.4). For example, early in the season (May 24), a female with a BCI in the top 20% (BCI = 1665.7) produced chicks that weighed 39.3 g (95% CI= 32.0-46.6), compared to 24.6 g (19.5-29.8) for a female with a BCI in the bottom 20% (1352.6). This relationship was less obvious in the middle of the season and reversed late in the season (Figure

3.4). In the middle of the season (June 15), chicks were comparable in weight for females with the highest (chick weight = 31.5 g, 28.5-34.5) and lowest BCI (29.8 g, 27.8-31.9). Late in the season (July 5), females with highest BCI produced chicks that weighed 24.0 g (16.1-31.8), compared to 34.9 g (30.3-39.4) for females with the lowest BCI.

Chick weights also varied among sage-types (Table 3.3). The heaviest chicks hatched from nests in threetip sagebrush (31.5 g, 95% CI = 30.5 - 32.5) and basin big sagebrush (31.0 g, 28.7 – 33.4) types, and the lightest chicks hatched from nests in mountain big sagebrush (30.2 g, 29.7 – 30.6). We did not detect evidence for other influences on chick weight (Table 3.3).

Discussion

We suggest conditions female sage-grouse experience during winter can influence chick weights and subsequent recruitment, which provides evidence of a carry-over effect (Harrison et al., 2011). Our results indicate pre-breeding body condition is important for producing high-quality (heavier) offspring early in the breeding season, but becomes less important as the breeding season progresses. Body condition may be important for chick formation early in the breeding season due to lower availability of high-quality foods during that period.

Sage-grouse rely on a combination of endogenous and exogenous reserves for reproduction, with exogenous reserves playing an important role in chick formation (Gregg, 2006). Forbs an important food source for pre-laying sage grouse because they have high levels of crude protein and are palatable compared to sagebrush; higher forb consumption increases the nutritional status of female sage-grouse (Barnett & Crawford, 1994). Forb consumption is related to availability, which changes with vegetation phenology throughout the year (Gregg, Barnett, & Crawford, 2008). In our study area, conditions early in the breeding season are typically cold and wet, with precipitation frequently falling in the form of snow (USDA Natural Resources Conservation Service, 2018). If spring green-up is delayed, high-quality food sources are not available and sage-grouse must instead consume lower-quality food and use endogenous reserves for reproduction (Gregg et al., 2008).

Females in better body condition often initiate nests earlier in the breeding season (Dubovsky & Kaminski, 1994), which can be advantageous, as chicks hatched from early nests are more likely to be recruited into the population (Dzus & Clark, 1998). Although we found some evidence that pre-breeding body condition influenced initiation of incubation, females with the highest and lowest body condition initiated early, suggesting that there are other driving factors. We suggest that this curvilinear relationship may be due to a combination of body condition and age differences.

In general, adult sage-grouse are better at all aspects of reproduction (including nest initiation) than juveniles (Aldridge & Brigham, 2001; Gregg, 2006; Wallestad & Pyrah, 1974). Differences in reproductive performance have largely been attributed to differences in foraging behaviors between age classes that result in variation in nutrition (Wunderle, 1991). In Nevada and Oregon, Gregg (2006) found adult sage-grouse females initiate nests earlier than yearlings, regardless of female body condition. Adult females in good body condition are likely to initiate nests early because they have ample fat reserves and can meet the nutritional demands of laying a nest (Devries et al., 2008; Gregg et al., 2008). In our study area, we found little difference in body condition between age classes. However, the nests initiated earliest (top 20%) during the season were laid mainly by adults (63%), such that body condition is likely not the only determinant of nest initiation. Adult females in poor body condition might initiate nests early due to previous breeding experience and social and physiological factors (Hannon, Simard, Zwickel, & Bendell, 1979; K. Martin, 1995; Zwickel, 1977).

Breeding propensity is an important determinant of lifetime reproductive success, with population-level implications for many avian taxa (Blums & Clark, 2004). Sage-grouse generally have high breeding propensity, with 89-96% of females attempting to nest every year (Taylor, Walker, Naugle, & Mills, 2012). Variation in breeding propensity has been attributed to nutrition before and during the breeding season; breeding propensity of sage-grouse in high-quality habitat is above average (N. Kaczor et al., 2011). We hypothesized females in better pre-breeding body condition would have higher breeding propensity, as in other avian taxa such as waterfowl, passerines, and galliformes (Devries et al., 2008; Porter, Nelson, & Mattson, 1983). Given that sage-grouse in our study area exhibited high breeding propensity (91%), pre-breeding body condition may have little influence on this trait.

Pre-breeding body condition is positively related to clutch size in other avian taxa (Devries et al., 2008; Gladbach et al., 2010; Krapu, 1981), but we did not detect evidence of this relationship. In our study, clutch size decreased throughout the breeding season and differed among years, which is consistent with previous research (Cowardin, Gilmer, & Shaiffer, 1985; Gladbach et al., 2010). Seasonal declines in clutch size have been linked to declining food supplies late in the breeding season (Murphy, 1986; Perrins & McCleery, 1989). Variation in clutch size among years could result from changes in environmental conditions that limit habitat quality and availability (Connelly et al., 2011). During the pre-laying period, forbs provide higher levels of protein, calcium, and phosphorus that likely affect clutch size (Barnett & Crawford, 1994); dry conditions during the pre-nesting period could limit forb production

(Wenninger & Inouye, 2008). Barnett and Crawford (1994) reported consumption of forbs by female sage-grouse decreased from 45-50% to 18% in two consecutive years, coinciding with a 40% reduction in precipitation. In our study, clutch size was lowest during 2015, the breeding season with the lowest precipitation (Figure 3.3B), highest temperature, and earliest snow-melt date. The apparent relationship between clutch size and precipitation suggests sage-grouse rely heavily on exogenous reserves for clutch formation.

Chick recruitment is somewhat dependent on the timing and weight at hatch, and chicks that hatch early and are heavier are most likely to be recruited into the population (Blomberg et al., 2014; Blums, Clark, & Mednis, 2002). Nutrients acquired during the winter are important for attaining high pre-breeding body condition and, in turn, producing heavy chicks early in the breeding season that may contribute greatly to the population. If individuals are unable to acquire ample nutrients during the winter and return to the breeding grounds in poor body condition, chick recruitment could decline the following year. Based on our work, variation in pre-breeding body condition has implications on subsequent reproduction, and potentially chick recruitment.

Conclusions

Carry-over effects have large consequences for capital breeding species that rely heavily on endogenous reserves for reproduction, where individuals with insufficient fat reserves have reduced reproductive performance (Drent & Daan, 1980). The influence of carry-over effects is less pronounced in income breeding species that rely on exogenous reserves for reproduction, where fat reserves have little influence (Drent & Daan, 1980; Meijer & Drent, 1999). The importance of carry-over effects on species such as sage-grouse that rely on a combination of endogenous and exogenous reserves is less obvious but could have population-level effects.

Carry-over effects may not influence all aspects of reproduction, but may be strong forces early in the breeding season, a time period that is important to recruitment.

Sage-grouse conservation has been focused on protecting core-regions of habitat, largely defined by using data surrounding lekking areas (Fedy & Aldridge, 2011). To meet all seasonal needs for sage-grouse and conserve migratory populations, conservation efforts also should include habitat distant from leks and brood-rearing areas (Doherty, Naugle, Copeland, Pocewicz, & Kiesecker, 2011; Fedy et al., 2012). Our findings support this assertion, given that distant areas are not only important for winter survival, but also can contribute to reproduction the subsequent breeding season. Quality of the overwintering habitat could be an important driver of sage-grouse reproduction, especially when high-quality food is less available in breeding areas. Although the core-region concept is a good starting point for sage-grouse conservation, areas outside of these core-regions also may be critical for the long-term conservation of this declining species.

Authors' contributions

Kyle Cutting and Bok Sowell conceived the ideas and designed methodology; Kyle Cutting and James Waxe collected the data; James Waxe and Andrea Litt analyzed the data; James Waxe and Andrea Litt led the writing of the manuscript.

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Figures and tables

Tables

Table 3.1. Covariates in the global model examining the relationship between body condition of female sage-grouse (BCI) and initiation of nest incubation, 174 nests, southwest Montana, 2014-2018. We used a backward variable selection procedure, sequentially removing terms that did not explain sufficient variation (*P* > 0.10, from Type II Wald chi-squared tests). Covariates included in the final model are listed in bold.

Variable	$\chi2$	*df*	*P*
Age	0.002	1	0.9669
Sage-type	0.667	2	0.7163
BCI*Age	0.062	1	0.8029
BCI*Sage-type	0.342	2	0.8428
BCI	**2.002**	**1**	**0.1571**
Year	**26.442**	**4**	**< 0.0001**
BCI*Year	**23.272**	**4**	**< 0.0001**
BCI^2	**4.017**	**1**	**0.0450**

Table 3.2. Covariates in the global model examining the relationship between body condition of female sage-grouse (BCI) and clutch size, 75 nests, southwest Montana, 2014-2018. We used a backward variable selection procedure, sequentially removing terms that did not explain sufficient variation (*P* > 0.10, from Type II Wald chi-squared tests); we always retained BCI. Covariates included in the final model are listed in bold.

† Type II Wald chi-squared tests were all on 1 degree of freedom except for Year and BCI*Year (*df* =4).

Variable	$\chi2^{\dagger}$	*P*
Age	0.342	0.5585
BCI^2	0.530	0.4668
BCI*Age	0.133	0.7150
BCI*Date	0.028	0.8667
BCI*Nesting Attempt	1.628	0.2020
BCI*Year	5.842	0.2113
BCI	**0.098**	**0.7544**
Nest #	**5.049**	**0.0246**
Year	**11.002**	**0.0266**
Date	**37.028**	**< 0.0001**

Table 3.3. Covariates in the global model examining the relationship between body condition of female sage-grouse (BCI) and chick weight, 33 females, 205 chicks, southwest Montana, 2014-2018. We used a backward variable selection procedure, sequentially removing terms that did not explain sufficient variation (*P* > 0.10, from Type II Wald chi-squared tests). Covariates included in the final model are listed in bold.

Variable	$\chi 2$	*df*	*P*
BCI^2	0.005	1	0.9462
BCI*Sage-type	0.493	2	0.7815
BCI*Age	2.695	1	0.1007
Nesting Attempt	<0.001	1	0.9921
Heat Loading Index	1.578	1	0.2009
Age	1.751	1	0.1858
BCI*Year	7.689	4	0.1037
BCI	**0.570**	**1**	**0.4503**
Year	**15.085**	**4**	**0.0045**
Date	**0.167**	**1**	**0.6824**
Sage-type	**6.973**	**2**	**0.0306**
BCI*Date	**5.278**	**1**	**0.0216**

Figures

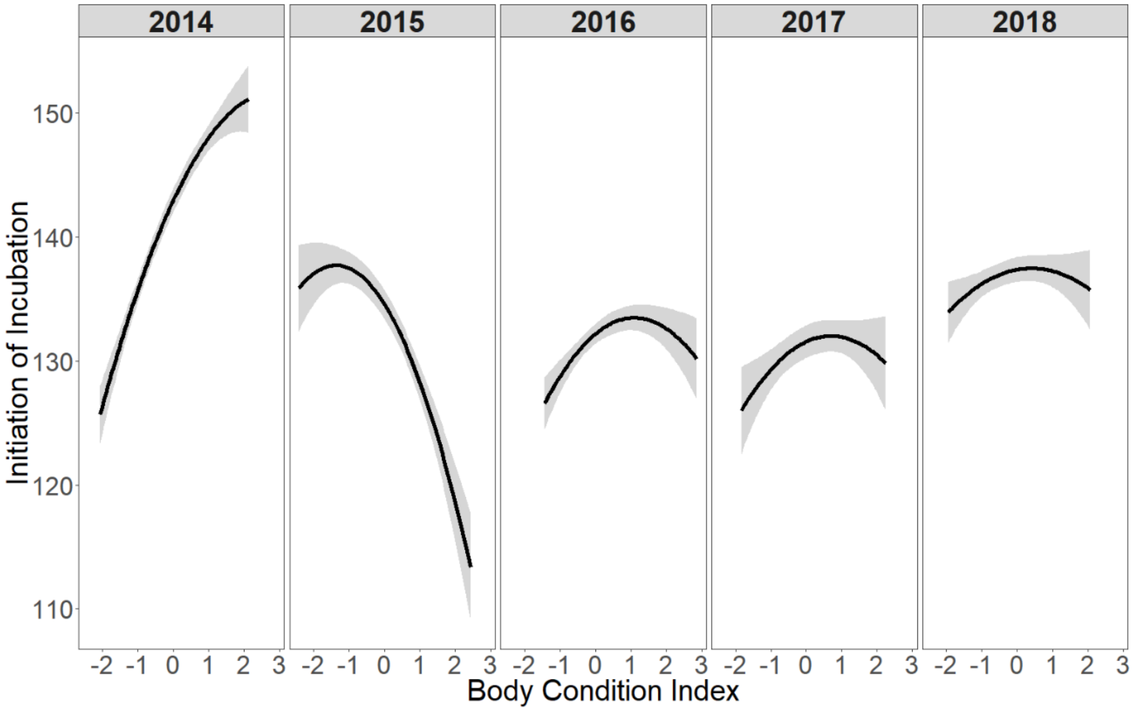

Figure 3.1. Predicted change in the date female sage-grouse initiated incubation based on body condition index, by year (including 95% CIs), based on the final model (Table 3.1), 174 nests, southwest Montana, 2014-2018.

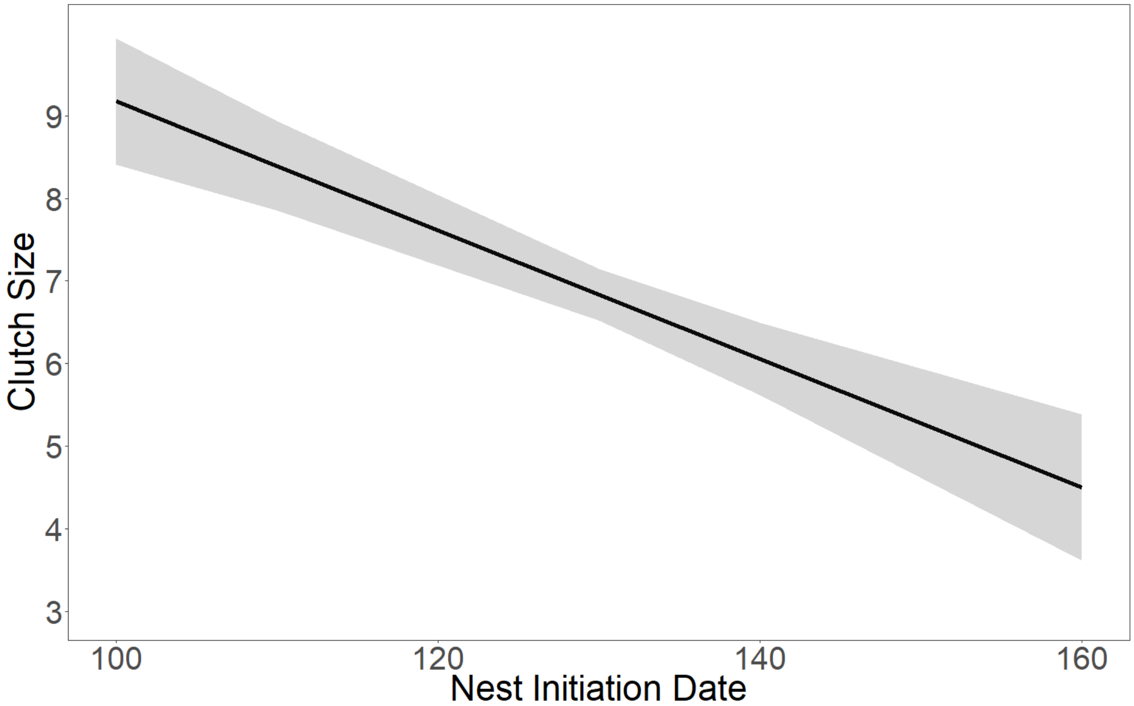

Figure 3.2. Predicted change in clutch size of sage-grouse throughout the breeding season (and 95% CI) based on the final model (Table 3.2), 75 nests, southwest Montana, 2014-2018.

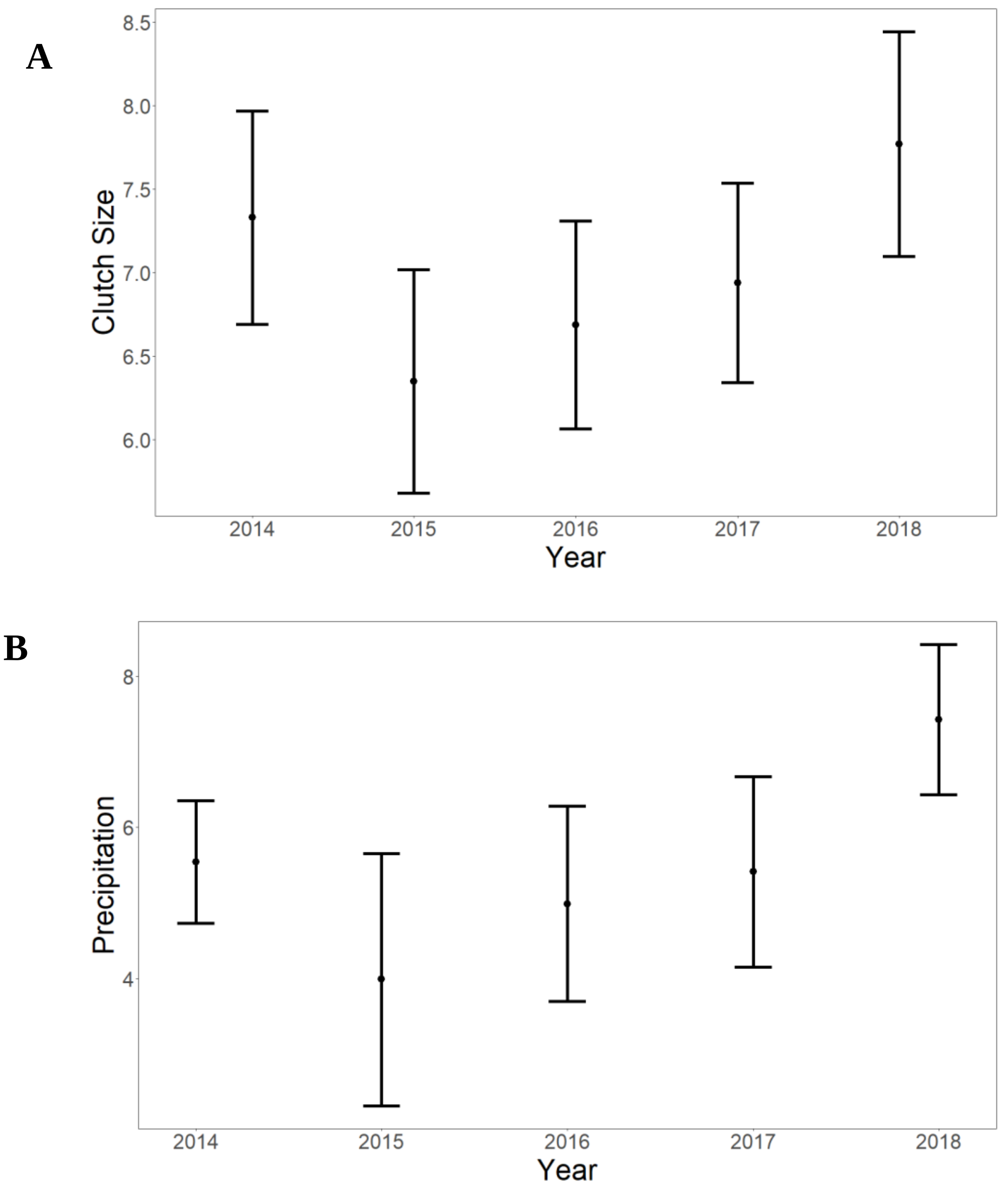

Figure 3.3. A) Predicted variation in clutch size of sage-grouse over time (and 95% CIs), 75 nests, southwest Montana, 2014-2018. B) Mean precipitation (cm) (and 95% CIs) for the breeding season (March – June) by year across the study area. We averaged extracted precipitation values for 4 separate 4-km^2 cells across the study area to obtain a single value for each breeding season (PRISM Climate Group 2018).

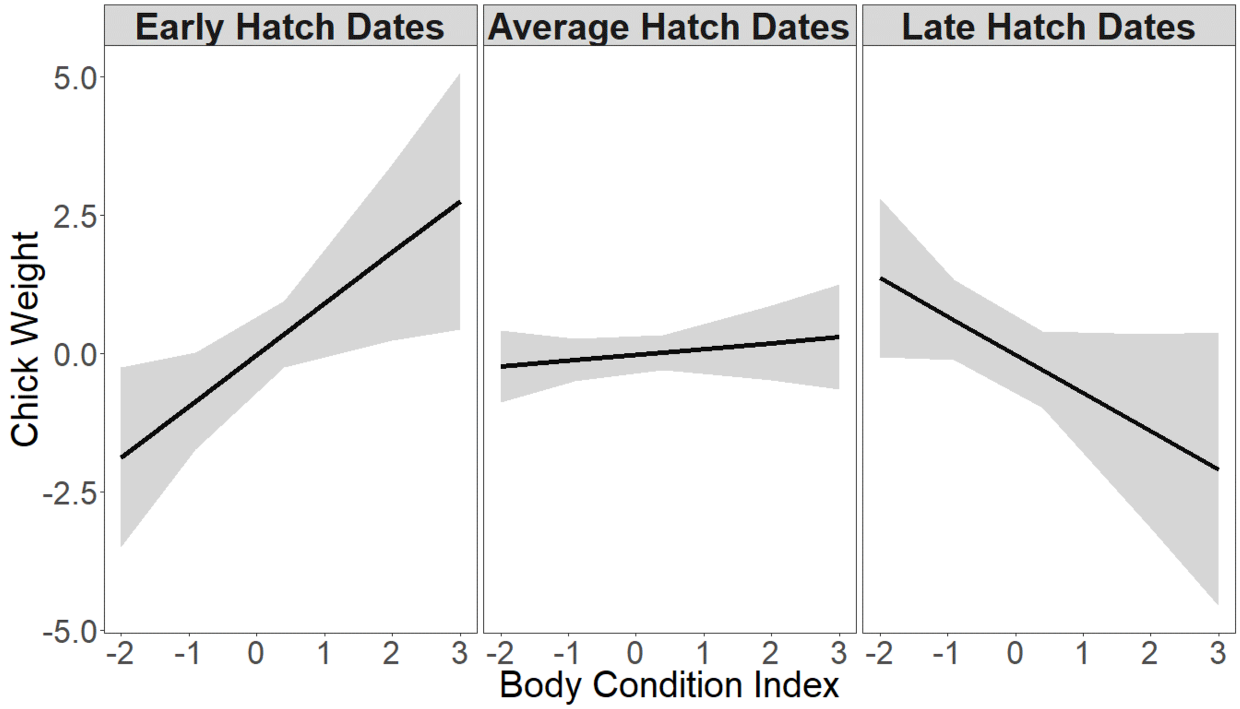

Figure 3.4. Predicted changes in chick weight as a function of body condition for early, average, and late hatch dates (including 95% CIs), based on the final model (Table 3.3), 33 female sage-grouse, 205 chicks, southwest Montana, 2014-2018.

CHAPTER FOUR

CONCLUSIONS

Our data suggest that carry-over effects influence sage-grouse, but the magnitude depended on environmental conditions and timing of breeding. Migration strategy and breeding habitat influenced pre-breeding body condition, with both effects largely driven by precipitation. Non-migratory individuals had higher pre-breeding body condition than migrants during dry winters. During winters with less precipitation, the costs of migration seemed to outweigh the benefits of remaining sedentary because non-migratory individuals were able to maintain body condition without enduring the energetic demands of migration. Precipitation during the breeding season also influenced body condition, as individuals attending leks that received less precipitation were in better condition than individuals that attended wetter leks. This relationship likely was driven by much of the precipitation falling in the form of snow, altering access to high-quality forage. We suggest conditions female sage-grouse experience during the winter and breeding seasons can influence their body condition, which provides evidence of a carry-over effect (Harrison et al., 2011).

Regardless of whether conditions during the winter or breeding season more strongly alter pre-breeding body condition, such changes have concomitant influences on future reproductive activities. Female sage-grouse in better body condition produced larger chicks early in the breeding season, although this relationship was less apparent later in the season. This reliance on body condition for reproduction early in the season could be due to lower availability of high-quality forage during that period. In our high-elevation study area, conditions early in the breading season are typically cold and wet, with frequent snowfall events that affect vegetation phenology (USDA Natural Resources Conservation Service, 2022). Delays in spring green-up reduce the availability of high-quality food sources (i.e., forbs), such that sage-grouse may need to supplement lower-quality foods (i.e., sagebrush) with fat and protein reserves to support reproduction (Gregg et al., 2008).

Abundance of sage-grouse populations fluctuate over time (Garton et al., 2011), which could be, in part, related to varying magnitudes of carry-over effects. During years with the right combination of environmental conditions and timing of breeding, carry-over effects may influence sage-grouse demographics. For example, a non-migratory individual that experiences favorable conditions during winter, attends a drier lek, and breeds early in the season likely would have some of the heaviest offspring in the population. These heavy offspring – that hatched early in the season – would have the best chance of being recruited into the population (Blomberg et al., 2014). During years with less winter precipitation, non-migratory individuals could be disproportionately contributing to the population. Conversely, during years with high amounts of winter precipitation, migratory individuals may play a key role in sustaining the population.

Although sage-grouse conservation has largely focused on areas around breeding grounds (Fedy & Aldridge, 2011), our data suggest that habitat quality during winter could influence the annual life cycle considerably; in migratory or partially migratory populations, these wintering locations could be far from the breeding grounds. Protecting a variety of winter habitat both near and distant from breeding areas will ensure the persistence and reproductive contribution of individuals with different migration strategies. Variation in winter habitat increases forage availability (i.e., sagebrush), and allows access to different sagebrush types with varying degrees of palatability. With increasing evidence of carry-over effects in sage-grouse populations managers should broaden their conservation strategies to account for all life stages (Blomberg et al., 2014).

Conservation efforts for sage-grouse also should focus on protecting a mosaic of wintering and breeding areas to meet the needs of more individuals over time. With climate change influencing weather patterns globally, habitat conditions may change such that sage-grouse in some areas can no longer complete their life cycle. Variation in life-history strategies and environmental conditions across the landscape allows at least some individuals to experience optimal conditions that support high body condition and reproductive success. Partially migratory populations of sage-grouse likely provide a buffer against environmental variability and protecting all known sage-grouse leks within a single population also allows for flexibility to respond to changing environments. Maintaining landscape-level habitat heterogeneity would allow more individuals to meet their life-history requirements, which is critical for conserving remaining sage-grouse populations.

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