DISSERTATION

SPRING AND AUTUMN STOPOVER RESOURCES AND LAND USE PATTERNS FOR THE ROCKY MOUNTAIN POPULATION OF SANDHILL CRANES IN THE SAN LUIS VALLEY, COLORADO

Submitted by

Rachel Ann Vanausdall

Department of Fish, Wildlife, and Conservation Biology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2024

Doctoral Committee:

Advisor: William L. Kendall

Daniel P. Collins
David N. Koons
Jeremy Sueltenfuss

ABSTRACT

SPRING AND AUTUMN STOPOVER RESOURCES AND LAND USE PATTERNS FOR THE ROCKY MOUNTAIN POPULATION OF SANDHILL CRANES IN THE SAN LUIS VALLEY, COLORADO

Stopover areas are important to migrant birds for resting and refueling on long journeys to and from their breeding grounds. Many birds use spring stopover areas to obtain adequate energy reserves to aid in reproduction, and the quality of habitat used during both spring and autumn migration can have cross-seasonal effects on vital rates, such as survival probability, later in the annual cycle. The Rocky Mountain Population of greater sandhill cranes (*Antigone canadensis tabida*) is a migrant population that stages in several western regions during the migratory period, but most of their time is spent on a single stopover area during the autumn and spring. While this population breeds throughout states within and around the Rocky Mountains and winters throughout parts of New Mexico, Arizona, and Mexico, over 90% of the RMP stopover in the San Luis Valley (SLV) in southcentral Colorado. Additionally, a smaller number of lesser sandhill cranes (*A. c. canadensis*) from the Midcontinent Population use the SLV during autumn and spring migraiton. During this time, sandhill cranes utilize riverine corridors, wetland complexes, wet meadows and pastures, and agricultural fields in the SLV on both private and public lands. A high proportion of their diet includes spilled barley and other grains leftover after harvest in autumn and before planting season the following spring. The Monte Vista National Wildlife Refuge (MVNWR) also provides supplemental barley for sandhill cranes in spring and manage water to provide emergent wetland and shallow water habitats for roosting and loafing. However, the SLV has experienced landscape changes that threaten important habitat for sandhill

cranes, and most of these changes center around the availability of water. As a semi-arid and snowpack driven region, the hydrology of the SLV relies mostly on precipitation that comes from the surrounding mountains and on aquifers that provide irrigation water and recharge other water sources. Over the years, efforts to divert surface water and pump water from aquifers have led to overappropriation of water rights and reduced water availability. In addition, increasing temperatures and a changing climate are contributing to increasing water scarcity. These changes will likely influence the land use patterns, which could ultimately affect the supply of energy on the landscape and energetic demand of sandhill cranes. In turn, this could affect abundance and distribution. Understanding migration phenology, along with their bioenergetics and land use patterns while at a primary stopover area, are important for informing management on both public and private land and for estimating the carrying capacity of an area for migrant species.

While the timing of RMP sandhill crane migration in the SLV has been documented previously, our first objective was to formally quantify their migration phenology in and out of the SLV and determine if there were weather or habitat covariates influencing their persistence probability. Migrant birds are thought to optimize migration timing and energy use by balancing the speed of migration with energetic consumption and expenditure. For example, migrating faster in the spring (i.e., time-minimization), and thus arriving earlier at the breeding grounds, may improve reproductive performance for some species. On the other hand, reducing the amount of energy (i.e., energy-minimization) used during migration may be preferred in autumn under reduced time constraints, so birds may take longer to migrate at this time of the year. Various factors will also influence how long birds remain at a stopover area, including weather patterns and habitat availability. As large birds, sandhill cranes may take advantage of various weather patterns, such as strong tailwinds or high wind speeds, to aid in flight and overall

migration. These factors may reduce the probability that a sandhill crane will remain at a stopover if they incur a higher energetic cost. We examined the arrival probability and persistence probabiltiy of RMP sandhill cranes in the SLV using data across eight years from birds fitted with global system for mobile communication (GSM) platform transmitter terminal (PTT) tags or Global Positioning System (GPS) units. Using an open robust design mark-recapture model, we examined the influence of temperature change, barometric air pressure, tailwinds, crosswinds, wind speed, and surface water on the persistence probability of RMP sandhill cranes. Stopover duration was longer in autumn than in spring and had higher variability across years. Arrival probability to the SLV peaked on 13 October in autumn and 21 February in spring. Persistence probability declined around mid-December in autumn and mid-March in spring. We found that several weather covariates influenced persistence in both seasons. In autumn, sandhill cranes departed the SLV with higher tailwinds, lower crosswinds, and higher surface water availability. In spring, sandhill cranes departed the SLV with lower crosswinds and higher barometric air pressure at the surface and higher wind speeds at altitudes of about 3,000 m. The effect of wind speed was stronger later in the spring. Given the lower variability of arrival and persistence probability and shorter stopover duration in spring compared to autumn, we suspect that RMP sandhill cranes are using a time-minimization strategy during spring. However, given the use of supportive winds and weather conditions ideal for soaring, RMP sandhill cranes appear to be using strategies that save energy in both seasons. This study identified the optimal timing of water management and surveys for RMP sandhill cranes and confirms that weather influences their persistence. Understanding differences in migration patterns between seasons and the factors that influence persistence at stopover sites will also be important for anticipating phenological impacts from climate change and land use alterations.

Next, we focused on how RMP sandhill cranes select habitat and use the SLV during their stopovers in autumn and spring. Sandhill cranes tend to show predictable movement patterns during migration in the SLV. They generally spend nights roosting in areas with shallow water (e.g., emergent wetlands, rivers, creeks, ponds) and leave the roosts around sunrise to forage primarily on grain fields. They spend midday loafing (i.e., resting and engaging in other behaviors) in various habitats, usually near or in water, and then return to feed one more time close to sunset before returning to the roost. This movement around a focal roosting point characterizes central place foragers. Given the risk of increasing water scarcity in the SLV and the potential for future landscape changes, quantifying the selection patterns of RMP sandhill cranes during their roosting, foraging, and loafing periods provides valuable information for habitat management. We used GSM/GPS data to examine the effects of water, sandbar, vegetation height, distance to the nearest grain field, landcover type, and ownership on roosting, loafing, and foraging habitat selection by RMP sandhill cranes. We found that sandhill cranes selected for areas with a high amount of water, relatively short vegetation (<5 m in autumn, <10 m in spring), close to grain fields (<5 km), and areas identified as open water for roosting. Loafing sandhill cranes also selected for areas with short vegetation and close to grain fields but that had less water and more sandbar than roosting areas and were identified as pastures or wetlands. While selection was higher for private land overall, we found evidence of avoidance of private lands and a stronger preference for public lands with increasing surface water for roosting in spring. For foraging areas, selection was highest for barley in both seasons, but triticale and other grains had relatively high selection in autumn. Our finding confirms the importance of providing roosting and loafing areas on both private and public lands close to foraging areas and

provides evidence that roosting and loafing opportunities may be most limited on public lands in the SLV.

We then examined foraging selection patterns more closely to define RMP sandhill crane distribution during migration and determine factors, in addition to habitat type, that affect selection for foraging areas. Flying is energetically expensive, so understanding some of the drivers of foraging preferences can inform management to aid in reducing the amount of energy required to find food. Greater sandhill cranes tend to forage within 2-5 km of their roost from the previous night. As food items in patches decline due to consumption and deterioration, sandhill cranes will move farther from their roost to forage. Other factors may motivate birds to switch patches. Tilling, for example, is a practice that takes place after harvest in many fields in the SLV and can also reduce seed availability. We sought to understand how tillage intensity in grain fields, along with crop type, distance to the nearest roost, and time, influence foraging selection by both greater sandhill cranes and lesser sandhill cranes. The same covariates were also used to examine their effects on the number of greater sandhill cranes. We completed roadside surveys to count greater and lesser sandhill cranes in autumn and spring and identify field-specific covariates. Lesser sandhill cranes were more concentrated in specific areas in the SLV, while greater sandhill cranes were more variable in their distribution. Selection in autumn was most influenced by an interaction between time and crop type for both subspecies, while spring selection was influenced by an interaction between crop type and roost distance. The probability of presence was highest on barley fields or other grains for both subspecies in mid-October and mid-March, but it declined as distance to the nearest roost increased for both subspecies. We only modeled covariates on abundance for greater sandhill cranes and found that an interaction between time and roost distance was the most influential model in autumn. The interaction

between time and crop type most influenced abundance in spring. The effect of roost distance was negative early in the autumn season but became positive later in the season. Greater sandhill cranes also showed a higher abundance in other crop types in spring compared to autumn. We found that both greater and lesser sandhill cranes were more likely to be on fields with idle or low intensity tillage practices than those with high intensity tillage practices. Overall, our results suggested that sandhill cranes are variable in their use of the SLV for foraging and prefer to fly farther from roosts to their preferred forage type but may also switch to other crop types.

While documenting phenology and selection patterns is useful for prioritizing areas for conservation and determining the appropriate habitat types to provide during migration, researchers and managers are lacking an understanding of how many sandhill cranes the SLV could theoretically support. Changing landscape and climate conditions in the SLV are contributing to increasing water scarcity, which may eventually reduce the amount of barley grown in the SLV or alter the juxtaposition of foraging and roosting areas. To understand how changes in barley tillage practices and amounts may influence RMP sandhill crane numbers in the SLV, our goals were to examine the influence of tillage intensity on barley availability, determine the energy demand of RMP sandhill cranes during autumn and spring, calculate the supply of energy available on the landscape from barley, and estimate current and potential carrying capacity under varying barley amounts. Idle fields (i.e., fields not tilled) had the greatest density of barley than fields that had low or high tillage intensity practices, and RMP sandhill cranes that used more tilled fields spent more time searching for forage. We also found an increase in lipid gain during spring migration, which increased the daily energetic expenditure (DEE) of RMP sandhill cranes during spring compared to autumn. Overall, we found that individual RMP sandhill cranes required between 458 to 566 kcal per day, which equated to

0.129 to 0.160 kg of barley per day, with a greater amount required during spring. The total energy demand required by the population for autumn was approximately 284.9 x 10^6 kcal (0.08 x 10^6 kg of barley), and this value increased to 435.4 x 10^6 kcal (0.1 x 10^6 kg of barley) for spring. The average energy supply was 5905.5 x 10^6 kcal (1.7 x 10^6 kg of barley) for early autumn and 1589.9 x 10^6 kcal (0.4 x 10^6 kg of barley) in late spring for the entire SLV. Overall, the supply of energy exceeded sandhill crane demand throughout both seasons. Based on bioenergetics models using the TRUEMET model, most scenarios also showed that energetic supply exceeded demand. Under all scenarios, barley declined by approximately 90% or more between early autumn to late spring, but supply was still greater than demand at the end of spring. While we made several assumptions using these models that could not be validated, we are confident that we provide evidence that there is currently enough barley in the SLV to support more sandhill cranes than the present population. Tillage intensity, particularly barley left idle in autumn and spring, appears to play a bigger role in barley availability than the presence of barley on public over private land.

Overall, our findings provide information that can aid in practical management objectives in the face of climate and land use challenges and describe baseline information on how current conditions influence the energetics of the RMP. While the RMP appears to be relatively stable and increasing, several environmental changes in the SLV are likely to impact the distribution, timing of migration, and habitat selection patterns of the population. In turn, these factors will affect how sandhill cranes use and expend energy, which may lead to reduced reproduction or survival. Current objectives for the RMP include providing suitable habitat to support a population goal of 17,000 – 21,000 individuals. Our results indicate that habitat is sufficient for the current population and potentially a larger population. However, given the role of water in

the movement and selection of sandhill cranes, increasing water scarcity is likely to temper the benefits of available forage over time, which may make meeting population objectives more challenging. Continued management of water and foraging resources on public and private lands are important, but our results also emphasize the need to integrate habitat management on both ownership types to ensure adequate resources are available during migration.

PREFACE

I first want to thank my advisor, Bill Kendall, for his guidance, support, and patience, especially given the ups and downs of the COVID19 pandemic. A special thanks to my committee members, who all contributed in valuable ways to my learning and research experiences. I am grateful for the research and field opportunities and career advice Dan Collins has provided over the years. Thank you to Dave Koons for being an amazing teacher and to Jeremy Sueltenfuss for pushing me to dive into better understanding ecosystem functions and services. I also have to give a warm thank you to students and faculty in the Animal Science Department at Colorado State University. Terry Engle provided resources and support that made an important piece of this project possible, and I thank him, along with Octavio Guimaraes, Huey Yi Loh, and his other students for their help and patience. Other faculty and staff at CSU have helped me immensely in my learning and teaching journey, and I'm grateful to have been a part of that community. A huge thank you goes to Gabriele Engler, Kim Samsel, and Melinda Neiblum for their support and for helping me out of some jams. Several FWCB and other CSU students and post-doctoral researchers were supportive and always willing to offer an ear and some advice when I was at my lowest points, and I will be forever grateful for that. I want to give a special thank you to Annie Hart, Sarah Albright and the rest of the Kendall lab for their friendship and help over the years. Thank you to the staff at the San Luis Valley Refuge Complex, including Suzanne Beauchaine, Scott Miller, Gabe Martinez, and several others for providing housing, vehicles, and support for this project. Thank you to Jim Gammonley and other Colorado Parks and Wildlife staff for their assistance in gathering additional information on sandhill cranes. I am grateful for the help and collaboration I received from Dave Olson, Patrick Donnelly, Jonathan Moore, Quentin Hays, Doug Osborne, and Matthew Buchholz. I am also

appreciative of the funding we received for this project, which was provided by the U.S. Fish and Wildlife Service and the U.S. Geological Survey. Finally, thank you to my family and friends for their unwavering support and encouragement, and thank you to the sandhill cranes for helping me cultivate a fulfilling PhD experience.

This dissertation is organized by chapters, and each chapter has been or is intended to be published in a peer-reviewed research journal. Citations have been formatted according to each journal's specifications. Below are the manuscript titles, authorship, and target journal.

Chapter 1: Time of year and weather influence departure decisions of sandhill cranes at a primary stopover

This chapter has been published in *Frontiers in Ecology and Evolution* (Volume 12, doi 10.3389/fevo.2024.1279279, pg 1-18). Its intended audience are those interested in migration phenology and the timing of sandhill crane migration in the San Luis Valley, Colorado.

Rachel A. Vanausdall[1], William L. Kendall[2], Daniel P. Collins[3], Quentin R. Hays[4]

[1]Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO, United States

[2]U. S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO, United States

[3]U. S. Fish and Wildlife Service, Migratory Bird Office, Albuquerque, NM, United States

[4]GeoSystems Analysis, Inc., Corvallis, OR, United States

Chapter 2: Habitat selection by Rocky Mountain Population greater sandhill cranes (*Antigone canadensis tabida*) during spring and autumn migration at a key stopover area

This chapter has been submitted to *Avian Conservation and Ecology* and is in review. The intended audience includes those wanting to understand management of roosting and loafing habitat for sandhill cranes and identify high-use areas in the San Luis Valley, Colorado.

Rachel A. Vanausdall[1], William L. Kendall[2], Daniel P. Collins[3], J. Patrick Donnelly[4], Quentin R. Hays[5]

[1]Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, USA

[2]U. S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, USA

[3]U. S. Fish and Wildlife Service, Migratory Bird Office, Albuquerque, New Mexico, USA

[4]Intermountain West Joint Venture, US Fish and Wildlife Service Migratory Bird Program, Missoula, Montana USA

[5]Geosystems Analysis, Corvallis, Oregon USA

Chapter 3: Sandhill crane foraging habitat selection during spring and autumn migration in an agriculturally dominated stopover

This chapter will be submitted to either *Ornithological Applications* or a similarly focused journal. It is meant for an audience interested in the effects of agriculture dynamics on sandhill crane distribution and selection.

Rachel A. Vanausdall[1,4], William L. Kendall[2], Daniel P. Collins[3]

[1]Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO, United States

[2]U. S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO, United States

[3]U. S. Fish and Wildlife Service, Southwest Region-Migratory Bird Program, Albuquerque, New Mexico, United States

Chapter 4: Energy availability for sandhill cranes during spring and autumn migration in the San Luis Valley, Colorado

This chapter is intended to be submitted to either the *Journal of Wildlife Management* or *Ecological Applications*. Its intended audience are those interested in food availability for migrating birds and bioenergetics.

Rachel A. Vanausdall[1,3], William L. Kendall[2],

[1]Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO, United States

[2]U. S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO, United States

TABLE OF CONTENTS

CHAPTER 1 – TIME OF YEAR AND WEATHER INFLUENCE DEPARTURE DECISIONS OF SANDHILL CRANES AT A PRIMARY STOPOVER

INTRODUCTION

Migration is energetically costly and exposes individuals to predators and sometimes unpredictable weather, but fast migration and early arrival to the breeding grounds can improve reproductive performance (Alerstam and Lindström, 1990; Kokko, 1999; Alerstam, 2011). Optimal migration theory predicts that birds should balance the time it takes to get to their destination with energy expenditure to maximize the benefits of migration (Alerstam and Lindström, 1990; Alerstam and Hedenström, 1998; Alerstam, 2011). There are several aspects of migration behavior that allow birds to optimize time and energy during migration, including the use of stopover areas, as they can provide refueling opportunities and allow individuals to rapidly increase nutrient reserves (e.g., lipids), which may improve fitness potential (Ankney and MacInnes, 1978; Alisauskas, 2002; Chapman et al., 2011; Schmaljohann et al., 2022). However, stopovers may increase the overall duration of migration, incur energetic settling costs, expose individuals to predation risk, and potentially result in decreased survival probability (Newton, 2007). Migratory behavior, such as total migration duration, the travel route, and optimal stopover departure timing, will vary among individuals and across seasons based on environmental and intrinsic factors (Weber et al., 1998; Karlsson et al., 2012; Nilsson et al., 2013; Åkesson and Helm, 2020). Understanding these decisions at known, key stopover areas can provide information on how populations respond to weather and habitat conditions, which may help identify potential impacts from climate and land use changes.

Migration in birds is hypothesized to evolve in response to temporal (e.g., seasonal) environmental variation, allowing for individuals to access high quality resources throughout the

year and respond to changing conditions (Cox, 1985; Lundberg, 1988; Winger et al. 2019). While some aspects of migration are genetically determined (e.g., response to day length; Møller, 2001; Pulido, 2011; Åkesson and Helm, 2020), migratory behaviors are also mediated and influenced by weather and habitat (Åkesson and Hedenström, 2007; Bauer et al., 2008; Haest et al., 2020). Previous work has identified temperature, wind assistance, cloud cover, precipitation, and barometric air pressure as factors influencing migratory decisions, such as departure probability (Richardson, 1978, 1990; Shamoun-Baranes et al., 2017). Often the effects of weather covariates on migration are related to the ability of birds to optimize time and energy (Åkesson and Hedenström, 2007; Shamoun-Baranes et al., 2017). For example, wind speed and wind assistance both have been cited as important in the departure decisions of many species (Schaub et al., 2004; Mellone et al., 2012; Gill et al., 2014; Panuccio et al., 2016; O'Neal et al., 2018). Higher wind speeds, increased tailwinds, and reduced crosswinds may all speed up migration and reduce energy use (Pennycuick et al., 1979; Panuccio et al., 2016; O'Neal et al., 2018; Roques et al., 2021; Rüppel et al., 2023). Temperature changes are often associated with arrival and departure during migration, where migration usually occurs in spring with rising temperatures and in autumn with falling temperatures (Richardson, 1990; Bauer et al., 2008). Both temperature and wind can interact or be correlated with barometric air pressure, which has been shown to influence departure decisions and other migratory behaviors (Richardson, 1978; Shamoun-Baranes et al., 2006; Cooper et al., 2023). Growing evidence indicates that birds can detect changes in barometric air pressure (Kreithen and Keeton, 1974; von Bartheld, 1994) and may change their flight or foraging behavior in response (Breuner et al., 2013; Metcalfe et al., 2013).

Topography and habitat may also influence the effects of environmental covariates on migratory behavior and impact migratory phenology. For example, orographic uplift (i.e., the movement of air over terrain) may be more important in migratory performance for birds flying over mountain ranges, whereas thermal uplift may have a greater impact on birds flying over flatter terrain (Mandel et al., 2011). Birds may also decide to go around ecological barriers, such as mountains or the open ocean, rather than over them, even if it increases overall migration duration (Åkesson and Hedenström, 2007). The suitability and availability of habitat can affect the stopover duration of migrating birds, where birds might remain at a stopover area longer if adequate resources are available (Obernuefemann et al., 2013; Jorgensen and Brown, 2017; Lawrence et al., 2021). The availability of resources can also interact with climatic shifts to alter migration phenology. In the Intermountain West, for example, increasing temperatures and changing precipitation and water regimes influence water availability, which can affect the availability of foraging and roosting sites for migrating waterbirds (Donnelly et al., 2019). Other studies have confirmed that some individuals and populations are departing wintering and stopover areas sooner or shifting their distribution in response to changing climate and habitat conditions (Jenni and Kéry, 2003; Visser et al., 2009; Usui et al., 2017; Cox et al., 2023). Understanding migratory behaviors and how individuals respond to weather, climate, and habitat is an important initial step to anticipating how climate and land use changes may adversely affect population numbers.

The importance of weather patterns and habitat may differ between northbound and southbound migration (Nilsson et al., 2013; Kemp et al., 2023) and based on other intrinsic factors of the bird, such as individual body condition and age or experience (Piersma and Jukema, 1990; Mueller et al., 2013; Mitchell et al., 2015). Considerable attention has been given

to whether birds migrate based on time-minimization or energy-minimization as the primary goal (Alerstam and Lindström, 1990; Alerstam and Hedenström, 1998; Duijns et al., 2019). Minimizing time is expected to be the preferred strategy during spring migration, as arriving to the breeding grounds at an optimal time may allow individuals to take advantage of high-quality resources and secure territory before the arrival of competitors (Kokko, 1999; Nilsson et al., 2013; Illan et al., 2017). In contrast, autumn migrants may be less time-constrained because they are not competing for breeding areas and may prioritize acquiring and saving energy (Nilsson et al. 2013). Several studies have confirmed that migrants travel faster in spring than in autumn (Karlsson et al., 2012; Mellone et al., 2012; Illan et al. 2017; Duijns et al., 2019), while others have found the opposite to be true (Shamoun-Baranes et al., 2003; Nolet 2006; Kölzsch et al., 2016). Migrants generally travel faster by reducing stopover time, which is the main determinant of total migration duration, but they may also increase their flight speed (Karlsson et al. 2012; Nilsson et al. 2013; Duijns et al. 2019).

Cranes in the subfamily *Gruinae* are composed of species known to be impacted by various weather conditions during migration, especially due to their relatively large size and reliance on a mix of flapping-powered and soaring flight (Pennycuick et al., 1979; Alonso et al., 1990a; Ojaste et al., 2020). There are six distinct migratory populations of sandhill cranes in North America, and they are composed of up to two subspecies (Collins et al. 2016; Petersen et al. 2003; Johnson et al. 2005). The greater sandhill crane (*Antigone canadensis tabida*) is the largest the subspecies of sandhill cranes and makes up the Rocky Mountain Population (RMP). The San Luis Valley (SLV) in Colorado has been identified as a key stopover site during spring and autumn migration for the RMP (Donnelly et al. 2021). During stopover, sandhill cranes rely on foraging areas (e.g., harvested grain fields) and roosting areas (e.g., wetland and riverine

habitat) in the SLV for up to 30 days and sometimes more as they move to breeding areas throughout several western states (i.e., Colorado, Idaho, Montana, Wyoming, and Utah) and their wintering areas in New Mexico, Arizona, and northern Mexico (Drewien and Bizeau, 1974; Donnelly et al., 2021). Water availability in the SLV is highly variable within and between seasons, which may impact stopover patterns, as the juxtaposition of nearby surface water with foraging areas may dictate distribution (Krapu et al., 1984; Boggie et al., 2018). A thorough examination of the stopover ecology and the role of weather and surface water in stopover decisions will be informative for both monitoring and management (e.g., survey timing, habitat manipulation), particularly as land use changes and increasing water scarcity have the potential to affect RMP cranes in the Intermountain West (Gerber et al. 2015; Donnelly et al., 2021, 2023).

Our specific objectives were to (1) determine stopover duration, (2) investigate entry and persistence probability (i.e., the probability of staying in the SLV during stopover), and (3) examine the influence of temperature, wind components (i.e., wind speed, tailwind, and crosswind) at the surface and higher altitudes, barometric air pressure, and surface water availability on the persistence probability of RMP sandhill cranes in autumn and spring in the SLV. Day of season or the amount of time an individual has been at a stopover (i.e., time-since-arrival) may be more influential than weather or other factors on persistence for an individual prioritizing the minimization of time over energy use (Alerstam and Lindström, 1990; Roques et al. 2022). Because the time spent at stopovers largely determines total migration duration, we expected RMP sandhill cranes to have a shorter stopover duration in spring than in autumn. There may also be less variability among years in the timing and duration of spring migration. For example, other studies have confirmed sandhill cranes migrate longer during autumn compared to spring and found evidence of greater variability in stopover duration and total

migration duration in autumn (Krapu et al., 2014; Fronczak et al., 2017; Donnelly et al., 2021). Thus, we predicted that there would be less variability in arrival and persistence probabilities in spring compared to autumn.

Several weather metrics have been shown to be correlated with the stopover decisions of other crane species and similarly sized migrants (Pennycuick et al., 1979; Shamoun-Baranes et al., 2006; Vansteelant et al., 2017; Ojaste et al. 2020). Specifically, the metrics wind speed, tailwinds, crosswinds, temperature, and barometric air pressure play a role in shaping conditions for migration and the amount of energy required to depart and fly (Richardson, 1990; Gordo, 2007). We predicted higher wind speeds, the presence of a tailwind, and reduced crosswinds would negatively influence persistence probability for RMP sandhill cranes in spring and autumn. We also predicted that wind covariates at higher altitudes would be more influential in spring than autumn because sandhill cranes must fly over or bypass mountains during northward migration. We hypothesized that barometric air pressure would have a negative influence on persistence probability in both seasons, as higher air pressure generally indicates light winds and no precipitation (Ahrens, 2013), which are favorable conditions for migration (Richardson, 1990). We also expected daily temperature change to negatively influence persistence probability in spring, as an increase in temperature might indicate more optimal migratory conditions (Richardson, 1990; Shamoun-Baranes et al., 2003; Panuccio et al., 2016). At the same time, temperature can influence habitat availability (Richardson, 1990; Ojaste et al., 2020). In the SLV, lower temperatures in early spring or late autumn may result in freezing conditions, which can incur thermoregulatory costs for sandhill cranes and limit roosting potential (Richardson, 1990). Water is becoming a limited resource in much of the Intermountain West (Llewellyn and Vaddey, 2013; Dettinger et al., 2015), and so it may affect the ability of sandhill cranes to roost and

forage while maintaining adequate energy reserves. As a result, we predicted that temperature and surface water availability would both positively influence persistence probability during autumn.

METHODS

Study Area

The SLV is in south-central Colorado, U.S.A., and is a high elevation, intermontane basin that is the northernmost part of the Upper Rio Grande Basin (Fig. 1.1). The average elevation is approximately 2,100 m, and the total area of the valley floor is about 8,200 km^2 (Emery et al., 1969). Climate in the SLV is largely driven by a combination of its location and elevation and the sea surface temperatures in the Pacific Ocean and the Gulf of Mexico, which in turn influence the movement of air masses throughout the year and the North American Monsoon in the summer (Ahrens, 2013; Llewellyn and Vaddey, 2013). The SLV is an arid region with an average annual precipitation of 180 mm but with evapotranspiration rates of 1150 to 1300 mm per year (U.S. Fish and Wildlife Service, 2015). The surrounding mountain ranges receive more precipitation (850 to 1100 mm on average) mostly in the form of snow. As a result, the major source of water input in the SLV is spring snowmelt from the Sangre de Cristo Mountains to the east and the San Juan Mountains to the west (Elias et al., 2015). Snowmelt is transported to the valley floor via the Rio Grande River and other creeks and tributaries (Emery et al., 1969). Monsoonal rains in the summer can provide water inputs, but surface water tends to become more limited throughout the summer and autumn due to evapotranspiration and irrigation withdrawals for agriculture (Rio Grande Basin Roundtable, 2015; U.S. Fish and Wildlife Service, 2015). Two aquifers also provide water for irrigation and natural inflows, which influence hydrological conditions. The annual average temperature in the SLV is approximately 6°C, but

temperatures range from as low as -20°C in winter to over 20°C in the summer (Western Regional Climate Center, 2013). Recent research has shown increasing temperatures in the Upper Rio Grande Basin (Llewellyn and Vaddey, 2013) and the SLV in recent decades (Mix et al., 2010). Winds are highly variable and are primarily from the south and southwest throughout the year.

Much of the SLV is composed of shrub-scrub habitat, privately-owned agricultural land, and interspersions of pastures and publicly managed wetland and wet meadow habitat. Willows (*Salix* sp.) and cottonwood (*Populus deltoides*) grow along the Rio Grande and its tributaries. Many of the remaining wetland habitats, composed of cattail (*Typha* sp.), rushes, and other emergent vegetation, exist on public lands, including the Monte Vista National Wildlife Refuge, Alamosa National Wildlife Refuge, and Russell Lakes State Wildlife Area. Agricultural production is the dominant economic driver in the SLV and the greatest user of water (Rio Grande Basin Roundtable, 2022). Agricultural fields are mostly irrigated by pivot sprinkler systems with water transported from ditches, canals, and underground wells. The primary crops grown include alfalfa, potatoes, grass hay, and barley (Rio Grande Basin Roundtable, 2022). Livestock ranching is also a major industry in the area. Irrigation water for crops come from both surface water and groundwater but diminishing surface water resources due to over-appropriation and increasing temperatures have resulted in a greater reliance on groundwater in recent decades (Rio Grande Basin Roundtable, 2022).

During the spring and the fall, RMP cranes will roost along the rivers and creeks and in emergent wetlands and wet meadows on both public and private lands. They forage primarily on waste grain (e.g., barley) remaining after autumn harvest or provided by the Monte Vista National Wildlife Refuge, but they will also forage in potato fields, grasslands, wetlands, and

pastures for other seeds, vegetation, and invertebrates. Greater sandhill cranes generally forage within 2-5 km of their roosting areas (Ivey et al., 2015; Boggie et al., 2018) and are central-place foragers that gradually move farther from the roost as foraging resources are depleted over time (Ashmole, 1963; Pearse et al., 2010; Ivey et al., 2015).

Transmitter deployment and data processing

A total of 106 greater sandhill cranes were captured and fitted with global system for mobile communication (GSM) platform transmitter terminal (PTT) tags (n = 72; Evolution Series-400, 15-g; Cellular Tracking Technologies, Rio Grande, New Jersey, USA) or global positioning system (GPS) PTT tags (n = 34; PTT-100, 22-g Solar Argos/GPS PTT, Microwave Telemetry, Columbia, Maryland, USA). Most RMP cranes (n = 86) were captured in wintering areas in New Mexico and Arizona, but a few individuals were captured in Colorado (n = 3), Idaho (n = 14), and Montana (n = 3) during the summer. Details on the capture methods can be found in Collins et al. (2016), Boggie et al. (2018), and Hays et al. (2021).

Data were formatted to an individual's presence or absence in the SLV on each day of autumn or spring for a given year (2015-2022). The GSM/GPS units were programmed to acquire positions every 15 minutes, while the GPS units acquired positions at specified time intervals throughout the day. Because we were only interested in presence or absence in the SLV, the different fix rates and the exact location of fixes in the SLV did not influence formatting. We did not use individuals for which we had data for less than three days in the SLV. Based on the GSM/GPS data, we identified the spring season to be between 18 January and 9 May and the autumn season to be between 20 August and 13 December.

All appropriate banding permits were acquired from the U.S. Geological Survey (USGS) Bird Banding Laboratory, the U.S. Fish and Wildlife Service, and New Mexico Department of Game and Fish permits to band and attach transmitters to sandhill cranes.

Covariate development

Weather data

Local weather covariates were acquired from up to five weather stations in the SLV through the National Oceanic and Atmospheric Administration (NOAA, 2022). We averaged daily maximum temperature (C°) from all five weather stations and calculated a daily change in temperature, where zero indicated no change in temperature, a positive value indicated an increase in temperature, and a negative value indicated a decrease in temperature. All other temperature covariates (e.g., daily maximum temperature) were highly correlated ($r > 0.70$) with time of season, so we did not consider other temperature covariates. Local wind covariates were available for one weather station in the SLV. In addition to using wind speed (m/s), we calculated a tailwind variable (b) according to Åkesson and Hedenström (2000) and Arizaga et al. (2011),

$$b = V\cos\big(\alpha_T - (180° + \alpha_W)\big),$$

where V is the wind speed, α_T is the departure direction, and α_W is the wind direction (i.e., the direction from which the wind comes). The departure direction differed for each season and was based on the mean departure direction of RMP cranes in autumn and spring during the study period. We determined departure direction by examining the bearing between the location of the sandhill crane on the last day it was observed in the SLV and the following location outside the SLV. Mean departure direction was less variable in autumn ($\bar{x}$=190°, standard deviation=10.97°) than in spring ($\bar{x}$=285°, standard deviation=91.59°), but both seasons showed a normal distribution in the frequency of departure directions among individuals. Positive values of b

corresponded to a tailwind, while negative values corresponded to a headwind (Arizaga et al., 2011). We also considered the influence of crosswinds c, which we calculated as

$$c = V \sin(\alpha_T - \alpha_W),$$

where a positive value indicates an easterly crosswind and a negative value indicates a more westerly crosswind. Values at or close to zero indicate no or minimal crosswind. We also considered the absolute value of c, which represents the effect of crosswind without consideration to direction.

Other covariates were obtained from the National Centers for Environmental Prediction (NCEP) and Department of Energy (DOE) Reanalysis II dataset (Kanamitsu et al., 2002) using the RNCEP package in R (Kemp et al., 2012). The data are publicly available and cover a spatial resolution of 2.5 x 2.5° (i.e., approximately 220 km x 250 km) and temporal resolution of 6-h intervals. We downloaded *u* (east-west) and *v* (north-south) wind components and wind direction at the pressure levels of 600 and 700 hPa, which correspond to approximately 4,500 and 3,000 m above sea level, respectively. These are altitudes where cranes have been documented during migratory flights (Gerber et al., 2020). We calculated wind speed as $\sqrt{u^2 + v^2}$ and wind direction (in radians) as $\arctan(\frac{u}{v})$. We then calculated the same tailwind and crosswind variables as with the local weather variables. Finally, we also considered barometric air pressure (hPa) measured at the surface of the study area and the daily change in barometric air pressure.

Water data

We used spectral mixture analysis to measure daily surface water availability in the SLV for each year and season. Spectral mixture analysis is a process that utilizes remotely sensed images and determines the proportion of habitat classes within pixels using endmembers (Adams and Gillespie, 2006; Jin et al., 2017). Endmembers are areas representative of the habitat class of

interest and are static. We used Landsat 8 and Landsat 9 Operational Land Imager satellite imagery corrected for surface reflectance. The spatial resolution is 30 x 30 m, and images are acquired approximately every two weeks. Images were processed to remove clouds, shadow, and snow. Although we were only interested in surface water, spectral mixture analysis requires that all pixels be classified into proportional habitat classes. We chose the classes sandbar, soil, shrub, and vegetation along with water. Static images of sandbar, soil, and shrub were chosen based on examination of satellite imagery, focusing on areas where there was little change in these classes over the study period. Endmembers for water were acquired using the mean of the 98^{th} percentile of the Normalized Difference Water Index for each two-week period in every year and season (Boggie et al., 2018). We used a similar method for vegetation, which was estimated using the Normalized Difference Vegetation Index. Spectral mixture analysis was completed in Google Earth Engine (Gorelick et al., 2017). To get daily values of surface water, we used cubic interpolation using the "ss" function (Bunting et al., 2022; Helwig, 2022) in Program R (R Core Team, 2022).

Statistical analysis

We examined stopover decisions using the within-season component of a multistate open robust design mark-recapture model (Kendall et al., 2019). For each season this model allows for estimation of arrival and persistence probabilities, in addition to detection probability. We modeled autumn and spring separately, so each season was composed of a different number of secondary occasions, and for each we used year as a grouping variable. Each season consisted of a set of J total secondary occasions (i.e., days), where individual i was either detected or not detected on day j. The start and end of each autumn and spring depended on the first and last encounter of all RMP cranes among all years. These dates were buffered by two additional

occasions to improve estimation of arrival and persistence probabilities. The parameters included arrival probability (β_{ij}), detection probability (p_{ij}), and persistence probability (φ_{ij}) of individual i on day j.

We were also interested in three derived parameters. The average total stopover duration was calculated using Method 1 described in Kendall et al. (2019), applicable where the arrival of the first individual and the departure of the last individual is bounded by sampling effort. We determined the expected arrival and departure periods across all years. Finally, the intensity parameter α_{ij} is the probability that individual i is present in period j (Kendall et al. 2019).

We examined a different set of covariates for β_{ij} and φ_{ij}. We assumed β_{ij} would likely be driven by conditions at areas prior to sandhill crane arrival in the SLV, so we only considered the effects of time (linear and quadratic). The list of covariates we considered for φ_{ij} included a linear trend of time and time since arrival, total surface water availability, the daily change in the maximum temperature, wind speed (daily and a five-day rolling average), crosswind speed (daily and a five-day rolling average), and barometric air pressure (daily and the daily change). We considered wind speed at the surface and at barometric air pressures of 600 hPa and 700 hPa, corresponding to 4,500 and 3,000 m above sea level, respectively. We did not include covariates with a correlation coefficient > 0.40 in the same model, including covariates that were correlated with time, as we were interested in modeling the effect to time or time-since-arrival on φ_{ij}. We also examined one-way interactions between time or time-since-arrival and a time-varying weather covariate to determine if weather covariates were more influential later in the season. We did not consider more than a one-way interaction to maintain simplicity and to avoid overfitting. Fixes from GSM/GPS units are sometimes unsuccessful and therefore detection is not perfect but is reliably high, so we constrained p_{ij} to vary only by year (i.e., $p(year)$) to

allow for the reduced fix rate of the older GSM/GPS units and the greater potential for missing a signal from cranes during the day. All weather covariates and surface water were scaled to have a mean of zero.

Model selection for φ_{ij} was composed of four steps using a build-up strategy to identify the best-supported models (Morin et al., 2020). First, we determined the best time trend for both β_{ij} and φ_{ij} by comparing all possible combinations of time and time-since-arrival. Time-since-arrival is an important covariate to consider because the decision to migrate on a given day may depend more on the accumulated time on site of an individual, rather than the day of the season (Roques et al., 2022). This is particularly pertinent for spring, when stopovers are used to build up energy reserves needed for reproduction and completing migration for some migrant birds (Hedenström and Alerstam, 1997). We also examined models with a time trend across years for φ_{ij} to allow for a trend in environmental conditions not accounted for by our chosen predictor variables. We compared models using Akaike's Information Criterion corrected for small sample sizes (AIC_c), and the time model with the lowest AIC_c score was used in the next step (Akaike, 1973; Burnham and Anderson, 2002). Second, we compared a set of models each with the best time covariate (on φ_{ij}) and a single time-varying covariate. Covariates in the models that improved the fit of the time-only model were used in the next step, but we removed covariates that were highly (> 0.40) correlated with one another or time. We used the covariate that produced a lower AIC_c value unless it was correlated with time. Third, covariates in the most competitive models from the previous step were used to examine the interaction of time with a time-varying weather covariate and additive effects of the remaining covariates. These models were compared to one another, and we included interactions from the most competitive models in the next step. Finally, we examined all combinations of covariates, including both main effects

only and interactive models, and identified the most competitive models (<2 ΔAIC_c from the top model). To remove potentially uninformative covariates, we did not consider models competitive at this stage if they were nested versions of other competitive models (Arnold, 2010).

There is currently no way to assess goodness-of-fit of multistate open robust design models directly (Kendall et al. 2019), so we used the median $\hat{c}$ approach described by Cooch and White (2017) and recommended by Kendall et al. (2019). Estimating $\hat{c}$ can reveal the amount of overdispersion in a model due to more variance in the capture history than expected (Cooch and White, 2017). Conditioning on first detection within a season and using the Cormack-Jolly-Seber framework (CJS; Cormack, 1964; Seber, 1965), we examined models for autumn and spring separately with a time trend on φ_{ij} and with *p(year)*.

To examine the change in φ_{ij} in response to covariates, we used the most competitive models to predict φ_{ij} across the range of observed values for the covariate being examined while keeping the other values at their means. If we found the interaction of time or time-since-arrival with a weather covariate to be influential, we examined the effect of the covariate during three periods of the season: early (day 15), middle (half the season length), and late (day 100). We estimated variances using the delta method. All model building, comparison, goodness-of-fit assessment, and predictions were completed directly in Program MARK (White and Burnham, 1999) or through RMark (Laake, 2013; R Core Team, 2022).

RESULTS

We monitored a total of 106 unique individual sandhill cranes across all years (2015-2022) in spring and 55 unique individuals across all years in autumn (Table 1.1). Some individuals (n =36) were only monitored during the spring following their initial capture due to transmitter failure, loss, or crane death. A total of 10 individuals never used the SLV in autumn

throughout their monitoring periods, and five individuals were removed from the autumn season due to too few (i.e., <3) daily fixes in the SLV. Finally, of the 106 individuals, one in autumn and eight in spring were last detected in the SLV, which might indicate the GSM/GPS units stopped transmitting while the individuals were in the study area. We reran the most competitive model for each season and censored the days after the first day of no detection for these individuals to determine if results were biased. We found no substantial differences in coefficient estimates, so we kept all data for these individuals uncensored.

Weather patterns in the SLV during this time showed declining temperature in autumn and increasing temperature in spring (Table 1.2, Figure S1.1). Surface winds primarily came from the west and southwest in both seasons (Table 1.2, Figure S1.2). Wind speeds at higher altitudes were more northerly on average (Table 1.2, Figure S1.2). Tailwinds were variable for both seasons but were generally more favorable in autumn than in spring (Table 1.2, Figure S1.3). Barometric air pressure was variable in both seasons and showed a slight positive trend in autumn (Table 1.2, Figure S1.4). Surface water declined throughout autumn and increased throughout spring on average (Table 1.2, Figure S1.5).

For the autumn CJS model, we estimated a $\hat{c}$ of 1.41 (95% CI -0.45, 3.27), so we used the quasi-likelihood adjusted AIC_c ($QAIC_c$) to compare autumn models (Burnham and Anderson, 2002). A value of $1 > \hat{c} < 3$ is likely due to overdispersion, rather than a lack of model fit (Lebreton et al., 1992). We did not detect overdispersion in the spring models and used AIC_c for model comparison. Models for β_{ij} in both seasons included a quadratic time trend. Based on the most competitive models, the probability of arriving in the SLV throughout the season peaked on 13 October in autumn and 21 February in spring (Figure 1.2). The value of φ_{ij} remained close to one for much of autumn and showed its greatest decrease around 12 December (Figure 1.3). The

value of φ_{ij} was also high at the beginning of the spring season but declined in mid-March (Figure 1.3). The average expected departure date varied across years in both seasons (Table 1.3). Autumn stopover duration was generally greater and more variable among years than spring stopover duration (Figure 1.4). The derived values of α_j indicated that the probability of presence peaked around 6 November in autumn and 6 March in spring (Figure 1.5).

The model with a time trend over years did not improve model fit for either the time-only models or the top model with covariates. There were small apparent trends in each season, negative for autumn and positive for spring (Table S1.1), but the 95% confidence intervals overlapped zero for both seasons.

The most competitive model for φ_{ij} in autumn included tailwind, crosswinds at 700 hPa, and surface water (Table 1.4). Several models with an interaction between time and temperature change or tailwind were also competitive. Surface water was included in all competitive models. The effect of tailwind indicated that RMP sandhill cranes were more likely to depart the SLV in autumn with greater tailwinds (Figure 1.6, Figure 1.7). The effect of crosswinds at 700 hPa showed that as winds became more easterly and perpendicular to the migratory direction, RMP sandhill cranes were more likely to remain in the SLV. The opposite was true as surface water increased, with RMP sandhill cranes less likely to stay as surface water increased.

The most competitive model for φ_{ij} in spring included barometric air pressure, crosswinds, and an interaction between time and wind speed at 700 hPa, but several other models were competitive (Table 1.4). Models with an interaction between time and crosswinds at 700 hPa were among the competitive models, as were models with main effects of temperature change and surface water. The most competitive model indicated that as the spring season progressed, the effect of wind speed at 700 hPa on φ_{ij} became stronger and RMP sandhill cranes

were less likely to remain in the SLV with strong wind speeds at 700 hPa (Figure 1.8). As local winds became more easterly and perpendicular to the preferred migratory direction (i.e., crosswinds), RMP sandhill cranes were more likely to remain in the SLV, while they were less likely to remain when barometric air pressure increased (Figure 1.9).

DISCUSSION

Patterns of sandhill crane phenology in the SLV during the spring and autumn of 2015-2022 confirmed our hypotheses that there was greater variability in the stopover patterns of RMP sandhill cranes in autumn than in spring and that autumn stopover duration was longer than spring stopover duration. Several of our hypotheses concerning the influence of weather covariates on persistence probability were confirmed, including the negative influence of tailwinds in autumn, the positive effect of barometric air pressure in spring, and the positive effects of wind speed and crosswinds in spring. In contrast to our expectation, surface water area had a negative influence on persistence probability in autumn and the daily change in temperature had no effect in either season. Our study provides information on migration phenology in the SLV and highlights the potential impacts of weather and habitat on the stopover ecology of RMP sandhill cranes.

Estimates of arrival and persistence probabilities provide support that RMP sandhill cranes in the SLV might prioritize minimizing time during spring migration when compared to autumn, which is consistent with findings from other studies of migrating birds in both spring and autumn (Mellone et al., 2012; Nilsson et al., 2013; Illan et al., 2017). The arrival day of RMP sandhill cranes in the SLV showed a quadratic pattern in both seasons, with greater within-year variability in autumn compared to spring. The RMP sandhill cranes also demonstrated a longer duration of high persistence probability and an overall greater stopover duration in autumn than

in spring. Other migratory populations of cranes, including sandhill cranes (Krapu et al., 2014; Fronczak et al., 2017; Donnelly et al., 2021) and whooping cranes (*Grus americana*; Pearse et al., 2020), also show greater variability in arrival and departure dates and longer stopover durations in autumn compared to spring. The higher variation in autumn compared to spring is likely due to several individual-specific intrinsic factors that we could not measure, such as experience and reproductive status. For example, during southbound autumn migration, adult RMP sandhill cranes that have successfully bred may be accompanied by 1-2 young, and these family units may depart breeding or stopover areas later than nonbreeding adults (Carlisle and Tacha, 1983; Tacha et al., 1985; Pearse et al., 2020). The timing of migration in spring is likely more related to the benefits of optimal arrival to the breeding grounds. Consistency in arrival to the breeding grounds, which is mediated by stopover duration in spring, can allow birds to arrive at a time that provides the best resources for egg-laying and raising young (Kokko, 1999; Both et al., 2004). Donnelly et al. (2021) estimated that total migration duration for RMP sandhill cranes is approximately 35 days in spring and 60 days in autumn. Our results indicate that RMP sandhill cranes spend most of their migration period in the SLV in both seasons, so conditions within the SLV are likely the main determinants of total migration duration for RMP sandhill cranes.

Identifying the peak of arrival probability, the change in persistence probability, and the length of stopover duration may ultimately be useful for focusing research, monitoring, and management efforts in both seasons. Annual productivity surveys in autumn provide information for hunting regulations of RMP sandhill cranes (Seamans, 2022), and productivity surveys are conducted when it is thought that the greatest proportion of RMP sandhill cranes are in the SLV (Collins and Vanausdall, 2023). Current monitoring efforts of the RMP align well with our findings, which suggested that the optimal timing for annual surveys is early to mid-October for

autumn and late-February to early March for spring when both the entry and persistence probabilities are relatively high. It will be important to continue to monitor potential changes in migration timing. Additional research on arrival and departure dates for other stopover areas may also be informative for annual autumn population surveys conducted to estimate the abundance of RMP sandhill cranes (Bunting et al., 2022).

Weather factors played an important role in the persistence probability of RMP sandhill cranes and were mostly consistent with our hypotheses. The importance of wind components may provide some evidence that RMP sandhill cranes prioritize energy maximization in both seasons but particularly autumn. Tailwind had a negative effect on persistence probability in autumn, while crosswinds at 700 hPa, equivalent to about 3,000 m in altitude, had a positive effect. Supportive winds can reduce the energetic costs of flight (Cooper et al., 2023), particularly for a large bird like a sandhill crane (Hedenström, 1993; Weber et al., 1998), as the cost of flapping flight increases with increasing body mass (Peters, 1986). Other studies have shown that tailwinds have a negative effect on persistence probability of migrating passerines (Schaub et al., 2004; Roques et al., 2022) and soaring raptors (Mellone et al., 2012; Limiñana et al., 2013). However, we did not find tailwinds at any altitude to be important for the spring season, which was inconsistent with our hypothesis. This could be due to the fact that winds at higher altitudes primarily come from the north, reducing the frequency of days with tailwinds (Supplementary Fig. 2). Because RMP sandhill cranes must fly over or bypass a mountain range, winds at higher altitudes are likely more important than at the surface. We found that crosswind at the surface and wind speed at 700 hPa had a positive effect on persistence in spring, with some evidence of a stronger wind speed effect later in the season. Other studies have found wind speed or wind support at higher altitudes to influence departure (Mateos-Rodríguez and Liechti, 2011;

Carneiro et al., 2020). Cranes use a mix of flapping powered and soaring flight and will take advantage of thermals to gain altitude and glide (Pennycuick et al., 1979; Galtbalt et al., 2022). Sandhill cranes in the SLV have been observed using thermals, and high wind speeds from the opposite direction at high altitudes are likely not favorable for northward migration.

The finding that barometric air pressure also had a negative influence on persistence probability provides evidence that ideal weather and/or soaring conditions might be important for spring departure, but this may require further validation. The influence or correlation of barometric air pressure with persistence has been documented in studies of both small and large migrants (Shamoun-Baranes et al., 2006; Sapir et al., 2011; Cooper et al., 2023), including other crane species (Pennycuick et al., 1979; Alonso et al., 1990a, 1990b). Increasing barometric air pressure is generally associated with calm, fair weather conditions with light winds. Studies have found spring migrants depart or increase migration intensity during high pressure conditions (Richardson, 1978, 1990; Maransky et al., 1997), as these conditions might be suitable for northbound migration and potentially provide better conditions for thermal uplift. There is also evidence that birds can detect changes in barometric air pressure (Kreithen and Keeton, 1974), an ability that might allow for maintaining a certain altitude during migration or detection of conditions favorable for migration.

The effect of surface water did not appear to be more important than time and weather covariates on persistence probability, but water is still a critical component to consider given its role in sandhill crane roosting and foraging (Boggie et al. 2018, Donnelly et al. 2021). We had hypothesized that surface water would have little to no effect on spring persistence and have a positive influence on persistence in autumn, as more surface water means more roosting potential. Our findings were consistent with our hypothesis in spring, but we found a negative

influence on persistence in autumn. Sandhill cranes typically choose roosting sites in areas with shallow water (Pearse et al., 2017; Boggie et al., 2018), and the proximity of foraging areas near roost sites tends to determine the distribution of sandhill cranes (Krapu et al., 1984; Sparling and Krapu, 1994). A negative effect of surface water on persistence in autumn could indicate that the water available is not ideal for roosting or foraging (e.g., too deep). It is also possible that with enough water, RMP sandhill cranes can acquire energetic requirements more efficiently and depart sooner. However, we acknowledge that our estimates of water were spatially and temporally coarse. Surface water is dynamic throughout spring and autumn in the SLV (Wetland Dynamics, 2019). Our seasonal estimates may not have been able to capture effects on persistence within seasons, such as late autumn, which may have a greater influence on persistence probability than total surface water throughout the season. The impact of water on RMP sandhill cranes will be important to investigate further, as water is an increasingly limited resource in the SLV and other parts of the Intermountain West due to over-allocation for irrigation and the effects of climate change (Ray et al., 2008; Mix et al., 2011). Our results provide information on when water can be distributed on the landscape for RMP sandhill cranes, particularly on public areas that are managed for waterbirds. Allocating water when the probability of arrival is high and persistence probability has not greatly declined will allow managers to use a depleting resource more efficiently throughout both seasons.

The finding that persistence is partially linked to weather and environmental covariates indicates that shifts in these cue values may alter migratory behavior and/or generate phenological mismatches if RMP sandhill cranes are unable to adapt or show plasticity when responding to climate and landscape changes (Visser et al., 2012; Visser and Gienapp, 2019). There is already documentation of weather and environmental covariates shifting in the western

United States (Llewellyn and Vaddey, 2013; Dettinger et al., 2015). Reduced streamflow and earlier spring snowmelt have been documented in mountainous areas due to increasing temperatures (Barnett et al., 2008; Dettinger et al., 2015; Elias et al., 2015), and temperatures are projected to continue to increase within the coming decades (Ray et al., 2008; Llewellyn and Vaddey, 2013). Mix et al. (2011) also reported evidence of increasing temperatures in the SLV in the last century, and Donnelly et al. (2021) showed a decline in surface water throughout the region. Furthermore, other weather covariates, including wind speed and precipitation, are projected to shift under climate change (Liu et al., 2013; La Sorte et al., 2019), which could influence migratory decisions of RMP sandhill cranes. On the one hand, a mistiming in the response to an environmental or climatic cue that initiates a migratory behavior and results in arriving at a destination when conditions are suboptimal may lead to reduced fitness potential and, in some cases, population decline (Both et al., 2006; Møller et al., 2008; Visser et al., 2012; Visser and Gienapp, 2019). On the other hand, there is evidence that species and populations that are more rapidly able to respond to climatic and environmental variation (i.e., show phenotypic plasticity) are less threatened by climate change and demonstrate a lower rate of decline (Møller et al., 2008). For example, while cranes and other long-lived, gregarious birds show evidence of a genetic component to migration, the experience of older individuals seems to play an important role and may allow these groups to respond to changing environmental conditions over time (Chernetsov et al., 2004; Mueller et al., 2013; Teitelbaum et al., 2016). However, a population-level shift in migratory performance or behavior may take years in long-lived birds (Mueller et al. 2013), making such species still susceptible to phenological mismatches. An analysis of migratory and movement decisions throughout the full annual cycle of RMP sandhill cranes

could provide more insight into the potential impacts of climate and land use change on this population.

There are other important factors that may influence the stopover decisions of migrating birds that we did not address, including waste grain availability, the accumulation of energy reserves at stopover areas, and the sex, age, or experience of individuals. Previous work on other migratory species has suggested that birds may delay the initiation of migration and remain at wintering or stopover areas longer if adequate resources are available and environmental conditions are favorable (Schummer et al. 2010, Thurber et al. 2020, Cox et al. 2023). Because waste grain is an important component of the diet of RMP sandhill cranes in the SLV, it is possible that the amount and distribution of grain may influence their stopover decisions. Indeed, other species of cranes have shown evidence of shifting their winter distributions and migratory timing in response to climate and availability of agricultural foods (Alonso et al. 2008, Jorgensen and Brown 2017). However, we were not able to assess waste grain availability throughout the SLV and estimates of grain planted would be an overestimate, but future work could consider its role in stopover decisions. Additionally, evidence from earlier studies suggests that cranes vary in their stopover decisions as they age and gain more experience (Mueller et al., 2013; Teitelbaum et al., 2016; Abrahms et al., 2021). Family groups may behave differently at stopover areas than adults without young (Gerber et al., 2020). While males are typically larger than females, there can be some overlap (Krapu et al., 1985; Gerber et al., 2020), so we were not able to sex all individuals or confidently identify family groups. Our analysis was also limited to adult individuals, and we were not able to determine body condition throughout migration. The rate of fuel deposition can be a major determinant in the timing of departure for migrant birds, particularly for those prioritizing time over energy (Alerstam and Lindström, 1990; Lindström,

1991; Hedenström and Alerstam, 1997). Departure probability has been found to be related to increasing lipid levels or body condition in other migrant birds (Pearse et al., 2011; Anderson et al., 2019; Vanausdall and Dinsmore, 2021). Given that sandhill cranes are rapidly depositing fat during spring migration in other populations at key stopover areas (Krapu et al., 1985, 2014; Fronczak et al., 2017), examining the influence of body condition on departure decisions of RMP sandhill cranes could be valuable.

TABLES AND FIGURES

Table 1.1: The number of sandhill cranes that were captured and tagged during the winter season and the number migrating through the San Luis Valley, Colorado the following spring and autumn. Captures of RMP sandhill cranes began in the winter of 2014-2015.

Year	Captured and tagged	Present in autumn	Present in spring
2014	27	-	-
2015	5	11	28
2016	2	13	22
2017	2	10	16
2018	18	9	16
2019	31	15	12
2020	24	27	47
2021	2	18	57
2022	-	11	31

Table 1.2: Mean (with standard error) values for weather covariates in the San Luis Valley, Colorado.

Year	Temperature change	Air pressure (hPa)	Daily air pressure change	Wind speed (m/s)	Wind speed 600 mb (m/s)	Wind speed 700 mb (m/s)	Crosswind	Crosswind 600 mb	Crosswind 700 mb	Tailwind	Tailwind 600 mb	Tailwind 700 mb	Surface water (ha)
						Autumn							
2015	-0.37	774.02	8.62	8.74	9.94	7.98	-1.43	-1.17	-0.14	-3.05	6.24	4.70	13413.12
	(0.33)	(0.45)	(34.54)	(0.33)	(0.51)	(0.38)	(0.51)	(0.71)	(0.6)	(0.64)	(0.51)	(0.39)	(558.51)
2016	-0.23	775.19	1.08	8.69	9.81	7.84	-2.43	-0.22	0.73	-2.42	7.16	5.44	12621.76
	(0.33)	(0.48)	(53.49)	(0.34)	(0.53)	(0.39)	(0.58)	(0.55)	(0.49)	(0.58)	(0.61)	(0.43)	(428.24)
2017	-0.26	775.14	1.16	9.9	11.54	8.71	-2.49	-2.66	-1.12	-2.93	7.54	5.7	18929.39
	(0.41)	(0.42)	(41.5)	(0.37)	(0.55)	(0.45)	(0.67)	(0.72)	(0.58)	(0.64)	(0.62)	(0.49)	(611.08)
2018	-0.28	774.00	-0.04	8.72	9.82	7.93	-2.67	-2.43	-1.22	-1.82	6.41	4.77	8162.03
	(0.40)	(0.40)	(37.57)	(0.34)	(0.43)	(0.38)	(0.56)	(0.61)	(0.57)	(0.61)	(0.49)	(0.39)	(341.89)
2019	-0.36	773.66	-7.56	8.62	11.31	8.31	-2.27	-2.07	-0.85	-2.62	8.16	5.73	13885.72
	(0.41)	(0.44)	(49.95)	(0.35)	(0.51)	(0.4)	(0.54)	(0.73)	(0.59)	(0.62)	(0.48)	(0.35)	(447.88)
2020	-0.53	775.29	13.1	8.11	10.35	7.68	-1.64	-3.20	-1.85	-1.74	6.30	4.13	8458.8
	(0.56)	(0.43)	(46.26)	(0.35)	(0.59)	(0.45)	(0.55)	(0.63)	(0.51)	(0.59)	(0.67)	(0.53)	(90.25)
2021	-0.33	774.76	16.96	8.08	10.06	7.95	-1.95	-2.49	-1.28	-2.75	6.94	5.33	12238.18
	(0.39)	(0.40)	(47.24)	(0.32)	(0.51)	(0.4)	(0.5)	(0.65)	(0.55)	(0.57)	(0.5)	(0.38)	(420.8)
2022	-0.33	774.35	-0.39	8.69	9.41	7.06	-1.19	-1.04	0.28	-2.06	5.59	4.02	5837.60
	(0.43)	(0.49)	(40.19)	(0.33)	(0.57)	(0.44)	(0.61)	(0.59)	(0.49)	(0.59)	(0.69)	(0.49)	(216.10)
						Spring							
2015	0.23	772.32	6.50	9.21	10.77	8.02	-1.81	6.28	3.98	-1.64	-3.62	-2.32	13413.12
	(0.50)	(0.38)	(43.93)	(0.38)	(0.47)	(0.38)	(0.65)	(0.56)	(0.49)	(0.66)	(0.70)	(0.54)	(558.51)
2016	0.27	771.71	-21.52	9.57	12.21	9.91	-2.26	6.91	5.07	-3.73	-5.50	-4.18	12621.76
	(0.54)	(0.45)	(49.53)	(0.41)	(0.51)	(0.42)	(0.69)	(0.57)	(0.49)	(0.58)	(0.76)	(0.66)	(428.24)
2017	0.30	770.36	3.86	9.74	13.03	10.21	-3.01	9.00	6.45	-3.53	-3.18	-1.99	18929.39
	(0.50)	(0.51)	(49.35)	(0.37)	(0.49)	(0.4)	(0.68)	(0.70)	(0.58)	(0.58)	(0.67)	(0.59)	(611.08)
2018	0.42	770.8	-13.46	11.19	13.89	10.33	-3.78	10.47	7.15	-5.43	-3.29	-2.11	8162.03
	(0.54)	(0.44)	(48.24)	(0.4)	(0.44)	(0.41)	(0.8)	(0.53)	(0.42)	(0.5)	(0.75)	(0.67)	(341.89)
2019	0.27	769.53	4.98	10.54	12.82	10.00	-3.52	9.35	6.50	-3.87	-3.57	-2.23	13885.72
	(0.50)	(0.46)	(47.76)	(0.39)	(0.5)	(0.42)	(0.71)	(0.58)	(0.50)	(0.63)	(0.7)	(0.64)	(447.88)
2020	0.34	771.33	14.78	10.26	12.49	8.89	-3.5	9.02	5.60	-4.62	-4.09	-2.95	8458.8
	(0.41)	(0.41)	(44.52)	(0.34)	(0.41)	(0.35)	(0.7)	(0.49)	(0.39)	(0.52)	(0.67)	(0.56)	(90.25)
2021	0.23	769.50	1.58	10.54	11.93	9.01	-3.24	8.51	5.50	-3.47	-3.06	-1.99	12238.18
	(0.57)	(0.48)	(49.74)	(0.39)	(0.48)	(0.39)	(0.7)	(0.59)	(0.52)	(0.67)	(0.65)	(0.55)	(420.8)
2022	0.24	770.3	-11.41	10.54	12.05	9.30	-2.82	7.76	4.9	-4.23	-4.16	-3.48	5837.60
	(0.55)	(0.47)	(51.32)	(0.42)	(0.46)	(0.39)	(0.76)	(0.6)	(0.50)	(0.6)	(0.68)	(0.6)	(216.10)

Table 1.3: Mean expected departure date (± days) derived from the multistate open robust design model for Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado.

Year	Expected departure date (± days)	
	Autumn	Spring
2015	11 Nov (± 2.58)	18 Mar (± 1.87)
2016	18 Nov (± 2.00)	22 Mar (± 1.89)
2017	15 Nov (± 3.01)	20 Mar (± 1.83)
2018	7 Nov (± 2.29)	21 Mar (± 1.70)
2019	9 Nov (± 2.73)	20 Mar (± 1.39)
2020	8 Nov (± 3.58)	18 Mar (± 1.78)
2021	12 Nov (± 2.71)	21 Mar (± 1.64)
2022	14 Nov (± 2.70)	22 Mar (± 1.97)

Table 1.4: Model selection results with the number of parameters (K), $\Delta QAIC_c$ (autumn models) or ΔAIC_c (spring models), model weights, and the negative log likelihood for the effects of weather covariates and surface water on persistence probability (φ) of sandhill cranes in the San Luis Valley, Colorado, 2015-2022.

Models (φ)	K	$\Delta QAIC_c$ /ΔAIC_c	$\Delta QAIC_c$ /ΔAIC_c weight	-LogLik
Autumn				
time + tailwind + crosswind (700 hPa) + water	11	0.00	0.15	2259.73
time*temperature change + tailwind + crosswind (700 mb) + water	13	0.50	0.12	2254.78
time*crosswind (700 hPa) + tailwind + temperature change + water	13	0.75	0.10	2255.14
time*tailwind + crosswind (700 hPa) + water	12	0.95	0.09	2258.24
time + tailwind + crosswind (700 hPa) + wind speed (700 mb) + water	13	1.05	0.09	2255.56
time*crosswind (700 hPa) + tailwind + water	12	1.67	0.07	2259.25
time*tailwind + crosswind (700 hPa) + temperature change + wind speed at (700 hPa) + water	14	1.86	0.06	2253.87
time + tailwind + crosswind (700 hPa) + wind speed (700 mb) + water	12	1.99	0.06	2259.69
Spring				
time*wind speed (700 hPa) + crosswind + air pressure	13	0.00	0.09	4185.893
time + wind speed (700 hPa) + crosswind + air pressure	12	0.40	0.07	4188.297
time*crosswind + air pressure	12	0.46	0.07	4188.365
time*crosswind + wind speed (700 hPa) + crosswind (600 hPa) + air pressure	14	0.95	0.05	4184.834
time*crosswind + wind speed (700 hPa) + air pressure + water	14	1.17	0.05	4185.059
time*wind speed (700 hPa) + crosswind + crosswind (600 hPa) + air pressure + temperature change	15	1.52	0.04	4183.395
time*crosswind + crosswind (600 mb) + wind speed (700 mb) + air pressure + temperature change	14	1.61	0.04	4185.496
time*wind speed (700 hPa) + crosswind (600 hPa) + crosswind + air pressure	14	1.80	0.04	4185.688
time*wind speed (700 hPa) + crosswind + air pressure + water	14	1.81	0.04	4185.7
time + crosswind + air pressure	11	1.94	0.03	4191.843

Models (φ)	K	$\Delta QAIC_c$ /ΔAIC_c	$\Delta QAIC_c$ /ΔAIC_c weight	-LogLik
time + wind speed (700 hPa) + crosswind + temperature change + water	14	1.94	0.03	4185.822
time + wind speed (700 hPa) + crosswind (600 hPa) + crosswind + air pressure	13	2.09	0.03	4187.987
time*crosswind + air pressure + water	13	2.10	0.03	4187.995
time + wind speed (700 hPa) + crosswind + air pressure + water	13	2.16	0.03	4188.054
time*crosswind + wind speed (700 hPa) + crosswind (600 hPa) + temperature change + air pressure + water	16	2.25	0.03	4182.118
time + crosswind + crosswind (600 hPa) + air pressure + temperature change	13	2.28	0.03	4188.172
time*crosswind + crosswind (600 hPa) + air pressure + temperature change + water	15	2.33	0.03	4184.207

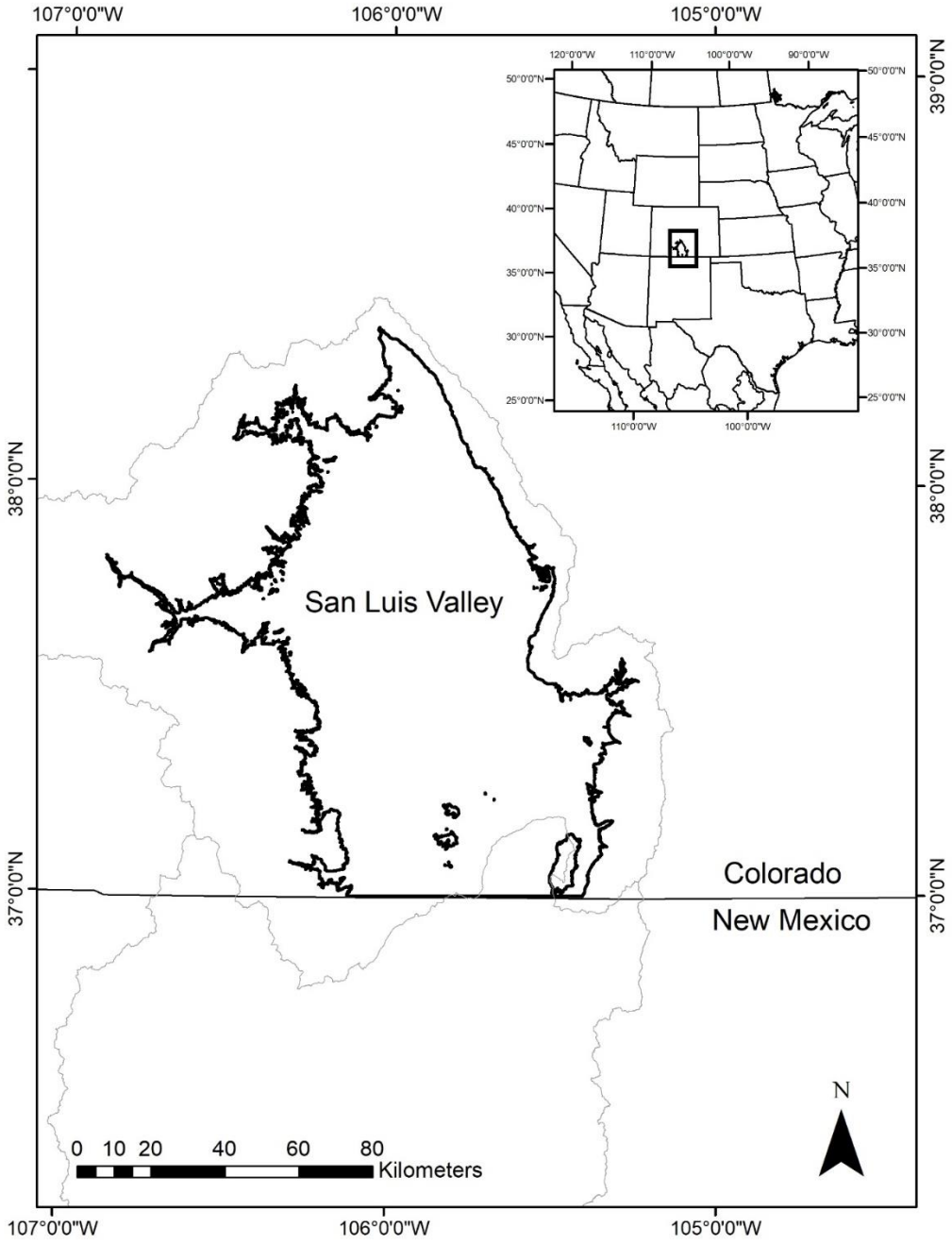

Figure 1.1: A map showing the location of the San Luis Valley, Colorado. The light gray lines indicate the boundaries of the Upper and Middle Rio Grande Basin.

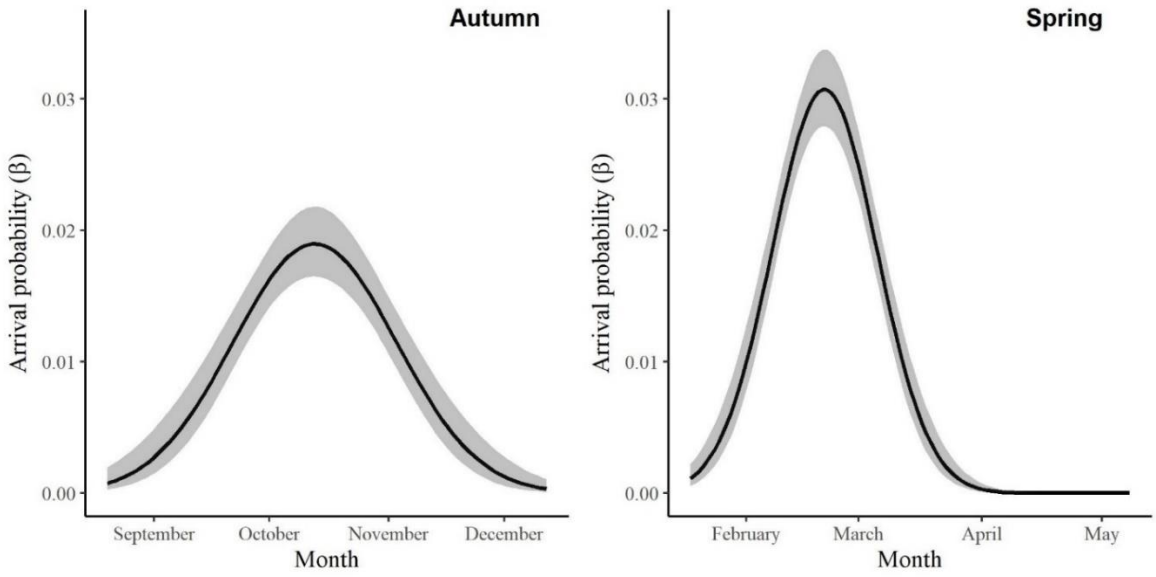

Figure 1.2: The change in the arrival probability (β) of migrating Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado, 2015-2022 in autumn and spring.

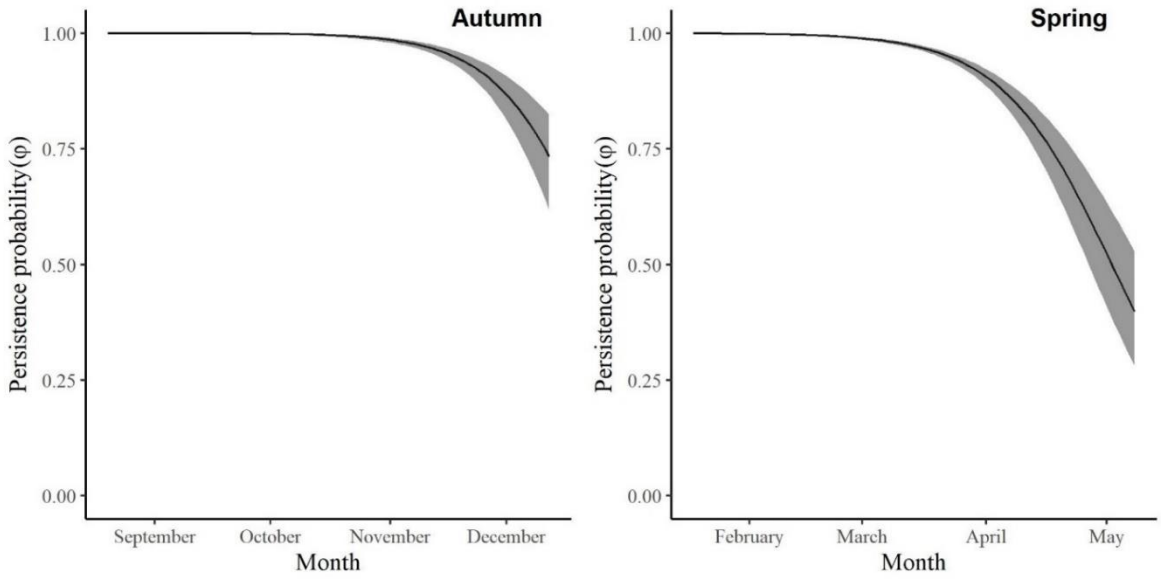

Figure 1.3: The change in the persistence probability (φ) of migrating Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado, 2015-2022 in autumn and spring.

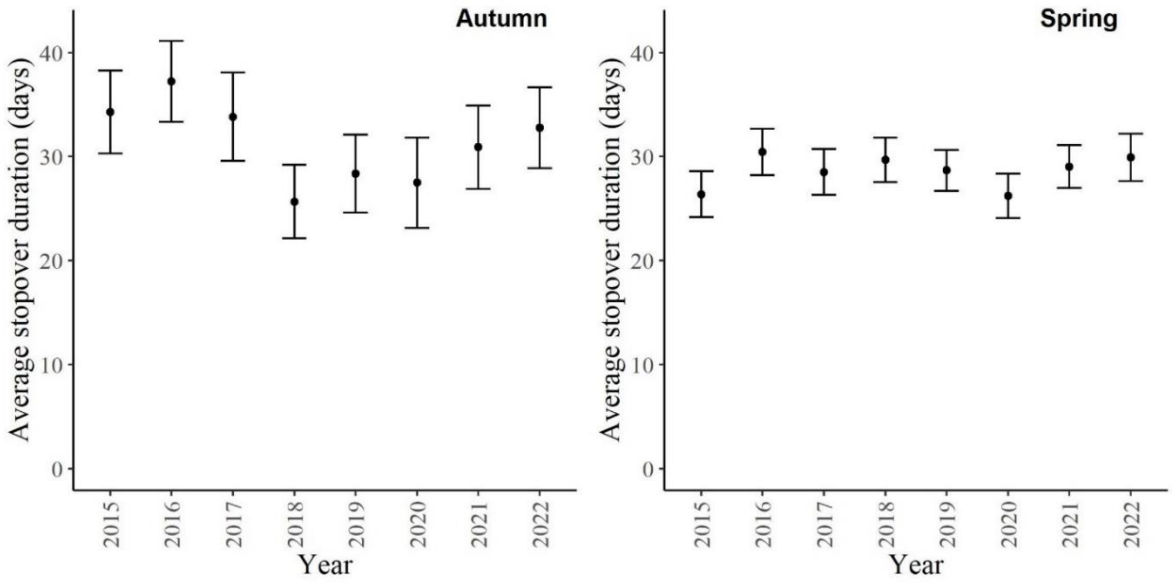

Figure 1.4: The stopover duration of migrating Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado, 2015-2022 in autumn and spring. The black bars are 95% confidence intervals.

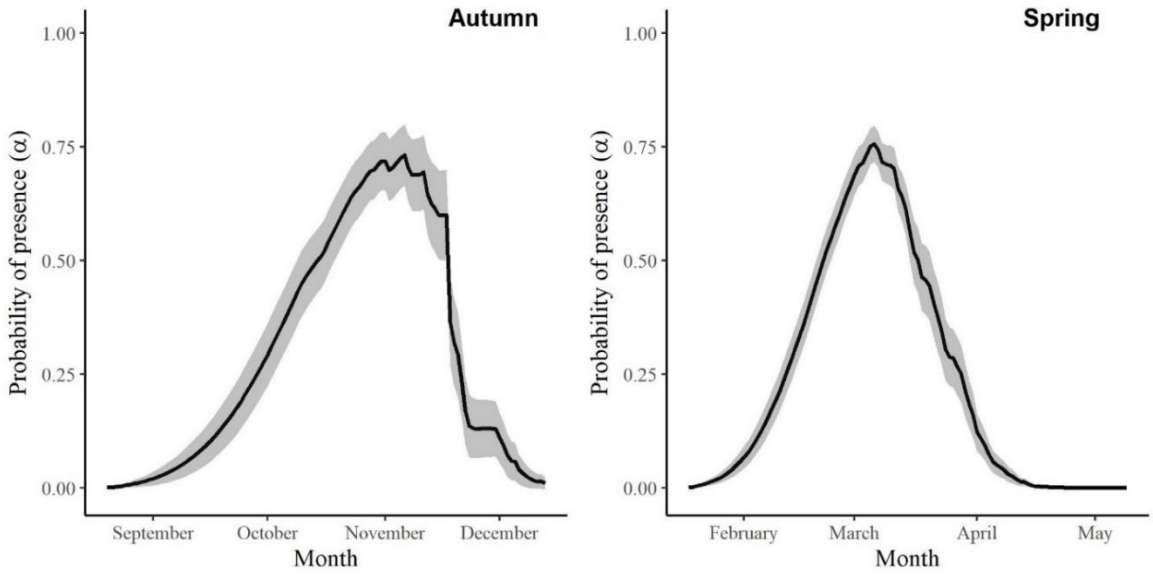

Figure 1.5: The probability of presence (α) of Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado, 2015-2022 in autumn and spring. The shaded area represents 95% confidence intervals.

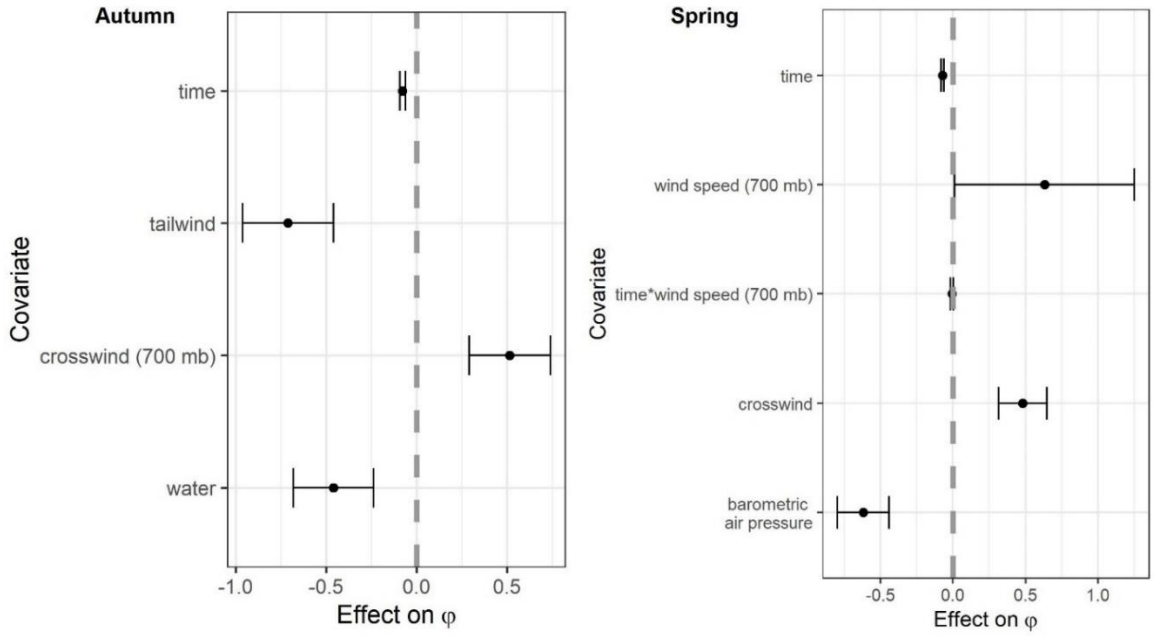

Figure 1.6: Coefficient estimates in the top models examining the effects of weather and habitat covariates on the probability of persistence (φ) of migrating Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado, 2015-2022 in autumn and spring. Covariates were standardized to have a mean of zero. The black bars are 95% confidence intervals.

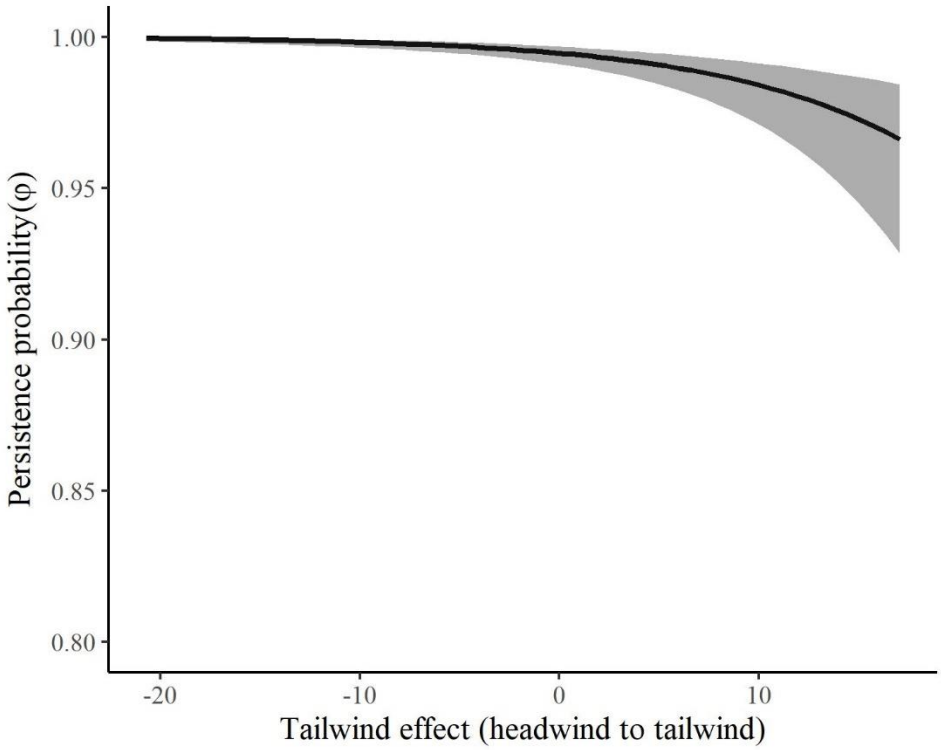

Figure 1.7: The effect of tailwinds on the persistence probability (φ) of migrating Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado, 2015-2022 in autumn. The shaded area represents 95% confidence intervals.

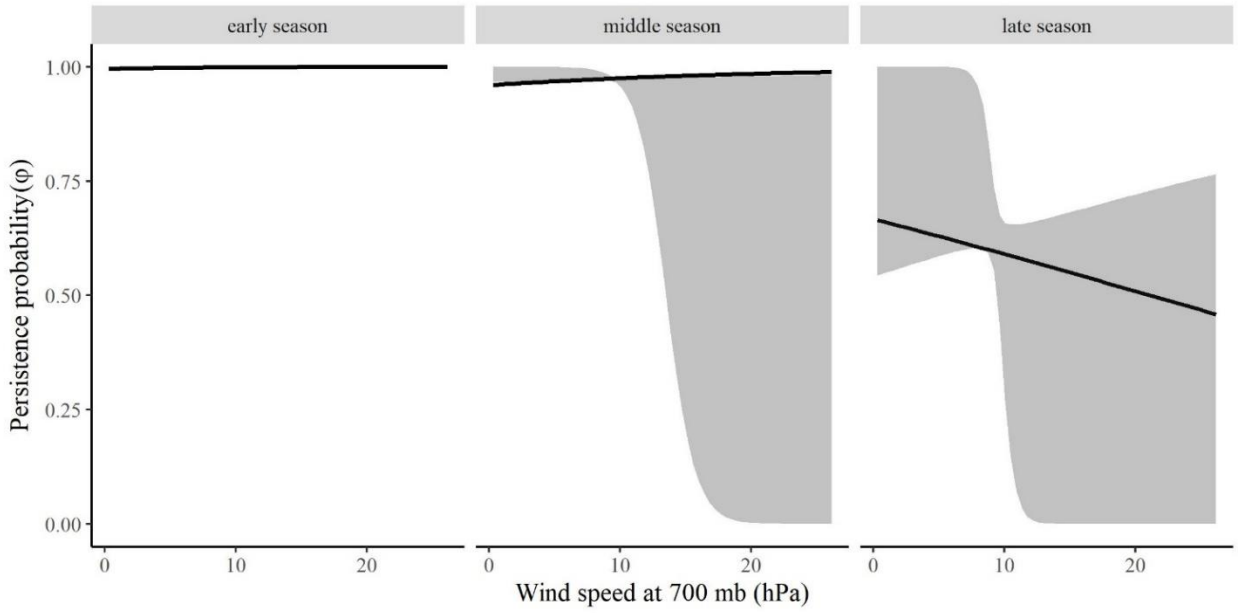

Figure 1.8: The effect of surface wind speed on the persistence probability (φ) of migrating Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado, 2015-2022 during early (1 February), middle (13 March), and late (27 April) spring. The shaded area represents 95% confidence intervals.

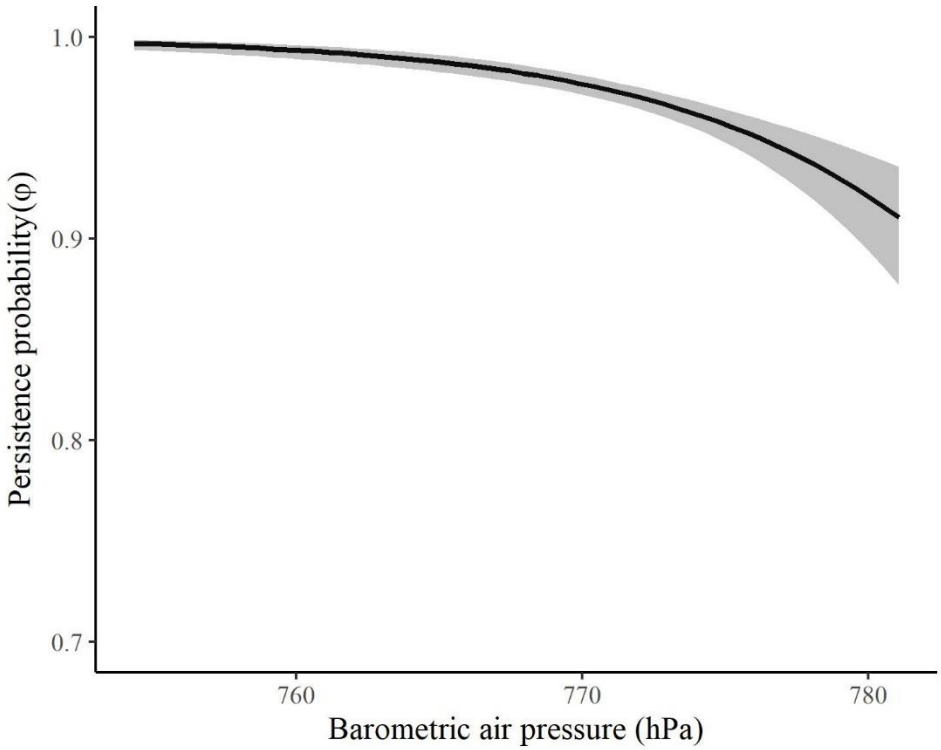

Figure 1.9: The effect of barometric air pressure on the persistence probability (φ) of migrating Rocky Mountain Population greater sandhill cranes in the San Luis Valley, Colorado, 2015-2022 in spring. The shaded area represents 95% confidence intervals.

LITERATURE CITED

Abrahms, B., Teitelbaum, C. S., Mueller, T., and Converse, S. J. (2021). Ontogenetic shifts from social to experiential learning drive avian migration timing. *Nat. Commun.* 12. doi: 10.1038/s41467-021-27626-5.

Adams, J. B., and Gillespie, A. R. (2006). *Remote Sensing of Landscapes with Spectral Images*. Cambridge: Cambridge University Press.

Ahrens, C. D. (2013). *Meteorology Today: An Introduction to Weather, Climate, and the Environment*. 10th ed. Belmont, CA: Brooks/Cole.

Akaike, H. (1973). "Information theory and an extension of the maximum likelihood principle," in *2nd International Symposium on Information Theory*, eds. B. N. Petran and F. Csaki (Budapest, Hungary: Akadémiai Kiadó), 276–281.

Åkesson, S., and Hedenström, A. (2000). Wind selectivity of migratory flight departures in birds. *Behav. Ecol. Sociobiol.* 47, 140–144.

Åkesson, S., and Hedenström, A. (2007). How migrants get there: migratory performance and orientation. *BioScience* 57, 123–133.

Åkesson, S., and Helm, B. (2020). Endogenous programs and flexibility in bird migration. *Front. Ecol. Evol.* 8. doi: 10.3389/fevo.2020.00078.

Alerstam, T. (2011). Optimal bird migration revisited. *J. Ornithol.* 152, S5–S23. doi: 10.1007/s10336-011-0694-1.

Alerstam, T., and Hedenström, A. (1998). The development of bird migration theory. *J. Avian Biol.* 29, 343–369.

Alerstam, T., and Lindström, A. (1990). "Optimal bird migration: the relative importance of time, energy, and safety," in *Bird Migration: Physiology and Ecophysiology*, ed. E. Gwinner (Springer-Verlag), 331–351.

Alisauskas, R. T. (2002). Arctic climate, spring nutrition, and recruitment in Midcontinent lesser snow geese. *J. Wildl. Manag.* 66, 181–193.

Alonso, J. A., Alonso, J. C., Cantos, F. J., and Bautista, L. M. (1990a). Spring crane *Grus grus* migration through Gallocanta, Spain: II. Timing and pattern of daily departures. *Ardea* 78, 379–388.

Alonso, J. C., Alonso, J. A., Cantos, F. J., and Bautista, L. M. (1990b). Spring crane *Grus grus* migration through Gallocanta, Spain: I. Daily variations in migration volume. *Ardea* 78, 365–378.

Alonso, J. A., Alonso, J. C., and Nowald, G. (2008). Migration and wintering patterns of a central European population of common cranes *Grus grus. Bird Study* 55, 1-7. doi: 10.1080/00063650809461499.

Ambrosini, R., Rubolini, D., Møller, A. P., Bani, L., Clark, J., Karcza, Z., et al. (2011). Climate change and the long-term northward shift in the African wintering range of the barn swallow Hirundo rustica. *Clim. Res.* 49, 131–141. doi: 10.3354/cr01025.

Anderson, A. M., Duijns, S., Smith, P. A., Friis, C., and Nol, E. (2019). Migration distance and body condition influence shorebird migration strategies and stopover decisions during southbound migration. *Front. Ecol. Evol.* 7. doi: 10.3389/fevo.2019.00251.

Ankney, C. D., and MacInnes, C. D. (1978). Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95, 459–471.

Arizaga, J., Belda, E. J., and Barba, E. (2011). Effect of fuel load, date, rain and wind on departure decisions of a migratory passerine. *J. Ornithol.* 152, 991–999. doi: 10.1007/s10336-011-0685-2.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manag.* 74, 1175–1178. doi: 10.2193/2009-367.

Ashmole, N. P. (1963). The regulation of numbers of tropical oceanic birds. *Ibis* 103b, 458–473.

Barnett, T. P., Pierce, D. W., Hidalgo, H. G., Bonfils, C., Santer, B. D., Das, T., et al. (2008). Human-induced changes in the hydrology of the western United States. *Science (1979)* 316, 1180–1183. doi: 10.1126/science.1139601.

Bauer, S., Gienapp, P., and Madsen, J. (2008). The relevance of environmental conditions for departure decision changes en route in migrating geese. *Ecology* 89, 1953–1960. doi: 10.1890/07-1101.1.

Boggie, M. A., Collins, D. P., Patrick Donnelly, J., and Carleton, S. A. (2018). Land use, anthropogenic disturbance, and riverine features drive patterns of habitat selection by a wintering waterbird in a semiarid environment. *PLoS One* 13, 1–26. doi: 10.1371/journal.pone.0206222.

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., et al. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc. R. Soc. B Biol.* 271, 1657–1662. doi: 10.1098/rspb.2004.2770.

Both, C., Bouwhuis, S., Lessells, C. M., and Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature* 441, 81–83. doi: 10.1038/nature04539.

Breuner, C. W., Sprague, R. S., Patterson, S. H., and Woods, H. A. (2013). Environment, behavior and physiology: Do birds use barometric pressure to predict storms? *J. Exp. Biol.* 216, 1982–1990. doi: 10.1242/jeb.081067.

Bunting, D. P., Boggie, M. A., Collins, D. P., Thorpe, P. P., and Donnelly, J. P. (2022). Linking ecological processes and animal movements to inform timing of long-term surveys of a migratory game bird. *Ecosphere* 13. doi: 10.1002/ecs2.4298.

Burnham, K. P., and Anderson, D. R. (2002). *Model selection and multimodal inference: A practical information-theoretic approach.* 1st ed. New York, New York: Springer-Verlag.

Carlisle, M. J., and Tacha, T. C. (1983). Fall migration of sandhill cranes in West Central North Dakota. *J. Wildl. Manag.* 47, 818–821.

Carneiro, C., Gunnarsson, T. G., and Alves, J. A. (2020). Linking weather and phenology to xtopover dynamics of a long-distance migrant. *Front. Ecol. Evol.* 8. doi: 10.3389/fevo.2020.00145.

Chapman, B. B., Brönmark, C., Nilsson, J. Å., and Hansson, L. A. (2011). The ecology and evolution of partial migration. *Oikos* 120, 1764–1775. doi: 10.1111/j.1600-0706.2011.20131.x.

Chernetsov, N., Berthold, P., and Querner, U. (2004). Migratory orientation of first-year white storks (Ciconia ciconia): Inherited information and social interactions. *J. Exp. Biol.* 207, 937–943. doi: 10.1242/jeb.00853.

Collins, D. P., Grisham, B. A., Conring, C. M., Knetter, J. M., Conway, W. C., Carleton, S. A., et al. (2016). New summer areas and mixing of two greater sandhill crane populations in the Intermountain West. *J. Fish Wildl. Manag.* 7, 141–152. doi: 10.3996/042015-JFWM-036.

Collins, D., and Vanausdall, R. A. (2023). October 2022 recruitment survey of the Rocky Mountain Population of greater sandhill cranes. *U.S. Fish and Wildlife Service*, 1–10. https://www.fws.gov/media/survey-rocky-mountain-population-greater-sandhill-cranes-2022.

Cooch, E. G., and White, G. C. (2017). Program MARK: a gentle introduction. www.phidot.org/software/mark/docs/book.

Cooper, N. W., Dossman, B. C., Berrigan, L. E., Brown, J. M., Cormier, D. A., Bégin-Marchand, C., et al. (2023). Atmospheric pressure predicts probability of departure for migratory songbirds. *Mov. Ecol.* 11. doi: 10.1186/s40462-022-00356-z.

Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* 51, 429–438.

Cox, A. R., Frei, B., Gutowsky, S. E., Baldwin, F. B., Bianchini, K., and Roy, C. (2023). Sixty-years of community-science data suggest earlier fall migration and short-stopping of waterfowl in North America. *Ornithol. App.* 125, 1-14. doi: 10.1093/ornithapp/duad041.

Cox, G. W. (1985). The evolution of avian migration systems between temperate and tropical regions of the world. *Am. Nat.* 126, 451–474.

Dettinger, M., Udall, B., and Georgakakos, A. (2015). Western water and climate change. *Ecol. App.* 25, 2069-2093.

Donnelly, J. P., Collins, D. P., Knetter, J. M., Gammonley, J. H., Boggie, M. A., Grisham, B. A., Nowak, M. C., and Naugle, D. E. (2023). Flood-irrigated agricultural mediates climate-induced wetland scarcity for summering sandhill cranes in western North America.

Donnelly, J. P., King, S. L., Knetter, J., Gammonley, J. H., Dreitz, V. J., Grisham, B. A., et al. (2021). Migration efficiency sustains connectivity across agroecological networks supporting sandhill crane migration. *Ecosphere* 12. doi: 10.1002/ecs2.3543.

Donnelly, J. P., Naugle, D. E., Collins, D. P., Dugger, B. D., Allred, B. W., Tack, J. D., et al. (2019). Synchronizing conservation to seasonal wetland hydrology and waterbird migration in semi-arid landscapes. *Ecosphere* 10. doi: 10.1002/ecs2.2758.

Drewien, R. C., and Bizeau, E. G. (1974). Status and distribution of greater sandhill cranes in the Rocky Mountains. *J. Wildl. Manag.* 38, 720–742.

Duijns, S., Anderson, A. M., Aubry, Y., Dey, A., Flemming, S. A., Francis, C. M., et al. (2019). Long-distance migratory shorebirds travel faster towards their breeding grounds, but fly faster post-breeding. *Sci. Rep.* 9. doi: 10.1038/s41598-019-45862-0.

Elias, E. H., Rango, A., Steele, C. M., Mejia, J. F., and Smith, R. (2015). Assessing climate change impacts on water availability of snowmelt-dominated basins of the Upper Rio Grande basin. *J Hydrol. Reg. Stud.* 3, 525–546. doi: 10.1016/j.ejrh.2015.04.004.

Emery, P. A., Boettcher, A. J., Snipes, R. J., and Mcintyre, H. J. (1969). Hydrology of the San Luis Valley, south-central Colorado. Denver, Colorado: U.S. Geological Survey.

Fronczak, D. L., Andersen, D. E., Hanna, E. E., and Cooper, T. R. (2017). Distribution and migration chronology of Eastern population sandhill cranes. *J. Wildl. Manag.* 81, 1021–1032. doi: 10.1002/jwmg.21272.

Galtbalt, B., Batbayar, N., Sukhbaatar, T., Vorneweg, B., Heine, G., Müller, U., et al. (2022). Differences in on-ground and aloft conditions explain seasonally different migration paths in Demoiselle crane. *Mov. Ecol.* 10. doi: 10.1186/s40462-022-00302-z.

Gerber, B. D., Dwyer, J. F., Nesbitt, S. A., Drewien, R. C., Littlefield, C. D., Tacha, T. C., et al. (2020). "Sandhill Crane (Antigone canadensis), version 1.0.," in *Birds of the World*, ed. A. F. Poole (Ithaca, NY, USA: Cornell Lab of Ornithology).

Gerber, B. D., Kendall, W. L., Hooten, M. B., Dubovsky, J. A., and Drewien, R. C. (2015). Optimal population prediction of sandhill cranes recruitment based on climate-mediated habitat limitations. *J. Anim. Ecol.* 84, 1299-1310. doi: 10.1111/1365-2656.12370.

Gill, R. E., Douglas, D. C., Handel, C. M., Tibbitts, T. L., Hufford, G., and Piersma, T. (2014). Hemispheric-scale wind selection facilitates bar-tailed godwit circum-migration of the Pacific. *Anim. Behav.* 90, 117–130. doi: 10.1016/j.anbehav.2014.01.020.

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim. Res.* 35, 37–58. doi: 10.3354/cr00713.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., and Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote. Sens. Environ.* 202, 18–27. doi: 10.1016/j.rse.2017.06.031.

Haest, B., Hüppop, O., and Bairlein, F. (2020). Weather at the winter and stopover areas determines spring migration onset, progress, and advancements in Afro-Palearctic migrant birds. *Proc. Nat. Acad. Sci.* 117, 17056–17062. doi: 10.5281/zenodo.3629178.

Hays, Q. R., Tredennick, A. T., Carlisle, J. D., Collins, D. P., and Carleton, S. A. (2021). Spatially explicit assessment of sandhill crane exposure to potential transmission line collision risk. *J. Wildl. Manag.* 85, 1440–1449. doi: 10.1002/jwmg.22100.

Hedenström, A. (1993). Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Philso. Trans. R. Soc. B* 342, 353–361. Available at: https://royalsocietypublishing.org/.

Hedenström, A., and Alerstam, T. (1997). Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. *J. Theor. Biol.* 189, 227–234. doi: 10.1006/jtbi.1997.0505.

Helwig, N. E. (2022). npreg: Nonparametric Regression via Smoothing Splines. R package version 1.0-9, https://CRAN.R-project.org/package=npreg.

Illan, J. G., Wang, G., Cunningham, F. L., and King, D. T. (2017). Seasonal effects of wind conditions on migration patterns of soaring American white pelican. *PLoS One* 12, 1–15. doi: 10.1371/journal.pone.0186948.

Ivey, G. L., Dugger, B. D., Herziger, C. P., Casazza, M. L., and Fleskes, J. P. (2015). Wintering ecology of sympatric subspecies of Sandhill Crane: Correlations between body size, site fidelity, and movement patterns. *Condor* 117, 518–529. doi: 10.1650/condor-14-159.1.

Jenni, L., and Kéry, M. (2003). Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proc. R. Soc. B Biol. Sci.* 270, 1467–1471. doi: 10.1098/rspb.2003.2394.

Jin, H., Huang, C., Lang, M. W., Yeo, I.-Y., and Stehman, S. V. (2017). Monitoring of wetland inundation dynamics in the Delmarva Peninsula using Landsat time-series imagery from 1985 to 2011. *Remote. Sens. Environ.* 190, 26–41. doi: 10.1016/j.rse.2016.12.001.

Jorgensen, J. G., and Brown, M. B. (2017). Temporal migration shifts in the Aransas-Wood Buffalo Population of whooping cranes (*Grus americana*) across North America. *Waterbirds* 40, 195–308.

Kanamitsu, M., Ebisuzaki, W., Woollen, J., Yang, S.-K., Hnilo, J. J., Fiorino, M., et al. (2002). NCEP-DOE AMIP-II REANALYSIS (R-2). doi: 10.1175/BAMS-83-11.

Karlsson, H., Nilsson, C., Bäckman, J., and Alerstam, T. (2012). Nocturnal passerine migrants fly faster in spring than in autumn: A test of the time minimization hypothesis. *Anim. Behav.* 83, 87–93. doi: 10.1016/j.anbehav.2011.10.009.

Kemp, J., Boyd, W. S., Forstner, T. M., Esler, D., Bowman, T. D., Douglas, D. C., et al. (2023). Pacific Barrow's Goldeneye refine migratory phenology in response to overwintering temperatures and annual snowmelt. *Ornithol*. doi: 10.1093/ornithology/ukad024.

Kemp, M. U., Emiel van Loon, E., Shamoun-Baranes, J., and Bouten, W. (2012). RNCEP: Global weather and climate data at your fingertips. *Methods Ecol. Evol.* 3, 65–70. doi: 10.1111/j.2041-210X.2011.00138.x.

Kendall, W. L., Stapleton, S., White, G. C., Richardson, J. I., Pearson, K. N., and Mason, P. (2019). A multistate open robust design: population dynamics, reproductive effort, and phenology of sea turtles from tagging data. *Ecol. Monogr.* 89. doi: 10.1002/ecm.1329.

Kokko, H. (1999). Competition for early arrival in migratory birds. *J. Anim. Ecol.* 68, 940–950. doi: 10.1046/j.1365-2656.1999.00343.x.

Kölzsch A., Müskens, G. J. D. M., Kruckenberg, H., Glazov, P., Weinzierl, R., Nolet, B. A., and Wikelski, M. (2016) Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. *Oikos*. 125, 1496–507. doi: 10.5441/001/1.31c2v92f.

Krapu, G. L., Brandt, D. A., Kinzel, P. J., and Pearse, A. T. (2014). Spring migration ecology of the Mid-Continent sandhill crane population with an emphasis on use of the Central Platte River Valley, Nebraska. *Wildl. Monogr.* 189, 1–41. doi: 10.1002/wmon.l013.

Krapu, G. L., Facey, D. E., Fritzell, E. K., and Johnson, D. H. (1984). Habitat use by migrant sandhill cranes in Nebraska. *J. Wildl Manag.* 48, 407–417.

Krapu, G. L., Iverson, G. C., Reinecke, K. J., and Boise, C. M. (1985). Fat deposition and usage by arctic-nesting Sandhill Cranes during spring. *Auk* 102, 362–368.

Kreithen, M. L., and Keeton, W. T. (1974). Detection of changes in atmospheric pressure by the homing pigeon, Columba livia. *J. Comp. Physiol.* 89, 73–82.

La Sorte, F. A., Horton, K. G., Nilsson, C., and Dokter, A. M. (2019). Projected changes in wind assistance under climate change for nocturnally migrating bird populations. *Glob. Chang Biol.* 25, 589–601. doi: 10.1111/gcb.14531.

Laake, J. L. (2013). RMark: An Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way, NE, Seattle, WA 98115.

Lawrence, K. B., Barlow, C. R., Bensusan, K., Perez, C., and Willis, S. G. (2021). Phenological trends in the pre- and post-breeding migration of long-distance migratory birds. *Glob. Chang. Biol.* 28, 375–389. doi: 10.1111/gcb.15916.

Lebreton, J.-D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Mon.* 62, 67-118.

Limiñana, R., Romero, M., Mellone, U., and Urios, V. (2013). Is there a different response to winds during migration between soaring and flapping raptors? An example with the Montagu's harrier and the lesser kestrel. *Behav. Ecol. Sociobiol.* 67, 823–835. doi: 10.1007/s00265-013-1506-9.

Lindström, Å. (1991). Maximum fat deposition rates in migrating birds. *Scandinavian Journal of Ornithol.* 22, 12–19.

Liu, Y., Goodrick, S. L., and Stanturf, J. A. (2013). Future U.S. wildfire potential trends projected using a dynamically downscaled climate change scenario. *For. Ecol. Manag.* 294, 120–135. doi: 10.1016/j.foreco.2012.06.049.

Llewellyn, D., and Vaddey, S. (2013). West-Wide Climate Risk Assessment: Upper Rio Grande Impact Assessment. Albuqurque, NM: Bureau of Reclamation.

Lundberg, P. (1988). The evolution of partial migration in birds. *Trends Ecol. Evol.* 3, 172–175.

Mandel, J. T., Bohrer, G., Winkler, D. W., Barber, D. R., Houston, C. S., and Bildstein, K. L. (2011). Migration path annotation: Cross-continental study of migration-flight response to environmental conditions. *Ecol. App.* 21, 2258–2268. doi: 10.1890/10-1651.1.

Maransky, B., Goodrich, L., and Bildstein, K. (1997). Seasonal shifts in the effects of weather on the visible migration of Red-Tailed Hawks at Hawk Mountain, Pennsylvania, 1992-1994. *Wilson Bulletin* 109, 246–252.

Mateos-Rodríguez, M., and Liechti, F. (2011). How to diurnal long-distance migrants select flight altitude in relation to wind. *Behav. Ecol.* doi: 10.1093/beheco/arr204.

Mellone, U., Klaassen, R. H. G., García-Ripollés, C., Limiñana, R., López-López, P., Pavón, D., et al. (2012). Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. *PLoS One* 7. doi: 10.1371/journal.pone.0039833.

Metcalfe, J., Schmidt, K. L., Bezner Kerr, W., Guglielmo, C. G., and MacDougall-Shackleton, S. A. (2013). White-throated sparrows adjust behaviour in response to manipulations of barometric pressure and temperature. *Anim. Behav.* 86, 1285–1290. doi: 10.1016/j.anbehav.2013.09.033.

Mitchell, G. W., Woodworth, B. K., Taylor, P. D., and Norris, D. R. (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. *Mov. Ecol*. 3. doi: 10.1186/s40462-015-0046-5.

Mix, K., Lopes, V. L., and Rast, W. (2011). Annual and growing season temperature changes in the San Luis Valley, Colorado. *Water Air Soil Pollut.* 220, 189–203. doi: 10.1007/s11270-011-0746-4.

Mix, K., Rast, W., and Lopes, V. L. (2010). Increases in growing degree days in the alpine desert of the San Luis Valley, Colorado. *Water Air Soil Pollut.* 205, 289–304. doi: 10.1007/s11270-009-0074-0.

Møller, A. P. (2001). Heritability of arrival date in a migratory bird. *Proc. R. Soc. B Biol. Sci.* 268, 203–206. doi: 10.1098/rspb.2000.1351.

Møller, P. A., Rubolini, D., and Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Nat. Acad. Sci.*105, 16195–16200.

Morin, D. J., Yackulic, C. B., Diffendorfer, J. E., Lesmeister, D. B., Nielsen, C. K., Reid, J., et al. (2020). Is your ad hoc model selection strategy affecting your multimodel inference? *Ecosphere* 11. doi: 10.1002/ecs2.2997.

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P., and Fagan, W. F. (2013). Social learning of migratory performance. *Science (1979)* 341, 999–1002. doi: 10.1126/science.1239794.

Newton, I. (2007). Weather-related mass-mortality events in migrants. *Ibis* 149, 453–467. doi: 10.1111/j.1474-919X.2007.00704.x.

Nilsson, C., Klaassen, R. H. G., and Alerstam, T. (2013). Differences in speed and duration of bird migration between spring and autumn. 181. doi: 10.5061/dryad.82d4q.

NOAA (2022). Climate Data Online. https://www.ncei.noaa.gov/cdo-web/. [Accessed August 31, 2022].

Nolet, B. A. (2006). Speed of migration of tundra swans *Cygnus columbianus* in accordance with income or capital breeding strategy? *Ardea*. 94, 579-591.

Obernuefemann, K. P., Collazo, J. A., and Lyons, J. E. (2013). Local movements and wetland connectivity at a migratory stopover of semipalmated sandpipers (*Calidris pusilla*) in the Southeastern United States. *Waterbirds* 36, 63–76. doi: 10.1675/063.036.0110.

Ojaste, I., Leito, A., Hedenström, A., Sepp, K., Leivits, M., Sellis, U., et al. (2020). From northern Europe to Ethiopia: long-distance migration of Common Cranes (*Grus grus*). *Ornis Fenn* 97, 12–25. Available at: https://www.researchgate.net/publication/339739195.

O'Neal, B. J., Stafford, J. D., Larkin, R. P., and Michel, E. S. (2018). The effect of weather on the decision to migrate from stopover sites by autumn-migrating ducks. *Mov. Ecol.* 6. doi: 10.1186/s40462-018-0141-5.

Panuccio, M., Barboutis, C., Chiatante, G., Evangelidis, A., Nicolantonio, &, Panuccio, A. M., et al. (2016). Pushed by increasing air temperature and tailwind speed: weather selectivity of raptors migrating across the Aegean Sea. *Ornis. Fenn.* 93, 159–171.

Pearse, A. T., Krapu, G. L., and Brandt, D. A. (2017). Sandhill crane roost selection, human disturbance, and forage resources. *J. Wildl. Manag.* 81, 477–486. doi: 10.1002/jwmg.21215.

Pearse, A. T., Krapu, G. L., Brandt, D. A., and Kinzel, P. J. (2010). Changes in agriculture and abundance of snow geese affect carrying capacity of sandhill cranes in Nebraska. *J. Wildl. Manag.* 74, 479–488. doi: 10.2193/2008-539.

Pearse, A. T., Metzger, K. L., Brandt, D. A., Bidwell, M. T., Harner, M. J., Baasch, D. M., et al. (2020). Heterogeneity in migration strategies of Whooping Cranes. *Condor* 122. doi: 10.1093/condor/duz056.

Pennycuick, C. J., Alerstam, T., and Larsson, B. (1979). Soaring migration of the common crane *Grus grus* observed by radar and from an aircraft. *Ornis Scand.* 10, 241-251.

Peters, R. H. (1986). *The ecological implications of body size*. Cambridge: Cambridge University Press.

Piersma, T., and Jukema, J. (1990). Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of bar-tailed godwits at successive spring staging sites. *Ardea* 78, 315–337.

Pulido, F. (2011). Evolutionary genetics of partial migration - the threshold model of migration revis(it)ed. *Oikos* 120, 1776–1783. doi: 10.1111/j.1600-0706.2011.19844.x.

R Core Team (2022). R version 4.2.3: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.

Ray, A. J., Barsugli, J. J., Averyt, K. B., Wolter, K., Hoerling, M., Doesken, N., et al. (2008). Climate change in Colorado: A synthesis to support water resources management and adaptation. Western Water Assessment.

Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: a review. *Oikos* 30, 224–272.

Richardson, W. J. (1990). Timing of bird migration in relation to weather: updated review. *Oikos* 30, 78–101.

Rio Grande Basin Roundtable (2015). Rio Grande Basin Implementation Plan. 1–164. https://engagecwcb.org/basin-implementation-plans. [Accessed August 31, 2022].

Rio Grande Basin Roundtable (2022). Rio Grande Basin Implementation Plan Volume 2. https://engagecwcb.org/basin-implementation-plans. [Accessed August 31, 2022].

Roques, S., Henry, P.-Y., Guyot, G., Bargain, B., Cam, E., and Pradel, R. (2022). When to depart from a stopover site? Time since arrival matters more than current weather conditions. *Ornithol.* 139. doi: 10.1093/ornithology/ukab057.

Roques, S., Lank, D. B., Cam, E., and Pradel, R. (2021). More than just refuelling: lengthy stopover and selection of departure weather by sandpipers prior to transoceanic and transcontinental flights. *Ibis* 163, 519–535. doi: 10.1111/ibi.12891.

Rüppel, G., Hüppop, O., Lagerveld, S., Schmaljohann, H., and Brust, V. (2023). Departure, routing and landing decisions of long-distance migratory songbirds in relation to weather. *R. Soc. Open. Sci.* 10. doi: 10.1098/rsos.221420.

Sapir, N., Wikelski, M., Avissar, R., and Nathan, R. (2011). Timing and flight mode of departure in migrating European bee-eaters in relation to multi-scale meteorological processes. *Behav. Ecol. Sociobiol.* 65, 1353–1365. doi: 10.1007/s00265-011-1146-x.

Schaub, M., Liechti, F., and Jenni, L. (2004). Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Anim. Behav.* 67, 229–237. doi: 10.1016/j.anbehav.2003.03.011.

Schmaljohann, H., C. Eikenaar, and Sapir, N. (2022). Understanding the ecological and evolutionary function of stopover in migrating birds. *Biol. Rev.* 97, 1231-1252. doi: 10.1111/brv.12839.

Schummer, M. L., Kaminski, R. M., Raedeke, A. H., and Graber, D. A. (2010). Weather-related indices of autumn-winter dabbling duck abundance in middle North America. *J. Wildl. Manag.* 74, 94-101. doi: 10.2193/2008-524.

Seamans, M. E. (2022). Status and harvests of sandhill cranes: Mid-Continent, Rocky Mountain, Lower Colorado River Valley and Eastern Populations. *U.S. Fish and Wildlife Service*, 1–17. https://www.fws.gov/library/collections/sandhill-crane-population-status-reports. [Accessed 6 June 2023].

Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika* 52, 249–259.

Shamoun-Baranes, J., Baharad, A., Alpert, P., Berthold, P., Yom-Tov, Y., Dvir, Y., and Leshem, Y. (2003). The effect of wind, season and latitude on the migration speed of white storks *Ciconia Ciconia*, along the eastern migration route. *J. Avian Biol.* 34, 97-104.

Shamoun-Baranes, J., Liechti, F., and Vansteelant, W. M. G. (2017). Atmospheric conditions create freeways, detours, and tailbacks for migrating birds. *J. Comp. Physiol. A.* 203, 509-529.

Shamoun-Baranes, J., van Loon, E., Alon, D., Alpert, P., Yom-Tov, Y., and Leshem, Y. (2006). Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Global Ecol. and Biog.* 15, 541–552. doi: 10.1111/j.1466-822x.2006.00261.x.

Sparling, D. W., and Krapu, G. L. (1994). Communal roosting and foraging behavior of staging sandhill cranes. *Wilson Bull.* 106, 62–77.

Tacha, T. C., Jorgenson, C., and Taylor, P. S. (1985). Harvest, migration, and condition of Sandhill Cranes in. *J. Wildl. Manag.* 49, 476–480.

Teitelbaum, C. S., Converse, S. J., Fagan, W. F., Böhning-Gaese, K., O'Hara, R. B., Lacy, A. E., et al. (2016). Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nat. Commun.* 7. doi: 10.1038/ncomms12793.

Thurber, B. C., Roy, C., and Zimmerling, J. R. (2020). Long-term changes in the autumn migration phenology of dabbling ducks in southern Ontario and implications for waterfowl management. *Wildl. Biol.* 2, 1-11. doi: 10.2981/wlb.00668.

U.S. Fish and Wildlife Service (2015). Comprehensive conservation plan: San Luis Valley National Wildlife Refuge Complex. Lakewood, Colorado.

Usui, T., Butchart, S. H. M., and Phillimore, A. B. (2017). Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. *J. Anim. Ecol.* 86, 250–261. doi: 10.1111/1365-2656.12612.

Vanausdall, R. A., and Dinsmore, S. J. (2021). Stopover ecology of the least sandpiper (Calidris minutilla) in Iowa: implications for reservoir management. *Lake Reserv. Manag.* 37, 300–312. doi: 10.1080/10402381.2021.1920071.

Vansteelant, W. M. G., Shamoun-Baranes, J., McLaren, J., van Diermen, J., and Bouten, W. (2017). Soaring across continents: decision-making of a soaring migrant under changing atmospheric conditions along an entire flyway. *J. Avian Biol.* 48, 887–896. doi: 10.1111/jav.01298.

Visser, M. E., and Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* 3, 879–885. doi: 10.1038/s41559-019-0880-8.

Visser, M. E., Marvelde, L., and Log, M. E. (2012). Adaptive phenological mismatches of birds and their food in a warming world. *J. Ornithol.* 153, 75–84. doi: 10.1007/s10336-011-0770-6.

Visser, M. E., Perdeck, A. C., van Balen, J. H., and Both, C. (2009). Climate change leads to decreasing bird migration distances. *Glob. Chang. Biol.* 15, 1859–1865. doi: 10.1111/j.1365-2486.2009.01865.x.

von Bartheld, C. S. (1994). Functional morphology of the paratympanic organ in the middle ear of birds. *Brain Behav. Evol.* 44, 61–73.

Weber, T. P., Alerstam, T., and Hedenström, A. (1998). Stopover decisions under wind influence. *J. Avian Biol.* 29, 552–560.

Western Regional Climate Center (2013). Cooperative Climatological Data Summaries. https://wrcc.dri.edu/Climate/summaries.php [Accessed August 31, 2022].

Wetland Dynamics, L. (2019). San Luis Valley wetland and wildlife conservation assessment. Monte Vista, CO.

White, G. C., and Burnham, K. P. (1999). Program mark: Survival estimation from populations of marked animals. *Bird Study* 46, S120–S139. doi: 10.1080/00063659909477239.

Winger, B. M., Auteri, G. G., Pegan, T. M., and Weeks, B. C. (2019). A long winter for the Red Queen: rethinking the evolution of seasonal migration. *Biol. Rev.* 94, 737-752. doi: 10.1111/brv.12467.

CHAPTER 2 – HABITAT SELECTION BY ROCKY MOUNTAIN POPULATION GREATER SANDHILL CRANES (ANTIGONE CANADENSIS TABIDA) DURING SPRING AND AUTUMN MIGRATION AT A KEY STOPOVER AREA

INTRODUCTION

Animals face survival and reproductive consequences depending on the type and quality of habitat and resources they use (Matthiopoulos et al. 2015). Resources include biotic and abiotic items, such as food or nesting material, and space needed for reproduction and survival (Johnson 1980, Aarts et al. 2008, Beyer et al. 2010, Gaillard et al. 2010). Theory predicts that individuals should use resources and thus habitat patches in such a way that their fitness is maximized (Fretwell 1969, Rosenzweig 1981, Northrup et al. 2022). An understanding of habitat use can inform management of populations, so habitat selection is of interest to managers and researchers.

An important consideration in habitat selection studies is that resource needs will change in seasonal environments, and animals will use different habitats depending on their stage in the annual cycle (Newton 2007, McLoughlin et al. 2010, Stanley et al. 2021). The seasonal changes in resource availability in time and space are ultimate reasons for the evolution of migratory behavior, particularly in birds (Cristol et al. 1999, Chapman et al. 2011). Migrants respond to environmental and habitat changes on their wintering and breeding areas to, in part, initiate migration, while stopover areas are used along the migration route and influence migratory decisions and duration (Newton 2007, Warnock 2010). Stopover areas are used for replenishing energy reserves through foraging and resting and sometimes as refugia from harsh conditions or predators (Schmaljohann et al. 2022). The energy acquired at stopover areas is critical for completing migration and, for some species, reproducing successfully during the following breeding season (Alisauskas 2002, Baker et al. 2004, Drent et al. 2007, Devries et al. 2008).

Managing habitat or resources associated with energy acquisition and maintenance is of concern to many managers in key stopover areas for species of interest (Albanese and Davis 2015, Ballard et al. 2021).

In North America, there are six migratory populations of Sandhill Cranes (*Antigone canadensis*) managed by state and federal agencies (Collins et al. 2016, Gerber et al. 2020), and all of them use stopover areas during autumn and spring migration (Drewien and Bizeau 1974, Krapu et al. 2011, Fronczak et al. 2017). Several populations show high fidelity to certain stopover areas each year and season, and these areas have been the target of research and management (Lovvorn and Kirkpatrick 1982, Krapu et al. 1984, Iverson et al. 1987, Bunting et al. 2022). For example, the San Luis Valley in Colorado is an important and well-known spring and autumn stopover area for Sandhill Cranes in the Rocky Mountain Population (Drewien and Bizeau 1974, Donnelly et al. 2021, Vanausdall et al. 2024). Similar to other stopover areas, Sandhill Cranes rapidly increase lipid levels in spring by foraging on grain leftover from harvest, and these reserves are likely used to fuel the remainder of migration (Kauffeld 1981, Krapu et al. 1985). Sandhill Cranes are not completely capital breeders, which include birds that acquire most or all of their nutrients needed for reproduction prior to arriving on the breeding grounds, but these reserves still likely assist with reproduction and egg laying (Krapu et al. 1985). Important stopover areas for other populations include the Central Platte River Valley in Nebraska (Krapu et al. 2014) and the Jasper-Pulaski Fish and Wildlife area for the Eastern Population (Lovvorn and Kirkpatrick 1982, Fronczak et al. 2017). Because of their status as a game species, a charismatic species, and a success story in terms of recovery from near extirpation (Walkinshaw 1949), Sandhill Cranes and their use of stopover areas has been of interest in recent decades.

The habitat requirements of Sandhill Cranes during the non-breeding period have been well documented, with a particular emphasis on spring migration owing to its potential impact on reproduction (Lovvorn and Kirkpatrick 1982, Krapu et al. 1984, Folk and Tacha 1990, Boggie et al. 2018). Slightly less work has examined habitat selection for Sandhill Cranes in autumn (but see Littlefield 1992, Donnelly et al. 2021), but there is evidence to suggest that preferred habitat is more variable among individuals when compared to spring (Lovvorn and Kirkpatrick 1982). The distribution of Sandhill Cranes is largely determined by the proximity of roosting areas and foraging areas (Iverson et al. 1987, Sparling and Krapu 1994). Roosting habitats at stopover areas include wetlands, wet meadows, and riverine habitats with shallow water (approximately 30 cm deep or less) and low vegetation, channel widths wider than 200 m, and at least 25 m from disturbance (Krapu et al. 1984, Davis 2003, Kinzel et al. 2009, Pearse et al. 2017, Kruse et al. 2017). Sandhill Cranes will also use wet areas, including wetlands and pastures, in between foraging bouts to loaf, which refers to behaviors such as resting, preening, and overall maintenance (Iverson et al. 1987, Tacha et al. 1987, Aborn 2011). Foraging habitat tends to include agricultural grains, but habitats such as wetlands, grasslands, and wet pastures are also important for providing other nutrients and minerals (Lewis 1979, Armbuster and Farmer 1982, Reinecke and Krapu 1986, Rowland et al. 1992). Sandhill Cranes show a preference for foods high in carbohydrates during migration, which allows for the synthesis and deposition of lipids (Krapu et al. 1985, Reinecke and Krapu 1986). Corn is more available and selected by Sandhill Cranes in the Mid-continent Population and Eastern Populations (Lovvorn and Kirkpatrick 1982, Krapu et al. 1984), whereas RMP Sandhill Cranes have access to more barley. Other crops, such as potatoes and alfalfa shoots, are also consumed in some areas (Kauffeld 1981, Armbuster and Farmer 1982, Walker and Schemnitz 1985). Sandhill Cranes will forage on invertebrates and

other plant parts in wetlands, wet meadows or pastures, and grasslands during migration and these items provide protein, calcium, minerals, and other nutrients that agricultural crops do not (Lewis 1979, Walker and Schemnitz 1985, Reinecke and Krapu 1986).

The San Luis Valley (hereafter, SLV) in south-central Colorado is of key interest for the RMP because most of the population is in the SLV during peak migration in spring and autumn (Drewien and Bizeau 1974), and it is an area critical to the migratory connectivity of the RMP (Donnelly et al. 2021). The RMP is composed solely of the greater Sandhill Crane (*A. c. tabida*), but lesser Sandhill Cranes (*A. c. canadensis*) from the Midcontinent Population also use this area during autumn and spring migration (Krapu and Brandt 2008, Krapu et al. 2011). Sandhill Cranes forage primarily on barley in the SLV and roost and loaf along the Rio Grande River and other tributaries, as well as wetlands and pastures on both public and private lands. A challenge facing the management of the RMP, as well as for people in the SLV and the Intermountain West, is the increasingly limited water resources due to over-appropriation, prolonged drought, and warming temperatures (Barnett et al. 2005, 2008, Mix et al. 2011, Dettinger et al. 2015). Irrigated agriculture is the main economic driver in the SLV (San Luis Valley Development Resources Group and Council of Governments 2023), and most fields are irrigated using surface water runoff from the surrounding mountain ranges, along with water pumped from underground aquifers. Due to increased groundwater pumping in response to prolonged drought and lowered aquifer levels in the early 2000s, groundwater subdistricts were created and tasked with bringing groundwater levels back to a sustainable level (Rio Grande Basin Roundtable 2015, 2022, Cody et al. 2015). An irrigation season also limits the time that most irrigators can divert surface water, with diversions generally restricted to between 1 April and 31 October for most users (Rio Grande Basin Roundtable 2015). At the same time, public areas in the SLV distribute water on

the landscape for migrating waterbirds, including Sandhill Cranes. The Monte Vista National Wildlife Refuge has adjudicated water rights to pump and divert water outside the irrigation season to provide roosting and foraging habitat for migrating Sandhill Cranes and waterbirds (U.S. Fish and Wildlife Service 2015). As a result, water availability differs spatially and temporally across the landscape in the SLV and can be dependent on whether property is privately or publicly owned. Temperatures are predicted to continue increasing in many parts of the Intermountain West, which will further reduce snowpack, the main provider of surface water for basins in the Southwest (Llewellyn and Vaddey 2013, Bureau of Reclamation 2021). Earlier spring runoff has already been documented (Barnett et al. 2008, Llewellyn and Vaddey 2013), which has the potential to create a temporal mismatch between migration patterns and water availability in the SLV (Donnelly et al. 2019). Efficient management of water resources on both public and private land will thus be important for migrating RMP Sandhill Cranes.

Examination of RMP habitat selection patterns at a key stopover area will provide a better understanding of where and when Sandhill Cranes most utilize habitat and inform how habitat could be managed to optimize limited resources (e.g., water) during the migratory period. Given continued water limitations, it would also be informative to understand the importance of publicly and privately managed lands to Sandhill Cranes, as the habitat management of each will likely require different strategies and include different stakeholders. We used Global Positioning System (GPS) data to (1) identify habitat attributes and landcover types that influence selection of roosting, loafing, and foraging Sandhill Cranes in the SLV, (2) determine if there is a preference for private or public lands for roosting and loafing, and (3) identify areas with the strongest selection strength throughout the SLV. We estimated the proportion of water and sandbar in roosting and loafing areas, along with mean vegetation height within 100 m of

Sandhill Crane locations, and distance to the nearest grain field. We also determined the ownership type and landcover type of these areas, and the crop type of foraging areas. We predicted that surface water would have a positive influence on selection by both roosting and loafing RMP Sandhill Cranes. We expected distance to grain and surrounding vegetation height to be negatively correlated with roosting and loafing selection, with a stronger selection strength in autumn for distance to grain due to the depletion of grain resources closer to roosting and loafing sites over time. We also expected Sandhill Cranes to use a greater diversity of landcover types while loafing than while roosting, with a greater selection for pastures and grasslands for loafing and of open water and wetlands for roosting. Due to limited water resources, we predicted Sandhill Cranes to use private areas (i.e., where more water is likely to be available) more than public areas for roosting and loafing. Finally, we expected barley to be the crop type with the greatest selection strength for foraging cranes in both seasons.

METHODS

Study area

The SLV is in the Upper Rio Grande Basin in southcentral Colorado, situated between the San Juan Mountains to the west and the Sangre De Cristo Mountains to the east (Figure 2.1). The area of the valley floor is approximately 8,200 km^2 and the average elevation is 2,100 m (Emery et al. 1969). The average temperature is 6°C but it can range between -20°C and 20°C throughout the year (Western Regional Climate Center 2013). Winds primarily come from the southwest and are highly variable. Considered an arid region, the SLV receives less than 200 mm annually, while the surrounding mountains receive 115 – 127 cm per year (Cooper et al. 2006). Hydrology in the SLV is driven by runoff from snowpack in the mountains, along with water coming from and discharging to underground aquifers (Emery et al. 1969). The headwaters of the

Rio Grande River are in the San Juan Mountains, and runoff from this mountain range provides 80% of the total runoff for the entire Upper Rio Grande Basin (Elias et al. 2015). Peak runoff occurs between April and June, but this has been shifting to earlier in the year in the Upper Rio Grande Basin and other parts of the Intermountain West (Barnett et al. 2008, Ficklin et al. 2013, Chavarria and Gutzler 2018). Monsoonal rains in the summer months can provide additional water, but surface water availability generally declines in autumn.

Agriculture is an important economic industry in the SLV. The main crops grown include alfalfa, potatoes, and barley. The main source of irrigation water in the Upper Rio Grande Basin comes from the Rio Grande River, but overuse in the last century has led to decreased water levels and depleted groundwater supplies utilized to compensate (Rio Grande Basin Roundtable 2022). Wetlands and wet meadows were historically more abundant throughout the SLV, but now they are mostly restricted to state and public lands. Cottonwoods (*Populus deltoides*) and willows (*Salix* sp.) occur along riparian areas, and emergent vegetation, such as cattails (*Typha* sp.) and bulrush (*Scirpus* sp.), occur in wetlands. Wet meadows include moist, short grass areas near riverine habitat or as part of wetlands, and many occur in areas used for ranching, which is also common in the SLV.

GPS deployment and formatting

Sandhill Cranes were captured and fitted with global system for mobile communication (GSM) platform transmitter terminal (PTT) tags (n = 95; Evolution Series-400, 15-g; Cellular Tracking Technologies, Rio Grande, NJ, USA) or global positioning system (GPS) PTT tags (n = 38; PTT-100, 22-g Solar Argos/GPS PTT, Microwave Telemetry, Columbia, MD, USA). Most Sandhill Cranes were captured in wintering areas in New Mexico at the Bosque del Apache National Wildlife Refuge and Bernardo Wildlife Area in Valencia and Socorro Counties, but a

few were captured in Arizona, Colorado, Idaho, and Montana. Details on the capture methods can be found in Collins et al. (2016) and Boggie et al. (2018). Data were acquired at different rates between the two types of transmitters, as the original acquisition and use of the transmitters were for different projects. The GSM units acquired locations at 15- to 30-min intervals, and we resampled these to approximately two-hour intervals. The GPS units were programmed to acquire points at scheduled times (07:00, 08:00, 10:00, 14:00, 18:00, 24:00) and applied to data gathered between the spring of 2015 and the spring of 2017. The location error for the GSM units was ±22 m for the GSM units and ±18 m for the GPS units.

Sandhill Cranes in the SLV have predictable movement patterns during the autumn and the spring and this influenced how we formatted GPS data. Their behavior patterns at different times of the day, namely roosting, loafing, and foraging, are also distinct in terms of behavior and, generally, habitat preference. We separated locations into either roosting, loafing, or foraging, depending on the time of day (Table 2.1) and analyzed models separately for each behavior (Suraci et al. 2019). Sandhill Cranes roost along rivers and in wetlands at night and fly to foraging locations around sunrise to begin feeding. After about 2-3 hours, flocks will fly to nearby wetlands, ditches, pastures, or moist grassy areas to loaf, where they rest, preen, drink water, and socialize with some occasional foraging. Approximately 2-3 hours before sunset, they will go back to foraging areas before returning to a roost around sunset. These patterns were observed in the field, but we also examined trajectories of Sandhill Cranes with transmitters to confirm their movement patterns. Based on the examination of trajectories, we considered the roosting period to be between one hour after sunset and 1.5 hours before sunrise. However, Sandhill Cranes moved an average of 140.52 m (SE = 6.65 m) in autumn and 36.27 m (SE = 1.72 m) in spring per night, indicating that movement is minimal once they choose a roost. As a result,

we used one location per crane per night for each season. We used the location acquired at or closest to midnight. We defined the foraging period to be between sunrise and two hours after sunrise and between two hours before sunset to sunset. The time in between was the loafing period, but we found considerable variation in the average distance moved during this period. The average distance between loafing locations within a day was 353.85 m (SE = 14.57 m) in autumn and 670.95 m (SE = 25.37 m) in spring. Sandhill Cranes were sometimes observed moving to different loafing locations during this timeframe, which likely explains the greater movement between these locations. Additionally, the difference in distances between the seasons is likely due to within-season and individual variation in when Sandhill Cranes leave and return to foraging locations. As a result, we decided to use one loafing location per day per individual at or closest to the time of day when movement was minimal, which was around noon. We used all locations for the foraging period and resampled them to every two hours.

Habitat covariates

To estimate surface water and sandbar for roosting and loafing areas, we used constrained spectral mixture analysis (SMA), which is a technique that uses remotely sensed images to determine the proportional amount of habitat classes within image pixels (Adams et al. 1995, Adams and Gillespie 2006). We used Landsat 8 and 9 satellite imagery corrected for surface reflectance for the years 2015-2022. Landsat images have a spatial resolution of 30 x 30 m, so our estimates of water and sandbar are the proportion of a pixel classified as those habitat types. To determine the fractional amount of habitat classes within pixels of an image, SMA requires reference endmembers, which are representative areas composed of pure or well-characterized habitat classes. All pixels must also be classified to a habitat type, but it is recommended to not use more habitat classes than the number of wavelength bands in an image (Adams and Gillespie

2006). We chose the classes shrub, soil, sandbar, water, and vegetation, but our main interests were in water and sandbar. For surface water and vegetation, endmembers were generated using the median band values of images for each season and year. Although Landsat images are available approximately every 16 days, there can be considerable variation in the quality of the images due to cloud cover and other factors. To account for this variation, we chose to take the median of all images for each season and year during the periods between 1 October and 15 November for autumn and 15 February and 1 April for spring. These are the primary times in which cranes are in the SLV and should be representative of the average conditions in the SLV during each season and year. We used the 98th percentile of Normalized Difference Water Index (NDWI) values to generate endmembers for each season-year. We used a similar approach for vegetation using the Normalized Difference Vegetation Index (NDVI). The endmembers for the remaining habitat classes were determined using static endmembers. Based on examination of various areas in the SLV, we chose polygons that did not significantly change in band values throughout the study period. The proportion of water and sandbar in each 30 x 30 m pixel were used in the resource selection analysis. We completed the SMA in the publicly available Google Earth Engine (Gorelick et al. 2017).

Vegetation height was also calculated using remote sensing techniques. We used Light Detection and Ranging (LiDAR) data collected in the SLV in 2011. This was the most recent source of LiDAR data for the SLV, but we did not expect there to be significant changes between then and the time of the study. Total precipitation in 2011 was approximately 17% below average in the SLV and 26% below average in the surrounding mountain ranges (Colorado Climate Center 2024), which provided relatively dry conditions for collecting elevation data using LiDAR. We generated a digital elevation model (DEM) and a digital surface model (DSM) at a

spatial resolution of 10 m from the LiDAR data. The DEM was subtracted from the DSM to get the height of objects. To smooth out the resulting layer, we used a 3 x 3 cell window around each cell and calculated the majority height value within each window. We excluded urban areas from this analysis. We then estimated the mean vegetation height within a circular buffer with a 100 m radius around each used and available crane location (Boggie et al. 2018).

Distance to the nearest grain field was identified using data from the Rio Grande Water Conservation District (RGWCD) and the Cropland data layer from the National Agricultural Statistics Service (NASS). The RGWCD completes an annual census of crop types in the counties of Rio Grande, Alamosa, and Saguache. We used the Cropland data layer for Costilla County. We considered all the most dominant grain types (i.e., barley, rye, triticale, and wheat) and other grains (e.g., corn) that were not as prevalent. We also identified the crop types used by foraging Sandhill Cranes and included the classes: potatoes, alfalfa, grains, pasture, and other crops.

We classified used and available locations for the roosting and loafing period into other landcover types and into public or private property. We used both the RGWCD and the National Landcover Database (NLCD) from 2016 (Dewitz 2019) and 2019 (Dewitz 2021) to determine landcover type: grassland, open water, pasture, wetland, and other. We used the 2016 NLCD data layer for crane locations from the years 2015 to 2017 and the 2019 NLCD layer for the remainder of the years.

Resource selection functions and habitat availability

We designed our study based on a use-availability framework to develop resource selection functions (RSF). A resource selection function estimates the selection strength by comparing a set of used locations, which were defined above, to a set of available locations

(Boyce and McDonald 1999, Manly et al. 2002). Habitats or resources that are used disproportionately to availability are "selected" by that animal (Johnson 1980, Boyce et al. 2002, Manly et al. 2002). To define the available distribution, we examined the average and median distances that RMP Sandhill Cranes moved between roosting or loafing locations on days for each season (Table 2). Distances were heavily skewed right for both periods and seasons. While the median values indicated that individuals typically moved within 1 km of roosting or diurnal locations between consecutive days, the average values represent cranes that moved greater distances as they likely continued to migrate south or north in the SLV. We wanted to encapsulate their ability to move greater distances between days, so we used a 5,000 m buffer around each used location to define the available area for all periods. Although individuals moved less between roosting and loafing areas in autumn than in spring, we decided to keep the available area consistent between seasons. We further restricted the available area for roosting and loafing locations to only include areas defined by a wetland polygon layer that delineated wetland, riparian, and wet meadow features (Figure 2.1). This also allowed for a more accurate estimation of some habitat features and excluded areas likely not used by roosting or loafing Sandhill Cranes. For each used location, individual, season, and year, we randomly placed 20 available locations within the 5-km buffered region (Pearse et al. 2021).

We built RSFs using generalized linear mixed effects models with random intercepts for each step and random slopes for each individual (Muff et al. 2019). Including random intercepts accounts for the unequal number of used and available locations per individual (Gillies et al. 2006, Muff et al. 2019), while random slopes allow for individual variation on selection (Gillies et al. 2006, Hebblewhite and Merrill 2008). For roosting and loafing periods, we examined models that included landcover types as dummy covariates (i.e., 1 if the location was the

specified landcover type, 0 otherwise), along with ownership type as a dummy covariate (i.e., 1 if location was specified as private, 0 otherwise). We included the habitat covariates proportion of water, proportion of sandbar, vegetation height, and distance to the nearest grain field. We examined both a linear effect of water and a quadratic effect of water, but we did not include any other interactions. We used a GLMM with a Poisson distribution and a log link. While the response variable is still binary (i.e., 1 for present, 0 for absent), the Poisson model with stratum-specific intercepts is equivalent to a conditional logistic regression model often used for habitat selection studies (McCullagh and Nelder 1989, Muff et al. 2019). Additionally, recent habitat selection studies refer to modeling selection as a function of location-specific covariates as step-selection functions (e.g., Fieberg et al. 2021), but we opted to keep the term resource selection function, as we were not examining a trajectory or step lengths. We used Akaike's Information Criterion (AIC) to compare models (Akaike 1973, Burnham and Anderson 2002). To examine covariate effects on selection strength, we removed the intercept from the top model, applied the coefficients to the observed values of the covariate of interest while holding the other covariates at their mean (i.e., zero), and exponentiated (Muff et al. 2019, Fieberg et al. 2021). We used the delta method to estimate the variance of the prediction. Next, we used a method described by Fieberg et al. (2021) to calculate the likelihood of a sandhill crane selecting one landcover type over another. Specifically, we calculated selection (above) across all observed covariate values and combinations, summed this value across all locations for the landcover type of interest, and divided it by the sum of selection for each of the other landcover types. Finally, using the population-level coefficient estimates to identify areas in the SLV where RMP Sandhill Cranes are most likely to roost and loaf, we projected our models to the most recent year (2022) of

environmental data across the SLV. We applied each of the top models for roosting and loafing to the entirety of the SLV and identified areas with relatively high selection strength.

Because we did not have continuous, measurable covariates for foraging areas, we only examined how crop type (alfalfa, potatoes, barley, rye, triticale, wheat, wetland, pasture, other crops) influenced selection in autumn and spring. We predicted that grains would have the greatest selection strength for both seasons, with barley being the highest, followed by other grains, and then potatoes, alfalfa, and pastures.

Model validation

We used methods from Boyce (2002) to ensure that our roosting and loafing models had good predictive capabilities using covariates from the top models. We used cross-validation by splitting the dataset into training and testing datasets, where 80% of the data was randomly assigned to the training dataset and the remainder was assigned to the testing dataset. The training data were used in the top model for each season, and the resulting model generated predictions using the testing data (Boyce et al. 2002, Fieberg et al. 2018). This was repeated for 1,000 iterations. We then examined the correlation between the expected and the observed observations and considered a value >0.90 to indicate a model with adequate predictive capabilities. We did not complete predictive checks for foraging models because we were only able to examine one covariate on selection and did not have continuous covariates.

Functional response

We used methods described by Holbrook et al. (2019) to examine if use of roosting and loafing areas changed with availability on public or private lands. We first converted proportion of water to area by multiplying NDWI values by 900 m^2, and we summed the total area each for used and available points on public and private lands for all individual Sandhill Cranes. We used

approach 2 described in Holbrook et al. (2019) and fit a general linear model (GLM) with the log of water area at used points as the response variable and the log of water area at available points as the explanatory variable. We also included ownership type and fit both an additive model and a model with an interaction between water area and ownership type. A slope of 1 for the covariates indicated selection of water (or ownership type) proportional to its availability, but a significant deviation from 1 indicates increasing or decreasing selection as availability increases.

RESULTS

The roosting model with a quadratic effect of water performed better than the model with a linear effect for both seasons. The proportion of water had a positive effect on selection in both seasons (Figure 2.2, Figure 2.3A), while the proportion of sandbar also had a positive effect (Figure 2.2). Vegetation height had a negative effect on selection for both seasons, but there was a stronger effect in autumn than in spring (Figure 2.2, Figure 2.4A). Selection strength dropped to zero above approximately 2.5 m in height in autumn, while there appeared to be a greater tolerance for taller vegetation in spring. Distance to the nearest grain field had a negative effect on selection (Figure 2.2, Figure 2.5A), but the effect was stronger in autumn than in spring. Selection for private land was higher than for public land (Figure 2.2). For both autumn and spring, RMP sandhill cranes were more likely to roost on open water than other landcover types, followed by wetland habitat (Table 2.3, Figure 2.2).

The loafing model with a quadratic effect of water performed better than the model with a linear effect for both seasons. Covariate effects on selection for loafing areas followed similar patterns as for roosting except for proportion of water and landcover type (Figure 2.2). In autumn, selection for the proportion of water peaked around 50% water, while it peaked around 30% water in spring (Figure 2.3B). Vegetation height had a negative effect on selection for both

seasons (Figure 2.2, Figure 2.4B). Distance to the nearest grain field also had a negative effect on selection similar to roosting, but selection dropped to zero more quickly (Figure 2.2, Figure 2.5B). Selection for private land was higher than for public land (Figure 2.2). For both autumn and spring, RMP sandhill cranes were more likely to loaf on wetlands than other landcover types, followed by pastures (Table 2.3, Figure 2.2).

Several areas showed a relatively high selection strength for both roosting and loafing in both seasons (Figure 2.6). Using Figure 2.6, the MVNWR showed a greater area of locations with high selection strength than the reference private area along the Rio Grande River in spring, but this pattern was less pronounced in autumn. There were fewer and smaller areas that showed a high selection strength for loafing across the SLV. Compared to roosting, loafing areas of moderate to high selection strength were more dispersed throughout the mapped region.

From the foraging model, for both seasons, selection was highest for grain crops overall, but there was a difference in the types of grain that had the highest selection strength between autumn and spring (Figure 2.7). While barley had the highest selection strength in both seasons, other grains and triticale also had relatively high selection strengths in autumn. Selection for these grains was lower in spring. There was also higher variability among individuals in selection for grains other than barley. Compared to wheat and rye, potatoes, pasture, and alfalfa had higher selection strengths in both seasons, but their confidence intervals overlapped.

Model validation

Overall, our models showed a relatively high predictive accuracy with the exception of the autumn roosting model. The correlation coefficient between the expected and observed RSF values for the roosting models were 0.66 and 0.92 for the autumn and spring models, respectively. The loafing models showed correlations of 0.94 for autumn and 0.95 for spring.

Functional response

We detected a functional response to water based on the ownership type for roosting selection in both autumn and spring but not for loafing selection (Figure 2.8). In all cases except spring roosting, the model with an interaction between water area and ownership type did not improve model fit, so interpretations are from the additive models (Table 2.4). For autumn roosting, use was proportional to availability for both private and public land, but the rate of increase declined as availability increased. There was also higher use on private than public land (Figure 2.8). We found that use also increased as water availability increased on public lands in spring, but use declined with increasing availability on private land, indicating avoidance of private lands and a stronger preference for public lands with increasing surface water for roosts. For the loafing period, we found little evidence of use as a function of availability. There was a slight apparent increase in the area used for private over public lands in autumn but no difference in spring.

DISCUSSION

Our results on the resource selection of roosting, loafing, and foraging RMP Sandhill Cranes in the SLV provide information on the habitat features important to this species during autumn and spring migration. The direction of the effects of vegetation height and distance to the nearest grain field were similar among roosting and loafing RMP Sandhill Cranes, but we found slight differences in their preference for the proportion of water and landcover type between roosting and loafing. In general, RMP Sandhill Cranes preferred to roost and loaf in wet areas with short vegetation and close to grain fields. Roosting cranes showed a stronger selection for open water and wetlands, whereas wetlands and pasture were more preferred for loafing. There were also several differences in the strength of selection when comparing autumn to spring.

Additionally, ownership type played an important role in selection and indicated that both public and private lands provide roosting and loafing habitat at different times of the year.

Consistent with other studies, vegetation, water, and sandbar influenced selection by roosting and loafing Sandhill Cranes in the SLV. Vegetation height had a negative influence on selection for roosting and loafing selection and in both seasons, which agreed with our hypothesis. Surrounding vegetation heights below 2.5 m within 100 m of roosting and loafing locations had the highest selection strength in autumn, while there appeared to be a greater tolerance for taller (but still < 5 m) vegetation in spring. Vegetation could include emergent vegetation, shrubs, and or trees along riverine habitats. Sandhill cranes rely on vision to detect predators or disturbance, so having relatively short vegetation is likely ideal (Krapu et al. 1984, Pearse et al. 2017). Additionally, areas with a greater proportion of water positively influenced selection for roosts and loafing areas, but selection strength peaked around 25 to 50% for loafing areas. Other studies have identified shorter vegetation heights with wide channel or bank widths and shallow water being selected by roosting Sandhill Cranes (Kauffeld 1981, Krapu et al. 1984, Folk and Tacha 1990, Pearse et al. 2017, Boggie et al. 2018). For example, Pearse et al. (2017) and Krapu et al. (1984) found that roosting Sandhill Cranes tended to select for areas with vegetation height no taller than approximately 8 m. Loafing RMP Sandhill Cranes also preferred areas with shorter vegetation, but the combination of a positive effect of sandbar and a peak in the selection of proportion of water may indicate dryer conditions than roosting areas. While we were not able to measure water depth directly, a mix of water and sandbar might represent shallow water (Iverson et al. 1987). Sandhill Cranes at other staging areas tend to roost in water depths < 30 cm (Kauffeld et al. 1982, Norling et al. 1992), and it is likely they also loaf in areas with shallow water. Boggie et al. (2018) found that RMP Sandhill Cranes used roosting areas

with a greater proportion of sandbar in their wintering areas, but they did not explicitly examine loafing areas. Although our results are consistent with RMP Sandhill Cranes selecting dryer areas when loafing than when roosting in the SLV, the presence of water was still an important factor.

We found distance to grain fields to be influential for both roosting and loafing RMP Sandhill Cranes, with selection decreasing with increasing distance from grain fields. Having both roosting and loafing areas close to foraging areas can reduce energy expenditure during migration (Sparling and Krapu 1994, Jankowiak et al. 2015), which is a time when maintaining adequate energy reserves may be important for reproduction or survival (Ankney and MacInnes 1978, Alisauskas 2002, Devries et al. 2008). At the same time, we expected the magnitude of the effect to differ between autumn and spring, as resources (i.e., waste grain) become depleted closer to roosting and loafing areas. We only found this to be true for roosting areas but not loafing areas. For autumn roosting and loafing and spring loafing, distances >5 km showed a selection strength near zero, whereas the decline was more gradual for spring roosting. A distance of 5 km has been shown to be the maximum distance greater Sandhill Cranes from other populations travel between roosting or loafing areas and foraging areas (Sparling and Krapu 1994, Ivey et al. 2015, Boggie et al. 2018). Collins et al. (2023) also found that wintering greater Sandhill Cranes from the Lower Colorado River Valley population flew further (up to 10 km) to grain than other potential foraging sites. We found that RMP Sandhill Cranes seemed to select roosts further from grain fields than when they select loafing sites, particularly in spring. Traveling shorter distances during the day, rather than going back to roosts, can also help Sandhill Cranes reduce energy expenditure (Collins et al. 2023). Loafing areas allow Sandhill Cranes to forage on other food sources (e.g., invertebrates) that provide nutrients (e.g., protein, calcium) less available in agricultural foods (Reinecke and Krapu 1986, Ballard et al. 2000).

Sandhill Cranes engage in other important behaviors during migration, such as courtship, preening, and drinking water, that are often observed more frequently during the loafing period (Tacha 1981, Tacha et al. 1987). Our results provide additional evidence that having adequate foraging areas nearby is important for both roosting and loafing RMP cranes in the SLV.

Roosting and loafing Sandhill Cranes showed preferences for certain landcover types in the SLV, and public and private land both played important roles in each season. For roosting, the highest selection strength was for open water compared to other landcover types in both seasons, and selection was higher for private areas than public areas overall. For loafing, pastures or wetland areas were more likely to be selected than open water, and private areas had a higher selection strength. Sandhill Cranes have been documented roosting or loafing in areas identified as pasture, wet meadows, and grasslands in other studies (Krapu et al. 1984, Iverson et al. 1987, Davis 2003). These areas are generally characterized by shallow water with relatively short vegetation. The use of open water areas for roosting may further emphasize preference for relatively unobstructed views and deeper water during this time of the day. Additionally, selection for open water areas was slightly stronger in autumn than in spring, which may be due to water availability. Water is more limited during autumn and could be restricted to more permanent or semi-permanent water bodies. While selection strength was higher for private areas, public areas like the MVNWR are better able to specifically manage water for roosting Sandhill Cranes (U.S. Fish and Wildlife Service 2015, Wetland Dynamics 2019), which may be particularly beneficial for Sandhill Cranes during autumn.

We detected a functional response to surface water availability by roosting, but not loafing, RMP Sandhill Cranes on both public and private land. Our results showed that as water availability increased during the roosting period, selection also increased on both public and

private land in autumn. We found a similar pattern for roosting RMP Sandhill Cranes in spring for public land but use decreased with availability on private land. Our results suggest that public areas are preferred for roosting in spring, as the functional response indicates a preference for water on public land (Holbrook et al. 2019). Availability, however, may be driving the use of private property, as more surface water is available on privately managed property. Despite the high availability of water available on private areas in spring, there appears to be a preference for public areas for roosting RMP Sandhill Cranes. For loafing RMP Sandhill Cranes, use did not change with availability on public or private land.

Grains were the dominant crop type used by foraging RMP Sandhill Cranes in both seasons, but barley was not the only important grain type, which was inconsistent with our original hypothesis. Autumn RMP Sandhill Cranes showed their highest selection strength for barley followed by triticale, while probability was highest for barley in spring. Grains provide a high amount of carbohydrates, which are used to synthesize the deposition of lipids, and often dictate Sandhill Crane distribution throughout their range (Anteau et al. 2011, Boggie et al. 2023, Collins et al. 2023). Migrant Sandhill Cranes in other populations also consume a diet high in carbohydrates and primarily select agricultural grains, including corn and wheat (Krapu et al. 1984, Anteau et al. 2011). The difference in the use of triticale in the SLV between spring and autumn is likely due to availability. Of the grains grown in the SLV, triticale makes up only approximately 1% of the total crop area (Rio Grande Water Conservation District 2022). Given the relatively low amount of triticale grown, these fields may be depleted soon after the arrival of Sandhill Cranes in autumn, leaving less triticale available the following spring. Preference for triticale may also be due to the chemical and physical properties of the grain type. Barley and triticale have similar energetic contents, but they can differ in carbohydrate content and other

chemical characteristics (Rodehutscord et al. 2016, Siegert et al. 2022), which may make triticale more favorable than barley to Sandhill Cranes.

While our study focused on the population-level decision patterns of RMP Sandhill Cranes, other methods exist that could elucidate individual-level behaviors related to habitat selection. Several covariates, including vegetation height and landcover type, showed high variation across individuals, indicating that other factors may influence selection by RMP Sandhill Cranes. For example, if pairs of Sandhill Cranes are successful breeders, their offspring will generally stay with the parents until the following spring (Gerber et al. 2020), and adults with young in autumn may select habitat differently than those without young. Additionally, another important consideration is body condition, or the overall health of an individual bird. Body condition can influence habitat selection and overall stopover time, as birds may need to remain at a stopover until they reach a threshold in energetic content and may select habitats that more rapidly increase their lipid accumulation (Hedenström and Alerstam 1997, Alerstam and Hedenström 1998, Eikenaar and Schläfke 2013). Further examination of individual-level habitat use patterns in the future will add to the growing body of work on Sandhill Cranes land use patterns.

Finally, we recognize that there are limitations to our models and acknowledge several other methods exist to determine habitat selection. Our analysis and model building were specific to the SLV in Colorado, and caution should be taken if extrapolating the RSF to other areas. Additionally, we were not able to provide a measure of accuracy in our estimates of habitat covariates (e.g., surface water) derived using SMA. Several other studies have utilized SMA to determine habitat use by animals using similar methods and have reported a high degree of accuracy (Donnelly et al. 2020, Bunting et al. 2022). At the same time, our approach to

validating our models showed a high degree of predictive ability in the SLV for spring roosting and both autumn and spring loafing Sandhill Cranes, which may indicate that our estimates for surface water and other covariates are suitable for predicting roosting and loafing areas for Sandhill Cranes in the SLV. However, the low predictive ability of the autumn roosting model could be due to missing covariates that may better explain roost selection during this time, such as disturbance from hunting for waterfowl or other covariates that may better explain roosting in autumn. There are several covariates that we did not consider due to a lack of data availability, but future work could assess the effects of attributes such as channel width and wetland type on habitat selection (Iverson et al. 1987, Pearse et al. 2017).

In summary, we identified habitat features important in the selection by RMP Sandhill Cranes for roosting, loafing, and foraging. We also found that ownership type was an important factor to consider, indicating that habitat characteristics and availability differ between public and private lands. Sandhill Cranes in the SLV are selecting for roosting and loafing areas with short vegetation (< 10 m), close to grain fields (< 5 km), and with >25% open water in both autumn and spring and showed a preference for open water areas, wetlands, and pastures. Our functional response analysis also indicated that RMP Sandhill Cranes select more strongly for public areas for roosting as water becomes more available.

Understanding the factors that drive habitat selection is important because habitat quality and resources may influence fitness components of populations (Alisauskas 2002, Devries et al. 2008, Sedinger and Alisauskas 2014, Matthiopoulos et al. 2015). As a long-lived bird, Sandhill Cranes may be particularly susceptible to habitat changes that affect their ability to meet energetic demands during migration. It is also informative for land managers when resources are limited or costly to obtain and manage. Resources and jurisdictions are often limited for either

private landowners or state and federal agencies managing property, which may reduce habitat availability for some species. Management on federal lands in the SLV, for example, is largely focused on Sandhill Cranes and waterfowl, but ranching and grazing greatly influence habitat on private lands even if water is available. Ultimately, we found that both public and private lands are important for the resource selection of RMP Sandhill Cranes, particularly for roosting and loafing cranes, and at different times of the year. Although we did not consider specific management actions, selection for public lands, particularly in spring, may indicate that management on public areas is providing the necessary resources migrating Sandhill Cranes need, particularly for roosting. At the same time, when roosting and loafing habitats are limited on public lands, private areas can provide appropriate habitat conditions throughout the year.

TABLES AND FIGURES

Table 2.1: The number (n) of unique telemetered RMP Sandhill Cranes and the mean number ($\bar{x}$) and standard deviation (SD) of roosting, loafing, and foraging locations they used in the San Luis Valley, Colorado.

	Roosting			Loafing			Foraging		
Year	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Autumn									
2015	9	16.44	10.22	10	11.80	6.27	11	36.55	20.09
2016	14	18.71	14.90	14	17.07	13.05	14	25.29	14.79
2017	9	22.78	16.98	9	25.67	12.48	10	37.30	25.31
2018	6	16.00	11.61	7	31.86	12.06	10	86.60	65.75
2019	10	18.90	13.06	15	29.27	19.90	17	102.65	80.82
2020	12	19.00	13.54	27	27.56	19.37	32	100.81	78.72
2021	14	24.57	19.96	16	31.56	22.71	22	95.09	94.07
2022	9	23.00	18.52	9	31.00	15.39	12	108.08	75.65
Spring									
2015	29	13.86	8.86	26	12.69	7.58	29	41.17	22.77
2016	23	12.78	12.30	21	16.14	12.68	21	30.52	12.03
2017	16	14.19	10.89	15	16.80	9.58	15	32.00	17.99
2018	14	16.07	12.33	15	26.47	12.11	14	70.14	51.55
2019	13	13.92	14.14	10	21.10	7.67	13	75.46	41.91
2020	46	19.89	14.79	46	22.91	13.69	48	94.02	53.76
2021	57	23.00	13.71	56	24.43	13.05	57	104.39	50.09
2022	31	19.90	15.07	29	22.52	11.30	31	96.68	54.18

Table 2.2: The mean and median distances (m) telemetered RMP Sandhill Cranes moved between consecutive days (i.e., < 1.5 days apart) during autumn and spring migration in the San Luis Valley, Colorado.

Season	Period	Mean distance (95% CI)	Median distance
Autumn	Roosting	2,419.39 (2,226.82, 2,611.96)	157.46
	Diurnal	2,130.86 (1,943.72, 2,318.001)	666.62
Spring	Roosting	5,165.03 (4,807.02, 5,523.04)	373.96
	Diurnal	4,457.451 (4,162.745, 4,752.16)	1100.66

Table 2.3: The likelihood of Rocky Mountain Population Sandhill Cranes roosting or loafing in one landcover type (rows) over another landcover type (columns) based on the top performing selection model and using methods described by Fieberg et al. (2021). Values with asterisks represent ratios where the value is greater than one, indicating the landcover type in the row is more likely to be selected than the landcover type in the column.

	wetland	grassland	open water	other	pasture	
wetland	1.00	21.57*	0.27	39.64*	25.07*	autumn roosting
grassland	0.05	1.00	0.01	1.84*	1.16*	
open water	3.74*	80.66*	1.00	148.26*	93.77*	
other	0.03	0.54	0.01	1.00	0.63	
pasture	0.04	0.86	0.01	1.58*	1.00	
wetland	1.00	45.33*	0.90	10.83*	4.62*	spring roosting
grassland	0.02	1.00	0.02	0.24	0.10	
open water	1.11*	50.24*	1.00	12.01*	5.12*	
other	0.09	4.18*	0.08	1.00	0.43	
pasture	0.22	9.81*	0.20	2.34*	1.00	
wetland	1.00	22.13*	33.72*	4.72*	3.18*	autumn loafing
grassland	0.05	1.00	1.52*	0.21	0.14	
open water	0.03	0.66	1.00	0.14	0.09	
other	0.21	4.69*	7.15*	1.00	0.67	
pasture	0.31	6.95*	10.60*	1.48*	1.00	
wetland	1.00	51.14*	29.17*	4.02*	4.81*	spring loafing
grassland	0.02	1.00	0.57	0.08	0.09	
open water	0.03	1.75*	1.00	0.14	0.16	
other	0.25	12.73*	7.26*	1.00	1.20*	
pasture	0.21	10.63*	6.06*	0.84	1.00	

Table 2.4: Coefficient (β) estimates and their standard errors for the effect of area of water available on the area of water used by roosting and loafing RMP Sandhill Cranes in the San Luis Valley, Colorado (2015-2022) during the autumn and spring.

	Water area β	Ownership β	Water area*ownership β
Autumn roosting	0.58 (0.22)	1.37 (0.49)	*NA*
Spring roosting	0.52 (0.17)	2.88 (1.21)	-0.94 (0.35)
Autumn loafing	0.08 (0.10)	1.10 (0.38)	*NA*
Spring loafing	0.06 (0.09)	0.33 (0.35)	*NA*

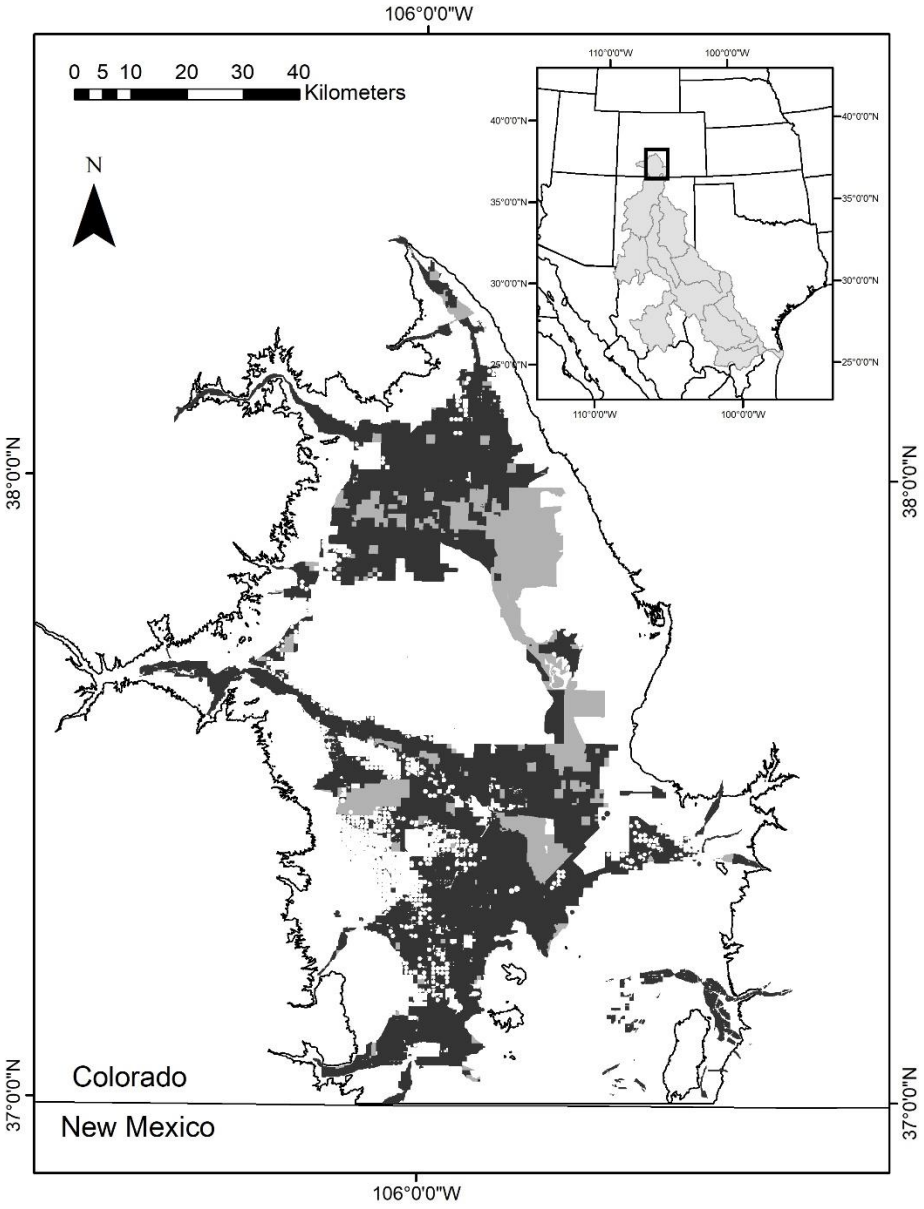

Figure 2.1: The study area used by greater Sandhill Cranes during autumn and spring, 2015-2022. The solid black line outlines the San Luis Valley, and the light gray lines outline the Rio Grande Basin. Within the San Luis Valley, the dark gray indicates private areas and the light gray indicates public areas.

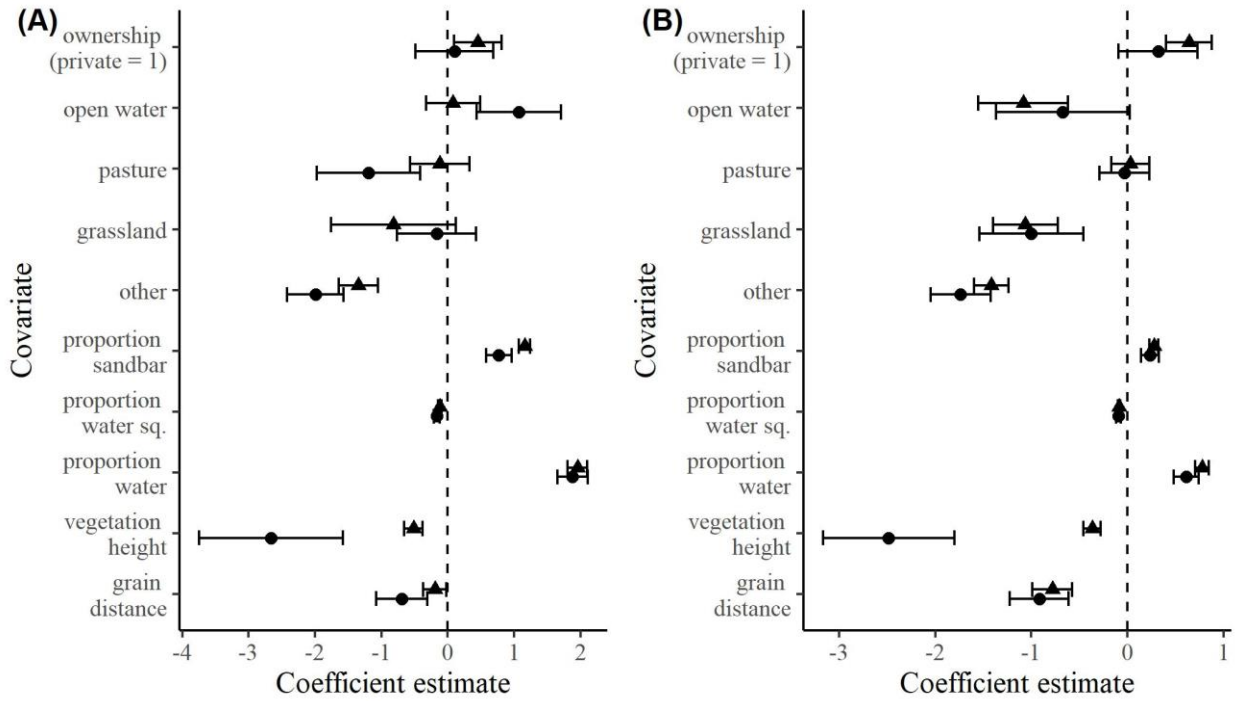

Figure 2.2: The effect of covariates on the selection strength of (A) roosting and (B) loafing areas by Rocky Mountain Population Sandhill Cranes in the San Luis Valley, Colorado 2015-2022 in autumn (●) and spring (▲). The reference level for landcover types (open water, pasture, grassland, other, and wetland) is wetland. The dashed vertical line represents zero, and the horizontal bars represent 95% confidence intervals. Covariates were scaled to have a mean of zero and standard deviation of one.

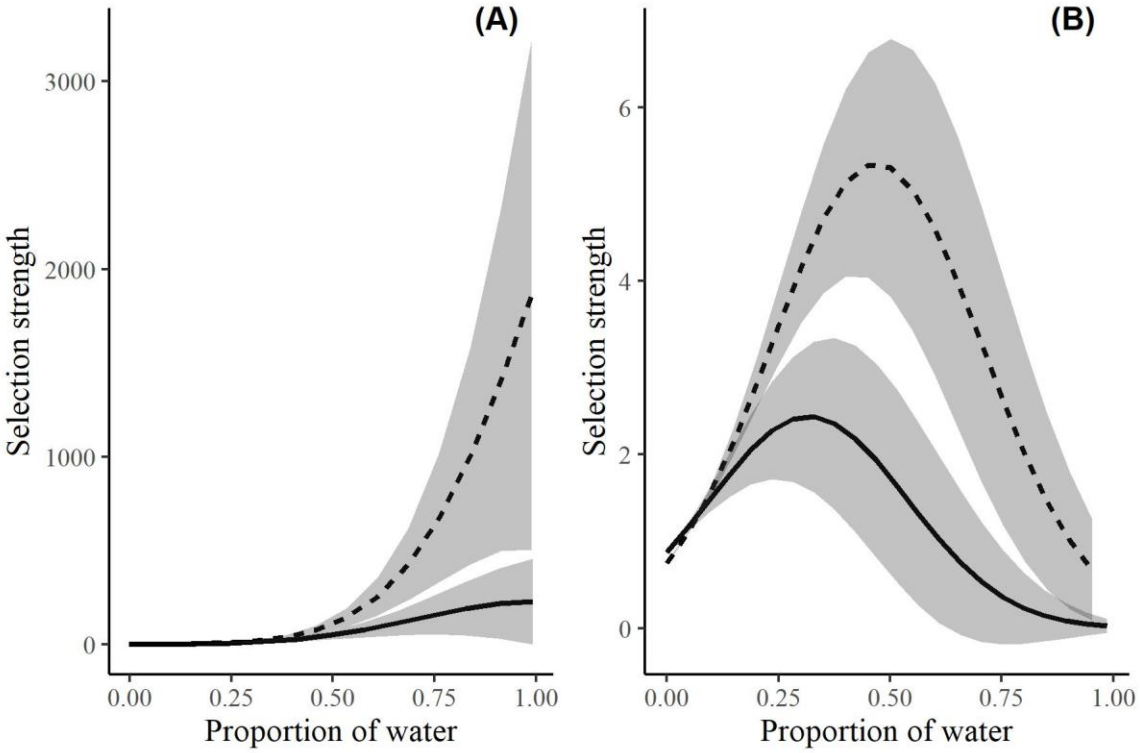

Figure 2.3: The effect of proportion of water on selection by (A) roosting and (B) loafing greater Sandhill Cranes during autumn (solid line) and spring (dashed line) migration in the San Luis Valley, Colorado, 2015-2022. The shaded regions are 95% confidence intervals. The y-axes are scaled differently.

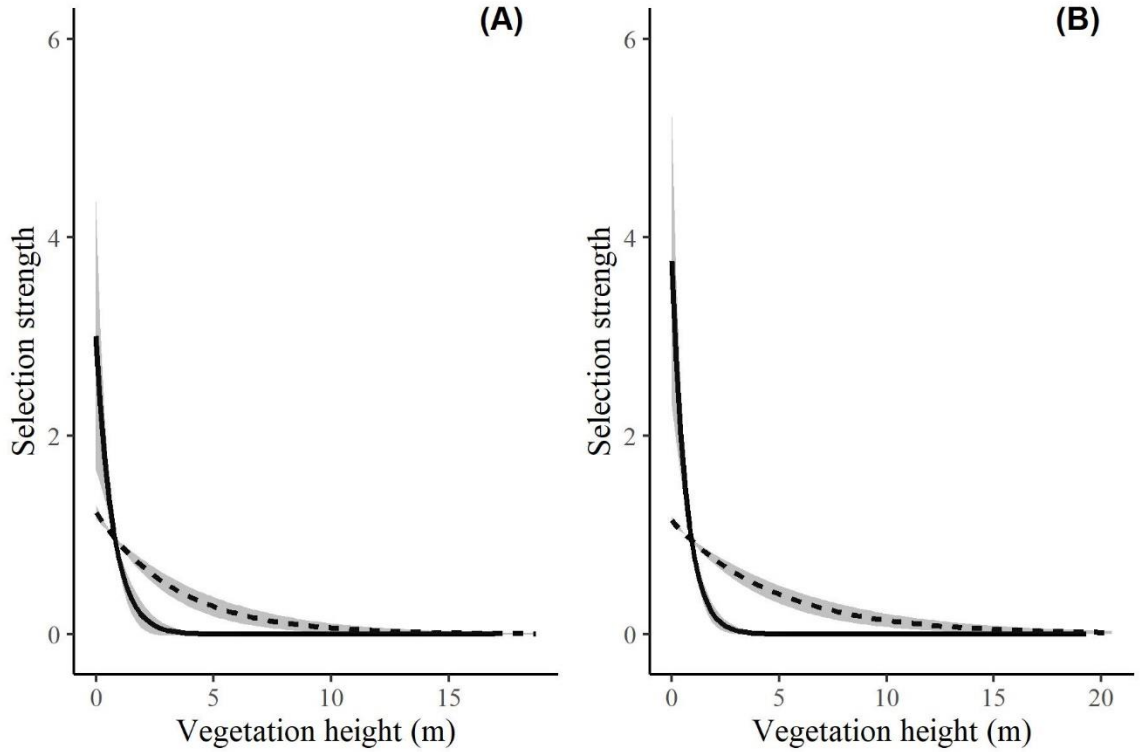

Figure 2.4: The effect of vegetation height on selection by (A) roosting and (B) loafing greater Sandhill Cranes during autumn (solid line) and spring (dashed line) migration in the San Luis Valley, Colorado, 2015-2022. The vertical bars are 95% confidence intervals. The y-axes are scaled differently.

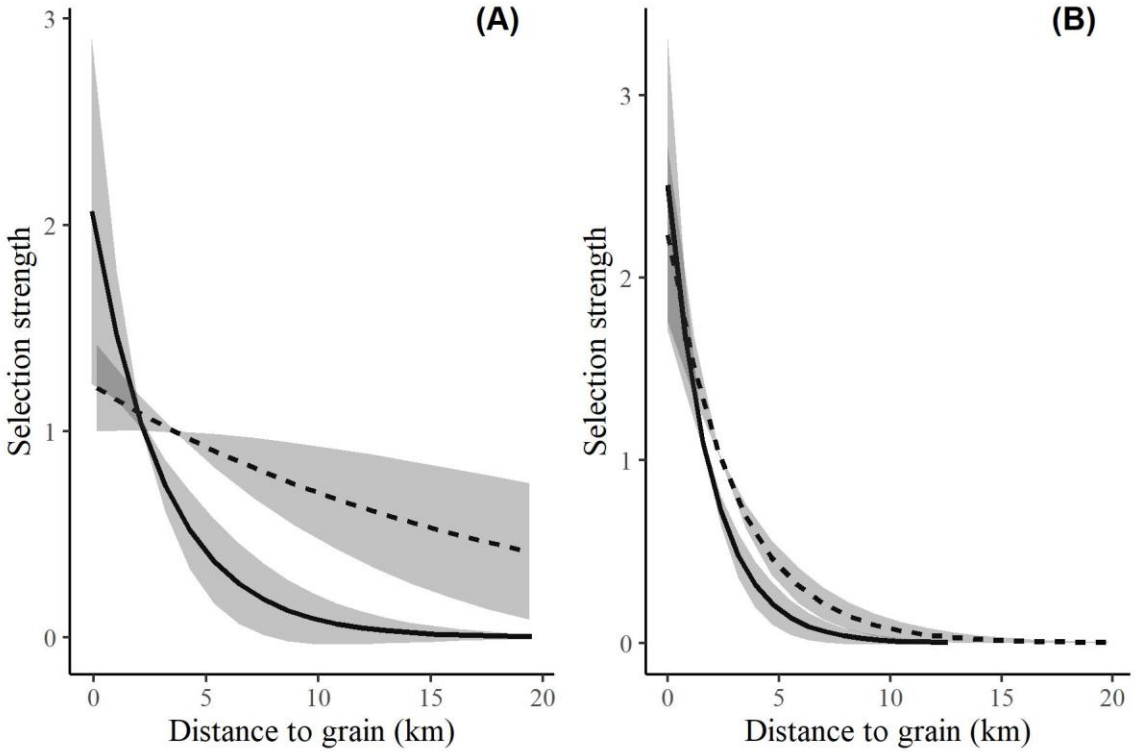

Figure 2.5: The effect of distance to the nearest grain field on selection by (A) roosting and (B) loafing greater Sandhill Cranes during autumn (solid line) and spring (dashed line) migration in the San Luis Valley, Colorado, 2015-2022. The vertical bars are 95% confidence intervals. The y-axes are scaled differently.

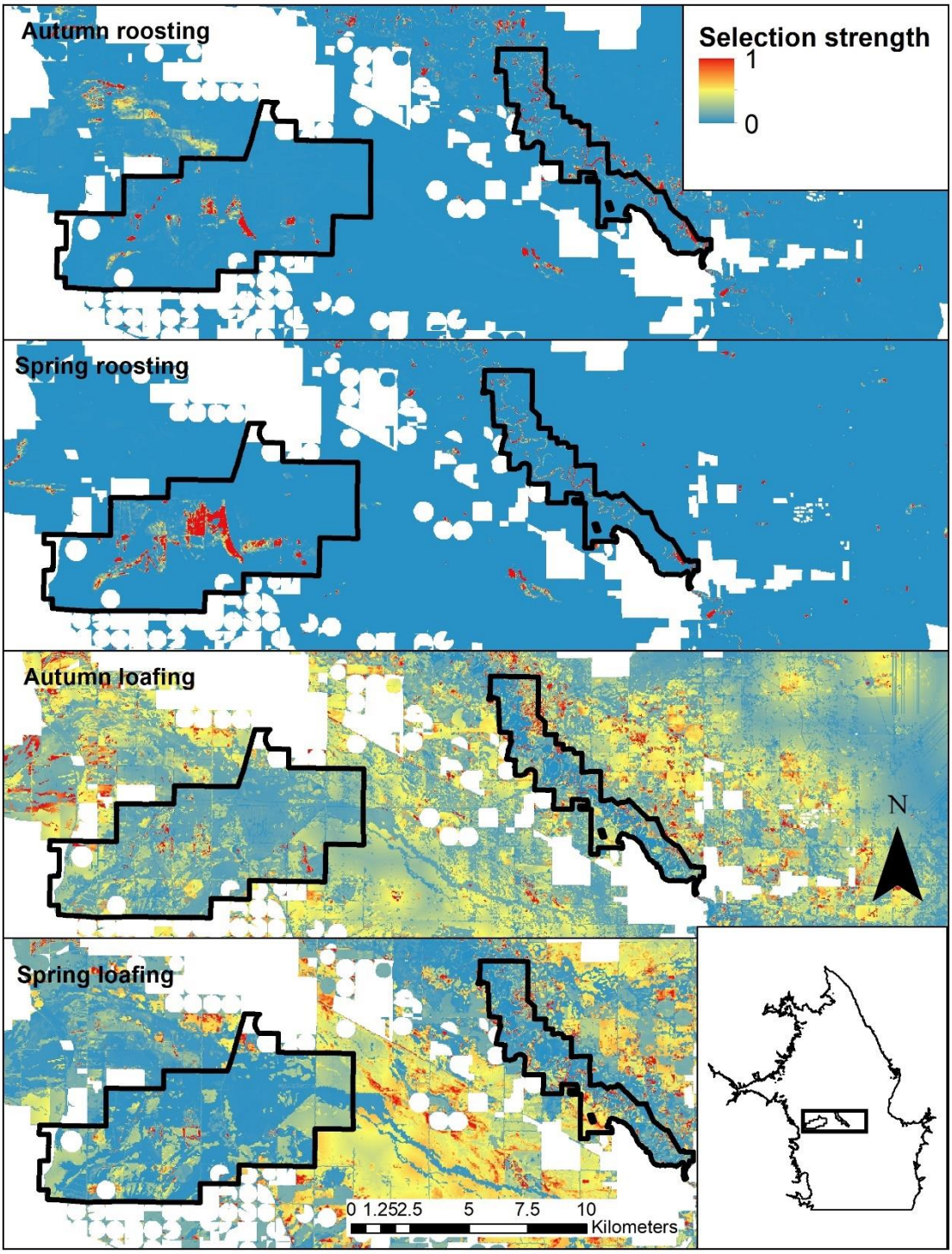

Figure 2.6: The selection strength for roosting and loafing areas across two example areas in the SLV during the autumn and spring of 2021. The public property is the Monte Vista National Wildlife Refuge (left), while the private property is along the Rio Grande River (right).

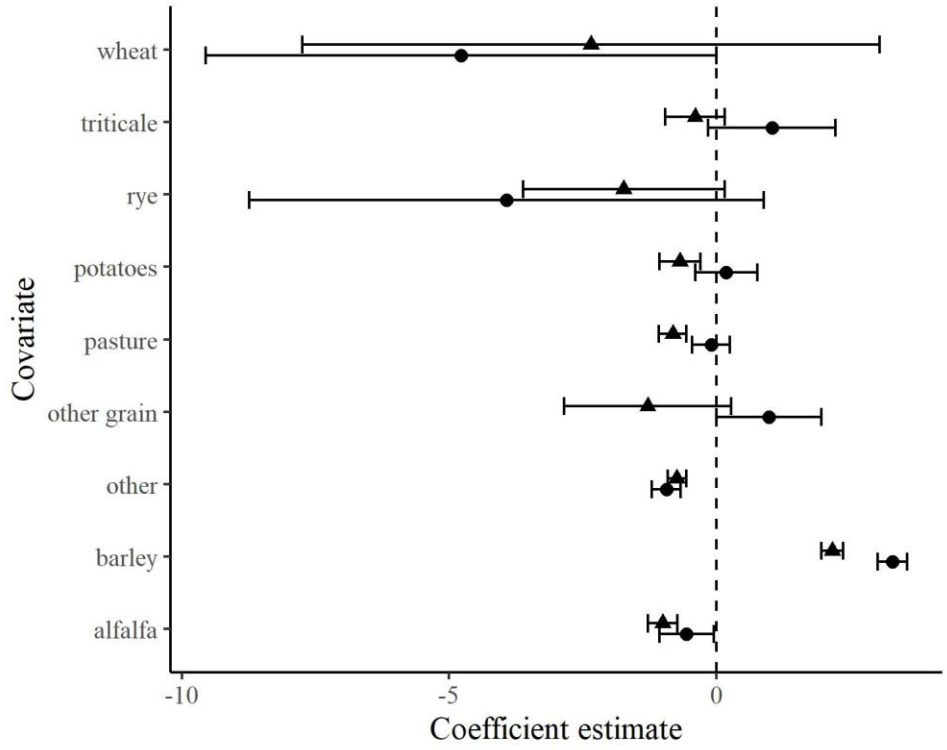

Figure 2.7: The effect of covariates on the selection strength of foraging areas by Rocky Mountain Population Sandhill Cranes in the San Luis Valley, Colorado 2015-2022 in autumn (●) and spring (▲). The reference level for landcover type was wetland. The dashed vertical line represents zero, and the horizontal bars represent 95% confidence intervals.

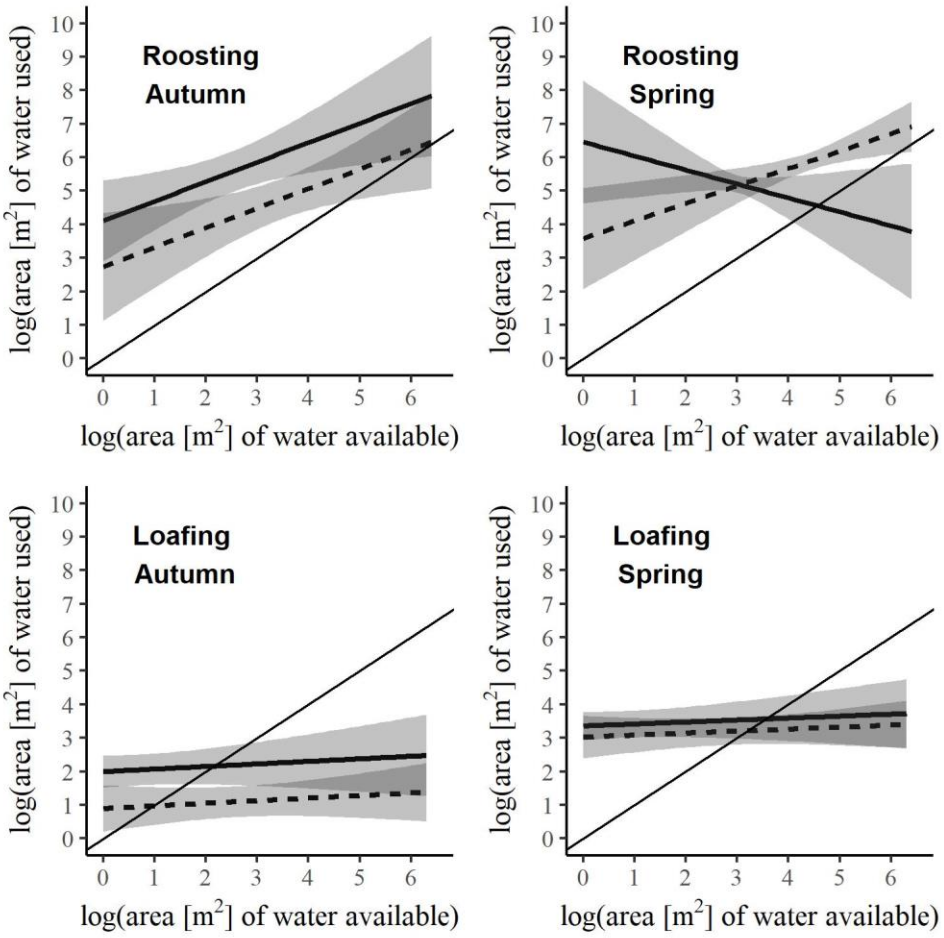

Figure 2.8: The log of the mean area of water used by roosting and loafing greater Sandhill Cranes as more water becomes available on private (solid line) and public (dashed line) land in the San Luis Valley, Colorado, 2015-2022. The reference line has a slope of 1 and represents use in proportion to availability.

LITERATURE CITED

Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008, February. Estimating space-use and habitat preference from wildlife telemetry data. https://doi.org/10.1111/j.2007.0906-7590.05236.x.

Aborn, D. A. 2011. Behavior and habitat use of greater sandhill cranes wintering in east Tennessee. Proceedings of the North American Crane Workshop 11:9–14.

Adams, J. B., and A. R. Gillespie. 2006. *Remote Sensing of Landscapes with Spectral Images*. Cambridge University Press, Cambridge.

Adams, J. B., D. E. Sabol, V. Kapos, R. Almeida Filho, D. A. Roberts, and A. R. Gillespie. 1995. Classification of multispectral images based on fractions of endmembers: application to land-cover change in the Brazilian Amazon. Remote Sensing and Environment 52:137–154.

Albanese, G., and C. A. Davis. 2015. Characteristics within and around stopover wetlands used by migratory shorebirds: Is the neighborhood important? Condor 117:328–340. https://doi.org/10.1650/CONDOR-14-166.1.

Alerstam, T., and A. Hedenström. 1998. The Development of Bird Migration Theory. Source: Journal of Avian Biology 29:343–369.

Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in Midcontinent lesser snow geese. Journal of Wildlife Management 66:181–193.

Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95:459–471. https://doi.org/https://doi.org/10.1093/auk/95.3.459.

Anteau, M. J., M. H. Sherfy, and A. A. Bishop. 2011. Location and agricultural practices influence spring use of harvested cornfields by cranes and geese in Nebraska. Journal of Wildlife Management 75:1004–1011. https://doi.org/10.1002/jwmg.135.

Armbuster, M. J., and A. H. Farmer. 1982. Draft sandhill crane habitat suitability model. Proceedings 1981 Crane Workshop:136–143.

Avgar, T., G. S. Betini, and J. M. Fryxell. 2020. Habitat selection patterns are density dependent under the ideal free distribution. Journal of Animal Ecology 89:2777–2787. https://doi.org/10.1111/1365-2656.13352.

Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. De Lima Serrano Do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: Fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proceedings of the Royal Society B: Biological Sciences 271:875–882. https://doi.org/10.1098/rspb.2003.2663.

Ballard, B. M., Thompson, and Jonathan E. 2000. Winter diets of sandhill cranes from central and coastal Texas. Wilson Bulletin 2:263–268. https://doi.org/10.1676/0043.

Ballard, D. C., O. E. Jones, and A. K. Janke. 2021. Factors affecting wetland use by spring migrating ducks in the southern Prairie Pothole Region. Journal of Wildlife Management 85:1490–1506. https://doi.org/10.1002/jwmg.22096.

Barnett, T. P., J. C. Adam, and D. P. Lettenmaier. 2005, November 17. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature Publishing Group. https://doi.org/10.1038/nature04141.

Barnett, T. P., D. W. Pierce, H. G. Hidalgo, C. Bonfils, B. D. Santer, T. Das, G. Bala, A. W. Wood, T. Nozawa, A. A. Mirin, D. R. Cayan, and M. D. Dettinger. 2008. Human-induced

changes in the hydrology of the western United States. Science 316:1180–1183. https://doi.org/10.1126/science.1139601.

Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use-availability designs. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2245–2254. https://doi.org/10.1098/rstb.2010.0083.

Boggie, M. A., D. P. Collins, and S. A. Carleton. 2023. Availability of supplemental corn for sandhill cranes, light geese, and dabbling ducks wintering in New Mexico. Journal of Fish and Wildlife Management 14:51–61. https://doi.org/10.3996/jfwm-22-013.

Boggie, M. A., D. P. Collins, J. Patrick Donnelly, and S. A. Carleton. 2018. Land use, anthropogenic disturbance, and riverine features drive patterns of habitat selection by a wintering waterbird in a semiarid environment. PLoS ONE 13:1–26. https://doi.org/10.1371/journal.pone.0206222.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution:268–272. https://doi.org/https://doi.org/10.1016/S0169-5347(99)01593-1.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300. https://doi.org/https://doi.org/10.1016/S0304-3800(02)00200-4.

Bunting, D. P., M. A. Boggie, D. P. Collins, P. P. Thorpe, and J. P. Donnelly. 2022. Linking ecological processes and animal movements to inform timing of long-term surveys of a migratory game bird. Ecosphere 13. https://doi.org/10.1002/ecs2.4298.

Bureau of Reclamation. 2021. *West-Wide Climate and Hydrology Assessment*.

Chapman, B. B., C. Brönmark, J. Å. Nilsson, and L. A. Hansson. 2011. The ecology and evolution of partial migration. Oikos 120:1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x.

Chavarria, S. B., and D. S. Gutzler. 2018. Observed changes in climate and streamflow in the Upper Rio Grande Basin. Journal of the American Water Resources Association 54:644–659. https://doi.org/10.1111/1752-1688.12640.

Cody, K. C., S. M. Smith, M. Cox, and K. Andersson. 2015. Emergence of collective action in a groundwater commons: irrigators in the San Luis Valley of Colorado. Society and Natural Resources 28:405–422. https://doi.org/10.1080/08941920.2014.970736.

Collins, D. P., M. A. Boggie, K. L. Kruse, C. M. Conring, J. P. Donnelly, W. C. Conway, and B. A. Grisham. 2023. Roost sites influence habitat selection of sandhill cranes (Antigone canadensis tabida) in Arizona and California. Waterbirds 45. https://doi.org/10.1675/063.045.0407.

Collins, D. P., B. A. Grisham, C. M. Conring, J. M. Knetter, W. C. Conway, S. A. Carleton, and M. A. Boggie. 2016. New summer areas and mixing of two greater sandhill crane populations in the Intermountain West. Journal of Fish and Wildlife Management 7:141–152. https://doi.org/10.3996/042015-JFWM-036.

Colorado Climate Center. 2024. Colorado Climate Center Information. Accessed 9 September 2024. https://climate.colostate.edu/general.html.

Cooper, D. J., J. S. Sanderson, D. I. Stannard, and D. P. Groeneveld. 2006. Effects of long-term water table drawdown on evapotranspiration and vegetation in an arid region phreatophyte community. Journal of Hydrology 325:21–34. https://doi.org/10.1016/j.jhydrol.2005.09.035.

Cristol, D. A., M. B. Baker, and C. Carbone. 1999. Differential migration revisited: Latitudinal Segregation by Age and Sex Class. Pages 33–88 *in* V. Nolan, E. D. Ketterson, and C. F. Thompson, editors. *Current ornithology*. Springer, Boston, MA.

Davis, C. A. 2003. Habitat use and migration patterns of sandhill cranes along the Platte River, 1998-2001. Great Plains Research 13:199–216.

Dettinger, M., B. Udall, and A. Georgakakos. 2015. *Western water and climate change*. Page *Ecological Applications*.

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in Mallards (Anas platyrhynchos). Auk 125:618–628. https://doi.org/10.1525/auk.2008.07055.

Dewitz, J. 2019. National Landcover Database (NLCD). U.S. Geological Survey.

Dewitz, J. 2021. National Landcover Database (NLCD). U.S. Geological Survey.

Donnelly, J. P., S. L. King, J. Knetter, J. H. Gammonley, V. J. Dreitz, B. A. Grisham, M. C. Nowak, and D. P. Collins. 2021. Migration efficiency sustains connectivity across agroecological networks supporting sandhill crane migration. Ecosphere 12. https://doi.org/10.1002/ecs2.3543.

Donnelly, J. P., S. L. King, N. L. Silverman, D. P. Collins, E. M. Carrera-Gonzalez, A. Lafón-Terrazas, and J. N. Moore. 2020. Climate and human water use diminish wetland networks supporting continental waterbird migration. Global Change Biology:1–18. https://doi.org/10.1111/gcb.15010.

Donnelly, J. P., D. E. Naugle, D. P. Collins, B. D. Dugger, B. W. Allred, J. D. Tack, and V. J. Dreitz. 2019. Synchronizing conservation to seasonal wetland hydrology and waterbird migration in semi-arid landscapes. Ecosphere 10. https://doi.org/10.1002/ecs2.2758.

Drent, R. H., G. Eichhorn, A. Flagstad, A. J. Van der Graaf, K. E. Litvin, and J. Stahl. 2007, December. Migratory connectivity in Arctic geese: Spring stopovers are the weak links in meeting targets for breeding. https://doi.org/10.1007/s10336-007-0223-4.

Drewien, R. C., and E. G. Bizeau. 1974. Status and distribution of greater sandhill cranes in the Rocky Mountains. Journal of Wildlife Management 38:720–742.

Eikenaar, C., and J. L. Schläfke. 2013. Size and accumulation of fuel reserves at stopover predict nocturnal restlessness in a migratory bird. Biology Letters 9. https://doi.org/10.1098/rsbl.2013.0712.

Elias, E. H., A. Rango, C. M. Steele, J. F. Mejia, and R. Smith. 2015. Assessing climate change impacts on water availability of snowmelt-dominated basins of the Upper Rio Grande basin. Journal of Hydrology: Regional Studies 3:525–546. https://doi.org/10.1016/j.ejrh.2015.04.004.

Emery, P. A., A. J. Boettcher, R. J. Snipes, and H. J. Mcintyre. 1969. *Hydrology of the San Luis Valley, south-central Colorado*. Denver, Colorado.

Ficklin, D. L., I. T. Stewart, and E. P. Maurer. 2013. Climate change impacts on streamflow and subbasin-scale hydrology in the Upper Colorado River Basin. PloS one 8. https://doi.org/10.1371/journal.pone.0071297.

Fieberg, J. R., J. D. Forester, G. M. Street, D. H. Johnson, A. A. ArchMiller, and J. Matthiopoulos. 2018. Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models. Ecography 41:737–752. https://doi.org/10.1111/ecog.03123.

Fieberg, J., J. Signer, B. Smith, and T. Avgar. 2021. A 'How to' guide for interpreting parameters in habitat-selection analyses. Journal of Animal Ecology 90:1027–1043. https://doi.org/10.1111/1365-2656.13441.

Folk, M. J., and T. C. Tacha. 1990. Sandhill crane roost site characteristics in the North Platte River Valley. Journal of Wildlife Management 54:480–486. https://doi.org/https://doi.org/10.2307/3809662.

Fretwell, S. D. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Institute of Statistics, Mimeograph Series No. 642.

Fronczak, D. L., D. E. Andersen, E. E. Hanna, and T. R. Cooper. 2017. Distribution and migration chronology of Eastern population sandhill cranes. Journal of Wildlife Management 81:1021–1032. https://doi.org/10.1002/jwmg.21272.

Gaillard, J. M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010, July 27. Habitat-performance relationships: Finding the right metric at a given spatial scale. Royal Society. https://doi.org/10.1098/rstb.2010.0085.

Gerber, B. D., J. F. Dwyer, S. A. Nesbitt, R. C. Drewien, C. D. Littlefield, T. C. Tacha, and P. A. Vohs. 2020. Sandhill Crane (Antigone canadensis), version 1.0. Page *in* A. F. Poole, editor. *Birds of the World*. Cornell Lab of Ornithology, Ithaca, NY, USA.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006, July. Application of random effects to the study of resource selection by animals. https://doi.org/10.1111/j.1365-2656.2006.01106.x.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27. https://doi.org/10.1016/j.rse.2017.06.031.

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834–844. https://doi.org/10.1111/j.1365-2664.2008.01466.x.

Hedenström, A., and T. Alerstam. 1997. Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234. https://doi.org/10.1006/jtbi.1997.0505.

Holbrook, J. D., L. E. Olson, N. J. DeCesare, M. Hebblewhite, J. R. Squires, and R. Steenweg. 2019. Functional responses in habitat selection: clarifying hypotheses and interpretations. Ecological Applications 29. https://doi.org/10.1002/eap.1852.

Iverson, G. C., P. A. Vohs, and T. C. Tacha. 1987. Habitat use by mid-continent sandhill cranes during spring migration. Journal of Wildlife Management 51:448–458. https://doi.org/https://doi.org/10.2307/3801033.

Ivey, G. L., B. D. Dugger, C. P. Herziger, M. L. Casazza, and J. P. Fleskes. 2015. Wintering ecology of sympatric subspecies of Sandhill Crane: Correlations between body size, site fidelity, and movement patterns. Condor 117:518–529. https://doi.org/10.1650/CONDOR-14-159.1.

Jankowiak, Ł., P. Skórka, Ł. Ławicki, P. Wylegała, M. Polakowski, A. Wuczyński, and P. Tryjanowski. 2015. Patterns of occurrence and abundance of roosting geese: the role of spatial scale for site selection and consequences for conservation. Ecological Research 30:833–842. https://doi.org/10.1007/s11284-015-1282-2.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71. https://doi.org/10.2307/1937156.

Kauffeld, J. D. 1981. Management of migratory crane habitat on Alamosa and Monte Vista National Wildlife Refuges. Proceedings 1981 Crane Workshop:117–121.

Kinzel, P. J., J. M. Nelson, and A. K. Heckman. 2009. Respones of sandhill crane (Grus canadensis) riverine roosting habitat to changes in stage and sandbar morphology. River Research and Applications 25:135–152. https://doi.org/10.1002/rra.1103.

Krapu, G. L., and D. A. Brandt. 2008. Spring and migratory habits and breeding distirbution of lesser sandhill cranes in west-central New Mexico and Arizona. Proceedings 2008 Crane Workshop:43–49.

Krapu, G. L., D. A. Brandt, K. L. Jones, and D. H. Johnson. 2011. Geographic distribution of the mid-continent population of sandhill cranes and related management applications. https://doi.org/10.1002/wmon.l.

Krapu, G. L., D. A. Brandt, P. J. Kinzel, and A. T. Pearse. 2014. Spring migration ecology of the Mid-Continent sandhill crane population with an emphasis on use of the Central Platte River Valley, Nebraska. Wildlife Monographs 189:1–41. https://doi.org/10.1002/wmon.l013.

Krapu, G. L., D. E. Facey, E. K. Fritzell, and D. H. Johnson. 1984. Habitat use by migrant sandhill cranes in Nebraska. Journal of Wildlife Management 48:407–417. https://doi.org/https://doi.org/10.2307/3801172.

Krapu, G. L., G. C. Iverson, K. J. Reinecke, and C. M. Boise. 1985. Fat deposition and usage by arctic-nesting Sandhill Cranes during spring. Auk 102:362–368. https://doi.org/https://doi.org/10.2307/4086780.

Kruse, K. L., D. P. Collins, C. M. Conring, B. A. Grisham, W. C. Conway, and J. M. Knetter. 2017. Summer habitat selection of the lower colorado river valley population of greater

sandhill cranes. Journal of Fish and Wildlife Management 8:436–448. https://doi.org/10.3996/042017-JFWM-037.

Lewis, J. C. 1979. Taxonomy, food, and feeding habitat of sandhill cranes, Platte Valley, Nebraska. Proceedings 1978 Crane Workshop:21–27.

Littlefield, C. D. 1992. Autumn sandhill crane migration in southeastern Oregon. Proceedings 1988 Crane Workshop:47–54.

Llewellyn, D., and S. Vaddey. 2013. *West-Wide Climate Risk Assessment: Upper Rio Grande Impact Assessment*.

Lovvorn, J. R., and C. M. Kirkpatrick. 1982. *Field Use by Staging Eastern Greater Sandhill Cranes*. Page *Source: The Journal of Wildlife Management*.

Manly, B., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*Second. Kluwer Academic Publishers, Dordrecht.

Matthiopoulos, J., J. Fieberg, G. Aarts, H. L. Beyer, J. M. Morales, and D. T. Haydon. 2015. Establishing the link between habitat selection and animal population dynamics. Ecological Monographs 85:413–436. https://doi.org/10.1890/14-2244.1.

McCullagh, P. and J. A. Nelder. 1989. Generalized Linear Models. Second Edition. Chapman and Hall, New York, USA.

McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010, January. Considering ecological dynamics in resource selection functions. https://doi.org/10.1111/j.1365-2656.2009.01613.x.

Mix, K., V. L. Lopes, and W. Rast. 2011. Annual and growing season temperature changes in the San Luis Valley, Colorado. Water, Air, and Soil Pollution 220:189–203. https://doi.org/10.1007/s11270-011-0746-4.

Muff, S., J. Signer, and J. Fieberg. 2019. Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. Journal of Animal Ecology 89:80–92. https://doi.org/10.1111/1365-2656.13087.

Newton, I. 2007. *The migration ecology of birds*. Academic Press Inc.

Northrup, J. M., E. Vander Wal, M. Bonar, J. Fieberg, M. P. Laforge, M. Leclerc, C. M. Prokopenko, and B. D. Gerber. 2022. Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. Ecological Applications 32. https://doi.org/10.1002/eap.2470.

Pearse, A. T., G. L. Krapu, and D. A. Brandt. 2017. Sandhill crane roost selection, human disturbance, and forage resources. Journal of Wildlife Management 81:477–486. https://doi.org/10.1002/jwmg.21215.

Pearse, A. T., K. L. Metzger, D. A. Brandt, J. A. Shaffer, M. T. Bidwell, and W. Harrell. 2021. Migrating Whooping Cranes avoid wind-energy infrastructure when selecting stopover habitat. Ecological Applications 31. https://doi.org/10.1002/eap.2324.

Reinecke, K. J., and G. L. Krapu. 1986. Feeding ecology of sandhill cranes during spring migration in Nebraska. Journal of Wildlife Management 50:71–79. https://doi.org/https://doi.org/10.2307/3801490.

Rio Grande Basin Roundtable. 2015. Rio Grande Basin Implementation Plan:1–164.

Rio Grande Basin Roundtable. 2022. Rio Grande Basin Implementation Plan Volume 2.

Rodehutscord, M., C. Rückert, H. P. Maurer, H. Schenkel, W. Schipprack, K. E. Bach Knudsen, M. Schollenberger, M. Laux, M. Eklund, W. Siegert, and R. Mosenthin. 2016. Variation in chemical composition and physical characteristics of cereal grains from different genotypes. Archives of Animal Nutrition 70:87–107. https://doi.org/10.1080/1745039X.2015.1133111.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62:327–335.

Rowland, M. M., L. Kinter, T. Banks, and D. C. Lockman. 1992. Habitat use by greater sandhill cranes in Wyoming. Proceedings 1988 North American Crane Workshop:82–86.

San Luis Valley Development Resources Group and Council of Governments. 2023. 2023 San Luis Valley Statistical Profile.

Schmaljohann, H., C. Eikenaar, and N. Sapir. 2022. Understanding the ecological and evolutionary function of stopover in migrating birds. Biological Reviews 97:1231–1252. https://doi.org/10.1111/brv.12839.

Sedinger, J. S., and R. T. Alisauskas. 2014. Cross-seasonal effects and the dynamics of waterfowl populations. Wildfowl 4:277–304.

Siegert, W., T. Zuber, and M. Rodehutscord. 2022. Variability and prediction of metabolisable energy of wheat, triticale, and rye in caecectomised laying hens. European Poultry Science 86. https://doi.org/10.1399/eps.2022.354.

Sparling, D. W., and G. L. Krapu. 1994. Communal roosting and foraging behavior of staging sandhill cranes. The Wilson Bulletin 106:62–77.

Stanley, C. Q., M. R. Dudash, T. B. Ryder, W. G. Shriver, K. Serno, S. Adalsteinsson, and P. P. Marra. 2021. Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking. Ecosphere 12. https://doi.org/10.1002/ecs2.3421.

Suraci, J. P., L. G. Frank, A. Oriol-Cotterill, S. Ekwanga, T. M. Williams, and C. C. Wilmers. 2019. Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. Ecology 100. https://doi.org/10.1002/ecy.2644.

Tacha, T. C. 1981. *Behavior and taxonomy of sandhill cranes from Mid-continental North America*.

Tacha, T. C., P. A. Vohs, and G. C. Iverson. 1987. Time and energy budgets of sandhill cranes from Mid-Continental North America. Journal of Wildlife Management 51:440–448.

U.S. Fish and Wildlife Service. 2015. *Comprehensive conservation plan: San Luis Valley National Wildlife Refuge Complex*. Lakewood, Colorado.

Vanausdall, R. A., W. L. Kendall, D. P. Collins, and Q. R. Hays. 2024. Time of year and weather influence departure decisions of sandhill cranes at a primary stopover. Frontiers in Ecology and Evolution 12. https://doi.org/10.3389/fevo.2024.1279279.

Walker, D. L., and S. D. Schemnitz. 1985. Food habits of sandhill cranes in relation to agriculture in central and southwestern New Mexico.

Warnock, N. 2010. Stopping vs. staging: The difference between a hop and a jump. Journal of Avian Biology 41:621–626. https://doi.org/10.1111/j.1600-048X.2010.05155.x.

Western Regional Climate Center. 2013. Cooperative Climatological Data Summaries. https://wrcc.dri.edu/Climate/summaries.php.

Wetland Dynamics, L. 2019. *San Luis Valley wetland and wildlife conservation assessment*. Monte Vista, CO.

CHAPTER 3 – SANDHILL CRANE FORAGING HABITAT SELECTION DURING SPRING AND AUTUMN MIGRATION IN AN AGRICULTURALLY DOMINATED STOPOVER

INTRODUCTION

Land use change around the world has created areas dominated by agriculture with refugia for wildlife interspersed throughout (Abraham et al., 2005; Krapu et al., 2004). While many species have declined or shown changes in distribution due to increases in farmland in the U.S. and Europe (Krebs et al., 1999; Stanton et al., 2018), a few species, such as cranes and waterfowl, now regularly use or rely on forage provided by agricultural crops at certain times of the year (Alisauskas and Ankney, 1992; Austin et al., 2018; Clausen et al., 2018; Ely and Raveling, 2011; Krapu et al., 1984). The reliance on agricultural forage is high enough that some population changes, distributional shifts, and variation in individual body condition have been linked to changes in agricultural area and practices (Abraham et al., 2005; Austin et al., 2018; Clausen et al., 2018; Fox et al., 2005; Moore et al., 2023). Agricultural crops can provide nutrients that are important to birds throughout their annual cycle (Ely and Raveling, 2011; Fox and Abraham, 2017). Understanding how agricultural areas influence the distribution and habitat use of certain species is of interest to inform management and to anticipate population responses to future landscape changes.

Agroecosystems are generally exploited by migrating birds due to the availability of foods high in energy and nutrients needed for migration, survival, and reproduction (Fox and Abraham, 2017; Overton and Casazza, 2023). Agriculture can offer foods that are consistently available each season, easily attainable and digestible, and high in energy and crude protein content that allow for rapid nutrient reserve accumulation (Fowler et al., 2020; Fox and Abraham, 2017; Prop and Black, 1998). For example, foods high in carbohydrates allow for lipid

deposition (Krapu et al., 1985), which provides some of the energetic demands needed during migration and egg production and is linked to reproductive success the following breeding season for some species (Alisauskas, 2002; Devries et al., 2008). Several studies have documented nonbreeding waterfowl and several crane species using and selecting corn (*Zea mays*), small grains, and other crop types, including rice (*Oryza sp.*), potatoes (*Solanum tuberosum*), and pastures, over natural foods (Alonso et al., 2008; Boggie et al., 2018a; Ely and Raveling, 2011; Gates et al., 2001). Diet studies have also shown that crops make up a majority or a significant proportion of the esophageal contents of some migrating birds in cases where natural foods (i.e., other plant and animal matter) exist and are also being consumed (Ballard and Thompson, 2000; Hemminger et al., 2022; Krapu et al., 2014). Grains in particular are often higher in fat, protein, and metabolizable energy compared to some natural foods, and require less handling time to find and consume (Fox and Abraham, 2017). There is evidence that several populations of cranes and waterfowl have shorter migrations and winter closer to their breeding grounds than they did historically due to the expansion and reliance of agricultural grains along with a decline in area of habitats with natural foods, such as wetlands (Alonso et al., 2008; Fox et al., 2005; Fronczak et al., 2017).

Crop dynamics coupled with other natural seasonal variations can influence the migration patterns of birds in stopover areas where agroecosystems make up most of the available habitat. Stopovers are areas birds use to rest and refuel during migration (Schmaljohann et al., 2022; Warnock, 2010), and migratory birds will use stopovers for variable lengths of time depending on the species, individual condition, and the time of the year (Duijns et al., 2019; Karlsson et al., 2012; Nilsson et al., 2013). Selection theory predicts that individuals will use habitat that will maximize fitness potential (Fretwell, 1969), and during migration this should mean choosing

habitat at a stopover that minimizes energetic output and maximizes energetic intake and nutrient storage (Alerstam and Lindström, 1990). In areas where migratory birds may stage for a considerable amount of time, changes in selection or use often occur in response to changing individual needs, the availability of certain food types, and competition (Collins et al., 2017; Ely and Raveling, 2011; English et al., 2017; Frederick and Klaas, 1982). For example, many migrating geese and waterfowl switch from a diet comprised of a significant amount of high energy foods in winter to one with a higher amount of protein in spring (Ely and Raveling, 2011; Hitchcock et al., 2021), which is important for the formation of eggs, body maintenance during incubation, and lipid transport (Afton and Ankney, 1991; Alisauskas and Ankney, 1985; Hepp et al., 1987; McWilliams et al., 2004). Other factors, such as the availability of certain foods over time, also influence habitat use (Askren et al., 2022; Combs and Fredrickson, 1996). Well-studied examples are the timing of harvest and postharvest treatment, which can influence the availability of seeds and other plant parts (Anteau et al., 2011; Baldassarre et al., 1983; Sherfy et al., 2011). For example, tilling fields (e.g., by discing or chiseling) can reduce the amount of seed available to granivores (Sherfy et al., 2011), and studies have shown birds preferring non-tilled (i.e., idle) crop fields over tilled (Baldassarre et al., 1983, Anteau et al., 2011, Matthews et al., 2022).

Sandhill cranes (*Antigone canadensis*) throughout North America use specific stopover areas every year, and many of these stopovers are dominated by agriculture. The Rocky Mountain Population (RMP) of greater sandhill cranes (*A. c. tabida*), for example, uses the San Luis Valley (SLV) in southcentral Colorado each spring and autumn as a stopover area for up to a month (Donnelly et al., 2021; Vanausdall et al., 2024). The RMP numbers approximately 23,000 individuals on average, but the most recent estimate was at 27,000 (Thorpe et al., 2024).

Approximately 5,000 lesser sandhill cranes (*A. c. canadensis*) from the Midcontinent Population (MCP) also utilize this area during migration each year (Krapu et al., 2011). Staging sandhill cranes roost in wetlands and habitat along rivers and creeks at night and feed in agricultural fields during the day. They primarily feed in barley (*Hordeum vulgare*) fields or less abundant grains, such as triticale (*Triticum aestivum x Secale cereale*), after harvest in September through October, but they have also been observed using pastures, alfalfa, and potatoes for loafing and foraging (Kauffeld, 1981). The Monte Vista National Wildlife Refuge (MVNWR) in the SLV provides roosting habitat and supplemental forage in the form of approximately 90 ha of barley for sandhill cranes and other migrant waterfowl each year. Sandhill cranes tend to prefer foraging areas within 2-5 km of roosting sites (Ivey et al., 2015; Pearse et al., 2017). Minimizing the amount of commuting time between areas reduces energetic expenditure (Austin and Humburg, 1992; Norberg, 1996), which allows individuals to better maintain nutrient reserves during stopover (Pearse et al., 2010). Thus, an important management practice in the SLV and other stopover areas for sandhill cranes is to ensure that there is adequate foraging habitat adjacent to roosting areas.

Several documented and potential future changes may influence how sandhill cranes utilize the SLV, which could ultimately affect their distribution and ability to acquire nutrient reserves. Barley is a major crop type in the SLV, but the amount of barley harvested in the SLV has declined by approximately 60% in the last 20 years and barley sales have declined in the last few decades (USDA National Agricultural Statistics Service Cropland Data Layer, 2023). At the same time, prolonged drought and a decrease in water availability have made growing irrigated crops more expensive and intensive in the SLV and other parts of the Intermountain West (Mix et al., 2011, 2010). The SLV is a snowpack driven region, with most of the water input coming

from snowmelt in the surrounding mountain ranges (Emery 1969). Increasing temperatures have reduced snowpack and increased the growing degree days in the SLV (Barnett et al., 2005; Mix et al., 2010; Pederson et al., 2011; Ray et al., 2008). Barley and potatoes are relatively high in their water needs (Katerji et al., 2008; Pohanková et al., 2018), so continued climate changes and increasing water scarcity may affect the crop types grown due to changes in water availability and temperature (Nie et al., 2021). While the RMP and MCP are relatively stable and appear to be increasing in numbers (Seamans, 2023), it is unknown what a decline in barley or other important resources may do to overall abundance. A better understanding of how they currently utilize foraging areas in the SLV and how they are affected by postharvest treatment (i.e., tillage intensity) will inform potential impacts from landscape changes.

We used data from 2.5 years of sandhill crane observations in the SLV to examine their foraging patterns during spring and autumn migration. The objectives of this study include: (1) identify the distribution of foraging sandhill cranes, (2) determine the effect of crop type, tillage intensity, and associated covariates on selection by sandhill cranes, and (3) determine the effect of the same covariates and number of lesser sandhill cranes present on the abundance of greater sandhill cranes given presence. We also compared results for the last two objectives to determine if there were covariates that influence selection but not abundance and vice versa. We predicted that sandhill cranes would show a gradual increase then decrease in abundance for each season, with a more diffuse pattern in autumn than spring (Vanausdall et al., 2024). We hypothesized that sandhill cranes would select barley or other grains in both seasons. Due to the greater availability of waste grain in autumn than spring, we predicted both roost distance and crop type to effect selection in autumn, with cranes selecting barley fields closer to roost sites. As grain becomes depleted in spring, we expected crop type to be more important than roost distance and that

sandhill cranes would fly farther from roosts to their preferred forage over switching to other crop types. Finally, we predicted that the probability of presence would be greatest on idle fields (i.e., no tilling) and lowest on fields with high intensity tillage.

METHODS

Study area

Our study took place in the SLV, which is in southcentral Colorado, USA and is the northern portion of the Rio Grande Basin (Figure 3.1). The valley floor is about 8,200 km^2 in area and the average elevation is 2,100 m. The SLV is bordered by the San Juan Mountains to the west and the Sangre de Cristo Mountains to the east. Considered a semi-arid region, the SLV receives less than 200 mm of precipitation annually, while the surrounding mountains receive 1,150 – 1,270 mm on average (Cooper et al. 2006). Hydrology is driven by mountain snowpack, which feeds the Rio Grande, the Conejos River, and other rivers, tributaries, and creeks (Emery 1969), but monsoonal rains in the summer can also increase water availability. As a result, surface water throughout the SLV is highly variable within and between seasons. Two aquifers also contribute to the hydrology in the SLV. The average temperature in the SLV is 6°C, but temperatures can range between -20°C to 20°C (Western Regional Climate Center 2013). Wind speeds are variable and primarily come from the south and southwest. Surface and groundwater are further constrained by diversion and extraction due to irrigation. Agriculture is the largest source of base jobs in the SLV, so it is an important economic driver in the region. Water is typically used to irrigate crops using pivot sprinklers, and the main crops grown include potatoes, alfalfa, and small grains, including wheat and barley. Ranching is also an important industry.

We identified six major regions throughout the SLV that together made up most of the area used by migrant sandhill cranes to survey sandhill cranes and summarize crop types and

tillage intensity (Figure 3.1). We identified these areas based on previous research in the SLV and observations of sandhill cranes. Areas varied in size and the amount of time it took to survey.

Roadside surveys

Count data were collected using weekly or bi-weekly roadside surveys conducted each season and year. Routes in each region were driven within a span of 2-4 days each week during the foraging hours of sandhill cranes. Morning surveys were conducted between a half hour before sunrise to approximately 4 hours after sunrise, and evening surveys were conducted between approximately 3 hours before sunset to a half hour after sunset. Survey times were based on both observations of sandhill cranes in the SLV during migration and data from sandhill cranes tagged with Global Positioning Systems in previous years. For each region, we alternated a morning and evening survey each week. During each survey, the same observer drove the route and counted every sandhill crane observed on fields adjacent to the road. We only counted birds that were within a field-width (approximately 1 km) of the road, as flocks that were farther away were difficult to accurately count. We also divided sandhill cranes into one of the two subspecies (greater or lesser) based on overall size and head shape (Schmitt and Hale 1997). We did not differentiate between adults and juveniles.

Habitat covariates

During the roadside surveys, we collected field-specific information for crop fields where sandhill cranes were observed. We determined the crop type (alfalfa, barley, pasture, potatoes, other grain, and other) and the tillage intensity for fields where sandhill cranes were observed. The category “other grain” included crops that were less commonly planted grain types, including winter wheat, triticale, rye wheat, oats, and corn. To determine crop type, we used data gathered annually by the Rio Grande Water Conservation District (RGWCD) for most of the

study area. These data are collected annually by observers who work for RGWCD. We were able to confirm those observations with fields used by sandhill cranes, and there were few instances when the crop type observed by RGWCD did not match our observations. The eastern-most area, Region 6, is in a different groundwater subdistrict, so we had to use a separate data source for this area. We used data from the Cropland Data Layer provided by the U.S. Department of Agriculture to determine crop type in Region 6 (USDA National Agricultural Statistics Service Cropland Data Layer, 2023). There were relatively few areas identified as unknown (n = 90). The proportion of crop types within the sampling area was similar to the entirety of the SLV (Table 3.1), so we are confident our sampling frame was representative of how sandhill cranes used the SLV as a whole.

Tillage intensity of grain fields refers to the degree of tilling that occurs postharvest, with some growers discing or plowing several times and others doing minimum or no tilling. Idle fields had standing stubble, while tilled fields showed variation in tillage intensity. We used the following visual index: idle or complete stubble (0), >75% stubble (1), 50-75% stubble (2), 25-50% stubble (3), and 0-25% stubble (4). We combined these indices into three categories: idle, low intensity till (index values 1 and 2), and high intensity till (index values 3 and 4). We also estimated tillage intensity for grain fields not used by sandhill cranes. These were fields that were surveyed but not assessed for tillage intensity because no sandhill cranes were observed. First, we used Random Forest Classification of satellite imagery to predict the tillage intensity of all fields throughout the study region. We sampled a random set of grain fields each season and year throughout all regions and identified tillage intensity using the index above. We used the tillage intensity classes from the randomly sampled fields, along with the fields used by sandhill cranes from that season and year, as training data in the Random Forest classifier. We used

satellite imagery collected from Landsat 9 Imagery and adjusted for surface reflectance to gather the following image properties to inform the classifier: Bands 1-5 and 7, Normalized Difference Soil Index (NDSI), Normalized Difference Vegetation Index (NDVI), soil cover, and stubble cover. We used the median band values for Landsat images collected between 1 February and 31 March for spring and between 1 September and 31 November for autumn. Soil and stubble cover were determined using spectral mixture analysis (SMA), a technique that classifies fractions of pixels into specified cover classes (Adams and Gillespie, 2006). We used grain fields classified into tillage intensity index value 4 (highly tilled) to generate endmembers of soil from median values of Landsat images and grain fields classified as no-till to generate endmembers of stubble. We included NDVI as a third class in SMA and used the 98th percentile of NDVI values to generate endmembers (Boggie et al. 2018). We then developed a classifier for each year and season because of the between-season variability in weather and environment in the SLV. Overall accuracy for our classifiers ranged between 0.77 for spring and 0.87 for autumn. The classification technique was used only for grain fields, as we expected spectral properties to differ for other crop types. We completed classification and SMA using the publicly available Google Earth Engine (Gorelick et al., 2017).

We determined distance to the nearest potential roost using information from sandhill cranes marked with transmitters fitted with global system for mobile communication (GSM) platform transmitter terminal (PTT) tags (Evolution Series-400, 15-g; Cellular Tracking Technologies, Rio Grande, NJ, USA) or global positioning system (GPS) PTT tags (PTT-100, 22-g Solar Argos/GPS PTT, Microwave Telemetry, Columbia, MD, USA). Data from 59 and 106 telemetered RMP sandhill cranes from 2014-2022 were used to determine potential roosting areas for autumn and spring, respectively. We refer to these roosting areas as “potential” because

we could not confirm that the sandhill cranes we counted and observed during this study were using the same roosting areas used by the sandhill cranes marked with GSM/GPS transmitters. Detailed methods for capture can be found in Collins et al. (2016) and Boggie et al. (2018b). We used these roosting points and generated a 1 km buffer around each point. Potential roosting areas included the entire buffered area for each roosting point. We dissolved the buffers for each season and calculated the distance between these roosting polygons and each individual field (used and not used by sandhill cranes).

Statistical analysis

We developed models using the presence and absence of sandhill cranes on individual crop fields to determine the influence of crop type and roost distance on selection. Our sampling units were the individual fields along each survey route (Anteau et al., 2011). We estimated selection by converting sandhill crane counts to present (1) or absent (0) and used a generalized linear mixed models (GLMM) approach to estimate the log-odds of presence (i.e., selection; Manly et al. 2002). We used a binomial distribution with a logit link and modeled the log-odds of presence as a function of the covariates time (i.e., survey week), distance to the nearest potential roost (roost distance), and crop type (i.e., alfalfa, barley, other grains, pasture, potatoes, and other crop type) as fixed effects and the crop field as a random effect to account for repeated observations. We used a quadratic effect of survey week for time. We compared a model that included only main effects of all covariates to models representing three other *a priori* hypotheses: an interaction between time and distance to the nearest roost, an interaction between time and crop type, and an interaction between crop type and distance to the nearest roost. All interaction models included the non-interactive covariates as main effects. We chose to compare a limited number of models to determine the relative importance of roost distance, crop type, and

roost distance conditional on crop type. Because sandhill cranes are central place foragers, we predicted the time and roost distance interaction model to be the most competitive model in autumn and show a negative effect of roost distance on the log-odds of presence. As resources become depleted near roosts, we predicted that roost distance would be less important in the spring. Sandhill cranes may switch crop types rather than move farther from roosts over time, so we expected the time and crop type interaction model or the crop type and roost distance interaction model to be the most competitive in spring. We scaled and centered roost distance. We compared models using the small-sample Akaike's Information Criterion (AIC_c) and considered models <2 ΔAIC_c to be competitive (Burnham and Anderson, 2002; Vaida and Blanchard, 2005). We examined the coefficients and their effects on the log-odds of presence. We used the inverse logit transformation to examine how changes in covariates influence the probability of presence. We used Program R and the 'glmmTMB' function (Brooks et al., 2017; R Core Team, 2022).

We used a GLMM to examine the number of greater sandhill cranes in response to time and habitat covariates conditional on presence. We used a zero-truncated model with either a Poisson or negative binomial distribution and a log link. We first compared a global, main effects model with either the Poisson or negative binomial distribution and used the distribution from the model with the lower AIC_c. We examined the same set of covariates as for the presence/absence models, but we also examined the influence of the number of lesser sandhill cranes. We again compared models using AIC_c and made inference from highly competitive models.

Finally, we examined a subset of data to determine the influence of tillage intensity on presence. We only included fields that were identified as barley or other grain. We examined a

binomial GLMM that included the fixed effects of time and tillage intensity with random effects of field. We exponentiated the coefficients to determine the odds of presence on idle and low intensity till fields compared to high intensity till fields (Dunn and Smyth, 2018). We considered there to be an effect of tillage intensity if confidence intervals did not include zero.

RESULTS

We completed a total of 79 surveys in autumn and 105 surveys in spring from 2020 to 2022. We began autumn surveys in late September or early October and completed surveys by mid-November, and for spring we began surveys in mid-February and completed surveys by late March (Table 3.2). There was one instance where only five out of six regions were surveyed during a week in the autumn of 2020, but all other regions were surveyed equally in each week for both seasons. We counted more sandhill cranes in spring than autumn overall and more greater sandhill cranes than lesser sandhill cranes in both seasons (Table 3.3, Table 3.4). The number of greater and lesser sandhill cranes showed a quadratic temporal trend within each season (Figure 3.2). Peak numbers of greater and lesser sandhill cranes occurred during mid-March in spring and during mid-October in autumn (Figure 3.2).

The area covered by crop types remained consistent across all years and regions (Table 3.4). Most areas were dominated by crop types other than barley or other grains, including alfalfa, potatoes, and pasture. Region 1 and Region 5 had the greatest amount of barley. In autumn, Region 3 tended to have the highest proportion of greater sandhill cranes in 2020, while Regions 1 and 2 had a higher proportion in 2021 (Figure 3.3). The greatest proportion of lesser sandhill cranes were in Region 3 in autumn for both years. Greater sandhill cranes showed a variable distribution in spring, with Regions 5 and 6 having a greater proportion throughout 2020 and 2021 (Figure 3.4). Spring 2022 showed an increase in the proportion of greater sandhill

cranes in Region 1. In contrast, lesser sandhill cranes were most prominent in Region 3 for the spring season in all years, but the proportion in Region 6 increased towards the end of the spring season.

The top-ranking model for greater sandhill crane selection in autumn included an interaction between time and crop type, but a model with an interaction between time and distance to the nearest roost was also competitive (Table 3.5). In the time and crop type interaction model, the probability of presence was greatest on barley fields, with a peak probability during the fifth week of surveys (Figure 3.5A). Distance to the nearest roost had a negative effect on the log-odds of presence (Table S2.1). In the time and roost distance interaction model, roost distance was negative for all survey weeks, and both barley and other grains positively influenced the log-odds of presence (Table S2.1, Figure 3.6A). The top-ranking model for spring included an interaction between crop type and distance to the nearest roost (Table 3.5). Roost distance was negative for all crop types, but barley showed the highest overall probability closer to roosts (Figure 3.7A).

The top-ranking models for lesser sandhill crane selection showed the same pattern as for greater sandhill cranes (Table 3.5) in both seasons. The model with an interaction between time and crop type showed a peak in probability of presence on barley fields in autumn during the fifth week of surveys (Figure 3.5B), with a similar pattern for other grains. In spring in this model, the probability of presence peaked during the fourth week on barley fields and during the fifth week on other grain fields. The model with an interaction between time and roost distance showed an overall negative effect of roost distance on the log-odds of presence across all time periods (Table S2.1, Figure 3.6B). Both barley and other grains had positive effects on the log-odds of presence (Table S2.1). For spring, the model with an interaction between crop type and

roost distance showed a negative effect of roost distance on the log-odds of presence on barley fields and other grains (Table S2.1, Figure 3.7B).

Abundance modeled with the negative binomial distribution performed better than when modelled with a Poisson distribution. The top-ranking abundance model for greater sandhill cranes in autumn included an interaction between time and distance to the nearest roost, but a competitive model included an interaction between crop type and roost distance (Table 3.6). The first model showed that roost distance had a negative influence on the number of greater sandhill cranes early in the season, but the relationship became positive after the fourth week of surveys (Figure 3.8). Barley, other grain, potatoes, and the number of lessers sandhill cranes all had positive effects on use by greater sandhill cranes in autumn (Table S2.2). The second model showed that roost distance was positive for barley fields in autumn, but this effect was negative for other crop types, including other grains and potatoes (Figure 3.9). The top-ranking model in spring included an interaction between time and crop type (Table 3.6). The number of greater sandhill cranes varied across habitat types, but there was a high degree of uncertainty early in the season (Figure 3.10). Compared to autumn, more greater sandhill cranes were predicted to be on pasture, potatoes, and other crop fields in spring. The number of lesser sandhill cranes positively influenced the number of greater sandhill cranes in all spring models (Table S2.2).

Both greater and lesser sandhill cranes were more likely to be present on idle fields or low intensity till fields compared to high intensity till fields in autumn and spring (Table 3.7). In autumn, the odds of presence on low-intensity till fields were highest for both subspecies. In spring, the odds of presence were greatest on idle fields.

DISCUSSION

We identified the distribution of foraging greater and lesser sandhill cranes throughout the SLV in autumn and spring and examined their selection patterns across crop types, roosting distances, and tillage intensity. Greater sandhill cranes consistently used a broader area of the SLV, while lesser sandhill cranes remained more concentrated in particular regions. Consistent with our hypothesis, sandhill cranes primarily foraged on barley or other grains close to potential roosting areas and moved farther from roosting areas throughout the season. There was evidence of birds switching to other forage types close to roosting areas, but there appeared to be a greater preference to fly farther for preferred forage types. Additionally, both greater and lesser sandhill cranes were more likely to utilize grain fields that were either not tilled or only moderately tilled over more intensively tilled fields.

The distribution of sandhill cranes throughout the SLV varied in both seasons and across subspecies, which may have implications for where management could be focused for foraging areas. Changes in the distribution of a population may indicate variation in resource availability or in preference for those resources (Fretwell, 1969). If sandhill cranes were selecting foraging resources proportional to availability of preferred forage types only, we might have expected them to utilize regions in the SLV where barley availability was the highest. Regions 1 and 5 tended to have the greatest amount of grain available. Indeed, we found that the proportion of greater sandhill cranes was relatively high in Region 1 in autumn and spring and Region 5 in spring, but this pattern was not consistent within seasons. Similarly, lesser sandhill cranes were primarily concentrated in Region 3, which had a relatively small area of grains compared to other regions. Other studies have suggested that the distribution of sandhill cranes tends to be determined more by the presence and condition of roosting areas than foraging areas (Collins et

al., 2023; Krapu et al., 1984; Sparling and Krapu, 1994), which could better explain the distribution of sandhill cranes in the SLV. Each survey region in the SLV has distinct wetland or riverine habitats traditionally used by sandhill cranes for roosting, including the MVNWR in Region 3 and the Rio Grande, which generally supports sandhill cranes using Regions 1, 2, and 3. We found that the number of greater sandhill cranes was greatest in areas north of the Rio Grande (Regions 1 and 2), and there were relatively high numbers in Region 3. Regions 1 and 2 were used throughout the spring, but there was an increase in the number and proportion of greater sandhill cranes in Regions 5 and 6. These regions have roosting areas managed by the state wildlife agency, Colorado Parks and Wildlife.

At the same time, the density of leftover seed may also be lower in some fields than others, and patch-specific seed density likely has a greater influence on selection than the area of grain fields. Although grain may be available in some fields, the density or availability of forage may be low enough that the energy gained from feeding in a patch does not offset the energetic cost of searching for food (Brown 1988). For example, Greer et al. (2009) found that ducks stopped foraging in fields after rice density declined to 50 kg/ha. Although Region 3 had a low area of barley, the MVNWR provides approximately 90 ha of barley specifically for sandhill cranes in spring. The barley is mowed but not harvested, which results in a relatively high density of seed in a few patches (see Chapter 4). This could explain the higher numbers of lesser sandhill cranes in this region in spring, in addition to the presence of optimal roosting area. It is not clear if the reason for mostly lesser sandhill cranes in Region 3 and fewer greater sandhill cranes is due to competition and limited roosting and foraging area in Region 3 or if greater sandhill cranes prefer roosting or foraging habitat elsewhere in the SLV. In either case, it remains critical to provide both adequate foraging habitat along with roosting habitat for sandhill cranes.

Additionally, management for the RMP specifically may prove most beneficial in other parts of the SLV.

Both subspecies showed similar patterns and preferences in crop types for foraging. The selection for barley by sandhill cranes in the SLV was consistent with our hypothesis, but there was evidence of an increase in the selection of other grains and crop types in spring. Agricultural grains have been identified as an important food resource for sandhill cranes and other crane species (Austin et al., 2018; Hemminger et al., 2022; Krapu et al., 2014). Sandhill cranes are habitat generalists and highly adaptable to land use changes, so the expansion of agriculture has been identified as a reason for their dramatic increase throughout North America in recent years (Hemminger et al. 2022). Barley's high energetic value in the form of carbohydrates and fats, high protein content and digestibility, and low fiber content (Rodehutscord et al., 2016), along with its more even distribution across the landscape compared to natural foods, make it an ideal food source for migrating cranes. Other grains, such as triticale, rye, wheat, and oats, also provide an energy-rich resource during migration (Rodehutscord et al., 2016; Siegert et al., 2022). Compared to autumn, selection for other grains was higher in spring for all years, and there was a slight increase in selection for potatoes and pasture. Sandhill cranes were observed consuming potatoes, but potato fields may also provide other food items, such invertebrates, including species in *Coleoptera* (Ballard and Thompson, 2000). Along with carbohydrates and fats, sandhill cranes require other nutrients and minerals, particularly during the spring when preparing for reproduction (Iverson et al., 1987; Krapu et al., 1985; Reinecke and Krapu, 1986). Pastures and grasslands can be a good source of foods that provide protein, calcium, and other essential nutrients in the form of invertebrates, seeds, and tubers (Avilés et al., 2002; Davis and Vohs, 1993; Iverson et al., 1987; Krapu et al., 1984). In the SLV, sandhill cranes were commonly

observed with cattle while in pastures, presumably foraging for invertebrates or seeds in vegetation or cow excrement (Avilés et al., 2002), but they were also observed foraging on seeds from hay left for cattle. While grain is an important resource for cranes, we have shown that other crop types and habitats can potentially provide other resources for sandhill cranes (Boggie et al., 2018a).

Along with crop type, distance to the nearest roost was an important covariate for crane distribution. The model with an interaction between time and roost distance was among the most competitive models in autumn for both subspecies, which was consistent with our hypothesis. The distance required to travel to foraging areas, the amount of time individuals spend foraging, and the predation risks associated with the foraging location influence the distance sandhill cranes and other central place foragers will commute (Austin and Humburg, 1992; Johnson et al., 2014; Link et al., 2011; Olsson et al., 2008). Other studies have documented sandhill cranes and other crane species preferring foraging areas closer to roosts but moving farther during foraging bouts as resources are depleted (Alonso et al., 1984; Anteau et al., 2011; Ivey et al., 2015). Remaining close to roosts is optimal particularly in autumn, as this is the time when waste grain is most available. However, the model with an interaction between time and crop type was also among the most competitive models for autumn. This model indicated that the probability of presence was greatest on barley and other grain fields around mid- to late October and that grains had the highest selection overall. Additionally, the juxtaposition of roosts and grain fields was influential in spring. The model with an interaction between crop type and roost distance was the top model and showed the highest selection on grain fields close to roosts. While we expected crop type to be important in spring, we did not expect roost distance to be as important as in

autumn. Together, these results emphasize the importance of the juxtaposition of grain fields and roosting areas for sandhill cranes in the SLV in both autumn and spring.

Despite a preference for grains close to roosts, there was evidence that the depletion of grains gradually pushed sandhill cranes farther from roosts. While we found a negative effect of roost distance on presence of sandhill cranes, roost distance showed a positive effect on the number of greater sandhill cranes in some cases. The abundance model with an interaction between time and roost distance showed that as the season progressed, the slope of roost distance went from negative to positive in autumn. Similarly, although not among the most competitive models for spring, roost distance showed a strong positive slope in the early part of the season. Additionally, the abundance model with an interaction between roost distance and crop type, which was the second-most competitive model in autumn, showed a positive effect of roost distance for barley in both seasons. This may indicate that while greater sandhill crane flocks are more likely to prefer foraging on areas close to roosts in both seasons, fewer, larger flocks were predicted to be found farther from roosting areas, particularly in the spring. Other studies have also found that cranes tend to forage where the density of food is highest and documented proportional changes in crane numbers with food abundance (Alonso et al., 1994). Although we did not find a clear pattern of sandhill crane numbers being proportional to the area of grain fields across regions, this pattern may also suggest that sandhill cranes opt for flying farther for preferred forage rather than switching crop types as grains become depleted close to roosts, particularly in spring. Collins et al. (2023) also found that sandhill cranes in the Lower Colorado River Valley Population preferred flying greater distances from roosts for grains than other crop types, such as alfalfa. The model that included an interaction between time and crop type was the most competitive model for spring abundance, which may indicate that distance to roost is less

important than crop type in spring and was consistent with our hypothesis. At the same time, there was some evidence of sandhill cranes switching to other crops. While barley showed a peak in the number of predicted greater sandhill cranes, other grains and potatoes showed an increase in numbers later in the season. Thus, in addition to flying greater distances for their preferred forage (i.e., barley), greater sandhill cranes may also switch forage types, which may allow them to forage closer to the roost, avoid large flocks, or access other nutrients available in different habitats (Krapu et al., 1984; Reinecke and Krapu, 1986). Similarly, Alonso et al. (1984) also found that while common cranes eventually moved greater distances as resources were depleted close to roosts to access their preferred forage (sunflower fields), they also foraged on other crop types as the season progressed. If barley production continues to decline in the SLV, sandhill cranes may need to switch to other forage types. However, it is not yet clear if other commonly grown crop types, such as potatoes and alfalfa, that sandhill cranes also use in the SLV will support the same population size.

In accordance with other studies, sandhill cranes in the SLV selected grain fields based on tillage intensity. The probability of presence was highest on idle fields and low-intensity fields for both subspecies, but there was a difference in which was more likely to be used across seasons. We found that the odds of greater sandhill cranes using low intensity fields compared to high intensity fields were higher than the odds of using idle fields compared to high intensity fields in autumn, but this relationship was reversed in spring. We found a similar pattern for lesser sandhill cranes. Tilled fields generally have less waste grain available than stubble, grazed, or mulched fields, with stubble having the most available (Matthews et al., 2022; Sherfy et al., 2011). We did not differentiate mulched from plowed or disced fields, but preference for low intensity tillage may indicate that these fields provide other benefits, such as reduced search

time, compared to fields left in stubble, which have more debris that needs to be sorted through in order to acquire seeds (Anteau et al. 2011). Indeed, Anteau et al. (2011) also found mulched fields to have a higher probability of use by sandhill cranes than idle fields in spring. At the same time, we found a higher preference for idle fields over low intensity fields in spring. This could be due to a difference in the availability of grain in idle fields compared to tilled fields. Along with tilling, many growers also irrigate grains after harvest, which causes the seeds to germinate. While sandhill cranes will still consume recently germinated barley (Hoffman 1976, Littlefield 2002), the seeds lose nutritional value over time. Sandhill cranes in Wisconsin, for example, did not consume grain that had been irrigated more than 17 days prior (Barzen et al. 2018). It could be that sandhill cranes have a greater preference for idle fields because more seed is still available after the autumn season with continued foraging on all grain fields and increased deterioration due to depletion.

Greater and lesser sandhill cranes concentrated in distinct areas throughout the SLV, which will be useful for identifying areas to prioritize for providing foraging or roosting habitat. Given that the distribution of the RMP is mostly concentrated in areas north of Rio Grande, the energetic needs of this population are mostly being met on privately operated crop fields. However, other work suggests that the MVNWR and other publicly managed lands are important for roosting greater sandhill cranes (see Chapter 2), and we found that a large proportion of the MCP used the area around the MVNWR. Rather than switching to other crop types as grains are depleted, we found evidence that sandhill cranes will likely fly farther for their preferred forage. Flying is energetically expensive for birds (McWilliams et al., 2004), particularly during the nonbreeding period, so sandhill cranes will require more energy to offset increased flight as resources are depleted near roosts. Additionally, the threshold density of food at which birds

cease foraging (Greer et al., 2007), has been shown to increase with increasing foraging flight distance (Johnson et al., 2014; Van Gils and Tijsen, 2007), resulting in less foraging time. Providing both publicly and privately managed roosting areas and foraging habitat will help sandhill cranes meet their energetic requirements during migration in the SLV, but emphasis should be placed on ensuring these areas are close together throughout the regions most used by sandhill cranes. Prioritizing the juxtaposition of roosting and foraging areas is consistent with the management suggestions of previous studies (Iverson et al., 1987; Pearse et al., 2010). Finally, sandhill cranes preferred to forage on idle or moderately tilled grain fields. Encouraging minimal tillage practices on grain fields will improve the suitability of grain fields to sandhill cranes, which may be more critical if the total area of barley continues to decline in the SLV.

TABLES AND FIGURES

Table 3.1: Proportion of crop types in the San Luis Valley (SLV) and the sampling frame used to count sandhill cranes within the SLV.

Crop type	2020		2021	
	SLV	Sampling area	SLV	Sampling area
Alfalfa	0.35	0.29	0.33	0.28
Barley	0.08	0.10	0.09	0.10
Other	0.21	0.25	0.18	0.25
Other grain	0.06	0.08	0.06	0.07
Potatoes	0.10	0.14	0.11	0.16
Wetland/Pasture	0.19	0.14	0.17	0.15

Table 3.2: Dates of surveys conducted for greater and lesser sandhill cranes in the San Luis Valley, Colorado.

		Autumn		Spring	
Year	Week number	Start date	End date	Start date	End date
2020	1	9/24/2020	9/26/2020	2/16/2020	2/18/2020
	2	10/2/2020	10/4/2020	2/24/2020	2/26/2020
	3	10/6/2020	10/9/2020	-	-
	4	10/13/2020	10/16/2020	3/13/2020	3/15/2020
	5	10/20/2020	10/24/2020	3/20/3030	3/22/2020
	6	10/29/2020	11/1/2020	3/27/2020	3/29/2020
	7	11/12/2020	11/17/2020	-	-
2021	1	-	-	2/15/2021	2/20/2021
	2	10/3/2021	10/6/2021	2/22/2021	2/25/2021
	3	10/10/2021	10/15/2021	3/1/2021	3/4/2021
	4	10/17/2021	10/20/2021	3/8/2021	3/11/2021
	5	10/24/2021	10/28/2021	3/15/2021	3/18/2021
	6	11/5/2021	11/8/2021	3/27/2021	3/31/2021
	7	11/13/2021	11/16/2021	-	-
2022	1	-	-	2/10/2022	2/13/2022
	2	-	-	2/18/2022	2/21/2022
	3	-	-	3/1/2022	3/4/2022
	4	-	-	3/8/2022	3/11/2022
	5	-	-	3/22/2022	3/25/2022
	6	-	-	3/29/2022	3/31/2022

Table 3.3: The mean ($\bar{x}$) and standard errors (SE) for the number of foraging greater and lesser sandhill cranes across flocks and survey weeks in the San Luis Valley, Colorado. The mean does not include fields with no sandhill cranes observed.

			Greaters			Lessers		
Season	Year	Survey week	$\bar{x}$	SE	No. flocks	$\bar{x}$	SE	No. flocks
Autumn	2020	1	37.92	9.42	13	4.00	NA	1
		2	171.09	41.96	51	117.06	20.21	31
		3	295.41	112.06	63	84.77	15.05	47
		4	74.08	19.04	79	93.96	0.63	57
		5	82.98	23.11	83	115.22	37.00	68
		6	83.41	24.41	82	96.68	12.06	65
		7	268.59	54.22	58	48.65	37.77	26
	2021	2	176.38	39.69	54	39.03	26.19	39
		3	170.35	41.38	55	64.68	13.26	37
		4	79.06	15.12	70	122.16	21.94	57
		5	103.16	20.44	67	97.46	21.28	59
		6	189.70	29.61	67	60.58	45.94	53
		7	182.75	41.30	51	64.34	20.64	35
Spring	2020	1	91.82	17.80	32	38.72	29.23	18
		2	117.26	21.64	39	72.77	27.31	22
		4	176.28	28.42	96	174.70	135.54	47
		5	156.90	28.64	73	186.03	66.74	34
		6	214.16	36.43	81	86.26	28.84	43
	2021	1	162.78	32.28	32	46.78	22.51	23
		2	113.91	25.29	65	66.95	23.78	42
		3	113.32	17.47	88	103.90	100.66	48
		4	158.12	43.60	68	135.82	60.43	44
		5	106.91	26.75	78	157.41	54.13	44
		6	88.62	19.27	61	53.07	26.42	42
	2022	1	146.42	29.46	38	3.23	19.23	13
		2	72.78	11.11	69	31.61	49.83	31
		3	45.43	11.58	83	54.33	18.40	48
		4	53.24	12.53	85	85.47	54.45	62
		5	73.17	17.65	103	113.15	38.21	55
		6	136.16	39.00	63	116.55	16.31	31

Table 3.4: The area of crop types and percent of total crop area for regions in the San Louis Valley, 2020-2022.

Region	Crop type	Area (ha)			Percent of total crop area by region		
		Autumn 2019/Spring 2020	Autumn 2020/Spring 2021	Autumn 2021/Spring 2022	Autumn 2019/Spring 2020	Autumn 2020/Spring 2021	Autumn 2021/Spring 2022
1	Alfalfa	1762.48	1873.25	1969.98	11.10	11.80	12.41
	Barley	4794.26	4430.03	4270.78	30.19	27.90	26.90
	Other	2903.37	3207.32	3534.22	18.29	20.20	22.26
	Other grain	375.27	190.72	177.73	2.36	1.20	1.12
	Pasture	578.70	602.68	680.04	3.64	3.80	4.28
	Potatoes	5464.28	5574.37	5245.62	34.41	35.11	33.04
2	Alfalfa	1088.87	974.81	684.67	7.49	6.71	4.71
	Barley	1280.54	918.40	1492.31	8.81	6.32	10.27
	Other	6828.92	7443.88	6876.01	46.98	51.22	47.31
	Other grain	920.70	1011.55	906.58	6.33	6.96	6.24
	Pasture	290.86	375.89	317.70	2.00	2.59	2.19
	Potatoes	4124.66	3810.03	4257.27	28.38	26.21	29.29
3	Alfalfa	6464.69	6678.06	6416.10	34.70	35.84	34.44
	Barley	619.73	1255.60	1221.97	3.33	6.74	6.56
	Other	4434.67	4468.55	4521.14	23.80	23.98	24.27
	Other grain	2088.48	1176.81	1173.18	11.21	6.32	6.30
	Pasture	4714.54	4736.49	4936.09	25.30	25.42	26.49
	Potatoes	309.91	316.50	363.54	1.66	1.70	1.95
4	Alfalfa	5655.76	5656.26	5417.06	34.88	34.88	33.41
	Barley	775.15	758.40	499.60	4.78	4.68	3.08
	Other	1554.55	1528.27	1629.14	9.59	9.42	10.05
	Other grain	1380.27	1318.30	1212.56	8.51	8.13	7.48
	Pasture	6453.36	6656.34	7083.88	39.80	41.05	43.69
	Potatoes	396.01	297.51	372.85	2.44	1.83	2.30
5	Alfalfa	1881.54	1764.53	1687.90	12.27	11.51	11.01
	Barley	2626.64	1902.65	2831.52	17.13	12.41	18.47
	Other	6420.68	6358.84	6398.84	41.88	41.47	41.74
	Other grain	368.61	1857.36	432.20	2.40	12.11	2.82
	Pasture	433.84	395.11	522.20	2.83	2.58	3.41
	Potatoes	3600.74	3053.58	3459.39	23.49	19.92	22.56
6	Alfalfa	2162.22	1780.35	1923.83	32.74	26.96	29.13
	Barley	541.30	471.12	714.78	8.20	7.13	10.82
	Other	3084.04	2748.97	2793.16	46.70	41.62	42.29
	Other grain	201.11	687.13	455.89	3.05	10.40	6.90
	Pasture	597.03	542.73	520.35	9.04	8.22	7.88
	Potatoes	18.64	374.05	196.32	0.28	5.66	2.97

Table 3.5: Model selection results for the log-odds of presence of greater and lesser sandhill cranes on crop fields in the San Luis Valley, Colorado (2020-2022) and fitted with fixed covariates of a quadratic effect of survey week ('time'), distance to the nearest roost ('roost distance'), and crop type. The crop types include alfalfa, barley, other, other grains, pasture, and potatoes. Results include the number of parameters (K), ΔAkaike's Information Criterion (AIC_c), and the AIC_c weight (w_i). Models include a random effect of unique field identification numbers.

Subspecies	Season	Model	K	ΔAIC_c	w_i
Greater	Autumn	$Time^2$*crop type + roost distance	20	0.00	0.50
		$Time^2$*roost distance + crop type	12	0.05	0.49
		$Time^2$ + crop type *roost distance	15	9.79	0.00
		$Time^2$ + crop type + roost distance	10	31.42	0.00
		$Time^2$	4	727.19	0.00
	Spring	$Time^2$ + crop type*roost distance	15	0.00	1.00
		$Time^2$*roost distance + crop type	12	30.77	0.00
		$Time^2$ + crop type + roost distance	10	33.83	0.00
		$Time^2$*crop type + roost distance	20	37.78	0.00
		$Time^2$	4	697.65	0.00
Lesser	Autumn	$Time^2$*crop type + roost distance	20	0.00	0.58
		$Time^2$*roost distance + crop type	12	0.65	0.42
		$Time^2$ + crop type *roost distance	15	11.98	0.00
		$Time^2$ + crop type + roost distance	10	19.42	0.00
		$Time^2$	4	428.37	0.00
	Spring	$Time^2$ + crop type*roost distance	15	0.00	1.00
		$Time^2$*roost distance + crop type	12	13.78	0.00
		$Time^2$ + crop type + roost distance	10	20.59	0.00
		$Time^2$*crop type + roost distance	20	23.40	0.00
		$Time^2$	4	393.51	0.00

Table 3.6: Model selection results for the number of greater sandhill cranes on crop fields in the San Luis Valley, Colorado (2020-2022) and fitted with fixed covariates of a quadratic effect of survey week ('time'), distance to the nearest roost ('roost distance'), crop type, and the number of lesser sandhill cranes. The crop types include alfalfa, barley, other, other grains, pasture, and potatoes. Results include the number of parameters (K), ΔAkaike's Information Criterion (AIC_c), and the AIC_c weight (w_i). Models include a random effect of unique field identification numbers.

Season	Model	K	ΔAIC_c	w_i
Autumn	$Time^2$*roost distance + crop type + lessers	14	0.00	0.48
	$Time^2$ + crop type *roost distance + lessers	17	0.14	0.44
	$Time^2$ + crop type + roost distance + lessers	12	3.88	0.07
	$Time^2$*crop type + roost distance + lessers	22	7.95	0.01
	$Time^2$	5	61.99	0.00
Spring	$Time^2$*crop type + roost distance + lessers	22	0.00	0.71
	$Time^2$ + crop type*roost distance + lessers	17	2.63	0.19
	$Time^2$*roost distance + crop type + lessers	14	3.87	0.10
	$Time^2$	5	71.91	0.00
	$Time^2$ + crop type + roost distance + lessers	12	8275.91	0.00

Table 3.7: Coefficient estimates (β with 95% confidence intervals [CI]) and odds ratios for the effect of tillage intensity on the presence of greater and lesser sandhill cranes in the San Luis Valley, 2020-2022.

Covariate	Greaters β (95% CI)	Odds ratio	Lessers β (95% CI)	Odds ratio
	Autumn			
Intercept (high intensity)	-9.85 (-11.09, -8.6)	0.00	-12.34 (-13.74, -10.93)	0.00
Time	1.61 (1.25, 1.97)	5.02	2.29 (1.82, 2.76)	9.86
$Time^2$	-0.16 (-0.2, -0.12)	0.85	-0.24 (-0.29, -0.19)	0.79
Low intensity	0.52 (0.13, 0.9)	1.68	0.76 (0.3, 1.22)	2.14
Idle	0.01 (-0.37, 0.4)	1.02	0.19 (-0.24, 0.63)	1.21
	Spring			
Intercept (high intensity)	-7.52 (-8.32, -6.72)	0.00	-10 (-11.13, -8.87)	0.00
Time	1.01 (0.72, 1.3)	2.75	1.24 (0.85, 1.63)	3.46
$Time^2$	-0.12 (-0.16, -0.08)	0.89	-0.15 (-0.21, -0.1)	0.86
Low intensity	0.57 (0.3, 0.83)	1.76	1.18 (0.82, 1.53)	3.24
Idle	2.79 (2.36, 3.23)	16.36	2.1 (1.59, 2.61)	8.20

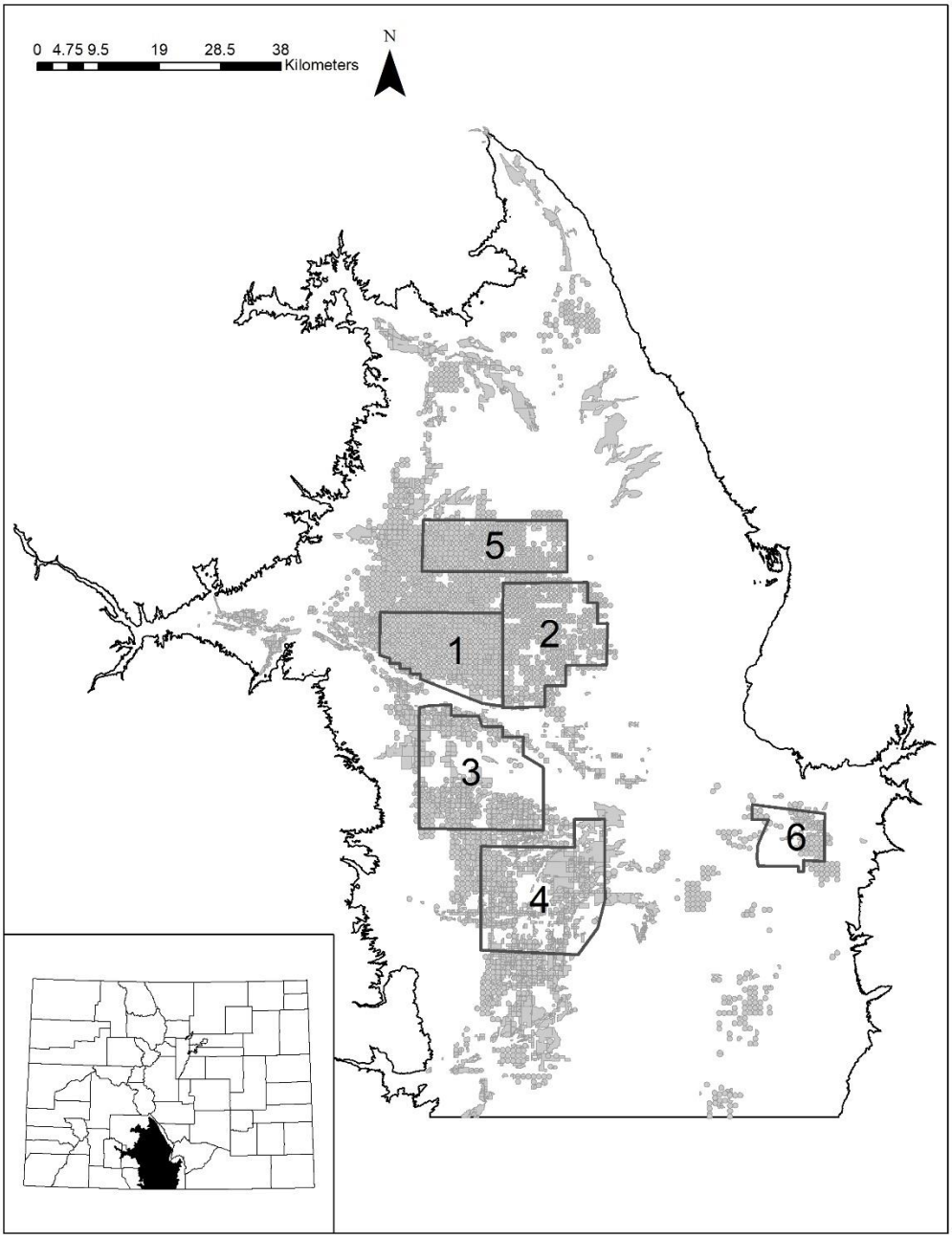

Figure 3.1: A map showing the San Luis Valley in Colorado and the regions in which surveys were conducted for greater and lesser sandhill cranes during the spring and autumn seasons, 2020-2022.

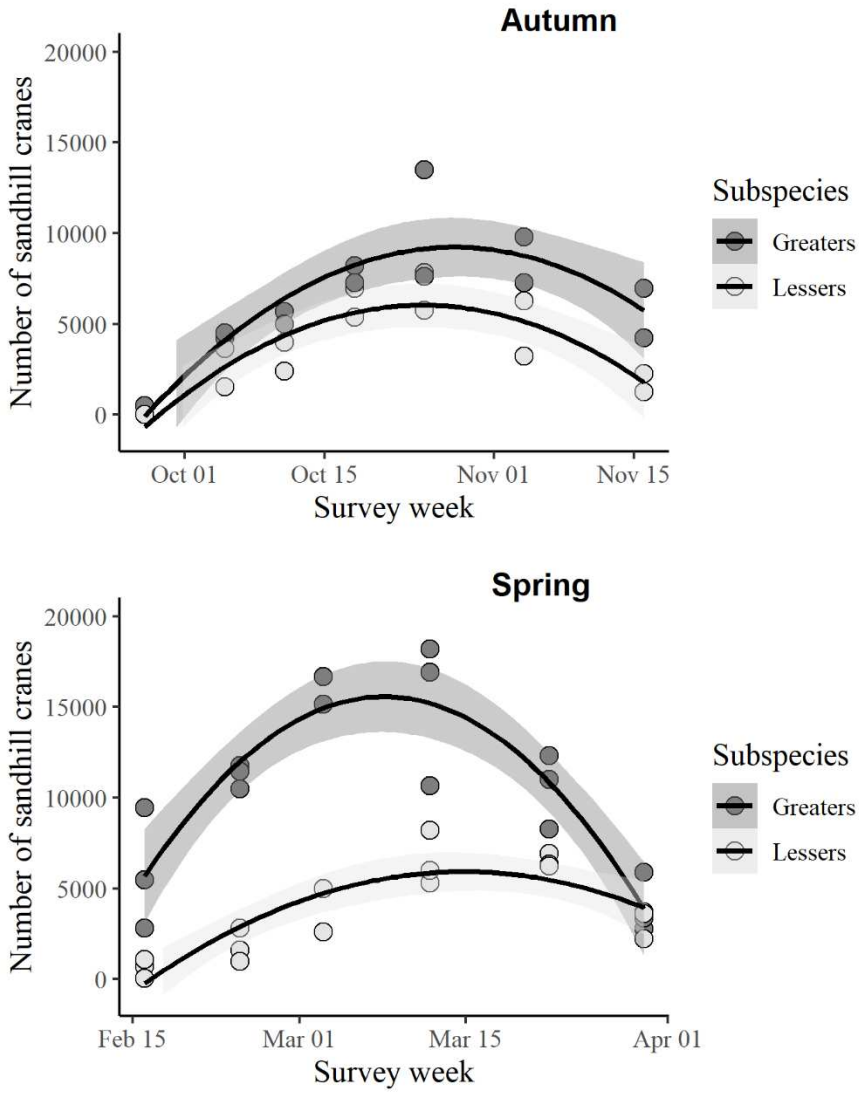

Figure 3.2: The total number of greater and lesser sandhill cranes in autumn and spring in the San Luis Valley, Colorado, 2020-2022. The dots represent the total number of sandhill cranes counted in each year and season. The black line is a smoothed curved fitted using a quadratic relationship between total sandhill cranes and survey week. The shaded regions are 95% confidence intervals for the fitted curves.

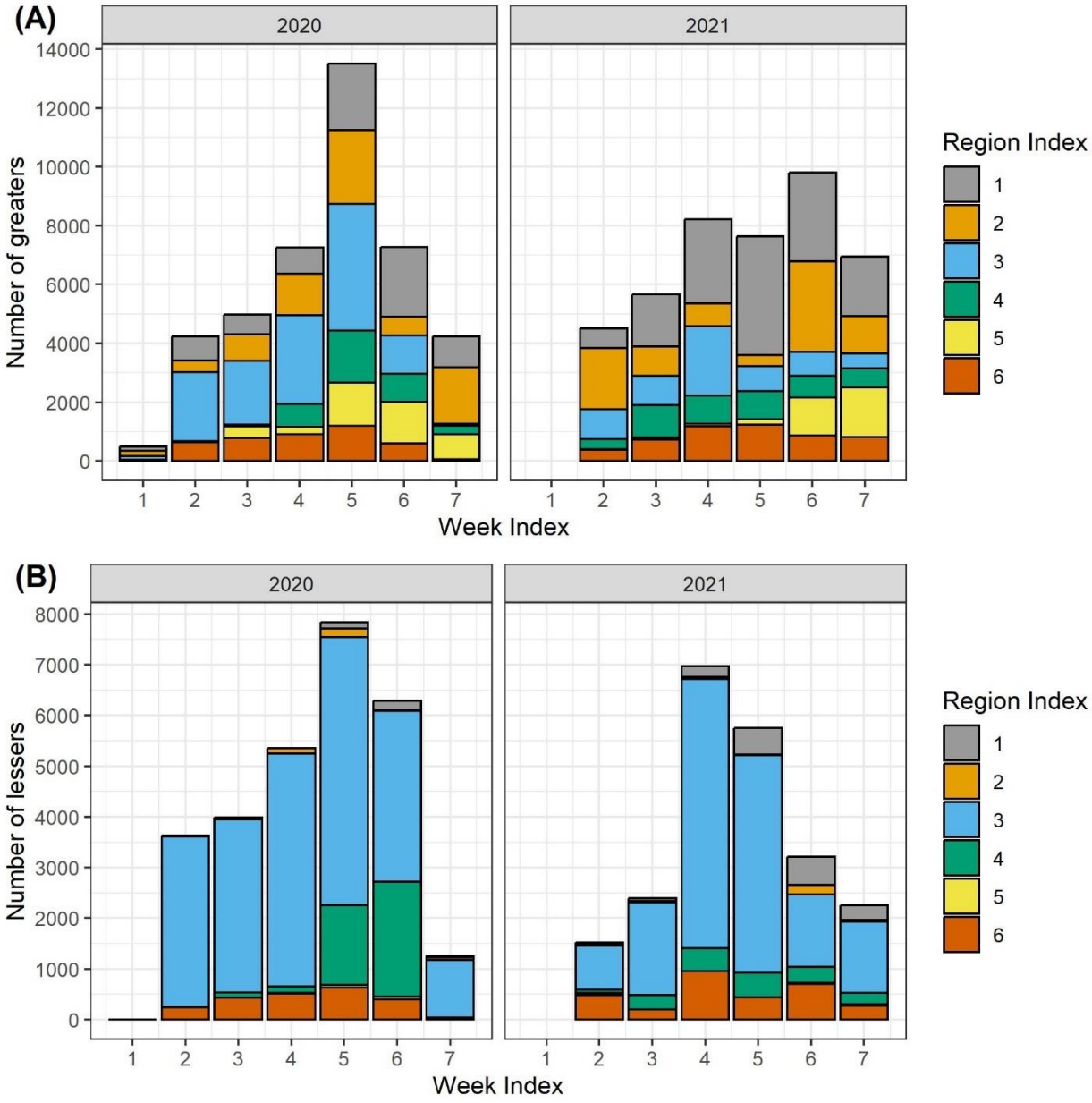

Figure 3.3: The number of (A) greater and (B) lesser sandhill cranes throughout six regions and across weekly surveys in autumn in the San Luis Valley, Colorado, 2020-2022.

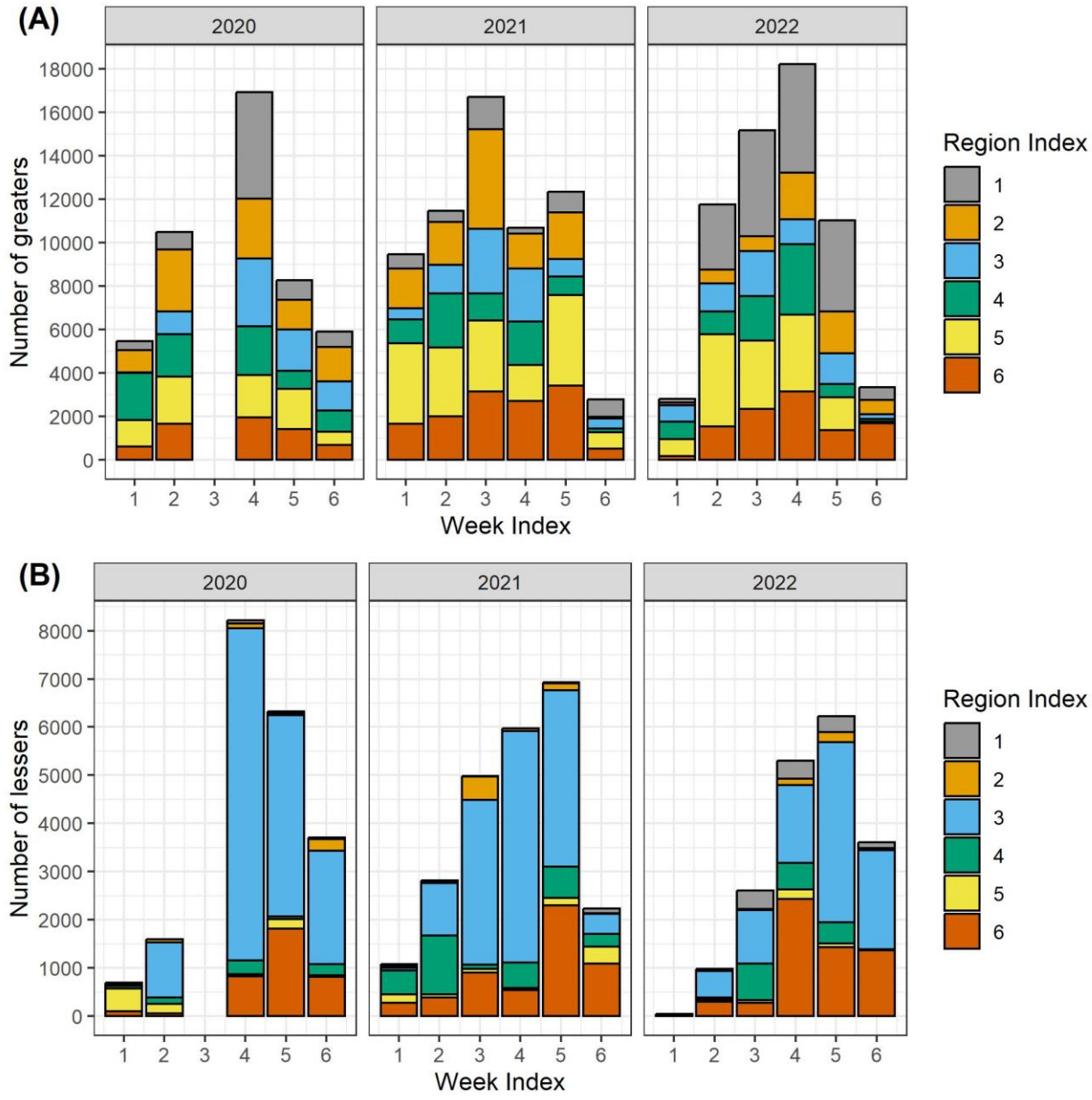

Figure 3.4: The number of (A) greater and (B) lesser sandhill cranes throughout six regions and across weekly surveys in spring in the San Luis Valley, Colorado, 2020-2022.

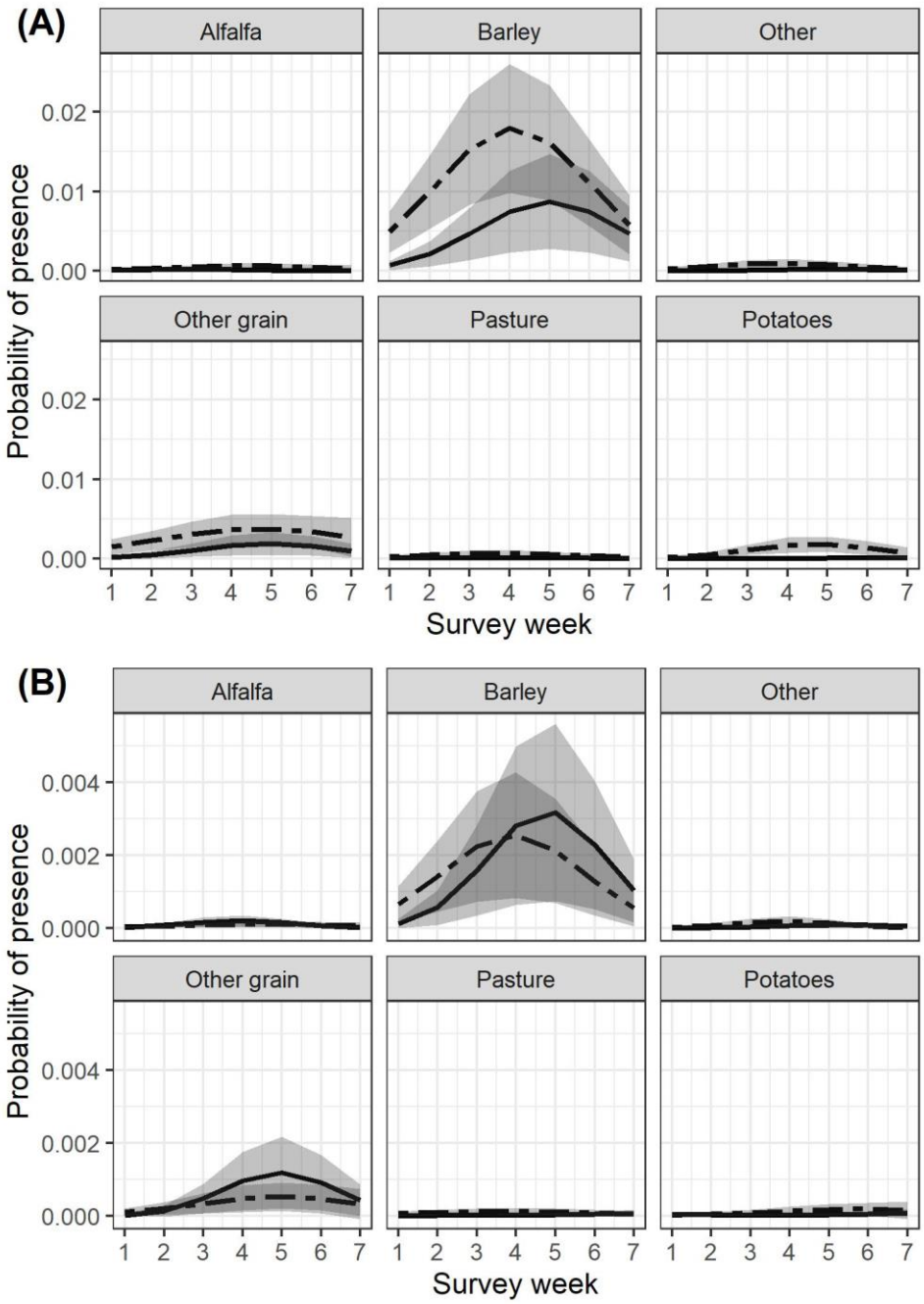

Figure 3.5: The probability of presence of (A) greater and (B) lesser sandhill cranes on crop types in the San Luis Valley, Colorado, during the autumn (solid lines) and spring (dashed lines) in 2020-2022. The shaded regions represent 95% confidence intervals.

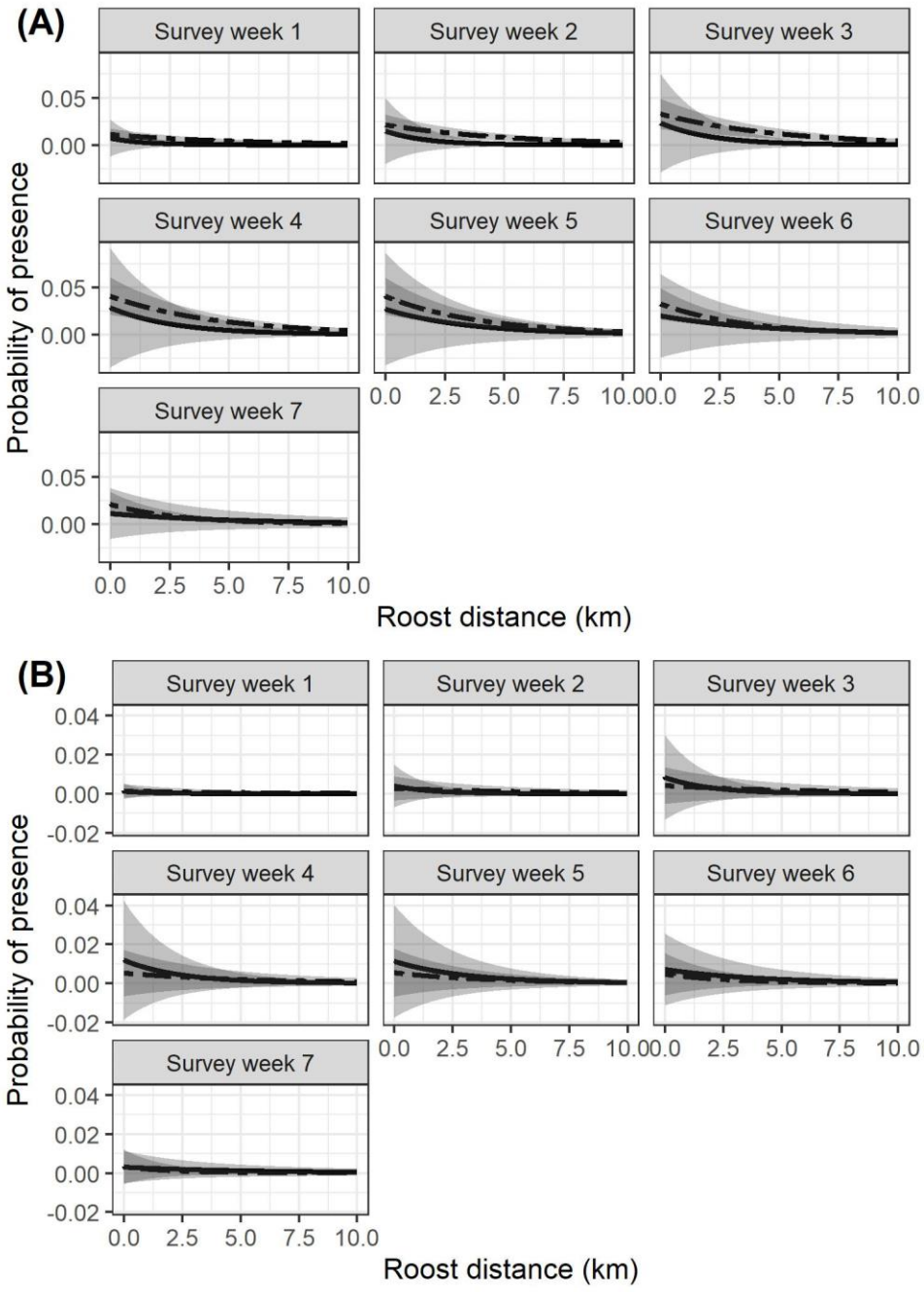

Figure 3.6: The probability of presence of (A) greater and (B) lesser sandhill cranes as distance to the nearest roost increases during the autumn (solid lines) and spring (dashed lines) in the San Luis Valley, Colorado, 2020-2022. The shaded regions represent 95% confidence intervals.

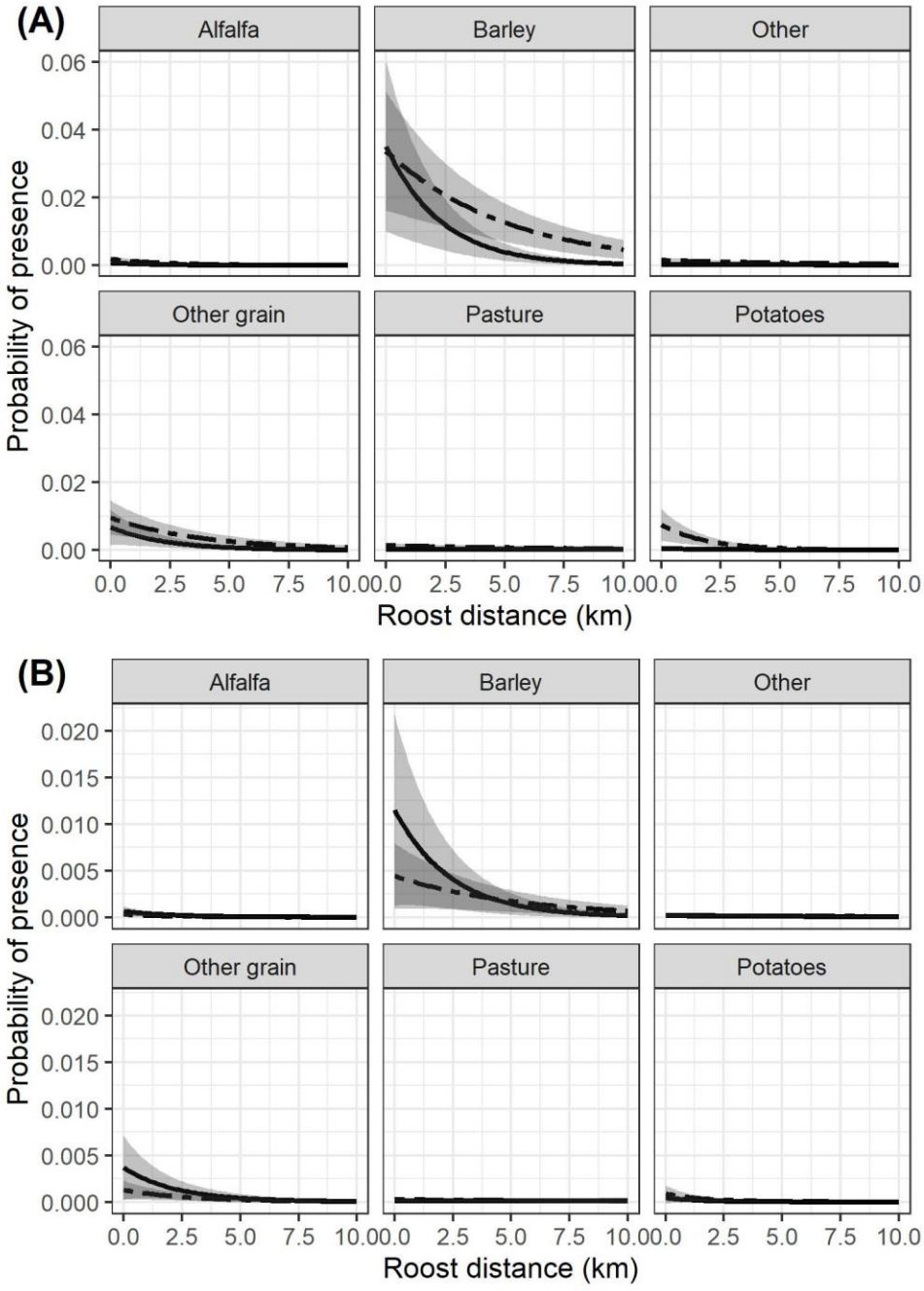

Figure 3.7: The probability of presence of (A) greater and (B) lesser sandhill cranes on crop types and changing roost distance during the autumn (solid lines) and spring (dashed lines) in the San Luis Valley, Colorado, 2020-2022. The shaded regions represent 95% confidence intervals.

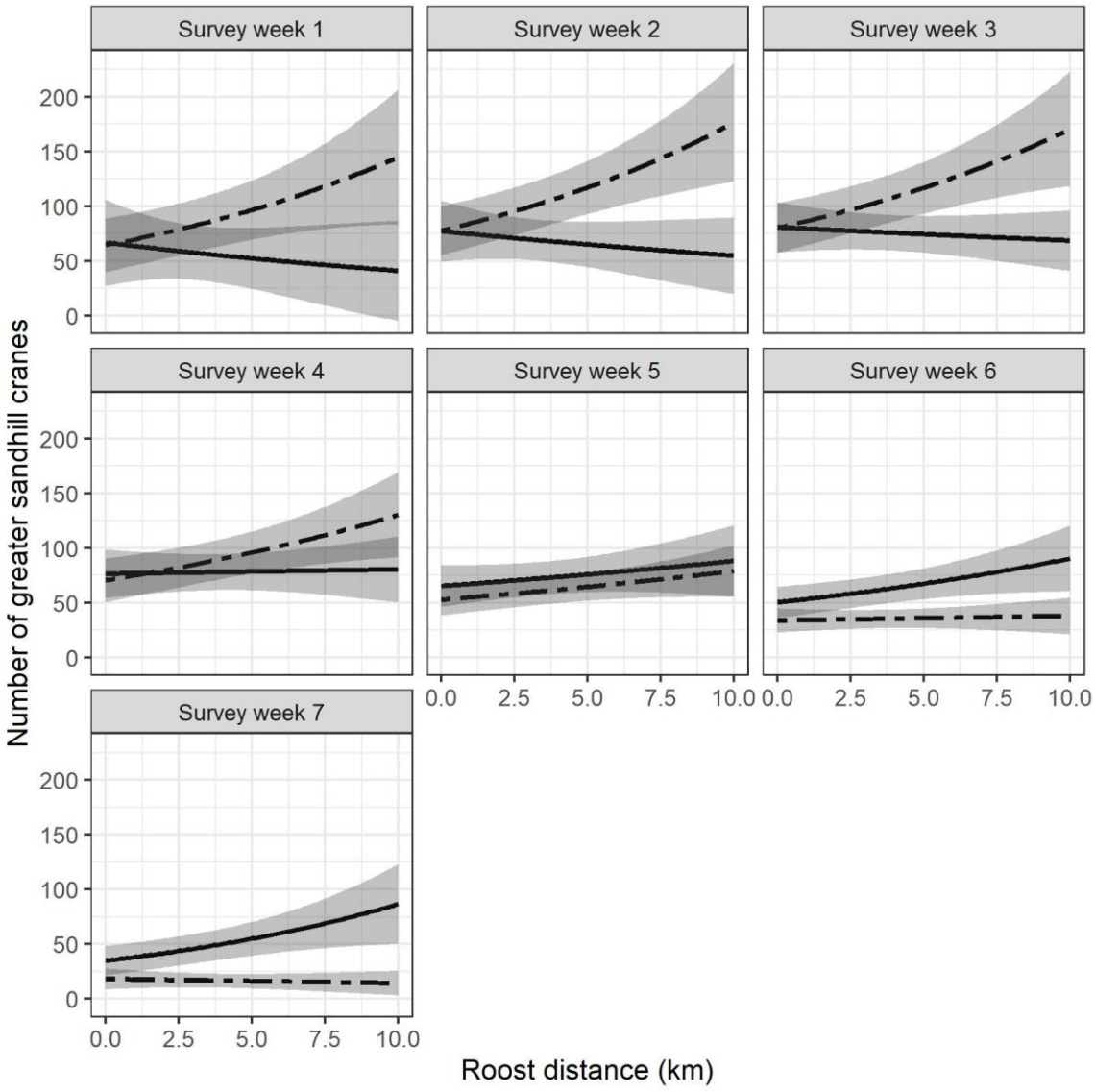

Figure 3.8: The predicted number of greater sandhill cranes in the autumn (solid line) and spring (dashed line) in the SLV, 2020-2022. The shaded region represents 95% confidence intervals.

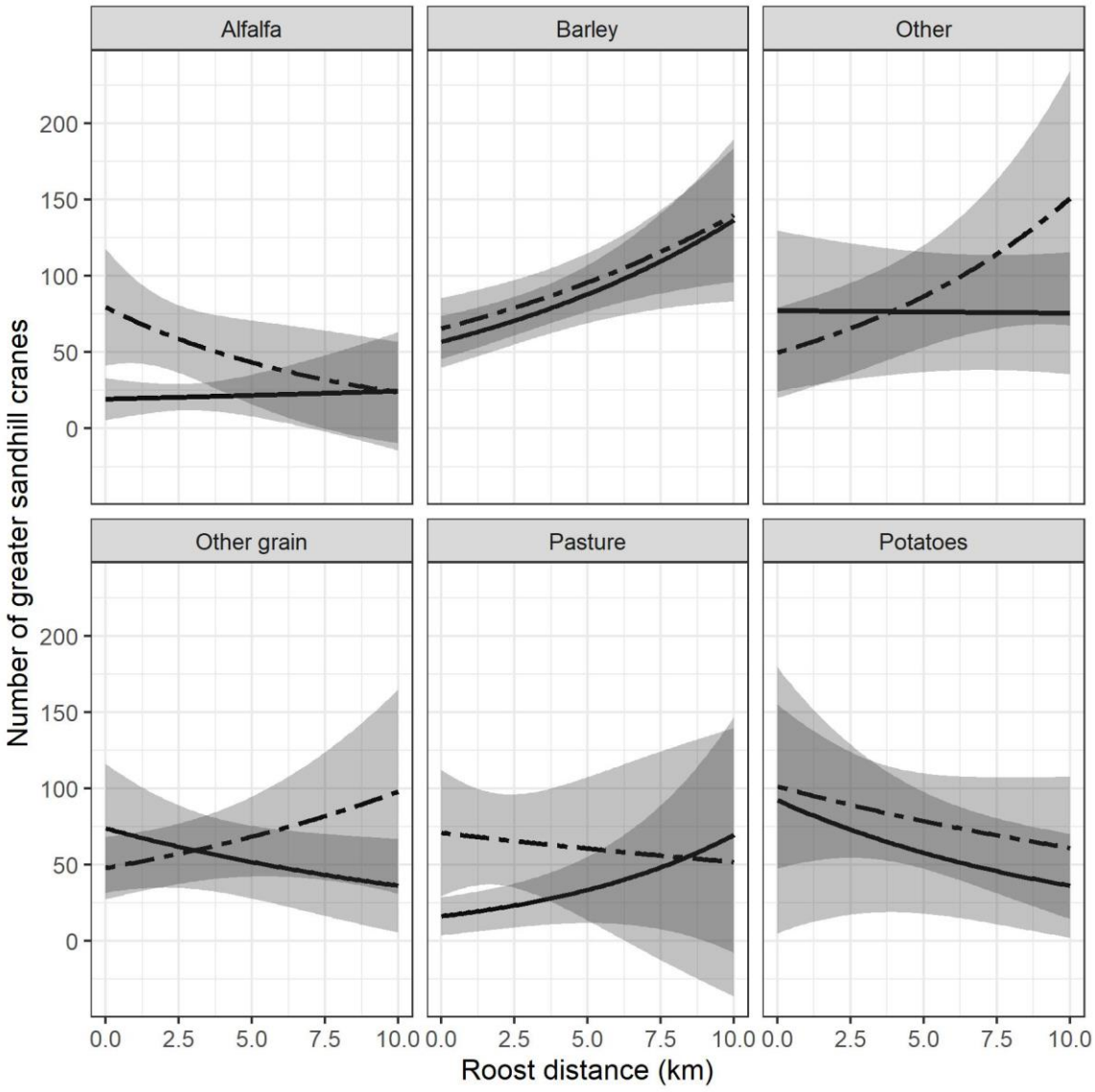

Figure 3.9: The predicted number of greater sandhill cranes in response to roost distance and crop type during the autumn (solid line) and spring (dashed line) in the SLV, 2020-2022. The shaded region represents 95% confidence intervals. The first week for potatoes in autumn was removed for clarity because the confidence intervals were large.

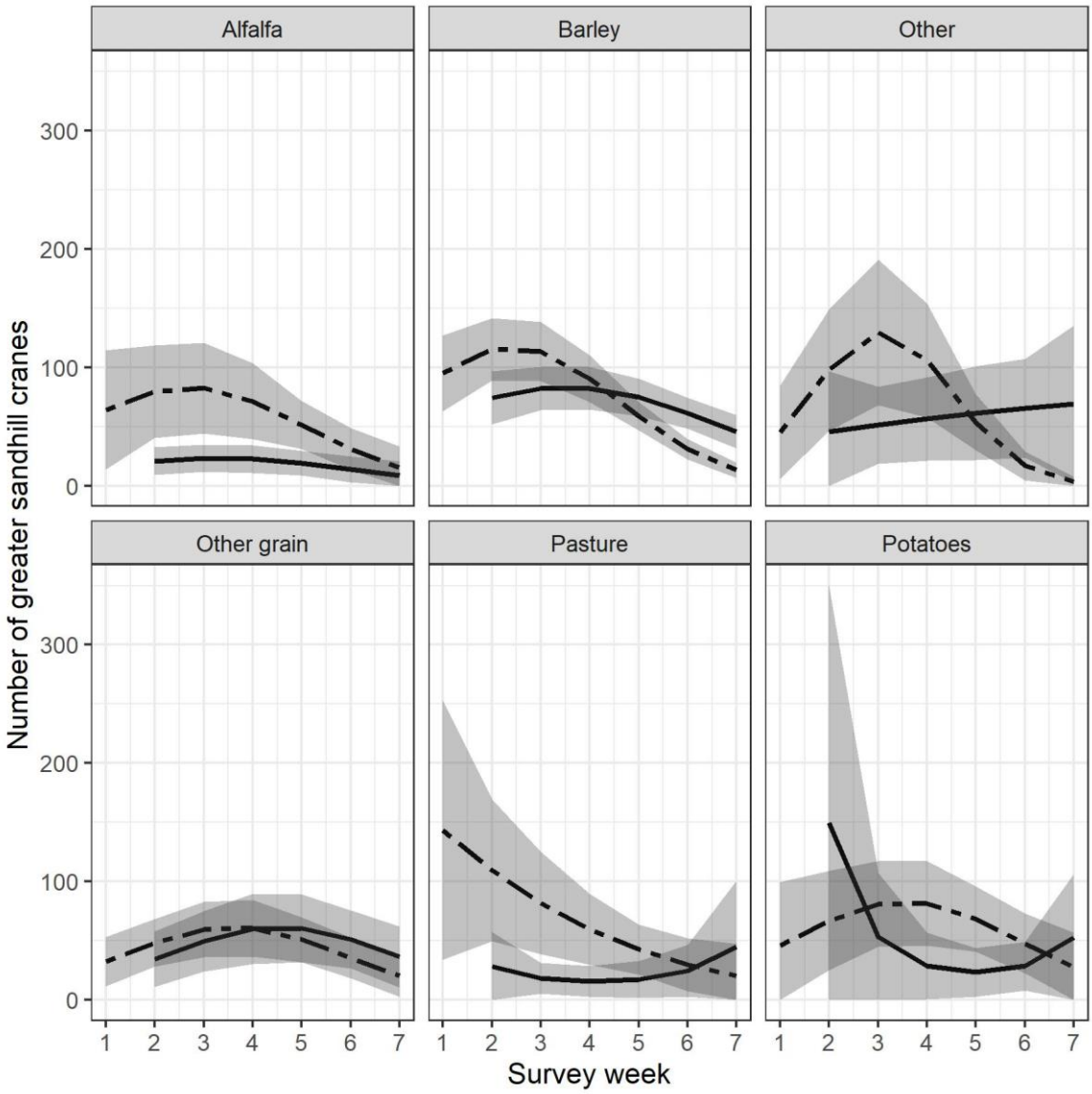

Figure 3.10: The predicted number of greater sandhill cranes in response to survey week and crop type during the autumn (solid line) and spring (dashed line) in the SLV, 2020-2022. The shaded region represents 95% confidence intervals. The first week for potatoes in autumn was removed for clarity because the confidence intervals were large.

LITERATURE CITED

Abraham, K.F., Jefferies, R.L., Alisauskas, R.T., 2005. The dynamics of landscape change and snow geese in mid-continent North America. Glob Chang Biol 11, 841–855. https://doi.org/10.1111/j.1365-2486.2005.00943.x

Adams, J.B., Gillespie, A.R., 2006. Remote Sensing of Landscapes with Spectral Images. Cambridge University Press, Cambridge.

Afton, A.D., Ankney, C.D., 1991. Nutrient-reserve dynamics of breeding lesser scaup: a test of competing hypotheses. Condor 93, 89–97.

Alerstam, T., Lindström, A., 1990. Optimal bird migration: the relative importance of time, energy, and safety, in: Gwinner, E. (Ed.), Bird Migration: Physiology and Ecophysiology. Springer-Verlag, pp. 331–351.

Alisauskas, R.T., 2002. Arctic climate, spring nutrition, and recruitment in Midcontinent lesser snow geese. Journal of Wildlife Management 66, 181–193. https://doi.org/http://dx.doi.org/10.2307/3802884

Alisauskas, R.T., Ankney, C.D., 1992. Spring habitat use and diets of Midcontinent adult lesser snow geese. Journal of Wildlife Management 56, 43–54. https://doi.org/https://doi.org/10.2307/3808789

Alisauskas, R.T., Ankney, C.D., 1985. Nutrient reserves and energetics of reproduction in American coots. Auk 102, 133–144. https://doi.org/10.2307/4086829

Alonso, J.A., Alonso, J.C., Nowald, G., 2008. Migration and wintering patterns of a central European population of Common Cranes Grus grus. Bird Study 55, 1–7. https://doi.org/10.1080/00063650809461499

Alonso, J.A., Alonso, J.C., Veiga, J., 1984. Winter feeding of the Crane in cereal farmland at Gallocanta, Spain. Wildfowl 35, 119–131.

Alonso, J.C., Alonso, J.A., Bautista, L.M., 1994. Carrying capacity of staging areas and facultative migration extension in common cranes. Journal of Applied Ecology 31, 212–222. https://doi.org/https://doi.org/10.2307/2404537

Anteau, M.J., Sherfy, M.H., Bishop, A.A., 2011. Location and agricultural practices influence spring use of harvested cornfields by cranes and geese in Nebraska. Journal of Wildlife Management 75, 1004–1011. https://doi.org/10.1002/jwmg.135

Askren, R.J., Massey, E.R., James, J.D., Osborne, D.C., 2022. Migration chronology and multi-scale habitat selection of wintering midcontinent greater white-fronted geese. Glob Ecol Conserv 39. https://doi.org/10.1016/j.gecco.2022.e02290

Austin, J.E., Humburg, D.D., 1992. Diurnal flight time of wintering Canada geese: consideration of refuges and flight energetics. Prairie Naturalist 24, 24–30.

Austin, J.E., Morrison, K.L., Harris, J.T., 2018. Cranes and agriculture: a global guide for sharing. Baraboo, Wisconsin, USA.

Avilés, J.M., Sánchez, J.M., Parejo, D., 2002. Food selection of wintering common cranes (Grus grus) in holm oak (Quercus ilex) dehesas in south-west Spain in a rainy season. J Zool 256, 71–79. https://doi.org/10.1017/s0952836902000092

Baldassarre, G.A., Whyte, R.J., Quinlan, E.E., Bolen, E.G., 1983. Dynamics and quality of waste corn available to postbreeding waterfowl in Texas. Bulletin 11, 25–31. https://doi.org/https://www.jstor.org/stable/3781078

Ballard, B.M., Thompson, J.E., 2000. Winter diets of sandhill cranes from central and coastal Texas. Wilson Bulletin 2, 263–268. https://doi.org/10.1676/0043

Barnett, T.P., Adam, J.C., Lettenmaier, D.P., 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature. https://doi.org/10.1038/nature04141

Boggie, M.A., Carleton, S.A., Collins, D.P., Vradenburg, J., Sroka, C.J., 2018a. Using stable isotopes to estimate reliance on agricultural food subsidies and migration timing for a migratory bird: Ecosphere 9. https://doi.org/10.1002/ecs2.2083

Boggie, M.A., Collins, D.P., Patrick Donnelly, J., Carleton, S.A., 2018b. Land use, anthropogenic disturbance, and riverine features drive patterns of habitat selection by a wintering waterbird in a semiarid environment. PLoS One 13, 1–26. https://doi.org/10.1371/journal.pone.0206222

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodal inference: A practical information-theoretic approach., 1st ed. Springer-Verlag, New York, New York.

Clausen, K.K., Madsen, J., Nolet, B.A., Haugaard, L., 2018. Maize stubble as foraging habitat for wintering geese and swans in northern Europe. Agric Ecosyst Environ 259, 72–76. https://doi.org/10.1016/j.agee.2018.03.002

Collins, D.P., Boggie, M.A., Kruse, K.L., Conring, C.M., Donnelly, J.P., Conway, W.C., Grisham, B.A., 2023. Roost sites influence habitat selection of sandhill cranes (Antigone canadensis tabida) in Arizona and California. Waterbirds 45. https://doi.org/10.1675/063.045.0407

Collins, D.P., Conway, W.C., Mason, C.D., Gunnels, J.W., 2017. Winter diet of Blue-winged Teal Anas discors, Green-winged Teal Anas carolinensis, and Northern Shoveler Anas Clypeata in east-central Texas. Wildfowl 67, 87–99.

Collins, D.P., Grisham, B.A., Conring, C.M., Knetter, J.M., Conway, W.C., Carleton, S.A., Boggie, M.A., 2016. New summer areas and mixing of two greater sandhill crane populations in the Intermountain West. J Fish Wildl Manag 7, 141–152. https://doi.org/10.3996/042015-JFWM-036

Combs, D.L., Fredrickson, L.H., 1996. Foods used by male mallards wintering in southeastern Missouri. Journal of Wildlife Management 60, 603–610. https://doi.org/https://doi.org/10.2307/3802078

Davis, C.A., Vohs, P.A., 1993. Role of macroinvertebrates in spring diet and habitat use of sandhill cranes. Transaction of the Nebraska Academy of Sciences 81–86.

Devries, J.H., Brook, R.W., Howerter, D.W., Anderson, M.G., 2008. Effects of spring body condition and age on reproduction in Mallards (Anas platyrhynchos). Auk 125, 618–628. https://doi.org/10.1525/auk.2008.07055

Donnelly, J.P., King, S.L., Knetter, J., Gammonley, J.H., Dreitz, V.J., Grisham, B.A., Nowak, M.C., Collins, D.P., 2021. Migration efficiency sustains connectivity across agroecological networks supporting sandhill crane migration. Ecosphere 12. https://doi.org/10.1002/ecs2.3543

Duijns, S., Anderson, A.M., Aubry, Y., Dey, A., Flemming, S.A., Francis, C.M., Friis, C., Gratto-Trevor, C., Hamilton, D.J., Holberton, R., Koch, S., McKellar, A.E., Mizrahi, D., Morrissey, C.A., Neima, S.G., Newstead, D., Niles, L., Nol, E., Paquet, J., Rausch, J., Tudor, L., Turcotte, Y., Smith, P.A., 2019. Long-distance migratory shorebirds travel

faster towards their breeding grounds, but fly faster post-breeding. Sci Rep 9. https://doi.org/10.1038/s41598-019-45862-0

Dunn, P.K., Smyth, G.K., 2018. Models for proportions: binomial GLMs, in: Generalized Linear Models with Examples in R. Springer Science + Business Media, New York, NY, pp. 333–369.

Ely, C.R., Raveling, D.G., 2011. Seasonal variation in nutritional characteristics of the diet of greater white-fronted geese. Journal of Wildlife Management 75, 78–91. https://doi.org/10.1002/jwmg.13

English, M.D., Robertson, G.J., Peck, L.E., Mallory, M.L., 2017. Agricultural food resources and the foraging ecologies of American black ducks (Anas rubripes) and mallards (Anas platyrhynchos) at the northern limits of their winter ranges. Urban Ecosyst 20, 1311–1318. https://doi.org/10.1007/s11252-017-0683-0

Fowler, D.N., Webb, E.B., Vrtiska, M.P., Hobson, K.A., 2020. Winter carry-over effects on spring body condition driven by agricultural subsidies to lesser snow geese (Anser caerulescens caerulescens). Avian Conservation and Ecology 15, 1–11. https://doi.org/10.5751/ACE-01743-150221

Fox, A.D., Abraham, K.F., 2017. Why geese benefit from the transition from natural vegetation to agriculture. Ambio 46, 188–197. https://doi.org/10.1007/s13280-016-0879-1

Fox, A.D., Madsen, J., Boyd, H., Kuijken, E., Norriss, D.W., Tombre, I.M., Stroud, D.A., 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. Glob Chang Biol 11, 881–893. https://doi.org/10.1111/j.1365-2486.2005.00941.x

Frederick, R.B., Klaas, E.E., 1982. Resource use and behavior of migrating snow geese. Journal of Wildlife Management 46, 601–614. https://doi.org/https://doi.org/10.2307/3808550

Fretwell, S.D., 1969. On territorial behavior and other factors influencing habitat distribution in birds. Institute of Statistics, Mimeograph Series No. 642.

Fronczak, D.L., Andersen, D.E., Hanna, E.E., Cooper, T.R., 2017. Distribution and migration chronology of Eastern population sandhill cranes. Journal of Wildlife Management 81, 1021–1032. https://doi.org/10.1002/jwmg.21272

Gates, R.J., Caithamer, D.F., Moritz, W.E., Tacha, T.C., 2001. Bioenergetics and nutrition of Mississippi Valley Population Canada geese during winter and migration. Wildlife Monographs 146, 1–65.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sens Environ 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Greer, A.K., Dugger, B.D., Graber, D. a., Petrie, M.J., 2007. The effects of seasonal flooding on seed availability for spring migrating waterfowl. Journal of Wildlife Management 71, 1561–1566. https://doi.org/10.2193/2006-376

Hemminger, K., König, H., Månsson, J., Bellingrath-Kimura, S.D., Nilsson, L., 2022. Winners and losers of land use change: A systematic review of interactions between the world's crane species (Gruidae) and the agricultural sector. Ecol Evol. https://doi.org/10.1002/ece3.8719

Hepp, G.R., Stangohr, D.J., Baker, L.A., Kennamer, R.A., 1987. Factors affecting variation in the egg and duckling components of wood ducks. Auk 104, 435–443. https://doi.org/https://doi.org/10.2307/4087542

Hitchcock, A.N., Schultheis, R., Straub, J.N., Coluccy, J.M., Yerkes, T., Eichholz, M.W., 2021. Variation in the diet of ducks during spring migration. Journal of Wildlife Management 85, 1601–1615. https://doi.org/10.1002/jwmg.22126

Iverson, G.C., Vohs, P.A., Tacha, T.C., 1987. Habitat use by mid-continent sandhill cranes during spring migration. Journal of Wildlife Management 51, 448–458. https://doi.org/https://doi.org/10.2307/3801033

Ivey, G.L., Dugger, B.D., Herziger, C.P., Casazza, M.L., Fleskes, J.P., 2015. Wintering ecology of sympatric subspecies of Sandhill Crane: Correlations between body size, site fidelity, and movement patterns. Condor 117, 518–529. https://doi.org/10.1650/CONDOR-14-159.1

Johnson, W.P., Schmidt, P.M., Taylor, D.P., 2014. Foraging flight distances of wintering ducks and geese: a review. Avian Conservation and Ecology 9, 2. https://doi.org/10.5751/ACE-00683-090202

Karlsson, H., Nilsson, C., Bäckman, J., Alerstam, T., 2012. Nocturnal passerine migrants fly faster in spring than in autumn: A test of the time minimization hypothesis. Anim Behav 83, 87–93. https://doi.org/10.1016/j.anbehav.2011.10.009

Katerji, N., Mastrorilli, M., Rana, G., 2008. Water use efficiency of crops cultivated in the Mediterranean region: Review and analysis. European Journal of Agronomy. https://doi.org/10.1016/j.eja.2007.12.003

Kauffeld, J.D., 1981. Management of migratory crane habitat on Alamosa and Monte Vista National Wildlife Refuges. Proceedings 1981 Crane Workshop 117–121.

Krapu, G.L., Brandt, D.A., Cox, R.R., 2004. Less waste corn, more land in soybeans, and the switch to genetically modified crops: trends with important implications for wildlife

management. Wildl Soc Bull 32, 127–136. https://doi.org/10.2193/0091-7648(2004)32[127:lwcmli]2.0.co;2

Krapu, G.L., Brandt, D.A., Jones, K.L., Johnson, D.H., 2011. Geographic distribution of the mid-continent population of sandhill cranes and related management applications. https://doi.org/10.1002/wmon.l

Krapu, G.L., Brandt, D.A., Kinzel, P.J., Pearse, A.T., 2014. Spring migration ecology of the Mid-Continent sandhill crane population with an emphasis on use of the Central Platte River Valley, Nebraska. Wildlife Monographs 189, 1–41. https://doi.org/10.1002/wmon.l013

Krapu, G.L., Facey, D.E., Fritzell, E.K., Johnson, D.H., 1984. Habitat use by migrant sandhill cranes in Nebraska. Journal of Wildlife Management 48, 407–417. https://doi.org/https://doi.org/10.2307/3801172

Krapu, G.L., Iverson, G.C., Reinecke, K.J., Boise, C.M., 1985. Fat deposition and usage by arctic-nesting Sandhill Cranes during spring. Auk 102, 362–368. https://doi.org/https://doi.org/10.2307/4086780

Krebs, J.R., Wilson, J.D., Bradbury, R.B., Siriwardena, G.M., 1999. The second Silent Spring? Nature 400, 611–612.

Link, P.T., Afton, A.D., Cox, R.R., Davis, B.E., 2011. Daily movements of female mallards wintering in Southwestern Louisiana. Waterbirds 34, 422–428. https://doi.org/10.1675/063.034.0404

Matthews, L.J., Petrie, M., Eadie, J.M., 2022. Impacts of changing postharvest agricultural practices on abundance of waste grain in California's Central Valley. J Fish Wildl Manag 13, 32–333. https://doi.org/10.3996/JFWM-21-061

McWilliams, S.R., Guglielmo, C., Pierce, B., Klaassen, M., 2004. Flying, fasting, and feeding in birds during migration: A nutritional and physiological ecology perspective. J Avian Biol. https://doi.org/10.1111/j.0908-8857.2004.03378.x

Mix, K., Lopes, V.L., Rast, W., 2011. Annual and growing season temperature changes in the San Luis Valley, Colorado. Water Air Soil Pollut 220, 189–203. https://doi.org/10.1007/s11270-011-0746-4

Mix, K., Rast, W., Lopes, V.L., 2010. Increases in growing degree days in the alpine desert of the San Luis Valley, Colorado. Water Air Soil Pollut 205, 289–304. https://doi.org/10.1007/s11270-009-0074-0

Moore, C.B., Osborne, D.C., Askren, R.J., Carlson, L.G., Brasher, M.G., 2023. Distributional shifts of wintering midcontinent greater white-fronted geese. Journal of Wildlife Management 87. https://doi.org/10.1002/jwmg.22401

Nie, W., Zaitchik, B.F., Rodell, M., Kumar, S. V., Arsenault, K.R., Badr, H.S., 2021. Irrigation water demand sensitivity to climate variability across the contiguous United States. Water Resour Res 57. https://doi.org/10.1029/2020WR027738

Nilsson, C., Klaassen, R.H.G., Alerstam, T., 2013. Differences in speed and duration of bird migration between spring and autumn. American Naturalist 181. https://doi.org/https://doi.org/10.1086/670335

Norberg, U.M., 1996. Energetics of flight, in: Avian Energetics. Chapman & Hall, New York, pp. 199–249.

Olsson, O., Brown, J.S., Helf, K.L., 2008. A guide to central place effects in foraging. Theor Popul Biol 74, 22–33. https://doi.org/10.1016/j.tpb.2008.04.005

Overton, C.T., Casazza, M.L., 2023. Movement behavior, habitat selection, and functional responses to habitat availability among four species of wintering waterfowl in California. Front Ecol Evol 11. https://doi.org/10.3389/fevo.2023.1232704

Pearse, A.T., Krapu, G.L., Brandt, D.A., 2017. Sandhill crane roost selection, human disturbance, and forage resources. Journal of Wildlife Management 81, 477–486. https://doi.org/10.1002/jwmg.21215

Pearse, A.T., Krapu, G.L., Brandt, D.A., Kinzel, P.J., 2010. Changes in agriculture and abundance of snow geese affect carrying capacity of sandhill cranes in Nebraska. Journal of Wildlife Management 74, 479–488. https://doi.org/10.2193/2008-539

Pederson, G.T., Gray, S.T., Woodhouse, C.A., Betancourt, J.L., Fagre, D.B., Littell, J.S., Watson, E., Luckman, B.H., Graumlich, L.J., 2011. The unusual nature of recent snowpack declines in the North American Cordillera. Science (1979) 333, 332–335. https://doi.org/10.1126/science.1201570

Pohanková, E., Hlavinka, P., Orság, M., Takáč, J., Kersebaum, K.C., Gobin, A., Trnka, M., 2018. Estimating the water use efficiency of spring barley using crop models. Journal of Agricultural Science 156, 628–644. https://doi.org/10.1017/S0021859618000060

Prop, J., Black, J.M., 1998. Food intake, body reserves and reproductive success of barnacle geese Branta leucopsis staging in different habitats. Nork Polarinstitutt 200, 175–193.

R Core Team, 2022. R: A language and environment for statistical computing.

Ray, A.J., Barsugli, J.J., Averyt, K.B., Wolter, K., Hoerling, M., Doesken, N., Udall, B., Webb, R.S., 2008. Climate change in Colorado: A synthesis to support water resources management and adaptation.

Reinecke, K.J., Krapu, G.L., 1986. Feeding ecology of sandhill cranes during spring migration in Nebraska. Journal of Wildlife Management 50, 71–79. https://doi.org/https://doi.org/10.2307/3801490

Rodehutscord, M., Rückert, C., Maurer, H.P., Schenkel, H., Schipprack, W., Bach Knudsen, K.E., Schollenberger, M., Laux, M., Eklund, M., Siegert, W., Mosenthin, R., 2016. Variation in chemical composition and physical characteristics of cereal grains from different genotypes. Arch Anim Nutr 70, 87–107. https://doi.org/10.1080/1745039X.2015.1133111

Schmaljohann, H., Eikenaar, C., Sapir, N., 2022. Understanding the ecological and evolutionary function of stopover in migrating birds. Biological Reviews 97, 1231–1252. https://doi.org/10.1111/brv.12839

Seamans, M.E., 2023. Status and harvests of sandhill cranes 2023: Mid-continent, Rocky Mountain, Lower Colorado River, and Eastern populations. Lakewood, Colorado.

Sherfy, M.H., Anteau, M.J., Bishop, A.A., 2011. Agricultural practices and residual corn during spring crane and waterfowl migration in Nebraska. Journal of Wildlife Management 75, 995–1003. https://doi.org/10.1002/jwmg.157

Siegert, W., Zuber, T., Rodehutscord, M., 2022. Variability and prediction of metabolisable energy of wheat, triticale, and rye in caecectomised laying hens. European Poultry Science 86. https://doi.org/10.1399/eps.2022.354

Sparling, D.W., Krapu, G.L., 1994. Communal roosting and foraging behavior of staging sandhill cranes. Wilson Bull 106, 62–77.

Stanton, R.L., Morrissey, C.A., Clark, R.G., 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agric Ecosyst Environ. https://doi.org/10.1016/j.agee.2017.11.028

Thorpe, P., Liddick, T., Collins, D., 2024. September 2023 survey of the Rocky Mountain Population of greater sandhill cranes. U.S. Fish and Wildlife Service. https://doi.org/10.1016/j.gecco.2023.e02715

USDA National Agricultural Statistics Service Cropland Data Layer, 2023. Published crop-specific data layer [Online] [WWW Document]. USDA-NASS, Washington, DC.

Vaida, F., Blanchard, S., 2005. Conditional Akaike information for mixed-effects models. Biometrika 92, 351–370. https://doi.org/https://doi.org/10.1093/biomet/92.2.351

Van Gils, J.A., Tijsen, W., 2007. Short-term foraging costs and long-term fueling rates in central-place foraging swans revealed by giving-up exploitation times. American Naturalist 169, 609–620. https://doi.org/10.1086/513114

Vanausdall, R.A., Kendall, W.L., Collins, D.P., Hays, Q.R., 2024. Time of year and weather influence departure decisions of sandhill cranes at a primary stopover. Front Ecol Evol 12. https://doi.org/10.3389/fevo.2024.1279279

Warnock, N., 2010. Stopping vs. staging: The difference between a hop and a jump. J Avian Biol 41, 621–626. https://doi.org/10.1111/j.1600-048X.2010.05155.x

CHAPTER 4 – ENERGY AVAILABILITY FOR SANDHILL CRANES DURING SPRING AND AUTUMN MIGRATION IN THE SAN LUIS VALLEY, COLORADO

INTRODUCTION

Energy availability is assumed to be the most limiting factor for several avian populations during the non-breeding period (Williams et al., 2014). During migration, birds require energy and nutrient reserves to travel and find resources, thermoregulate, secure mates, and eventually reach their breeding or wintering grounds (Jenni & Jenni-Eiermann, 1998; Williams et al., 2014). An inability to acquire adequate energy and nutrients during migration has been shown to have cross-seasonal effects on survival (Fowler et al., 2020; Haramis et al., 1986; Hepp et al., 1986; Sedinger & Alisauskas, 2014) and reproduction (Alisauskas, 2002; Ankney & MacInnes, 1978; Devries et al., 2008). As a result, management strategies often involve improving the quantity and quality of foraging habitats for migrant birds to ensure they can meet their energetic needs. To determine if population goals are being met, many regional management plans operate on the idea that food limitation will have the greatest impact on the carrying capacity of an area (Central Valley Joint Venture, 2006; Intermountain West Joint Venture, 2013; Lancaster & Wilson, 2021). Carrying capacity generally refers to the number of birds of a particular species or group an area can support for a given length of time (Goss-Custard et al., 2002, 2003). Identifying the carrying capacity of areas intensively managed for migrant birds is a critical step to ensuring adequate resources are available and anticipating effects from management or landscape changes.

Carrying capacity can be estimated using bioenergetics models, which incorporate the energy demand of individual birds and energy supply of habitat types used by species of interest (Beatty et al., 2015; Fino et al., 2017; Petrie et al., 2016; Williams et al., 2014). The amount of energy and the type of nutrients a single bird needs to survive and/or reproduce will vary

depending on the time of the year (Baldwin et al., 2022; Reinecke et al., 1982; Winker et al., 1992). During spring, individuals are often focused on acquiring nutrient reserves (e.g., lipids, protein) needed for successfully migrating and reproducing, so birds may spend more time foraging and choosing foods that are easily digestible and have a higher lipid content, which is the major energy source for birds (Gates et al., 2001; Jenni & Jenni-Eiermann, 1998; Krapu et al., 1995; McLandress & Raveling, 1981). At the same time, the increase in lipid deposition also incurs an energetic cost to the individual (Gates et al., 2001). In contrast to spring, autumn migrants may allocate more of their time budget to resting, maintenance during molt, or to care for young (Gates et al., 2001; Portugal et al., 2007). As a result of this variation in demand, individuals will also vary in their energy expenditure as they go about their daily activities, such as foraging, maintenance, and flying (Pearse et al., 2010; Tacha et al., 1987). Environmental conditions, such as temperature and precipitation, will also influence energy demand, as these factors affect the ability of birds to thermoregulate (Baldassarre & Bolen, 1984). Quantifying the energetic requirements of birds allows for determining the amount of energy available on the landscape at specific times of the year. Different foods will provide different levels of energy and nutrients, and their prevalence in the diets of certain species will vary throughout the year. Estimating forage biomass and converting it to energetic availability is a commonly used method for determining energetic availability (Brasher et al., 2007; Fino et al., 2017; Heitmeyer, 2010; Williams et al., 2014)

Agricultural crops provide a significant amount of energy for several migrant populations, including sandhill cranes (*Antigone canadensis*) and some species of waterfowl (English et al., 2017; Gates et al., 2001; Krapu et al., 2004). As a result, growing crops is often incorporated into management practices at nonbreeding areas (Boggie et al., 2023; English et al.,

2017), including stopovers, which are areas used by migrant birds to rest and refuel during migration (Schmaljohann et al., 2022). Several stopover areas used by sandhill cranes throughout their range in North America are dominated by cereal grains, such as corn (*Maize sp.*), wheat (*Triticum sp.*), and barley (Krapu et al., 2014; Lovvorn & Kirkpatrick, 1982), and some public areas provide supplemental forage in the form of crops (Boggie et al., 2023). The San Luis Valley (SLV) in southcentral Colorado is one such stopover area for the Rocky Mountain Population (RMP) of greater sandhill cranes (*A. c. tabida*). The RMP stage in the SLV for 30-40 days in spring as they migrate from their wintering areas in New Mexico, Arizona, and Mexico to their breeding areas throughout the Rocky Mountains in Wyoming, Montana, Utah, Idaho, and northwestern Colorado (Drewien & Bizeau, 1974; Vanausdall et al., 2024). In autumn, most of the RMP spends a longer period in the SLV, with some individuals remaining for up to 60 days (Donnelly et al., 2021; Vanausdall et al., 2024). Additionally, a smaller number of lesser sandhill cranes (*A. c. canadensis*) from the Midcontinent Population (MCP) also use the SLV during spring and autumn migration (Krapu et al., 2014).

Agriculture is the main economic driver in the SLV, and barley is one of the main crops grown in the region, along with potatoes (*Solanum tuberosum*) and alfalfa (*Medicago sativa*; Rio Grande Basin Roundtable, 2022). Sandhill cranes primarily forage on waste barley that is left over after autumn harvest and remains during the following spring (see Chapter 2). Barley and other grains provide protein and a significant amount of carbohydrates (Rodehutscord et al., 2016), which allows sandhill cranes to deposit lipid important for migration and breeding (Krapu et al., 1985). Most of the barley comes from private property, but the Monte Vista National Wildlife Refuge (MVNWR) also provides supplemental barley specifically for sandhill cranes and waterfowl (U.S. Fish and Wildlife Service, 2015). Previous work on sandhill cranes in the

SLV and populations in other parts of their range confirm that cereal grains make up a significant portion of their diet in spring (Ballard & Thompson, 2000; Kauffeld, 1981; Reinecke & Krapu, 1986).

Although numbers of RMP and MCP sandhill cranes have been relatively stable and even increasing in the last 20 years (Seamans 2023), several factors influence the energetics of sandhill cranes in the SLV and some may pose challenges to management of sandhill cranes in the future. After crop harvest, for example, many growers in the SLV plow and irrigate fields to germinate seeds and prepare fields for planting in late spring. Tillage decreases the waste seed available to sandhill cranes and other granivores (Krapu et al., 2004; Kross et al., 2008; Matthews et al., 2022; Sherfy et al., 2011). Previous research has also shown that sandhill cranes and geese that rely on waste grain spend less time in tilled agricultural fields than non-tilled fields (Anteau et al., 2011).

Barley production and harvest overall have declined in the SLV in the last few decades (USDA National Agricultural Statistics Service Cropland Data Layer, 2023). Part of this decline could be due to decreases in barley demand, but increasing water scarcity and temperatures may also make growing water-intensive crops more difficult and costly (Lobell et al., 2011; Mix et al., 2011). Most of the water used for irrigation in the SLV comes from surface water diverted from the Rio Grande and other tributaries, but groundwater from underground aquifers is also used to supplement water needs (Rio Grande Basin Roundtable, 2022). However, surface water has declined in the SLV and other regions in the Intermountain West due to climate change and overuse (Barnett et al., 2008; Chavarria & Gutzler, 2018; Donnelly et al., 2020). Extreme drought and limited surface water has also led to significant depletions in groundwater. These conditions are likely to influence overall crop dynamics and the type of crops grown. While

sandhill cranes will forage on other crops, particularly other grains (e.g., triticale), barley is the dominant crop used and the most abundant grain throughout the SLV. Given the role of barley in the diet of migrant sandhill cranes and its importance in improving body condition, a significant decline in barley or changes in postharvest may influence the energetics of sandhill cranes, which may subsequently affect reproduction and survival.

The management plan for the RMP includes an objective to provide sufficient habitat to support a population of 17,000 – 21,000 sandhill cranes (Pacific Flyway Council and Central Flyway Council, 2016). Gathering baseline information on the bioenergetics of sandhill cranes during migration in the SLV will help inform future habitat management to support this objective, particularly under changing climate, agricultural, and landscape conditions. Specifically, determining the amount of barley required to support current and future numbers of RMP sandhill cranes and how that is influenced by season and tillage intensity (i.e., postharvest) is important for habitat managers. Our objectives were to (1) determine the influence of tillage intensity on barley availability to cranes, (2) examine the temporal variation in energy requirements of RMP sandhill cranes in spring and autumn, (3) estimate average barley availability and demand in the spring and autumn in the SLV, (4) relate energy demand to energy availability from barley using a bioenergetics model, and (5) use this model to determine the carrying capacity of the SLV for sandhill cranes. We predicted that waste barley would be lowest in the most intensively tilled fields and highest in fields that are not tilled (i.e., idle fields). We also predicted energy demand to increase in spring compared to autumn due to the continued depletion of waste barley after harvest, the need to fly farther from roosts, and increasing needs for fat accumulation. Sandhill cranes are central-place foragers foraging closer to roosting sites if adequate forage is available (Ivey et al., 2015; Johnson et al., 2014). As waste barley is depleted

due to granivory, germination, and deterioration, sandhill cranes must fly farther from roosts to obtain the necessary energy requirements (Collins et al., 2023; Johnson et al., 2014). Thus, waste barley is likely to be most depleted by the end of spring prior to planting for the following season.

METHODS

Study area

The SLV is a high elevation, intermontane basin and part of the Upper Rio Grande Basin (Figure 4.1). The area of the valley floor is approximately 8,200 km^2. The surrounding mountain ranges include the San Juan Mountains to the west and the Sangre de Cristo Mountains to the east. The headwaters of the Rio Grande are in the San Juan Mountains, and snowmelt from the mountains run from the river and its tributaries and provide surface water throughout the SLV. Peak runoff from snowmelt occurs in spring, and monsoonal rains in the summer also increase surface water on the valley floor. Annual precipitation, which averages less than 200 mm, is lower in the SLV than in the surrounding mountains, making it an arid region (Cooper et al., 2006) confined and an unconfined aquifer contribute to hydrology in the SLV and are replenished by surface water (Emery et al., 1969). Temperatures range between -20°C to 20°C (Western Regional Climate Center, 2013) throughout the year, with average temperatures around 6°C.

Agriculture is the most important economic sector in the SLV (Rio Grande Basin Roundtable, 2022). The primary crops produced are alfalfa, barley, potatoes, and other grains, such as oat hay. During this study, alfalfa made up 27% of the total crop area in the SLV, while barley made up 12%, potatoes made up 11%, and other grains made up 12%. Crops are generally irrigated using center pivots, and the majority of water comes from the diversion of surface water

from the Rio Grande and other rivers and channels (Emery et al., 1969). Irrigation water is also supplemented with groundwater. Severe drought during the 2000-2004 period and overuse have resulted in decreased groundwater levels and resulted in the formation of groundwater subdistricts to improve management of groundwater withdrawals (Rio Grande Basin Roundtable, 2015). An irrigation season limits groundwater pumping to between 1 April and 31 October.

Much of the SLV was once composed of extensive wetland networks, but most of these are limited to areas managed by the state (i.e., Colorado Parks and Wildlife) and federal governments. The MVNWR allocates water to flood approximately 5,000 ha of wetland habitat for migrating waterfowl and sandhill cranes, along with wintering and breeding waterfowl and waterbirds (Heitmeyer & Aloia, 2013). Wet meadows and scrub-shrub habitat composed of greasewood and rabbitbrush are other habitat types that make up many of these properties (U.S. Fish and Wildlife Service, 2015). However, much of the surface water is on private areas in the SLV (Donnelly et al., 2021), which makes the area that can be managed intentionally more limited.

Barley collection

We focused on selection of barley fields on private property within 15 km of potential sandhill crane roost sites. Before autumn of each year, we randomly selected barley fields to sample post-harvest. We attempted to contact property owners of the barley fields selected, but we were not always able to successfully reach all property owners or were denied access. When we could not obtain permission to access a particular property, we selected another barley field within 1-2 km of the original field until we were able to gain access. Growers in the SLV typically have multiple fields that they manage, so in some cases we sampled more than one field for a specific property owner.

We sampled barley at four different time periods based on the arrival and departure of sandhill cranes in the autumn and spring: early autumn (pre-arrival), late autumn (post-arrival), early spring (pre-arrival), and late spring (post-arrival). During each sampling occasion, we randomly selected points within a field to collect waste barley. The number of points in each field varied based on the size of the field. We sampled 4-6 points for fields < 24 ha and 10-12 points for fields > 24 ha. The number of points also varied based on logistical constraints and timing. We used a 0.25 m^2 quadrat to sample barley (A. Lanssen pers. comm.). We opted for more small quadrats rather than fewer large quadrats to try to capture variability within a field. We avoided placing points within 10 m of a field edge (Foster et al., 2010). We collected only un-sprouted barley on the surface of the ground and within 5 cm of the surface of the soil. Although there is evidence that sandhill cranes will consume germinated grain up to 17 days after sprouting (Barzen et al., 2018), timing of irrigation varies widely, and it was logistically difficult to determine the age of sprouted waste grain during collection. Additionally, sandhill cranes generally prefer un-sprouted or recently germinated grain when the endosperm is still intact over sprouted grain and tend to cease use in fields when seedlings reach 5-10 cm (Littlefield, 2002). To examine differences in waste grain among fields with different tillage intensities, each field was classified based on the percentage of standing stubble still visible: no tillage or complete stubble ("idle"), >50% stubble ("low intensity"), and <50% stubble ("high intensity"). The collected barley was frozen at a temperature of -20°C until processing. We cleaned thawed samples, removed seeds still attached to the spike, and removed any awns. Grain seeds were dried to a constant weight at 60°C for approximately 48 hours and then weighed (0.001 g) to estimate biomass.

Unlike privately managed barley fields, the MVNWR does not harvest planted barley. The barley is left standing through autumn and early spring, mowed, and the cut barley is left prior to the peak arrival time (mid-March) of sandhill cranes in spring. We sampled all three barley fields for the MVNWR each year, but the first three samples were composed of both spilled barley and barley still left on the spike. The location of the fields did not change over the years. We randomly selected quadrats within each field for each season and year and sampled at the same time periods as for the private barley fields. We summarized these fields by averaging across all plots and years for each season.

To get an estimate of the total barley available throughout the entire SLV to sandhill cranes and derive estimates of barley available in different tillage intensities, we used remote sensing techniques to classify barley fields into one of the three tillage indices. We created a classifier in the publicly available Google Earth Engine (Gorelick et al., 2017) to classify fields into idle, low intensity till, and high intensity till using training data collected on the ground in the SLV and from Landsat imagery. We trained the classifier using postharvest data gathered from fields sampled for barley and from fields used by RMP sandhill cranes during roadside counts (see Chapter 3). We used imagery from Landsat Operational 8 and 9 adjusted for surface reflectance to obtain spectral data for both the training data and the classified area. We first delineated barley fields for the study period (2020 and 2021) using data from the Rio Grande Water Conservation District (RGWCD) and the Cropland Data Layer from the U.S. Department of Agriculture's National Agricultural Statistics Service (NASS). Technicians from the RGWCD classify agricultural fields into crop types throughout most of the SLV each year, but the area in Costilla County is not surveyed. We used NASS data for this region only. We used spectral mixture analysis to differentiate pixels in stubble (i.e., idle), bare soil, and green vegetation (i.e.,

Normalized Difference Vegetation Index [NDVI]). Spectral mixture analysis is a remote sensing technique that uses reference endmembers to classify the proportional amount of habitat classes within pixels (Adams and Gillespie 2006). We used static endmembers from fields known to be in stubble and bare soil (i.e., highly tilled) in 2020 and 2021. We used the 98th percentile of NDVI to generate endmembers for 2020 and 2021. We then estimated the proportion of stubble, bare soil, and NDVI to classify pixels into these proportional habitat classes. To identify tillage intensity at the field level, we then obtained the following spectral information to inform a classifier: NDVI, Normalized Difference Soil Index (NDSI), and spectral bands 1-5 and 7. Along with these data layers, stubble and bare soil from spectral mixture analysis were used in the classifier to further differentiate fields into one of the three tillage intensity types. We assessed the accuracy of our classifier by comparing observed values and predicted values of tillage intensity at the field level. Our estimates of the proportion correctly classified (i.e., accuracy) were 0.82 for the 2020-2021 season and 0.81 for the 2021-2022 season.

Behavioral observations

We used behavioral observations to summarize behaviors across different habitats and tillage intensities and to inform the amount of energy allocated to different daily activities (Paulus, 1988). We completed focal observations of individuals throughout the primary habitats used by RMP sandhill cranes in the SLV. The focal habitats were described as barley, other grain, potatoes, alfalfa, wetland/pasture, and other habitats (e.g., grassland). We focused only on the diurnal period, as there is evidence that cranes spend 95% to 100% of their time resting during the nocturnal period (Tacha et al., 1987). Surveys began between a half hour before sunrise and ended at a half hour after sunset, and we attempted to survey 1-2 birds in each hour of the diurnal period each week. To select an individual from a flock (>20 individuals), we set up a scope,

looked away, and moved the scope sideways and up and down to randomly position it. We then used a die to randomly choose the individual and the side from which to count (even numbers to count from the right, odd numbers to count from the left). We used a similar random process for groups comprised of <20 individuals but did not move the scope randomly. For 15 minutes, we recorded behaviors every 10 seconds. We assigned behaviors to the following categories: walking (i.e., head up, walking forward, not looking at the ground), searching (i.e., walking while looking at the ground, searching for food), maintenance (preening, stretching, or scratching), resting, foraging (jabbing or probing), alert, and other (i.e., drinking, social, flying, or out-of-sight). We separated searching from walking to try to separate when a bird was apparently walking from one destination to another from when it was actively looking for food while walking (Barzen et al., 2018). Social behaviors included agonistic and courtship displays and were based on descriptions by Tacha (1988). We also recorded other variables including the number of conspecifics using the area, habitat type, and tillage intensity. The number of other cranes included cranes within approximately 100 m of the selected individual (Tacha et al., 1987). For agricultural areas, we recorded the crop type, while tillage intensity was recorded for grain fields using the indices described above.

Because we only observed sandhill cranes when they were not flying, we used another data source to estimate the proportion of time RMP sandhill cranes spent flying. We used data from birds fitted with global system for mobile communication (GSM) platform transmitter terminal (PTT) tags (n = 95; Evolution Series-400, 15-g; Cellular Tracking Technologies, Rio Grande, NJ, USA) or global positioning system (GPS) PTT tags (n = 38; PTT-100, 22-g Solar Argos/GPS PTT, Microwave Telemetry, Columbia, MD, USA) during the years 2015-2022. Details for the selection and capture of RMP sandhill cranes can be found in Boggie et al. (2018)

and Conring et al. (2019). We separated locations in the SLV into either roosting, loafing, or foraging. Descriptions on how we differentiated locations into these behaviors can be found in Chapter 1. We calculated the distance between foraging and roosting locations and between foraging and loafing locations for each year and season across all sandhill cranes. We used the median of these distances in each season and assumed an average speed of 47 km during flight to calculate the amount of time RMP sandhill cranes fly per day (Pearse et al., 2010). The average speed was calculated using the GSM/GPS data for all RMP sandhill cranes.

Sandhill crane collection and proximate analysis

We collected adult RMP sandhill cranes in the SLV to examine the temporal trends in body mass and body condition (i.e., lipid or fat mass) and to estimate the daily gain in fat throughout the spring migration period. We used data from collections that occurred in the spring 1999-2001 for a different project, along with collections from spring 2021. We focused on collecting foraging RMP sandhill cranes between February through April in the SLV using a rifle or shotgun. Because these studies were also a part of other projects examining the food contents of collected sandhill cranes, individuals were observed for approximately 20 minutes to ensure the esophagus would contain forage. We distinguished adults from juveniles using plumage characteristics (Tacha, 1988). We immediately froze collected specimens.

We obtained fresh carcass weight in the lab after thawing specimens. Individuals collected during the 1999-2001 period were weighed ±10 g, while individuals from the 2021 sample were weighed ±1 g. We removed internal organs and feathers and reweighed carcasses to adjust lipid estimates. We sexed individuals by using observations from the field and examining internal organs in the lab. However, for individuals that could not be confidently sexed, we used genetics testing. Genomic DNA (gDNA) was isolated from 0.1 g of frozen muscle using the

Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, California). The CHD gene, located on the sex chromosome, was amplified using polymerase chain reaction (PCR) using the primers CHD1 R and CHD1 F (Lee et al. 2010). PCR reactions to amplify CHD followed the standard HotStarTaq (Qiagen Inc., Valencia, CA, USA) protocol: 25 µL reactions containing 30 ng gDNA, 12.5 µL HotStarTaq premix, 0.6 µL of each 10 µM primer, and 8.3 µL of distilled water (ddH2O). The thermal profile was as follows: hot start of 80°C, initial denaturation at 95°C for 2 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 49°C for 45 s, and extension at 73°C for 1 min, with a final extension at 73°C for 15 min. Sex was then assessed by running the PCR product on a 1% agarose gel by gel electrophoresis. The presence of 2 bands in the gel at ~550 and ~350 bp indicated the presence of both the Z and W chromosomes (i.e. female), whereas the presence of a single band at ~550 bp indicated the presence of only the Z chromosome (i.e. male; (Lee et al., 2010)).

The ingesta-free carcasses were homogenized, and a 100-300 g sample of each carcass was dried to a constant weight at 80°C. Based on the period of collection, samples were processed for lipids using two separate but similar methods. For the 1999-2001 samples, lipids were extracted from the dried sample using petroleum ether in a modified Soxhlet apparatus (Dobush et al., 1985). The samples were then placed in a muffle furnace at 550 °C to obtain protein. For the 2021 samples, a 1.0-2.0 g sample of the dried homogenate was head-sealed in an Ankom filter bag (Ankom Technology, Macedon, New York USA) and weighed (± 0.1 mg). Lipids were extracted using an Ankom XT15 Lipid Extractor. The samples were reweighed to obtain a lean sample mass. We extrapolated sample lipids and carcass lipids by multiplying the sample lipid amount by the inverse of the proportion of carcass mass represented by each homogenate, and we used a similar method for protein content.

Collection of sandhill cranes was approved by the Colorado State University Institutional Animal Care and Use Committee (IACUC; Protocol ID 1273). The appropriate permits at the federal level (Permit MB89291D-0) and for New Mexico (Permit BIO 2021-016) and Colorado (License 1849839645) were obtained.

Sandhill crane surveys

We conducted weekly or bi-weekly surveys of sandhill cranes throughout the SLV to estimate a population index for calculating carrying capacity. Survey routes were divided into six major regions throughout the SLV where sandhill cranes are historically the most abundant. We drove survey routes within a span of 2-4 days each week during the foraging hours of sandhill cranes. Morning surveys occurred between a half hour before sunrise to approximately 4 hours after sunrise, and evening surveys were conducted between 3 hours before sunset and a half hour after sunset. Survey times were determined using a combination of observations of sandhill cranes and data from Global Positioning Systems in previous years. Morning and evening surveys were alternated weekly for each region. During a survey, the same observer drove the route and counted both greater (RMP) and lesser (MCP) sandhill cranes on fields immediately adjacent (i.e., within approximately 1 km) to the road. Determining subspecies was based on overall size and head shape (Schmitt & Hale, 1997). We did not differentiate between adults and hatch-year birds. For more information on roadside surveys, see Chapter 3.

Energetics parameters and model

We examined the energetic demand and availability of barley by RMP sandhill cranes using two steps (Figure 4.2). The first step involved using basic energetics equations to estimate average energy demand required per day by individual RMP sandhill cranes, energy supply at two-week periods based on biomass estimates, and extrapolating to total supply available

throughout autumn and spring. We divided each season into 15-day intervals (i.e., time periods) to improve precision and account for the limited temporal scale of some of the data inputs. For spring, we defined early spring (15 February – 28 February), mid-spring (1 March – 15 March), and late spring (16 March – 31 March). Similarly, we partitioned autumn into early autumn (1 October – 15 October), mid-autumn (16 October – 31 October), and late autumn (1 November – 15 November). The second step used biomass estimates and RMP sandhill crane numbers as inputs for a *daily* energetics model to calculate total daily energy demand and supply in the SLV under different scenarios of barley availability.

Effect of tillage intensity and time on biomass and estimates of biomass

We used the unweighted observations (i.e., individual plots within fields) following Sherfy et al. (2011) to examine the effect of tillage intensity (i.e., idle, low intensity, high intensity), season, and period (i.e., autumn pre-arrival, autumn post-arrival, spring pre-arrival, and spring post-arrival) on biomass in privately owned barley fields. For this part, we did not include fields managed by the MVNWR because they did not harvest barley or manage their fields like private growers. We included tillage intensity, an interaction of season and period, and year as fixed effects and field as a random effect in a general linear model. We scaled observations to have a mean of zero and a standard deviation of one. We used the package *nlme* in Program R (Pinheiro & Bates, 2000; Pinherio et al., 2023). We identified significant effects for coefficients if their 95% confidence intervals did not overlap zero.

Effect of tillage intensity on behavior

To examine the effects of tillage intensity on behavioral observations, we used the unadjusted, diurnal behavioral observations. We used the average time sandhill cranes spent in behaviors (i.e., alert, foraging, maintenance, resting, searching, social, and walking) during the

diurnal period to examine trends in behavior differences across habitat and season. To determine if there was an effect of tillage intensity on behavior, we only examined foraging and searching behavior by RMP sandhill cranes that used grain fields and used Analysis of Variance (ANOVA). We considered fixed effects to be significant at α=0.05. For significant effects, we used the Tukey-Kramer post-hoc test to determine significant (P<0.05) differences.

Temporal trends in body mass and lipids

To examine differences in body mass and lipid content of collected RMP sandhill cranes in spring, we grouped specimens into the three time periods for spring described above. We did this for both periods of collection. We used ANOVA with Type III sums of squares to determine the effects of time period and sex on both body mass and fat content. We first examined models with an interaction between time period and sex, but we discarded the interaction if it was not significant at α=0.05.

Energy demand

We generated estimates for energy required by an individual RMP sandhill crane in the SLV to calculate the energy demand (*ED*) required by the population (Figure 4.2). Values of ED_t in kcal at time *t* were calculated as

$$ED_t = DEE_t * N_t$$

where DEE_t is the daily energy expenditure at time period t for an individual RMP sandhill crane and N_t is the total number of RMP sandhill cranes in the SLV at time period *t*. Calculations of DEE_t were different for both autumn and spring, as we wanted to account for the cost of lipid production in spring. For spring, we calculated DEE_t as

$$DEE_t = LP + CF_t + \sum_{i=1}^{n} (RMR_t a_i T_i)$$

where LP is the cost of lipid production, CF_t is the cost of flight at time period t, RMR_t is the resting metabolic rate at time period t, a_i is the correction factor for behavior i, and T_i is the proportion of time in a 24-hour period that RMP sandhill cranes are engaged in behavior i. We calculated RMR (kcal) at time *t* using the allometric equation

$$RMR_t = (0.239006)(422M_t^{0.74})$$

based on Miller & Eadie (2006) and Boggie et al. (2023), where M_t is the average body mass (kg) of RMP sandhill cranes at time period t. The constant 0.239006 converts RMR from kJ to kcal. We used data from the collected RMP sandhill cranes and averaged body mass across the three time periods for spring. We set the cost of lipid production (LP) as 9.38 kcal/g of fat gained (Reinecke & Krapu, 1986). To estimate the daily rate of fat gain, we used the ANOVA result from the analysis described above. Specifically, we used the coefficient from the ANOVA that describes the relative difference between fat in late spring compared to early spring. We converted this value to daily fat gain.

We used results from behavioral observations to apply correction factors to *RMR* (Williams et al. 2014). We averaged the proportion of time RMP sandhill cranes spent in the following behaviors for each season and applied the associated correction factor based on Tacha et al. (1988): alert (1.0), drinking (1.0), foraging (2.4), maintenance (1.2), out-of-sight (2.5), resting (1.0), searching (2.2), social (3.0), and walking (2.7). For estimates of energy demand, we adjusted the proportion of time spent in each behavior to a diel (24-hr) period by assuming that sandhill cranes mostly rested at night, because we were unable to observe flocks on the roost. Tacha et al. (1988) found that sandhill cranes in the Midcontinent Population spent an average of 50-60% of time resting over a 24-hr period that included both diurnal and nocturnal observations.

We also included the proportion of time spent flying in the diel activity budgets and accounted for the cost of flight (*CF*; Pearse et al. 2010), rather than using a correction factor. We first estimated the metabolic power (*P*) required for flight using the allometric equation

$$P_t = 57.3M_t^{0.813}$$

where P_t is in Watts and based on equation 7.35 from Norberg (1996). We converted P_t to kcal/h and multiplied it by the average daily hours RMP sandhill cranes were in flight based on the GSM/GPS data to get the daily cost of flight in kcal (Pearse et al., 2010). Based on examining average daily flight distances (described above), we converted the average total daily distance RMP sandhill cranes were in flight for each season and week to the average time (hr) spent flying. The value of *CF* varied by time period in spring along with body mass.

We used the same equations for autumn, but we did not include the cost of lipid production. While RMP sandhill cranes are likely depositing fat in autumn, we did not have body mass or fat estimates for this time of the year. For both seasons, we calculated separate values for each sex. We did not vary DEE by age because the GSM/GPS data and fat content data were from adult RMP sandhill cranes. We used the resulting DEE values to estimate the amount of energy and barley required by an individual RMP sandhill crane in autumn and spring. We obtained average estimates of the amount of energy and barley required for all RMP sandhill cranes for a two-week period in both seasons and approximated the total requirements for each season.

Energy supply

Our estimates of energy supply were based on the area (ha) of barley identified by RGWCD and NASS, biomass estimates (kg/ha), and true metabolizable energy (TME) of barley. We found no evidence that there was depletion in low intensity fields throughout the season. This

was likely due to limited sample size for this category and sampling variation. For subsequent analyses, we combined the low and high intensity fields into a single "till" category for estimating energy supply and bioenergetics models. The total energy supply (ES_{th}) in kcal at time period *t* and in tillage intensity type *h* was calculated as:

$$ES_{th} = D_{th}A_hTME$$

where D_{th} is the biomass estimates at time period *t* and tillage intensity type *h*, A_h is the area of barley available in tillage intensity *h*, and TME is the true metabolizable energy of barley.

We only considered barley to be available under three scenarios, one where barley across the entire SLV is available and the others where barley is available within 5 km or 10 km of known roosting areas. Based on previous work, we determined that RMP sandhill cranes generally fly no further than approximately 10 km from their roost to forage (see Chapter 2). Based on GSM/GPS data, average commuting distance is approximately 3 km in spring and 2.6 km in autumn, but we wanted to consider the potential distance RMP sandhill cranes could fly to forage. We summed the area of barley available in each tillage intensity type using results from the classification of barley fields. True metabolizable energy (TME) is an estimate for the energy available to an individual after accounting fecal and urinary loss. We used the value 3540 kcal/kg (Gammonley and Laubhan, unpubl. data).

We also accounted for the depletion of barley over time using the barley density estimates for each tillage intensity type. We aligned the collection of barley during the four collection periods (pre-arrival and post-arrival in autumn and spring) with the 15-day time intervals for each season. However, we did not have estimates of barley density for the second interval in each season, so we only reported estimates for the early and late time periods. To convert biomass to energy availability we multiplied biomass estimates for each tillage intensity by the

TME value, which provides an estimate of energy density (kcal/ha). We then used this value and barley area to estimate the average amount of energy available per two-week periods for the entire SLV. We also estimated the average supply for early autumn and late spring for all tillage types and for idle fields only. We then determined the percent decline in energy availability and compared both *ED* and *ES* across each period within spring and autumn to assess potential deficits in the amount of energy available to RMP sandhill cranes over time.

Next, we estimated crane-energy days (*CED*; kcal/ha/crane/day) using the equation

$$CED_{th} = \frac{(D_{th})(TME)}{DEE_t}$$

to examine the number of cranes a ha of barley in tillage intensity type *h* can support during time period *t*. We extrapolated *CED* to the entire SLV, the area within 5 km of potential roost sites, and the area within 10 km of potential roost sites by multiplying each value by the area of barley in each tillage intensity type to estimate the total number of RMP sandhill cranes that can be supported given the area of barley available.

TRUEMET Simulations

We next used TRUEMET to calculate daily energy supply and demand over a specified time period and to simulate different scenarios of barley availability (Penmetcha et al., 2016; Petrie et al., 2016). Several Joint Ventures utilize the TRUEMET model to determine if energetic demands are being met under current and future habitat availability scenarios (Central Valley Joint Venture, 2006; Intermountain West Joint Venture, 2013). The TRUEMET model is a daily ration model and assumes that birds are ideal foragers and there are no costs associated with traveling between patches (Petrie et al., 2016). To generate daily estimates of energy demand and supply, we used average values calculated above as inputs into the TRUEMET model at specified time periods and then interpolated daily values across the entire period from October 1

to March 31. We modeled energy demand and supply over the entire season length (i.e., autumn to spring) to account for the continued depletion of barley throughout the wintering period. A total of eight parameters were required as input for TRUEMET: 1) the number of days being simulated, 2) population estimates of the target species during the time period being modeled, 3) daily energy expenditure, 4) habitat types used by birds for foraging, 5) area of habitat available in each time period, 6) biomass of food in habitat types, 6) nutritional quality or energetic availability of each food type, and 7) decomposition rate of each food type. Specifications of the complete TRUEMET model and its inputs can be found at Petrie et al. (2016), but we provide a brief description here. We used symbols and terminology similar to Petrie et al. (2016).

For each season, total energy demand (TED_k) on day *k* was calculated as

$$TED_k = DEE_k N_k$$

where N_k is the number of RMP sandhill cranes in the SLV on day *k* and DEE_k is the daily energy expenditure of an individual bird on day *k*. This is the same equation used to calculate energy demand above, except that is calculated for each day *k*. We used DEE values derived from the above methods for males and females and each two-week time period. Total energy supply (TES_k) on day *k* was calculated as

$$TES_k = \sum_{i=1}^{H} NEFH_{kh}$$

where $NEFH_{kh}$ is the net energy available in tillage intensity type *h* on day *k* and *H* is the total number of foraging types (i.e., tillage intensity types). Values of $NEFH_{kh}$ are the cumulative sum of total energy available on the landscape for each day of the time period and are calculated as

$$NEFH_{kh} = \left\{ \sum_{k=1}^{k} EFH_{k-1,h} - CFH_{k-1,h} - DFH_{k-1,h} \right\} + EFH_{kh}$$

where EFH_{kh} is the energy (kcal) of barley in tillage intensity type h available at the beginning of day k, CFH_{kh} is the loss of energy (kcal) in tillage intensity type h available at the beginning of day k due to consumption, and DFH_{kh} is the loss of energy (kcal) in tillage intensity type h available at the beginning of day k due to decomposition. Next, EFH_{kh} is calculated as

$$EFH_{k-1,h} = D_{k-1,h} * A_h * TME$$

which is similar to the estimate of ES_{th}, but the biomass ($D_{k-1,h}$) is estimated for each day k. For our starting value of $D_{k-1,h}$, we used the average biomass estimate across years for the first time period in autumn and spring. The consumption of energy (CFH_{kh}) is calculated as

$$CFH_h = \sum_{i=1}^{H} w_h \min(TED_k, TES_k)$$

where w_h is preference for tillage intensity type h. The value of w_h is between 0 and 1 and assumes that forage is consumed in proportion to availability and represents the proportion of forage consumed on each day k across all tillage intensity types. We determined w_h using roadside counts and examining the proportion of RMP sandhill cranes using fields in the tillage intensity types. Ideally, demand will remain lower than supply (i.e., $\min(TED_k, TES_k) = TED_k$), but a foraging type will be exhausted on day k if supply is lower than demand (i.e., $\min(TED_k, TES_k) = TES_k$).

Finally, to account for the decomposition of forage, we calculated DFH_{kh} as

$$DFH_{kh} = NEFH_{kh} * e^R$$

where R is the decomposition rate of barley. This value cannot vary temporally in the TRUEMET model. We fixed this value at -0.01 based on the approximate change in biomass from the end of autumn to the beginning of spring. While granivory is still occurring throughout

the winter, we assumed it was much less than when sandhill cranes were present and would be the best approximation for decomposition.

We examined eight scenarios using values calculated in the previous sections as input (Table 4.1). The scenarios represented varying availability of barley depending on the total area of privately managed barley fields, the presence or absence of publicly managed barley fields, and varying numbers of RMP sandhill cranes in the SLV during autumn and spring. In scenarios where barley is available on public land, we assumed it would not be available until mid-spring, which is consistent with how the MVNWR manages barley fields. In the first scenario, we assumed conditions (i.e., area of barley and number of RMP sandhill cranes) were similar to what we observed throughout the study period. In the second scenario, we assumed no barley on public land was available and only considered privately managed fields. In the third scenario, we assumed no fields were left in stubble but that all fields in idle became tilled fields. In the fourth scenario, we assumed that only idle barley fields were available but the area of barley did not increase. Public fields were still present. For the last four scenarios, we ran each of the other scenarios again, but we assumed the entire population of the RMP were eventually in the SLV in both seasons. We adjusted the number of RMP sandhill cranes in the SLV by multiplying the latest three-year average (23,000) by the proportion of the total number RMP sandhill cranes counted in each season. We examined simulations by plotting the resulting availability of energy to the total demand of energy. All simulations were completed in Program R and using code provided by Penmetcha et al. (2016).

RESULTS

Effect of tillage intensity and time on biomass

There was higher biomass density on publicly managed fields than privately owned fields (Table 4.2). For private fields, idle fields had higher biomass compared to fields with low intensity and high intensity tillage. The model without year and main effects of tillage intensity type, season, and migration timing had the lowest AIC_c (Table 4.3). Biomass density was significantly higher on idle fields compared to fields with high intensity tillage (Figure 4.3). The effect of spring was significantly lower compared to autumn, indicating biomass decreased between the autumn and spring seasons.

Effect of tillage intensity on behavior

We completed focal observations on a total of 87 RMP sandhill cranes in autumn and 252 RMP sandhill cranes in spring (Table 4.4). In autumn, the average proportion of time RMP sandhill cranes spent in diurnal behaviors were: alert 0.148 (SE=0.020), drinking 0.001 (SE=0.004), foraging 0.526 (SE=0.330), maintenance 0.104 (SE=0.189), resting 0.061 (SE=0.107), searching 0.071 (SE=0.107), social 0.005 (SE=0.010), and walking 0.081 (SE=0.119). In spring, the average proportion of time RMP sandhill cranes spent in diurnal behaviors were: alert 0.101 (SE=0.151), drinking 0.002 (SE=0.008), foraging 0.549 (SE=0.355), maintenance 0.097 (SE=0.187), resting 0.082 (SE=0.178), searching 0.047 (SE=0.089), social 0.007 (SE=0.028), and walking 0.084 (SE=0.120). Sandhill cranes spent most of their time foraging in all habitat types (Figure 4.4). We did not find an effect of tillage intensity on foraging behavior ($F_{2,174}$=0.653, P=0.522) for sandhill cranes in grain fields, but we did find an effect of tillage intensity on searching behavior ($F_{2,175}$=20.393, P<0.001). Sandhill cranes spent more time

searching in high intensity grain fields compared to low intensity grain fields (P=0.003) and fields in idle (P<0.001).

Temporal trends in body mass and lipids

We collected a total of 108 adult RMP sandhill cranes during 1999-2001 (n=84) and in 2021 (n=24). For both body mass and fat content, the interaction of time period and sex was not significant. Males were heavier than females ($F_{1,104}$=41.435, P<0.001). There was a general increasing trend in body mass over time, but the effect was not significant ($F_{2,104}$=2.532, P= 0.120; Fig. 5A). Time period was significant for fat content ($F_{2,104}$=14.292, P<0.001), with both mid-spring (P=0.003) and late spring (P<0.001) having greater fat content overall than early spring. There was no significant difference between mid-spring and late spring. Males had slightly higher fat content than females (Figure 4.5B), but the effect was not significant ($F_{1,104}$=2.910, P=0.067). Based on the model without an interaction, fat content was predicted to be approximately 0.147 kg higher for both males and females between early spring and late spring, which equates to 3.267 g gained per day.

Energy demand

Males showed higher DEE than females in both seasons (Table 4.5), particularly in spring. Without the cost of lipid production, values of DEE were comparable across time periods in both seasons but slightly higher in the late part of spring. Spring overall showed higher energy demands due to increased mass in both males and females and a greater amount of time spent flying in spring compared to autumn (Figure 4.6). When including the cost of lipid production, the amount of energy required per day increased by approximately 30.673 kcal. For spring, we used values of DEE that incorporated the cost of lipid production in subsequent analyses.

Using the estimates of DEE, individual RMP sandhill cranes required between 0.129 to 0.160 kg of barley per day to meet energy requirements (Table 4.5). When extrapolating to the population by using the roadside counts of sandhill cranes, the total amount of barley needed ranged between approximately 717 kg of barley per day to 5,000 kg of barley per day (Table 4.6). We estimated the total energy required by the population per two-week time period for autumn to be 95.0 x 10^6 kcal (95% CI = 63.0 x 10^6 – 127.0 x 10^6 kcal), and the total demand for the autumn season was approximately 284.9 x 10^6 kcal (0.08 x 10^6 kg of barley). In spring, the two-week requirement averaged 145.1 x 10^6 kcal (95% CI = 100.6 x 10^6 – 189.7 x 10^6 kcal), and the total demand for the season was approximately 435.4 x 10^6 kcal (0.1 x 10^6 kg of barley).

Energy supply

We estimated the area of barley in the SLV across each year to be 18,362 ha in the 2020-2021 season and 17,182 ha in the 2021-2022 season (Table 4.7). Most of the area was in high intensity till in both seasons, and this was true for the areas within 5 km and 10 km of potential roost sites. For combining tilled fields, we used average estimates of 49.49 kcal/ha in early autumn, 20.34 kcal/ha in late autumn, and 17.08 kcal/ha for both early and late spring. For the latter value, we did not find evidence of depletion for tilled fields overall, so it represents the weighted average of tilled fields in both early and late spring. Using a TME of 3,540 kcal/kg, we estimated the total energetic availability of barley throughout the entire SLV to range between approximately 9.1 x 10^6 kcal on public managed barley fields in spring and 5086.0 x 10^6 kcal on privately managed idle barley fields in autumn (Table 4.8). The average energy supply per two-week time period was 2533.9 x 10^6 kcal (95% CI = 1462.0 x 10^6, 3604.7 x 10^6 kcal) in autumn and 805.5 x 10^6 kcal (95% CI = 324.2 x 10^7, 1286.8 x 10^6 kcal) in spring for the entire SLV. The average energy supply was 5905.5 x 10^6 kcal (1.7 x 10^6 kg of barley) for early autumn and

1589.9 x 10^6 kcal (0.4 x 10^6 kg of barley) in late spring for the entire SLV. When only considering idle fields, energy supply averaged 3728.9 x 10^6 kcal (1.1 x 10^6 kg of barley) in early autumn and 832.7 x 10^6 kcal (0.2 x 10^6 kg of barley) in late spring. The changes in energy availability represented a 73% decline for all tillage types combined and a 78% decline for idle barley fields, but energy supply still far exceeded demand in both cases.

Barley fields on public lands that are left idle in spring could support the highest densities of RMP sandhill cranes (Figure 4.7), followed by idle fields on private land. However, when extrapolating to the area of barley available each year within 5 km of roosts, idle fields on private land could support the greatest number of RMP sandhill cranes overall in both seasons and time periods (Figure 4.8). An average total of 7.7 x 10^6 RMP sandhill cranes (95% CI = 4.5 x 10^6, 10.9 x 10^6) could be supported per day in autumn and 2.2 x 10^6 RMP sandhill cranes (95% CI = 0.9 x 10^6, 3.6 x 10^6) could be supported per day in spring given the area of barley available within 5 km of roosts. Within 10 km of roosts, an average of 9.7 x 10^6 RMP sandhill cranes (95% = 5.5 x 10^6 – 14.0 x 10^6) and 2.8 x 10^6 RMP sandhill cranes (95% CI = 1.1 x 10^6 – 4.5 x 10^6) could be supported per day in autumn and spring, respectively. The entire SLV could support 10.5 x 10^6 RMP sandhill cranes (95% CI = 6.1 x 10^6 – 15.0 x 10^6) and 3.0 x 10^6 RMP sandhill cranes (95% CI = 1.2 x 10^6 – 4.9 x 10^6) in autumn and spring, respectively.

TRUEMET Simulations

In most scenarios under the TRUEMET model, energy availability far exceeded demand (Figure 4.9, Figure 4.10). At peak migration, RMP sandhill cranes required 4.7 x 10^6 kcal and 8.8 kcal x 10^6 kcal per day in autumn and spring, respectively, for the first four scenarios. These values were 11.3 x 10^6 kcal in autumn and 12.5 x 10^6 kcal in spring for the other scenarios. Across the entire timeframe examined (October 1 – March 31), a total of 463.5 x 10^6 kcal was

required for the first four scenarios, while a total of 853.4 x 10^6 kcal was required for the other scenarios. Supply at peak migration varied across scenarios, except that there was little difference in supply between scenarios with publicly managed barley and scenarios without it (Table 4.9). Under Scenarios 1, 2, 3, and 4, energy supply declined by 86%, 90%, 90%, and 87% from its original amount, respectively (Table 4.9). Scenarios 5, 6, 7, and 8 showed declines of 90%, 93%, 97%, and 93%, respectively (Table 4.9). The scenarios where no grain fields were left idle (Scenarios 3 and 6) showed the lowest energy supply at the end of spring.

DISCUSSION

Sandhill cranes rely on a spatially variable but abundant food source in the SLV. We found that the density of waste barley leftover after harvest declined from autumn to spring and was greatest in fields that were not tilled or only moderately tilled. Variations in barley availability contributed to changes in body mass and lipid content of RMP sandhill cranes in spring, with both sexes showing a positive trend in lipid gain throughout the season, and this ultimately influenced their overall energy requirements. Other factors, including increased flight distances due to depleting resources and potential changes in behavior due to tillage practice, also likely influenced energy expenditure. However, despite there being only a small area of barley managed specifically for sandhill cranes on public lands in the SLV, the supply of barley currently seems to exceed energetic demands based on our estimates and simulations.

While we are confident in the determination that adequate forage is available to sandhill cranes in the SLV, there are some factors we did not incorporate into our estimates and simulations that could be assessed in future studies. First, we did not account for a foraging threshold, which is the amount of forage at which a bird abandons a patch (Brown 1988, Pearse and Stafford 2014). For example, Greer et al. (2009) observed that waterfowl abandoned rice

fields below a biomass of 50 kg/ha. As a result, even if grain is present in fields that are idle or moderately tilled, they may be abandoned at lower densities, which would drastically decrease the amount of barley available on the landscape compared to our estimates. There is currently no foraging threshold estimated for sandhill cranes and future work could improve understanding of available energy on the landscape. However, our estimates of energy availability from idle fields, which provide the most waste seed on average, still supplied enough forage for the RMP. Second, using bioenergetics models requires making several assumptions that we were not able to validate. For example, we assumed that RMP sandhill cranes depleted resources at a constant rate throughout the season. Rate of consumption or how much time a bird spends foraging may vary based on temperature, individual condition, and disturbance (Ladin et al., 2011; Morton et al., 2018), all factors for which we did not account. Boggie et al. (2018), for example, found that sandhill cranes increased foraging throughout the winter due to increased energetic demands. Third, we recognize total energetic demands may be underestimated because (1) we did not include lesser sandhill cranes in the MCP in our estimates of energy demand and (2) sandhill cranes may start arriving in the SLV prior to October 1 (Vanausdall et al 2024). Both factors would increase the amount of energy required during a season. It is estimated that approximately 5,000 MCP sandhill cranes use the SLV during autumn and spring (see Chapter 3). Our focus was on the RMP sandhill cranes, so we did not complete focal observations of MCP sandhill cranes nor have data on their body condition and movement patterns. Finally, barley is not the only food consumed by RMP sandhill cranes during migration, so our estimates of energy supply are likely underestimated. In both autumn and spring, sandhill cranes will consume a variety of natural foods and agricultural crops, including invertebrates from wetlands and grasslands (Davis

& Vohs, 1993; Littlefield, 2002; Reinecke & Krapu, 1986). Future research may incorporate the contribution of other food items to their diet and the overall energetic supply on the landscape.

The finding that waste barley is the densest in idle fields is consistent with several studies that have examined biomass of agricultural foods consumed by birds (Baldassarre et al., 1983; Foster et al., 2010; Sherfy et al., 2011). Values for idle fields (~200 kg/ha in early autumn; ~45 kg/ha in late spring) are within range of those estimated by Gammonley and Laubhan (unpubl. data) in 1999-2001 in the SLV in spring. Our estimates of biomass in intensely tilled fields (~50 kg/ha in early autumn; 17 kg/ha in late spring) were greater than their estimates (0.04 kg/ha from three fields), but we sampled considerably more fields that had a higher variability of waste seed. The greater amount of waste seed available on barley fields is also consistent with findings that greater sandhill cranes in the SLV select idle fields over tilled fields (results in Chapter 3). Similarly, sandhill cranes in the MCP were found to spend more time in idle fields where waste corn seed was highest (Anteau et al., 2011; Krapu et al., 2014). We found that waste barley decreased significantly between autumn and spring, which may influence use by RMP sandhill cranes over time. While this decline is partly due to foraging by sandhill cranes, other factors, such as granivory by other species (e.g., waterfowl, elk) and seed deterioration, contribute to seed depletion. We also were not always able to account for additional tillage by growers, which could lead to further decline in waste seed. Depletion will likely influence energetics, as sandhill cranes tend to move farther from roosting sites as resources are depleted nearby to find more high-quality patches (Alonso et al., 1984; Collins et al., 2023).

The decrease in waste barley was concomitant with changes in body condition in RMP sandhill cranes. Consistent with our hypothesis, RMP sandhill cranes showed an increase in lipid mass and body mass between early spring and late spring. Studies of MCP sandhill cranes have

found similar trends in lipid gain during spring migration (Krapu et al., 1985), and others have found rapid lipid increases in waterfowl (Austin & Fredrickson, 1987; Skalos et al., 2021) and shorebirds (Battley et al., 2004) during spring migration. Lipids are the main source of energy during migration (Jenni & Jenni-Eiermann, 1998; McWilliams et al., 2004; Odum & Connell, 1956), and acquiring adequate nutrient reserves has been associated with improved reproductive performance (Alisauskas, 2002; Devries et al., 2008), as they may improve body condition and contribute to egg formation (Hobson et al., 2011). Other nutrients, such as protein, are also important to reproduction, but protein is not stored like lipids and is catabolized from muscle tissue, which may adversely affect flight performance and overall body condition during migration (Hobson et al., 2011; Jenni & Jenni-Eiermann, 1998). Krapu et al. (1985) postulated that compared to other species, such as Arctic-nesting geese, sandhill cranes likely allocate relatively less of their nutrient reserves to egg formation and instead rely more on resources acquired at the breeding grounds. At the same time, increased lipid reserves buffers against poor weather or habitat conditions that may affect energy expenditure and improve survival in subsequent seasons (Morrison et al., 2007), so it is still advantageous to increase lipid levels during this period. Our estimate of daily lipid gain was less than that found for MCP sandhill cranes, where Krapu et al. (1985) found a daily gain of approximately 12-15 g of lipids during the entire spring migration. Our values may be an underestimate due to sample size limitations or examining trends over a shorter timeframe.

We also estimated an increase in DEE values for greater sandhill cranes from autumn to spring, which is consistent with an increase in body mass and lipid gain in spring. Our estimates are comparable to DEE estimated for sandhill cranes in the MCP. Tacha et al. (1987) found that approximately 536 kcal were required for sandhill cranes during spring in Nebraska, but they did

not differentiate DEE among greater and lesser sandhill cranes. They also found an increase in energy requirements as sandhill cranes flew north to their breeding grounds. While our spring estimates incorporated lipid gain whereas autumn did not, increases in energy requirements could additionally be explained by other factors. For example, we found evidence that RMP sandhill cranes are flying greater distances in spring than in autumn, which is likely related to depletion of barley near roosts and may require sandhill cranes to acquire higher energetic reserves. Other studies have examined movement of waterfowl in relation to roosts and forage depletion and found evidence that some species will move farther for preferred foods (Frederick et al., 1987; Johnson et al., 2014). Collins et al. (2023) also found that greater sandhill cranes in the Lower Colorado River Valley population are more likely to use grain fields farther from roosts than other crop types at the same distance. Our results indicate that sandhill cranes spend more time searching in fields with less waste barley, which may also influence energetic expenditure. Similarly, Krapu et al. (2014) observed a higher proportion of walking by sandhill cranes in years with less corn available. Overall, our results are consistent with other work showing the higher energetic demands of spring due to various factors.

The density of waste seed contributed to an overall high supply of barley available to sandhill cranes in the SLV that exceeded population demand. We estimated that an average of approximately 5900 million kcal and 1600 million kcal were available in early autumn and late spring, respectively, for sandhill cranes. While most of the barley fields were tilled, the area of publicly managed barley fields coupled with the area of idle fields meant that a considerable amount of energy was on the landscape. Considering that we estimated total energy demands of 285 million kcal in autumn and 435 million kcal in spring for the observed number of RMP sandhill cranes, our estimates of energy supply indicate that the SLV could support more sandhill

cranes than are currently observed. Additionally, while we did not estimate energy demands for MCP sandhill cranes, the availability of more barley would support lesser sandhill cranes too. While there are other factors, such as social organization, forage availability in other parts of their range, or limitations in roosting habitat, that would limit such a high density of sandhill cranes, this result emphasizes the high availability of barley on publicly managed and idle barley fields in the SLV.

Our TRUEMET models also showed high amounts of energy available under various scenarios. Under scenarios where idle fields covered a large area and the number of RMP sandhill cranes represented the three-year average population size, energy supply was near 3 billion kcal higher than energy demand at its peak in autumn and 600 million kcal higher than energy demand in spring. Given our decomposition rate in addition to foraging by sandhill cranes, barley declined relatively rapidly throughout the season. Additionally, the availability of publicly managed fields only moderately increased energy supply. While our scenario of no idle fields represents an extreme case, our results provide evidence that supplemental forage alone will not provide enough energy for RMP sandhill cranes in the SLV. This is in contrast to the situation in one of their main wintering areas in New Mexico, where supplemental corn is provided for sandhill cranes and waterfowl (Boggie et al. 2023). Boggie et al. (2023) estimated that about 4.8 billion kcal were on state and federal land providing corn and able to feed the population of sandhill cranes and waterfowl that winter there for up to 101 days. In the SLV, supplemental forage may need to exist in addition to grain on private lands, with an emphasis on idle postharvest practices. Scenarios 4 and 8 were also extreme cases where only idle and publicly managed grain fields were available, but they still provided enough energy for the RMP.

The SLV appears to currently provide enough barley to meet the energetic needs of RMP sandhill cranes and likely those of MCP sandhill cranes during autumn and spring migration. Tillage intensity greatly influences barley availability, and continued monitoring of tillage practices throughout the area will inform management decisions. While grains provided by the MVNWR contributed relatively little to overall energetic availability, the refuge still provides a reliable source of energy each spring. The increase in lipid levels of RMP sandhill cranes also emphasizes the importance of assessing their energetics and movement patterns to gauge the overall health of the population. Other factors, such as the distance between barley fields and roosts, will also affect energy expenditure. Consideration of roosting areas near private or public grain fields should also be a part of management decisions.

TABLES AND FIGURES

Table 4.1: Scenario descriptions for the TRUEMET model simulating changes in Rocky Mountain Population greater sandhill crane numbers and area of grain fields under different tillage intensity practices in the San Luis Valley, Colorado. Simulations estimated the energy supply and demand under each scenario for a period between 1 October to 31 March.

Scenario	Crane population	Idle (ha)	Till (ha)	Public (ha)	Description
1	Observed	4016	8685	95	Observed RMP sandhill crane numbers; average grain area
2	Observed	4016	8685	0	Observed RMP sandhill crane numbers; average grain area but no publicly grown grain
3	Observed	0	12701	95	Observed RMP sandhill crane numbers; 50% idle fields become low intensity and 50% become high intensity
4	Observed	4016	0	95	Observed RMP sandhill crane numbers; only idle private and public fields remain
5	Maximum 23000	4016	8685	95	Three-year average RMP sandhill crane numbers; average grain area
6	Maximum 23000	4016	8685	0	Three-year average of RMP sandhill crane numbers; average grain area but no publicly grown grain
7	Maximum 23000	0	12701	95	Three-year average of RMP sandhill crane numbers; 50% idle fields become low intensity and 50% become high intensity
8	Maximum 230000	4016	0	95	Three-year average of RMP sandhill crane numbers; only idle private and public fields remain

Table 4.2: The average ($\bar{x}$) biomass (kg/ha) estimated using 0.25 m^2 quadrats for barley fields with varying levels of tillage intensity across autumn (2020-2021) and spring (2021-2022) in the San Luis Valley, Colorado.

Tillage intensity	Season	$\bar{x}$	95% lower CI	95% upper CI	No. samples	No. fields
High intensity till	Autumn sample 1	51.762	38.335	65.190	262	29
	Autumn sample 2	14.466	10.416	18.515	455	48
	Spring sample 1	16.684	4.975	28.392	166	18
	Spring sample 2	15.557	6.004	25.110	447	43
Low intensity till	Autumn sample 1	42.899	29.081	56.717	80	10
	Autumn sample 2	79.796	17.976	141.617	45	7
	Spring sample 1	14.860	5.090	24.630	6	1
	Spring sample 2	27.928	19.942	35.914	70	9
Idle	Autumn sample 1	198.671	140.264	257.077	263	30
	Autumn sample 2	175.466	94.176	256.756	196	17
	Spring sample 1	121.593	85.255	157.930	166	13
	Spring sample 2	44.364	35.634	53.094	135	9
Public	Autumn sample 1	1693.667	1157.390	2229.944	44	3
	Autumn sample 2	1180.462	838.706	1522.219	68	3
	Spring sample 1	632.490	453.279	811.702	73	3
	Spring sample 2	26.928	21.183	32.672	76	3

Table 4.3: Model selection results for the effect of tillage intensity (idle, low intensity till, high intensity till), season (autumn, spring), and migration timing (pre-arrival, post-arrival) on biomass (kg/ha) in barley fields used by RMP sandhill cranes in the San Luis Valley, Colorado, 2020-2022).

Model	K	AIC_c	ΔAIC_c
Tillage intensity + season + migration timing	7	5333.032	0.000
Tillage intensity + season + migration timing + year	8	5334.098	1.066
Tillage intensity + season*migration timing	8	5335.045	2.013
Tillage intensity + season*migration timing + year	9	5336.109	3.076

Table 4.4: The number of RMP sandhill cranes observed and with recorded behaviors in the San Luis Valley, Colorado, 2020-2022.

Habitat	Autumn	Spring
Alfalfa	2	16
Grain	64	120
Potatoes	0	17
Pasture/wetland	20	85
Other	1	14

Table 4.5: The daily energy expenditure (DEE) and barley requirements of individual RMP sandhill cranes at time period *t* (early, mid, late) during the autumn and spring in the San Luis Valley, Colorado.

Season	Time period	DEE_t (kcal)		Barley required/day (kg)	
		Male	Female	Male	Female
Autumn	Early	502	462	0.142	0.130
	Mid	498	458	0.141	0.129
	Late	501	460	0.141	0.130
Spring	Early	553	500	0.156	0.141
	Mid	566	513	0.160	0.145
	Late	562	522	0.159	0.148

Table 4.6: The daily energy expenditure (DEE; kcal) and energy demand (ED; kcal) of all RMP sandhill cranes at time period *t* (early, mid, late) during the autumn and spring in the San Luis Valley, Colorado.

Season	Year	Time period	No. greaters	ED_t male (thousands of kcal)	ED_t female (thousands of kcal)	ED_t total (thousands of kcal)	Barley required/day (kg)
Autumn	2020	Early	13942	3502	3220	6722	1899
		Mid	22802	5682	5225	10907	3081
		Late	5285	1323	1216	2539	717
	2021	Early	10178	2557	2351	4907	1386
		Mid	15840	3947	3630	7577	2140
		Late	16767	4196	3858	8054	2275
Spring	2020	Early	15950	4412	3984	8395	2372
		Mid	17717	5018	4541	9559	2700
		Late	14176	3985	3703	7689	2172
	2021	Early	20922	5787	5226	11013	3111
		Mid	29666	8402	7604	16005	4521
		Late	13239	3722	3459	7180	2028
	2022	Early	14569	4030	3639	7669	2166
		Mid	33375	9452	8554	18006	5087
		Late	14368	4039	3754	7793	2201

Table 4.7: Area and proportion of barley in different tillage intensities and within 5 km and 10 km of RMP sandhill crane roosts and throughout the entire San Luis Valley (SLV) in Colorado.

		Area (ha) within			Proportion of total within		
Year	Tillage intensity	5 km	10 km	SLV	5 km	10 km	SLV
2020-2021	Idle	2745	3324	3493	0.23	0.20	0.19
	Low intensity till	3976	5605	6429	0.33	0.34	0.35
	High intensity till	5385	7373	8440	0.44	0.45	0.46
2021-2022	Idle	5287	6894	7301	0.40	0.44	0.42
	Low intensity till	1279	1798	2366	0.10	0.12	0.14
	High intensity till	6731	6827	7515	0.50	0.44	0.44

Table 4.8: The energy supply (*ES*) for time period *t* and tillage intensity *h* provided by barley in the San Luis Valley, Colorado during the autumn and spring migration of Rocky Mountain Population sandhill cranes.

Tillage intensity	Year	Season	Time period	ES_t within 5 km (millions of kcal)	ES_t within 10 km (millions of kcal)	ES_t in SLV (millions of kcal)
Idle (private)	2020-2021	autumn	early	1863.72	2270.56	2389.75
			late	1668.78	2033.07	2139.79
		spring	early	1140.65	1389.65	1462.60
			late	416.18	507.03	533.64
	2021-2022	autumn	early	3651.19	4781.54	5068.01
			late	3269.28	4281.40	4537.91
		spring	early	2234.64	2926.45	3101.78
			late	815.33	1067.74	1131.71
Idle (public)	2020-2021	spring	early	212.84	212.84	212.84
			late	9.06	9.06	9.06
	2021-2022	spring	early	212.84	212.84	212.84
			late	9.06	9.06	9.06
Till	2020-2021	autumn	early	1646.46	2282.80	2615.38
			late	673.98	934.47	1070.61
		spring	early	565.92	784.65	898.96
			late	565.92	784.65	898.96
	2021-2022	autumn	early	1408.94	1517.16	1737.95
			late	576.75	621.06	711.43
		spring	early	484.28	521.48	597.37
			late	484.28	521.48	597.37

Table 4.9: The energy supply (millions of kcal) available at the beginning of the season (early autumn), at the end of the season (late spring), peak migration in autumn, and peak migration in spring under six scenarios modeled using TRUEMET for RMP sandhill cranes in the San Luis Valley, Colorado.

Scenario	Initial supply	Supply end of spring	Supply at peak autumn migration	Supply at peak spring migration
1	4366.36	621.58	3293.97	803.96
2	4366.36	454.90	3293.97	748.17
3	2248.08	226.30	1660.67	343.97
4	2829.11	367.47	2108.67	480.93
5	4366.36	464.05	3190.28	675.76
6	4366.36	297.37	3190.28	619.97
7	2248.08	68.78	1556.98	215.77
8	2829.11	209.95	2004.99	352.73

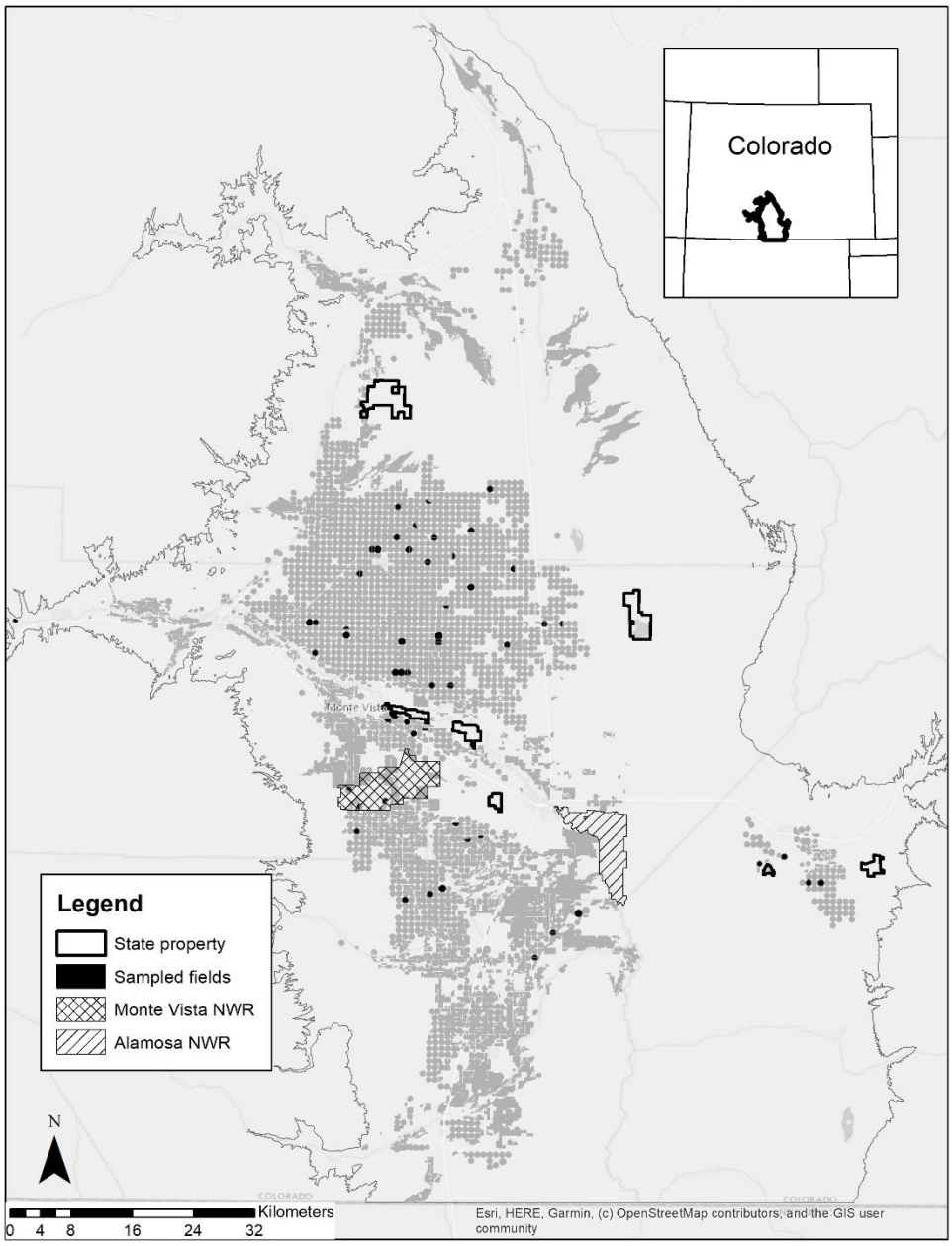

Figure 4.1: The San Luis Valley, Colorado, with agricultural fields, sampled barley fields, and state and federal properties historically used by sandhill cranes.

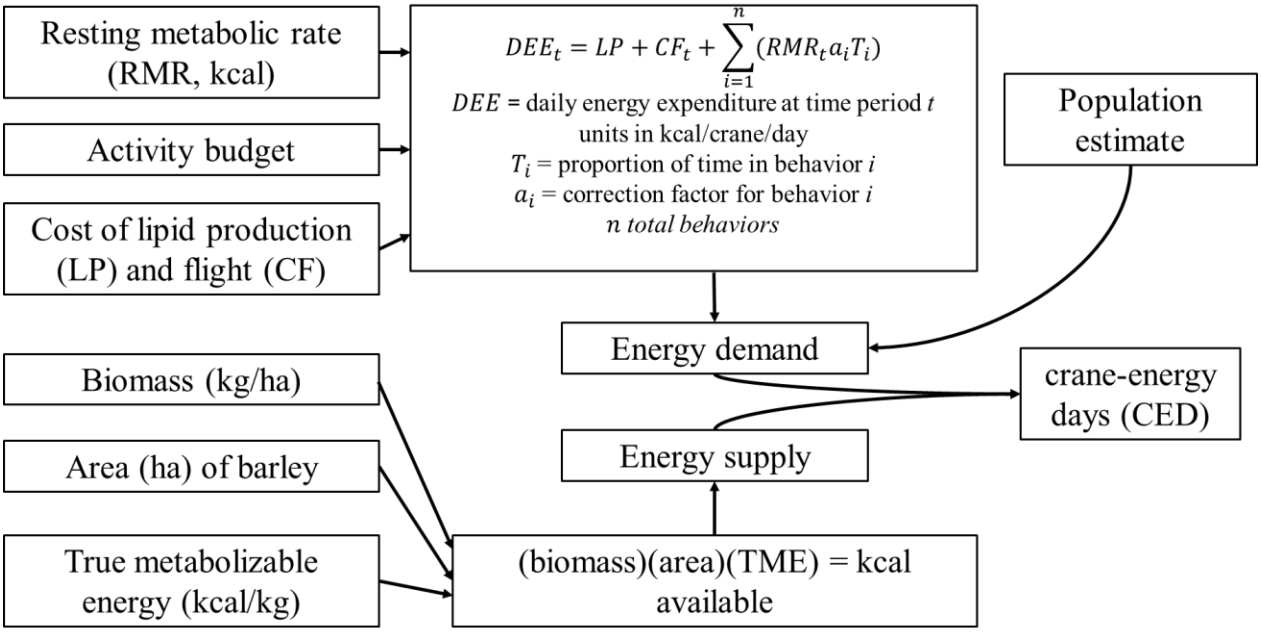

Figure 4.2: A diagram of the inputs used to calculate energy demand per day and individual and total energy supply for sandhill cranes in the San Luis Valley, Colorado during autumn and spring migration.

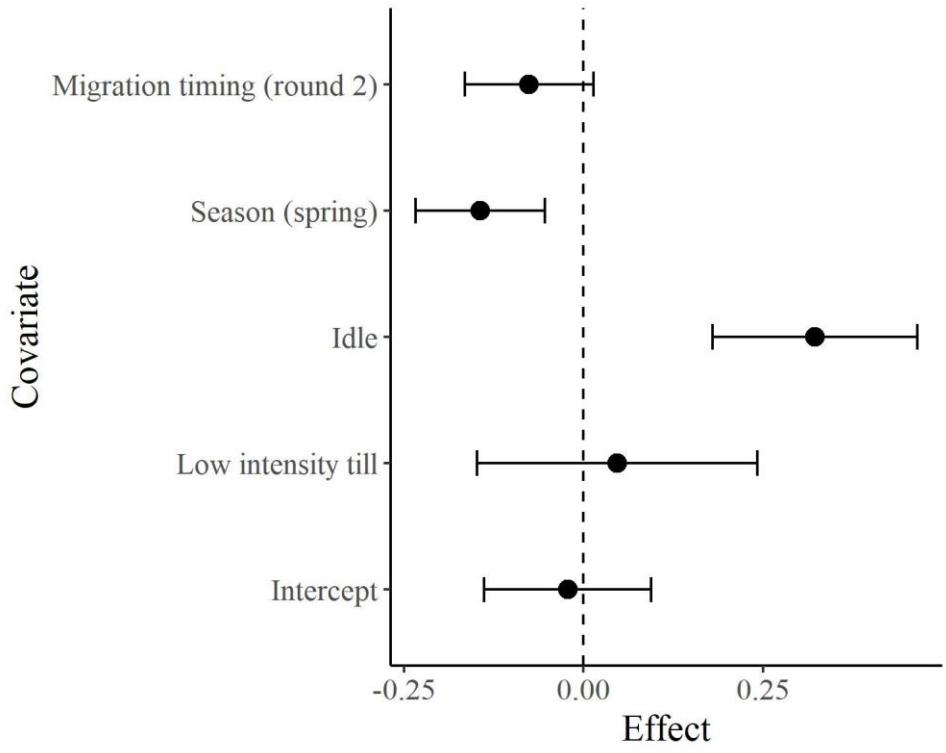

Figure 4.3: Coefficient estimates for covariates related to tillage intensity, season, and migration timing and their effects on biomass (kg/ha) in barley fields during the autumn and spring in the San Luis Valley, Colorado, 2020-2022. The reference level is the high intensity postharvest treatment during autumn and the first sampling event. The dashed line intersects zero, and the horizontal bars are 95% confidence intervals.

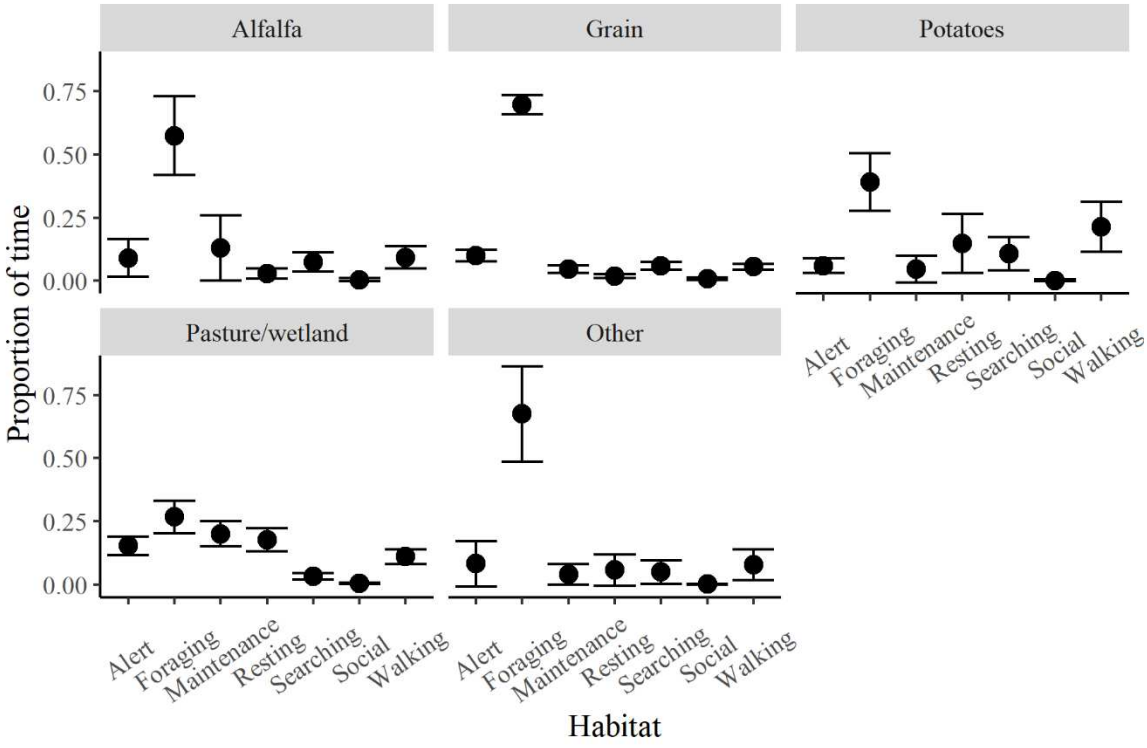

Figure 4.4: The average proportion of time RMP sandhill cranes spent in different behaviors during autumn and spring migration (2020-2022) in the San Luis Valley, Colorado. The vertical lines represent 95% confidence intervals.

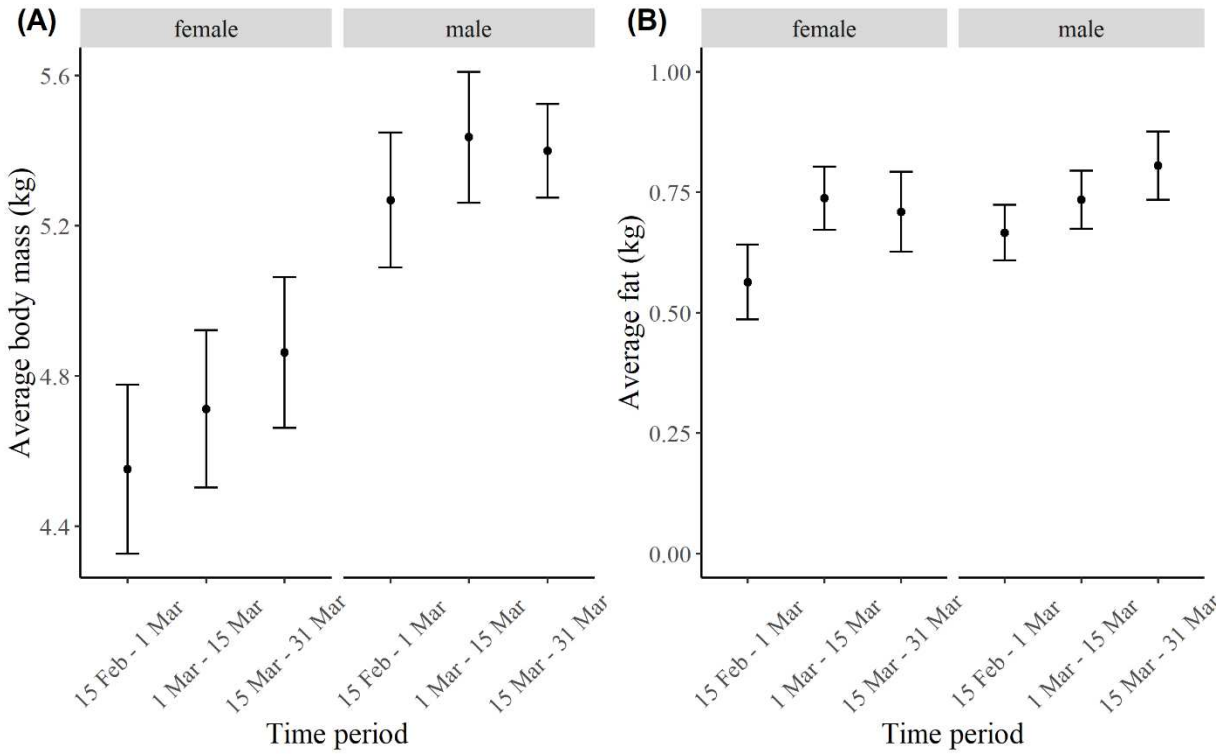

Figure 4.5: The average (A) body mass and (B) fat content for adult RMP sandhill cranes collected during the springs of 1999-2001 and 2021 in the San Luis Valley, Colorado.

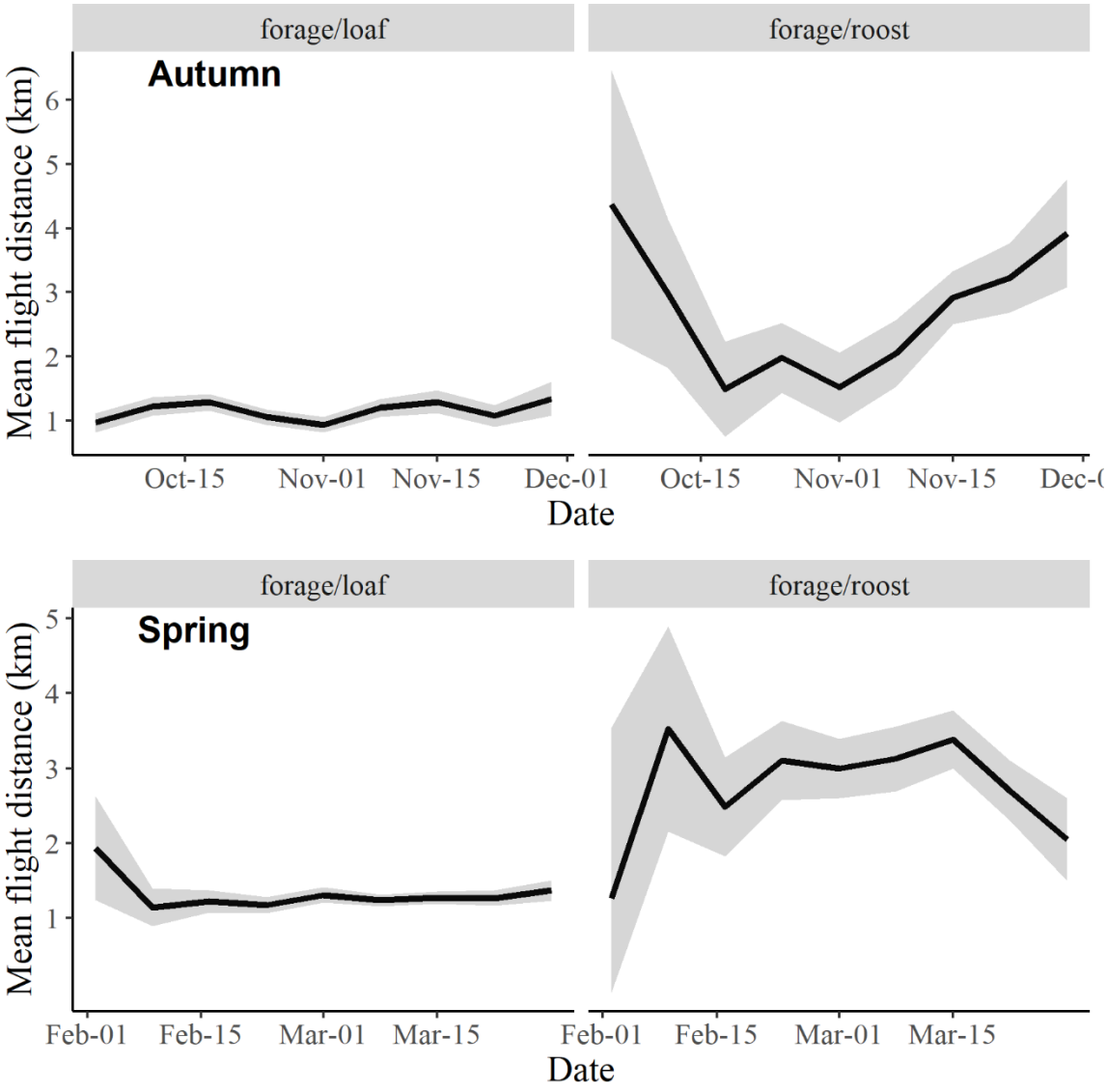

Figure 4.6: The mean weekly flight distance of RMP sandhill cranes traveling between foraging areas and loafing areas (forage/loaf) and between forage areas and roosting areas (forage/roost) in the San Luis Valley, Colorado, 2015-2022. The shaded regions are 95% confidence intervals.

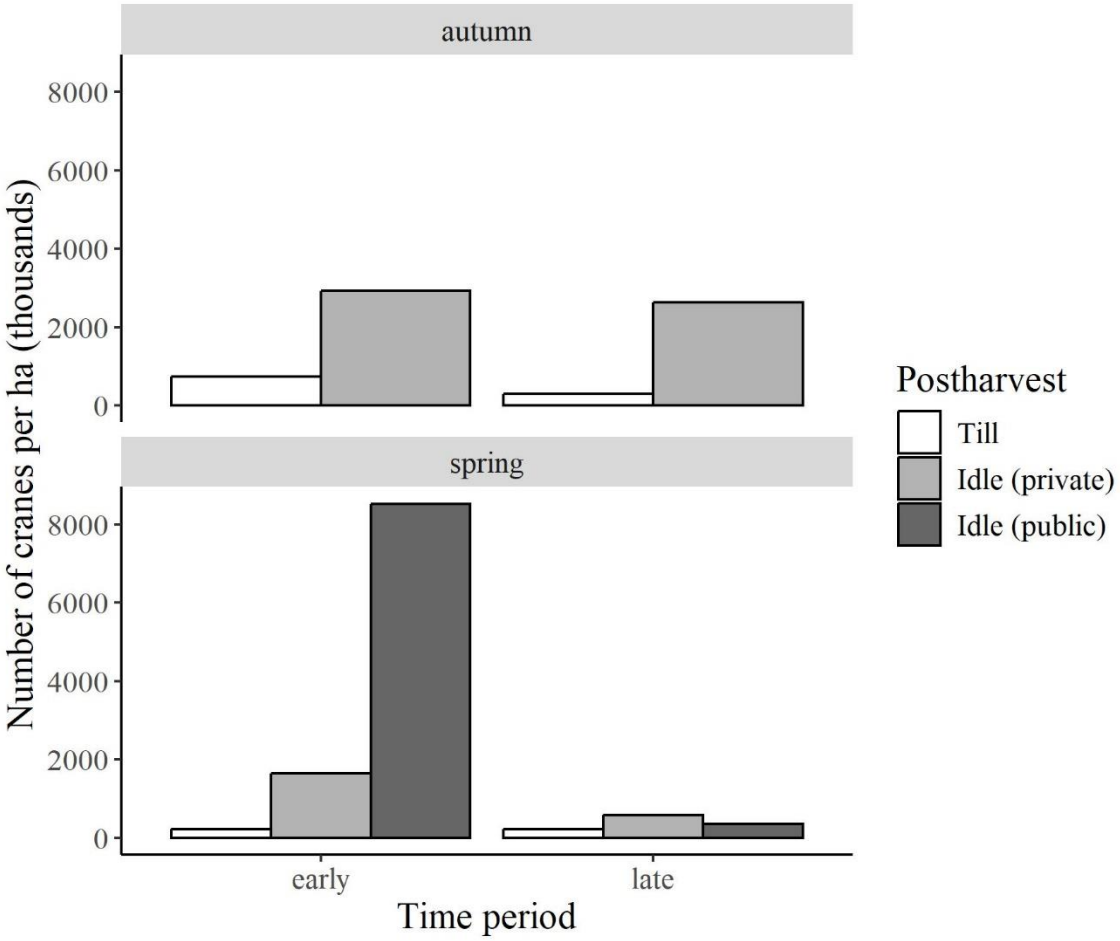

Figure 4.7: The number of sandhill cranes per ha that barley fields in different tillage intensity types can support per day in the San Luis Valley, Colorado. The values are based on the true metabolizable energy of barley (3,540 kcal/kg), the daily energy expenditure of Rocky Mountain Population sandhill cranes, and the biomass (kg/ha) of waste barley sampled during the early and late part of the autumn and spring seasons.

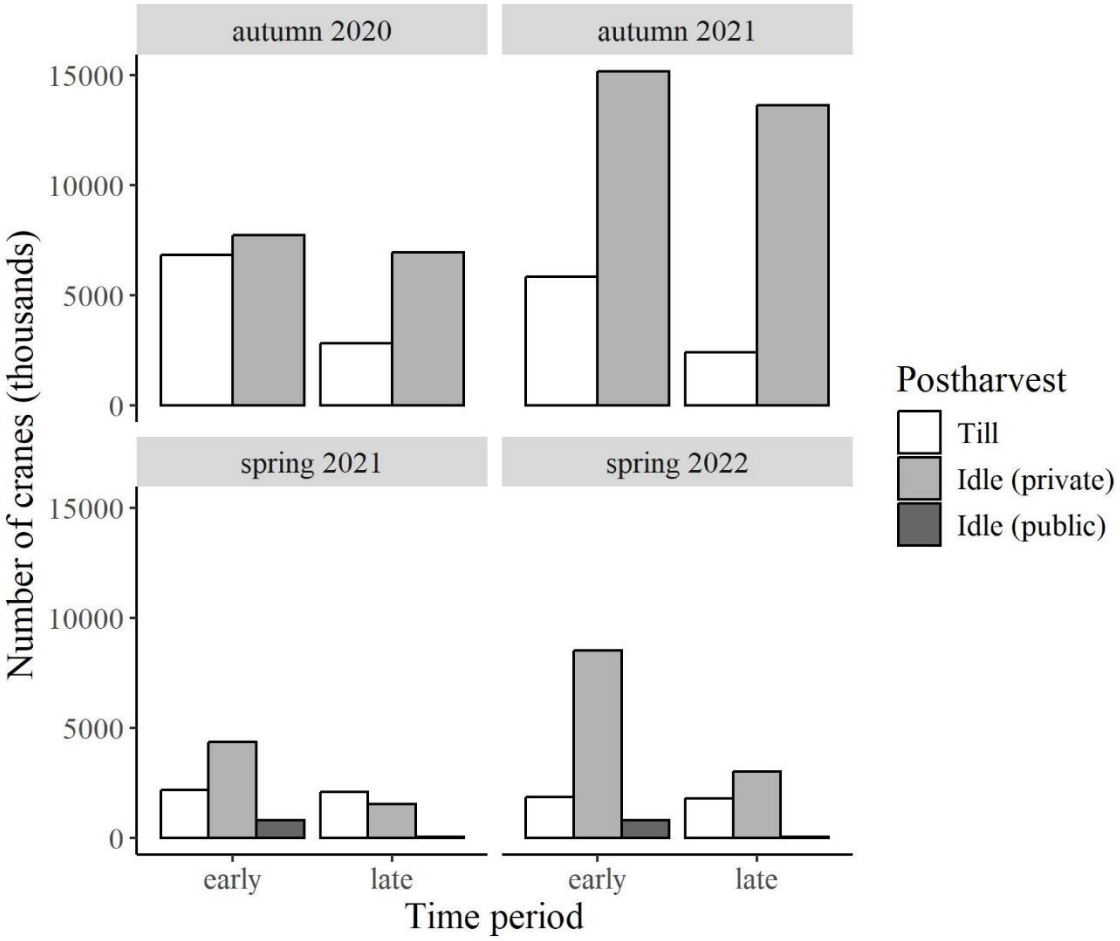

Figure 4.8: The number of sandhill cranes that barley fields in different tillage intensity types and within 5 km of potential roost sites can support per day in the San Luis Valley, Colorado. The values are based on the true metabolizable energy of barley (3,540 kcal/kg), the daily energy expenditure of Rocky Mountain Population sandhill cranes, and the biomass (kg/ha) of waste barley sampled during the early and late part of the autumn and spring seasons.

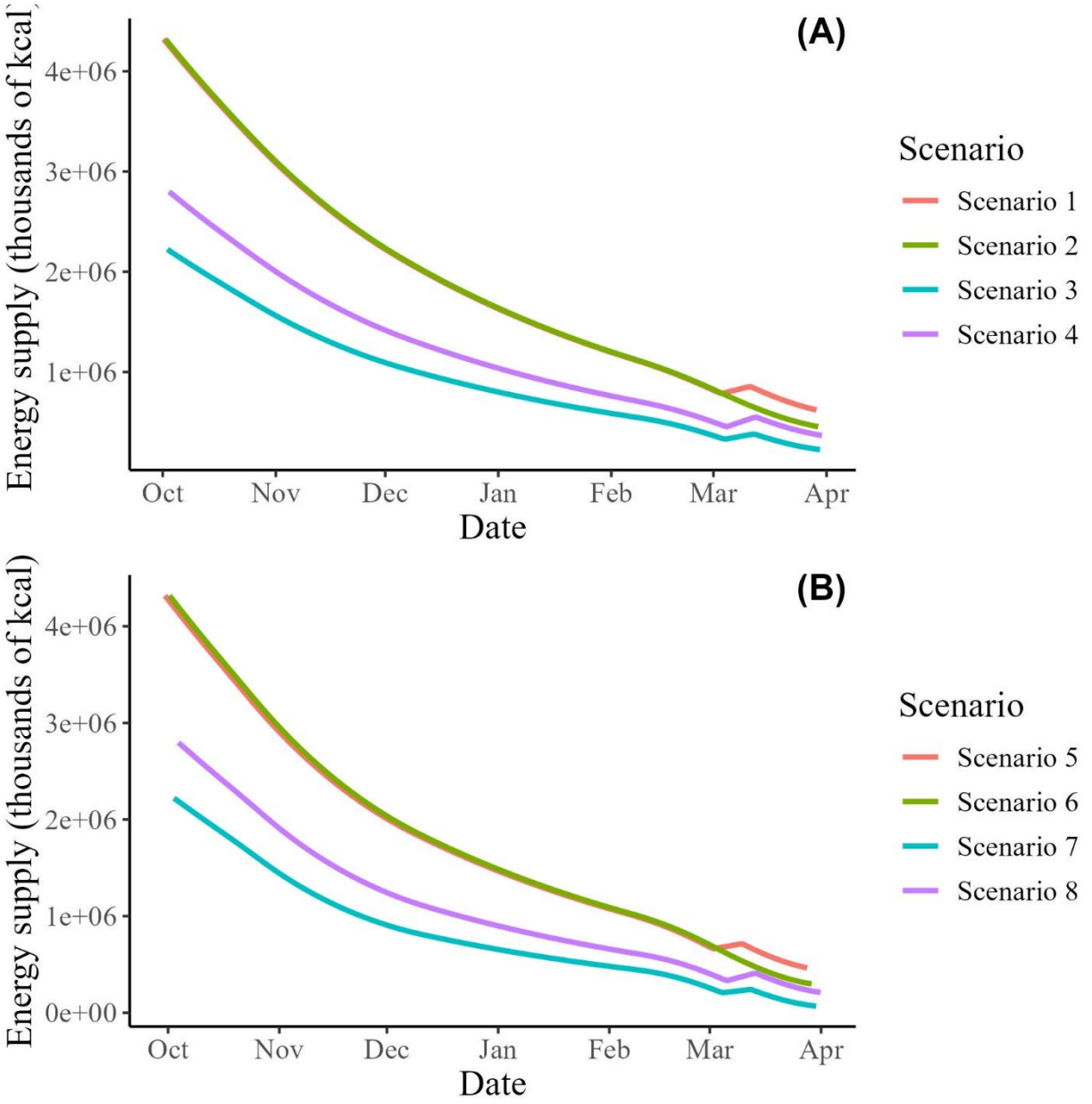

Figure 4.9: Energy supply under scenarios with (A) observed Rocky Mountain Population (RMP) sandhill crane numbers and (B) a maximum of 23,000 RMP sandhill crane numbers using the TRUEMET model for autumn and spring migration periods in the San Luis Valley, Colorado.

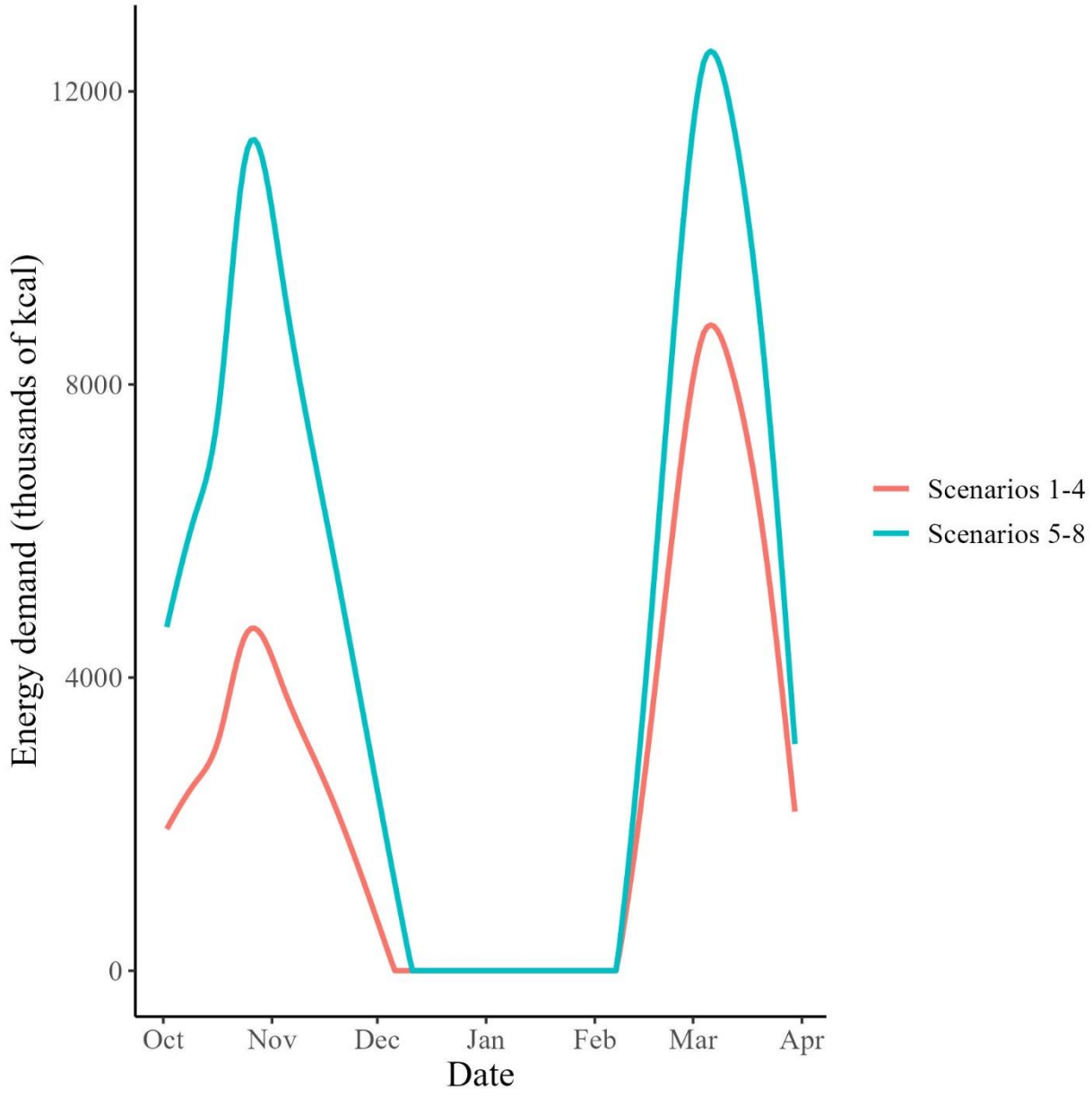

Figure 4.10: Energy demand under scenarios with observed Rocky Mountain Population (RMP) sandhill crane numbers (solid line) and three-year average RMP sandhill crane numbers (dashed line) using the TRUEMET model for autumn and spring migration periods in the San Luis Valley, Colorado.

LITERATURE CITED

Alisauskas, R. T. (2002). Arctic climate, spring nutrition, and recruitment in Midcontinent lesser snow geese. *Journal of Wildlife Management*, *66*(1), 181–193. https://doi.org/http://dx.doi.org/10.2307/3802884

Alonso, J. A., Alonso, J. C., & Veiga, J. (1984). Winter feeding of the Crane in cereal farmland at Gallocanta, Spain. *Wildfowl*, *35*, 119–131.

Ankney, C. D., & MacInnes, C. D. (1978). Nutrient reserves and reproductive performance of female lesser snow geese. *Auk*, *95*(3), 459–471. https://doi.org/https://doi.org/10.1093/auk/95.3.459

Anteau, M. J., Sherfy, M. H., & Bishop, A. A. (2011). Location and agricultural practices influence spring use of harvested cornfields by cranes and geese in Nebraska. *Journal of Wildlife Management*, *75*(5), 1004–1011. https://doi.org/10.1002/jwmg.135

Austin, J. E., & Fredrickson, L. H. (1987). Body and organ mass and body composition of postbreeding female lesser scaup. *Auk*, *104*(4), 694–699.

Baldassarre, G. A., & Bolen, E. G. (1984). Field-feeding ecology of waterfowl wintering on the southern high plains of Texas. *Journal of Wildlife Management*, *48*(1), 63–71.

Baldassarre, G. A., Whyte, R. J., Quinlan, E. E., & Bolen, E. G. (1983). Dynamics and quality of waste corn available to postbreeding waterfowl in Texas. *Bulletin*, *11*(1), 25–31. https://doi.org/https://www.jstor.org/stable/3781078

Baldwin, F. B., Alisauskas, R. T., & Leafloor, J. O. (2022). Dynamics of pre-breeding nutrient reserves in subarctic staging Lesser Snow Geese (Anser caerulescens caerulescens) and Ross's Geese (Anser rossii): implications for reproduction. *Avian Conservation and Ecology*, *17*(2). https://doi.org/10.5751/ACE-02326-170238

Ballard, B. M., & Thompson, J. E. (2000). Winter diets of sandhill cranes from central and coastal Texas. *Wilson Bulletin*, *2*, 263–268. https://doi.org/10.1676/0043

Barnett, T. P., Pierce, D. W., Hidalgo, H. G., Bonfils, C., Santer, B. D., Das, T., Bala, G., Wood, A. W., Nozawa, T., Mirin, A. A., Cayan, D. R., & Dettinger, M. D. (2008). Human-induced changes in the hydrology of the western United States. *Science*, *316*, 1180–1183. https://doi.org/10.1126/science.1139601

Barzen, J. A., Gossens, A. P., & Lacy, A. E. (2018). Sandhill crane foraging behavior and damage estimates in cornfields during spring. In J. E. Austin & R. P. Urbanek (Eds.), *Proceedings of the Fourteenth North American Crane Workshop* (pp. 67–80). North American Crane Working Group.

Battley, P. F., Piersma, T., Rogers, D. I., Dekinga, † Anne, Spaans, B., & Van Gils, J. A. (2004). Do body condition and plumage during fuelling predict northwards departure dates of Great Knots Calidris tenuirostris from north-west Australia? In *Ibis* (Vol. 146). https://doi.org/https://doi.org/10.1111/j.1474-919X.2004.00210.x

Beatty, W. S., Webb, E. B., Kesler, D. C., Naylor, L. W., Raedeke, A. H., Humburg, D. D., Coluccy, J. M., & Soulliere, G. J. (2015). An empirical evaluation of landscape energetic models: Mallard and American black duck space use during the non-breeding period. *Journal of Wildlife Management*, *79*(7), 1141–1151. https://doi.org/10.1002/jwmg.920

Boggie, M. A., Collins, D. P., & Carleton, S. A. (2023). Availability of supplemental corn for sandhill cranes, light geese, and dabbling ducks wintering in New Mexico. *Journal of Fish and Wildlife Management*, *14*(1), 51–61. https://doi.org/10.3996/jfwm-22-013

Boggie, M. A., Collins, D. P., Patrick Donnelly, J., & Carleton, S. A. (2018). Land use, anthropogenic disturbance, and riverine features drive patterns of habitat selection by a

wintering waterbird in a semiarid environment. *PLoS ONE*, *13*(11), 1–26. https://doi.org/10.1371/journal.pone.0206222

Brasher, M. G., Steckel, J. D., & Gates, R. J. (2007). Energetic carrying capacity of actively and passively managed wetlands for migrating ducks in Ohio. *Journal of Wildlife Management*, *71*(8), 2532–2541. https://doi.org/10.2193/2006-401

Central Valley Joint Venture. (2006). *Central Valley Joint Venture Implementation Plan - Conserving Bird Habitat*.

Chavarria, S. B., & Gutzler, D. S. (2018). Observed changes in climate and streamflow in the Upper Rio Grande Basin. *Journal of the American Water Resources Association*, *54*(3), 644–659. https://doi.org/10.1111/1752-1688.12640

Collins, D. P., Boggie, M. A., Kruse, K. L., Conring, C. M., Donnelly, J. P., Conway, W. C., & Grisham, B. A. (2023). Roost sites influence habitat selection of sandhill cranes (Antigone canadensis tabida) in Arizona and California. *Waterbirds*, *45*(4). https://doi.org/10.1675/063.045.0407

Conring, C. M., Brautigam, K., Grisham, B. A., Collins, D. P., & Conway, W. C. (2019). Identifying the migratory strategy of the lower colorado river valley population of greater sandhill cranes. *Avian Conservation and Ecology*, *14*(1). https://doi.org/10.5751/ACE-01352-140111

Cooper, D. J., Sanderson, J. S., Stannard, D. I., & Groeneveld, D. P. (2006). Effects of long-term water table drawdown on evapotranspiration and vegetation in an arid region phreatophyte community. *Journal of Hydrology*, *325*(1–4), 21–34. https://doi.org/10.1016/j.jhydrol.2005.09.035

Davis, C. A., & Vohs, P. A. (1993). *Role of macroinvertebrates in spring siet and habitat use of sandhill cranes*. https://digitalcommons.unl.edu/tnas

Devries, J. H., Brook, R. W., Howerter, D. W., & Anderson, M. G. (2008). Effects of spring body condition and age on reproduction in Mallards (Anas platyrhynchos). *Auk*, *125*(3), 618–628. https://doi.org/10.1525/auk.2008.07055

Dobush, G. R., Davison, C., & Krementz, D. G. (1985). The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. *Canadian Journal of Zoology*, *63*, 1917–1920. https://doi.org/https://doi.org/10.1139/z85-285

Donnelly, J. P., King, S. L., Knetter, J., Gammonley, J. H., Dreitz, V. J., Grisham, B. A., Nowak, M. C., & Collins, D. P. (2021). Migration efficiency sustains connectivity across agroecological networks supporting sandhill crane migration. *Ecosphere*, *12*(6). https://doi.org/10.1002/ecs2.3543

Donnelly, J. P., King, S. L., Silverman, N. L., Collins, D. P., Carrera-Gonzalez, E. M., Lafón-Terrazas, A., & Moore, J. N. (2020). Climate and human water use diminish wetland networks supporting continental waterbird migration. *Global Change Biology*, *December 2019*, 1–18. https://doi.org/10.1111/gcb.15010

Drewien, R. C., & Bizeau, E. G. (1974). Status and distribution of greater sandhill cranes in the Rocky Mountains. *Journal of Wildlife Management*, *38*(4), 720–742.

Emery, P. A., Boettcher, A. J., Snipes, R. J., & Mcintyre, H. J. (1969). Hydrology of the San Luis Valley, south-central Colorado. In *U.S. Geological Survey* (pp. 1–22).

English, M. D., Robertson, G. J., Peck, L. E., & Mallory, M. L. (2017). Agricultural food resources and the foraging ecologies of American black ducks (Anas rubripes) and

mallards (Anas platyrhynchos) at the northern limits of their winter ranges. *Urban Ecosystems*, *20*(6), 1311–1318. https://doi.org/10.1007/s11252-017-0683-0

Fino, S. R., Williams, C. K., Livolsi, M. C., Ringelman, K. M., Coluccy, J. M., Devers, P. K., & Castelli, P. M. (2017). Carrying capacity of wintering American black ducks in forested wetlands. *Journal of Wildlife Management*, *81*(5), 943–950. https://doi.org/10.1002/jwmg.21242

Foster, M. A., Gray, M. J., & Kaminski, R. M. (2010). Agricultural seed biomass for migrating and wintering waterfowl in the southeastern United States. *Journal of Wildlife Management*, *74*(3), 489–495. https://doi.org/10.2193/2008-588

Fowler, D. N., Webb, E. B., & Vrtiska, M. P. (2020). Condition bias of decoy-harvested Light Geese During the Conservation Order. *Journal of Wildlife Management*, *84*(1), 33–44. https://doi.org/10.1002/jwmg.21770

Frederick, R. B., Clark, W. R., & Klaas, E. E. (1987). Behavior, energetics, and management of refuging waterfowl: a simulation model. *Wildlife Monographs*, *96*, 3–35. https://www.jstor.org/stable/3830584?seq=1&cid=pdf-

Gates, R. J., Caithamer, D. F., Moritz, W. E., & Tacha, T. C. (2001). Bioenergetics and nutrition of Mississippi Valley Population Canada geese during winter and migration. *Wildlife Monographs*, *146*, 1–65.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Goss-Custard, J. D., Stillman, R. A., Caldow, R. W. G., West, A. D., & Guillemain, M. (2003). Carrying capacity in overwintering birds: When are spatial models needed? *Journal of Applied Ecology*, *40*(1), 176–187. https://doi.org/10.1046/j.1365-2664.2003.00785.x

Goss-Custard, J. D., Stillman, R. A., West, A. D., Caldow, R. W. G., & McGrorty, S. (2002). Carrying capacity in overwintering migratory birds. *Biological Conservation*, *105*(1), 27–41. https://doi.org/10.1016/S0006-3207(01)00175-6

Greer, D. M., Dugger, B. D., Reinecke, K. J., & Petrie, M. J. (2009). Depletion of Rice as Food of Waterfowl Wintering in the Mississippi Alluvial Valley. *Journal of Wildlife Management*, *73*(7), 1125–1133. https://doi.org/10.2193/2008-250

Haramis, G. M., Nichols, J. D., Pollock, K. H., & Hines, J. E. (1986). The relationship between body mass and survival of wintering canvasbacks. *Auk*, *103*, 506–514. https://academic.oup.com/auk/article/103/3/506/5191468

Heitmeyer, M. E. (2010). A manual for calculating duck-use-days to determine habitat resource values and waterfowl population energetic requirements in the Mississippi Alluvial Valley. Greenbrier Wetland Services Report 10-01. In *Blue Heron Conservation Design and Printing LLC, Bloomfield, MO* (pp. 1–69).

Heitmeyer, M. E., & Aloia, C. M. (2013). *Hydrogeomorphic evaluation of ecosystem restoration and management options for Monte Vista National Wildlife Refuge. Prepared for U.S. Fish and Wildlife Service, Region 6, Lakewood, CO.* (pp. 1–70).

Hepp, G. R., Blohm, R. J., Reynolds, R. E., Hines, J. E., & Nichols, J. D. (1986). Physiological condition of autumn-banded mallards and its relationship to hunting Vulnerability. *Journal of Wildlife Management*, *50*(2), 177–183. https://www.jstor.org/stable/3801893

Hobson, K. A., Sharp, C. M., Jefferies, R. L., Rockwell, R. F., & Abraham, K. F. (2011). Nutrient allocation strategies to eggs by lesser snow geese (Chen caerulescens) at a sub-arctic colony. *The Auk*, *128*(1), 156–165. https://doi.org/https://doi.org/10.1525/auk.2010.10086

Intermountain West Joint Venture. (2013). *Intermountain West Joint Venture. 2013 Implementation Plan - Strengthening Science and Parternships*. www.iwjv.org

Ivey, G. L., Dugger, B. D., Herziger, C. P., Casazza, M. L., & Fleskes, J. P. (2015). Wintering ecology of sympatric subspecies of Sandhill Crane: Correlations between body size, site fidelity, and movement patterns. *Condor*, *117*(4), 518–529. https://doi.org/10.1650/CONDOR-14-159.1

Jenni, L., & Jenni-Eiermann, S. (1998). Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology*, *29*(4), 521–528. https://doi.org/https://doi.org/10.2307/3677171

Johnson, W. P., Schmidt, P. M., & Taylor, D. P. (2014). Foraging flight distances of wintering ducks and geese: a review. *Avian Conservation and Ecology*, *9*(2), 2. https://doi.org/10.5751/ACE-00683-090202

Kauffeld, J. D. (1981). Management of migratory crane habitat on Alamosa and Monte Vista National Wildlife Refuges. *Proceedings 1981 Crane Workshop*, 117–121.

Krapu, G. L., Brandt, D. A., & Cox, R. R. (2004). Less waste corn, more land in soybeans, and the switch to genetically modified crops: trends with important implications for wildlife management. *Wildlife Society Bulletin*, *32*(1), 127–136. https://doi.org/10.2193/0091-7648(2004)32[127:lwcmli]2.0.co;2

Krapu, G. L., Brandt, D. A., Kinzel, P. J., & Pearse, A. T. (2014). Spring migration ecology of the Mid-Continent sandhill crane population with an emphasis on use of the Central Platte

River Valley, Nebraska. *Wildlife Monographs*, *189*, 1–41. https://doi.org/10.1002/wmon.l013

Krapu, G. L., Iverson, G. C., Reinecke, K. J., & Boise, C. M. (1985). Fat deposition and usage by arctic-nesting Sandhill Cranes during spring. *Auk*, *102*(2), 362–368. https://doi.org/https://doi.org/10.2307/4086780

Krapu, G. L., Reinecke, K. J., Jorde, D. G., & Simpson, S. G. (1995). Spring-staging ecology of Midcontinent greater white-fronted geese. *Journal of Wildlife Management*, *59*(4), 736–746. https://doi.org/https://doi.org/10.2307/3801950

Kross, J. P., Kaminski, R. M., Reinecke, K. J., & Pearse, A. T. (2008). Conserving waste rice for wintering waterfowl in the Mississippi Alluvial Valley. *Journal of Wildlife Management*, *72*(6), 1383–1387. https://doi.org/10.2193/2007-226

Ladin, Z. S., Castelli, P. M., Mcwilliams, S. R., & Williams, C. K. (2011). Time energy budgets and food use of Atlantic brant across their wintering range. *Journal of Wildlife Management*, *75*(2), 273–282. https://doi.org/10.1002/jwmg.58

Lancaster, J. D., & Wilson, B. C. (2021). Gulf Coast Joint Venture wintering waterfowl population and habitat objective model refinement 2021. In *Gulf Coast Joint Venture* (pp. 1–75).

Lee, J. C. I., Tsai, L. C., Hwa, P. Y., Chan, C. L., Huang, A., Chin, S. C., Wang, L. C., Lin, J. T., Linacre, A., & Hsieh, H. M. (2010). A novel strategy for avian species and gender identification using the CHD gene. *Molecular and Cellular Probes*, *24*(1), 27–31. https://doi.org/10.1016/j.mcp.2009.08.003

Littlefield, C. D. (2002). Winter foraging habitat of greater sandhill cranes in northern California. *Western Birds*, *33*, 51–60.

Lobell, D. B., Schlenker, W., & Costa-Roberts, J. (2011). Climate trends and global crop production since 1980. *Science*, *333*, 616–620. https://doi.org/10.1126/science.1206376

Lovvorn, J. R., & Kirkpatrick, C. M. (1982). Field use by staging eastern greater sandhill cranes. *Journal of Wildlife Management*, *46*(1), 99–108. https://doi.org/https://doi.org/10.2307/3808412

Matthews, L. J., Petrie, M., & Eadie, J. M. (2022). Impacts of changing postharvest agricultural practices on abundance of waste grain in California's Central Valley. *Journal of Fish and Wildlife Management*, *13*(2), 32–333. https://doi.org/10.3996/JFWM-21-061

McLandress, M. R., & Raveling, D. G. (1981). Changes in diet and body composition of Canada geese before spring migration. *Auk*, *98*(1), 65–79. https://doi.org/https://doi.org/10.1093/auk/98.1.65

McWilliams, S. R., Guglielmo, C., Pierce, B., & Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: A nutritional and physiological ecology perspective. In *Journal of Avian Biology* (Vol. 35, Issue 5, pp. 377–393). https://doi.org/10.1111/j.0908-8857.2004.03378.x

Miller, M. R., & Eadie, J. M. (2006). The allometric relationship between resting metabolic rate and body bass in wild waterfowl (Anatidae) and an application to estimation of winter habitat requirements. *Condor*, *108*(1), 166–177. https://doi.org/10.1093/condor/108.1.166

Mix, K., Lopes, V. L., & Rast, W. (2011). Annual and growing season temperature changes in the San Luis Valley, Colorado. *Water, Air, and Soil Pollution*, *220*(1–4), 189–203. https://doi.org/10.1007/s11270-011-0746-4

Morrison, R. I. G., Davidson, N. C., & Wilson, J. R. (2007). Survival of the fattest: body stores on migration and survival in red knots Calidris canutus islandica. *Journal of Avian Biology*, *38*(4), 479–487. https://doi.org/10.1111/j.2007.0908-8857.03934.x

Morton, J. M., Fowler, A. C., & Kirkpatrick, R. L. (2018). Time and energy budgets of American black ducks in winter. *Journal of Wildlife Management*, *53*(2), 401–410. https://doi.org/https://doi.org/10.2307/3801143

Norberg, U. M. (1996). Energetics of flight. In *Avian Energetics* (pp. 199–249). Chapman & Hall.

Odum, E. P., & Connell, C. E. (1956). Lipid levels in migrating birds. *Science*, *123*(3203), 892–894. https://doi.org/10.1126/science.123.3203.892.b

Pacific Flyway Council and Central Flyway Council. (2016). *Pacific and Central Flyways management plan for the Rocky Mountain population of greater sandhill cranes*.

Paulus. (1988). Time-activity budgets of nonbreeding Anatidae: a review. In *Waterfowl in winter: selected papers from symposium and workshop in Galveston, Texas* (pp. 135–152).

Pearse, A. T., Krapu, G. L., Brandt, D. A., & Kinzel, P. J. (2010). Changes in agriculture and abundance of snow geese affect carrying capacity of sandhill cranes in Nebraska. *Journal of Wildlife Management*, *74*(3), 479–488. https://doi.org/10.2193/2008-539

Penmetcha, S., Feng, F., Petrie, M. J., Reiter, M. E., Sartwell, J., & Richmond, O. M. W. (2016). *A user guide for the TRUEMET Program, Version 2.2*.

Petrie, M. J., Fleskes, J. P., Wolder, M. A., Isola, C. R., Yarris, G. S., & Skalos, D. A. (2016). Potential effects of drought on carrying capacity for wintering waterfowl in the central valley of California. *Journal of Fish and Wildlife Management*, *7*(2), 408–422. https://doi.org/10.3996/082015-JFWM-082

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-Effects Models in S and S-PLUS*. Springer, New York. https://doi.org/doi:10.1007/b98882

Pinherio, J., Bates D, & R Core Team. (2023). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-164.

Portugal, S. J., Green, J. A., & Butler, P. J. (2007). Annual changes in body mass and resting metabolism in captive barnacle geese (Branta leucopsis): The importance of wing moult. *Journal of Experimental Biology*, *210*(8), 1391–1397. https://doi.org/10.1242/jeb.004598

Reinecke, K. J., Stone, T. L., & Owen, R. B. (1982). Seasonal carcass composition and energy balance of female black ducks in Maine. *Condor*, *84*(4), 420–426. https://doi.org/https://doi.org/10.2307/1367447

Reinecke, & Krapu, G. (1986). Feeding ecology of sandhill cranes during spring migration in Nebraska. *Journal of Wildlife Management*, *50*(1), 71–79. https://doi.org/https://doi.org/10.2307/3801490

Rio Grande Basin Roundtable. (2015). *Rio Grande Basin Implementation Plan*. 1–164. https://engagecwcb.org/basin-implementation-plans

Rio Grande Basin Roundtable. (2022). *Rio Grande Basin Implementation Plan Volume 2*. https://engagecwcb.org/basin-implementation-plans

Rodehutscord, M., Rückert, C., Maurer, H. P., Schenkel, H., Schipprack, W., Bach Knudsen, K. E., Schollenberger, M., Laux, M., Eklund, M., Siegert, W., & Mosenthin, R. (2016). Variation in chemical composition and physical characteristics of cereal grains from different genotypes. *Archives of Animal Nutrition*, *70*(2), 87–107. https://doi.org/10.1080/1745039X.2015.1133111

Schmaljohann, H., Eikenaar, C., & Sapir, N. (2022). Understanding the ecological and evolutionary function of stopover in migrating birds. *Biological Reviews*, *97*(4), 1231–1252. https://doi.org/10.1111/brv.12839

Schmitt, C. G., & Hale, B. (1997). Sandhill crane hunts in the Rio Grande Valley and southwest New Mexico. *North American Crane Workshop Proceedings*, *7*, 219–231. http://digitalcommons.unl.edu/nacwgproc/232

Sedinger, J. S., & Alisauskas, R. T. (2014). Cross-seasonal effects and the dynamics of waterfowl populations. *Wildfowl*, *4*, 277–304.

Sherfy, M. H., Anteau, M. J., & Bishop, A. A. (2011). Agricultural practices and residual corn during spring crane and waterfowl migration in Nebraska. *Journal of Wildlife Management*, *75*(5), 995–1003. https://doi.org/10.1002/jwmg.157

Skalos, D. A., Eadie, J. M., Yparraguirre, D. R., Weaver, M. l., Oldenburger, S. L., Ely, C. R., Yee, J. L., & Fleskes, J. P. (2021). Body condition of wintering Pacific greater white-fronted geese. *Journal of Wildlife Management*, *85*(3), 484–497. https://doi.org/10.1002/jwmg.21997

Tacha, T. C. (1988). Social organization of sandhill cranes from midcontinental North America. *Wildlife Monographs*, 3–37. https://doi.org/10.1002/jwmg.ll3

Tacha, T. C., Vohs, P. A., & Iverson, G. C. (1987). Time and energy budgets of sandhill cranes from Mid-Continental North America. *Journal of Wildlife Management*, *51*(2), 440–448. https://www.jstor.org/stable/3801032?seq=1&cid=pdf-reference#references_tab_contents

U.S. Fish and Wildlife Service. (2015). *Comprehensive conservation plan: San Luis Valley National Wildlife Refuge Complex*.

USDA National Agricultural Statistics Service Cropland Data Layer. (2023). *Published crop-specific data layer [Online]*. USDA-NASS, Washington, DC.

Vanausdall, R. A., Kendall, W. L., Collins, D. P., & Hays, Q. R. (2024). Time of year and weather influence departure decisions of sandhill cranes at a primary stopover. *Frontiers in Ecology and Evolution*, *12*. https://doi.org/10.3389/fevo.2024.1279279

Western Regional Climate Center. (2013). *Cooperative Climatological Data Summaries*. https://wrcc.dri.edu/Climate/summaries.php

Williams, C. K., Dugger, B. D., Brasher, M. G., Coluccy, J. M., Cramer, D. M., Eadie, J. M., Gray, M. J., Hagy, H. M., Livolsi, M., Mcwilliams, S. R., Petrie, M., Soulliere, G. J., Tirpak, J. M., & Webb, E. B. (2014). Estimating habitat carrying capacity for migrating and wintering waterfowl: Considerations, pitfalls and improvements. *Wildfowl*, *4*, 407–435.

Winker, K., Warner, D. W., & Weisbrod, A. R. (1992). Daily mass gains among woodland migrants at an inland stopover site. *Auk*, *109*(4), 853–862. https://doi.org/https://doi.org/10.2307/4088159

APPENDIX S1

Table S1.1: Coefficient estimates for the effects of a time trend within years and a time trend over years on the persistence probability (φ) of sandhill cranes in the San Luis Valley, Colorado, 2015-2022.

Covariate	Coefficient estimate (95% confidence intervals)
Autumn	
intercept	9.24 (7.97, 10.51)
time	-0.07 (-0.09, -0.06)
time trend over years	-0.06 (-0.14, 0.03)
Spring	
intercept	6.83 (6.21, 7.45)
time	-0.07 (-0.08, -0.06)
time trend over years	0.05 (-0.01, 0.11)

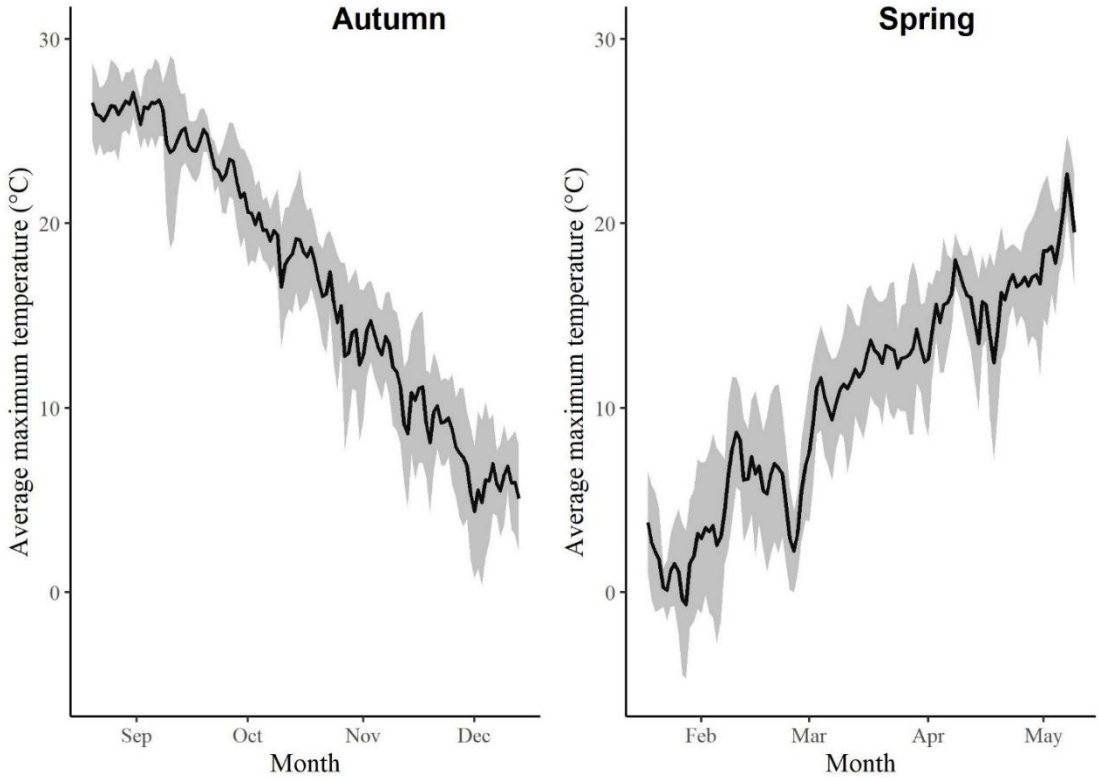

Figure S1.1: Average maximum temperature during the autumn and spring periods in the San Luis Valley, Colorado, 2015-2022.

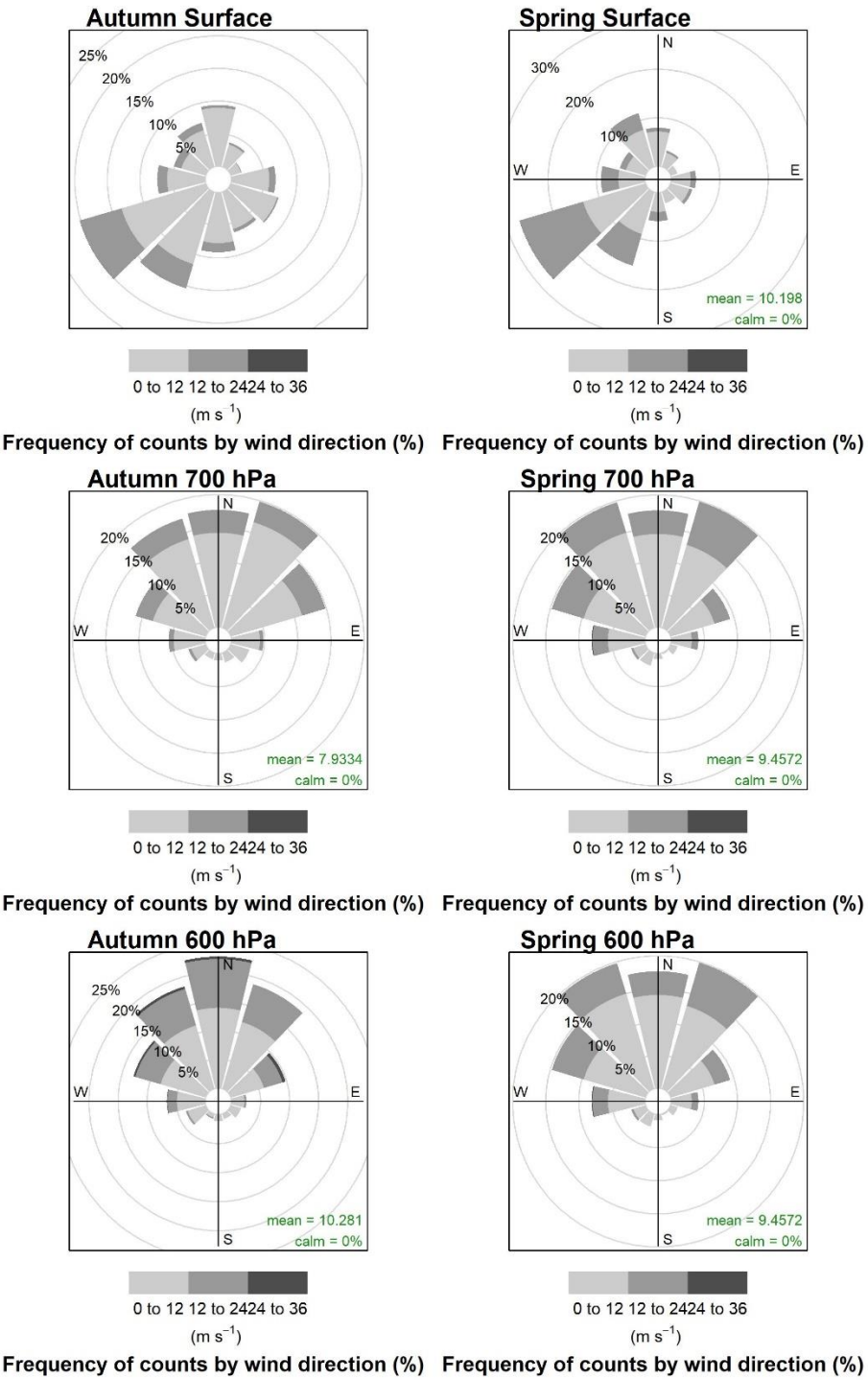

Figure S1.2: Proportion of counts of wind direction and wind speed at the surface and altitudes of 700 hPa (3,000 m above sea level) and 600 hPa (4,500 m above sea level) for the autumn and spring periods in the San Luis Valley, Colorado, 2015-2022.

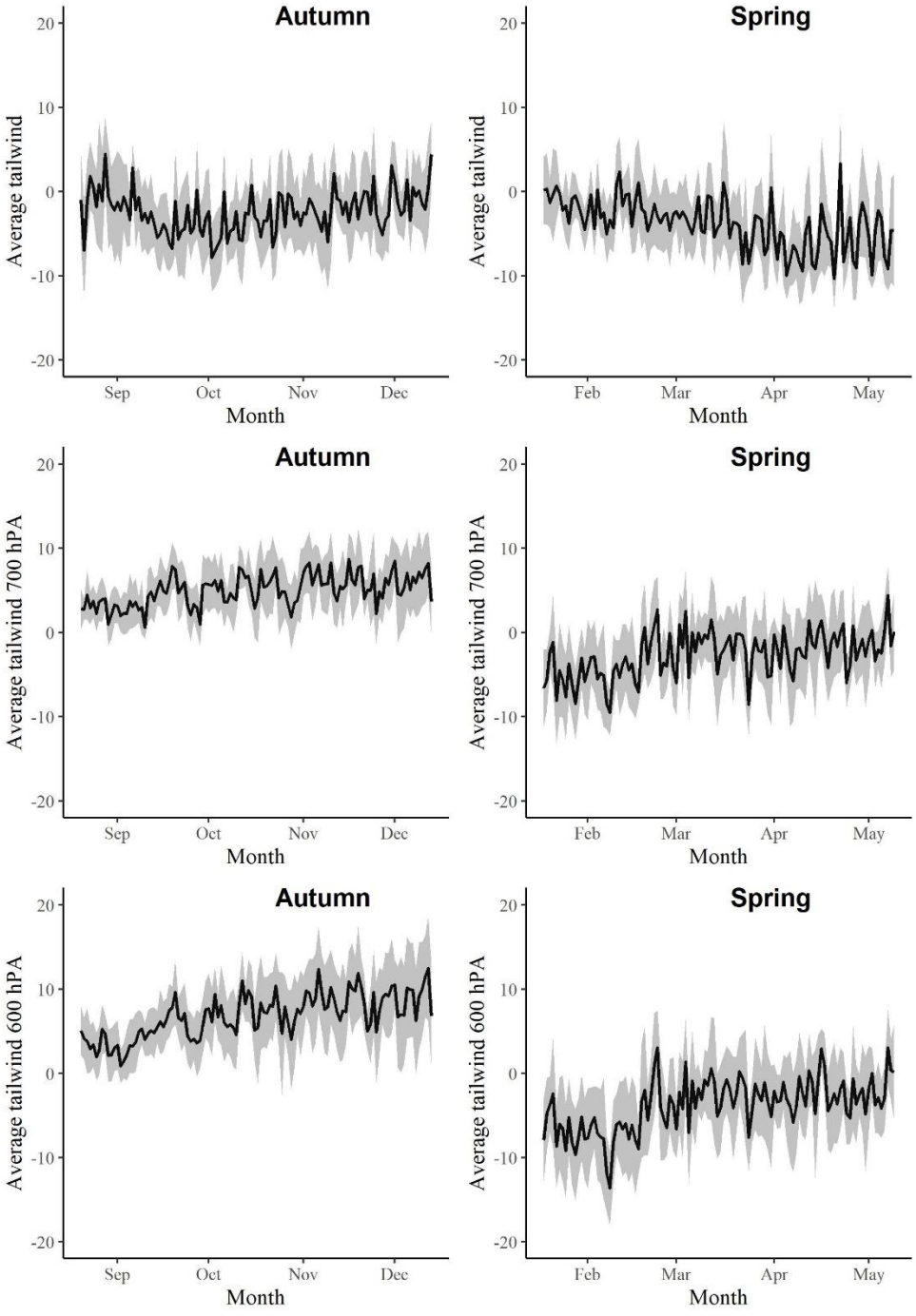

Figure S1.3: Average tailwind at the surface and altitudes of 700 hPa (3,000 m above sea level) and 600 hPa (4,500 m above sea level) during the autumn and spring periods in the San Luis Valley, Colorado, 2015-2022. The shaded area represents 95% confidence intervals.

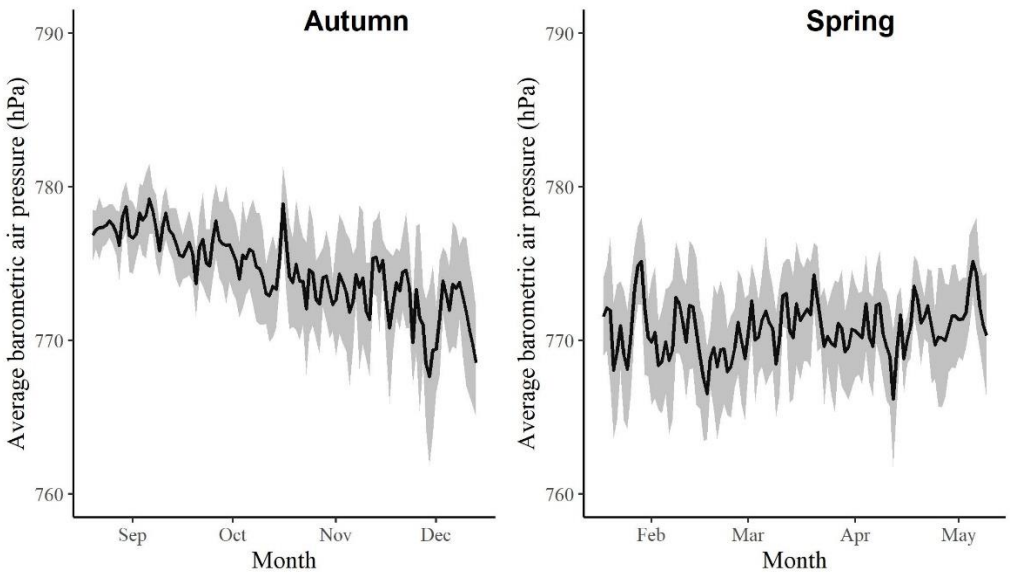

Figure S1.4: Average barometric air pressure during the autumn and spring periods in the San Luis Valley, Colorado, 2015-2022. The shaded area represents 95% confidence intervals.

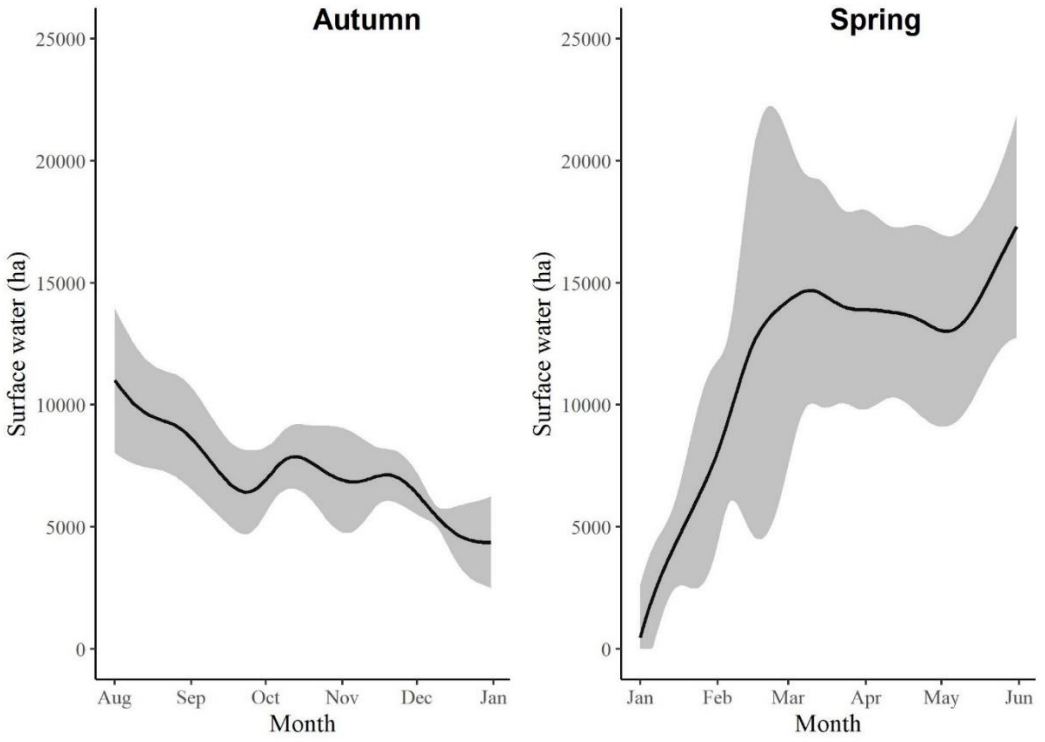

Figure S1.5: Average surface water area during the autumn and spring periods in the San Luis Valley, Colorado, 2015-2022. The shaded area represents 95% confidence intervals.

APPENDIX S2

Table S2.1: Coefficient estimates (with 95% confidence intervals [CI])) for the effect of covariates on the log-odds of presence of greater and lesser sandhill cranes on crop fields in the San Luis Valley, Colorado, 2020-2022. Roost distance is the distance (m) to the nearest potential roost. Time represents the survey week during which roadside surveys were conducted.

		Greaters		Lessers	
Model	Covariate	Autumn	Spring	Autumn	Spring
$Time^2$ + crop type*roost distance	Intercept (alfalfa)	-11.59 (-12.84, -10.34)	-9.95 (-10.71, -9.18)	-12.99 (-14.4, -11.57)	-11.95 (-13.05, -10.84)
	Barley	4.01 (2.99, 5.02)	3.86 (3.25, 4.46)	3.13 (2.09, 4.17)	3.65 (2.81, 4.49)
	Other	0.50 (-0.57, 1.57)	0.92 (0.30, 1.55)	0.00 (-1.12, 1.11)	0.83 (-0.06, 1.72)
	Other grain	2.36 (1.25, 3.47)	2.35 (1.69, 3)	1.90 (0.7, 3.11)	1.83 (0.87, 2.79)
	Pasture	0.84 (-0.35, 2.04)	0.89 (0.06, 1.72)	0.07 (-1.31, 1.44)	1.05 (-0.10, 2.20)
	Potatoes	0.28 (-0.86, 1.42)	1.11 (0.45, 1.78)	-1.09 (-2.92, 0.73)	0.44 (-0.57, 1.46)
	Roost distance	-1.72 (-2.93, -0.52)	-1.64 (-2.31, -0.98)	-1.75 (-2.96, -0.54)	-1.67 (-2.59, -0.75)
	Roost distance*barley	0.10 (-1.16, 1.36)	0.91 (0.22, 1.61)	0.21 (-1.07, 1.49)	0.97 (0.01, 1.93)
	Roost distance*other	1.40 (0.14, 2.67)	1.12 (0.41, 1.84)	1.30 (0, 2.61)	1.31 (0.32, 2.3)
	Roost distance*other grain	0.13 (-1.23, 1.49)	0.69 (-0.05, 1.43)	0.14 (-1.35, 1.63)	0.41 (-0.66, 1.49)
	Roost distance*pasture	1.71 (0.26, 3.16)	1.19 (0.24, 2.15)	1.81 (0.15, 3.47)	1.26 (-0.06, 2.57)
	Roost distance*potatoes	0.79 (-0.58, 2.16)	-0.26 (-1.06, 0.53)	-0.72 (-3.07, 1.63)	-0.6 (-1.81, 0.61)
	Time	1.26 (0.98, 1.54)	1.02 (0.81, 1.24)	1.87 (1.52, 2.23)	1.13 (0.84, 1.42)
	$Time^2$	-0.13 (-0.16, -0.10)	-0.12 (-0.15, -0.09)	-0.20 (-0.24, -0.16)	-0.13 (-0.17, -0.1)
$Time^2$*crop type + roost distance	Intercept (alfalfa)	-10.08 (-11.57, -8.59)	-9.27 (-10.41, -8.13)	-12.34 (-14.06, -10.62)	-11.08 (-12.6, -9.56)
	Barley	1.41 (-0.21, 3.03)	2.98 (1.78, 4.19)	1.43 (-0.5, 3.35)	2.65 (1.08, 4.22)
	Other	-1.84 (-4.53, 0.86)	0.01 (-1.57, 1.59)	-1.07 (-4.48, 2.35)	-1.32 (-3.7, 1.06)
	Other grain	0.08 (-2.11, 2.28)	2.22 (0.81, 3.63)	-0.34 (-3.18, 2.49)	0.88 (-1.16, 2.92)
	Pasture	0.14 (-2.27, 2.55)	0.31 (-1.26, 1.89)	0.37 (-4.42, 5.15)	0.92 (-1.09, 2.93)
	Potatoes	0.09 (-2.84, 3.01)	-0.98 (-2.85, 0.89)	2.83 (-0.54, 6.2)	-0.68 (-3.31, 1.94)
	Roost distance	-1.15 (-1.47, -0.83)	-0.86 (-1.06, -0.67)	-1.24 (-1.65, -0.84)	-0.81 (-1.10, -0.52)
	Time	1.04 (0.29, 1.78)	0.85 (0.22, 1.47)	1.96 (1.16, 2.75)	0.83 (0.02, 1.65)

Model	Covariate	Greaters		Lessers	
		Autumn	Spring	Autumn	Spring
	Time*barley	0.54 (-0.3, 1.37)	0.27 (-0.44, 0.97)	0.22 (-0.72, 1.15)	0.42 (-0.49, 1.33)
	Time*other	0.32 (-0.99, 1.63)	0.35 (-0.58, 1.27)	-0.34 (-1.93, 1.24)	1.12 (-0.23, 2.47)
	Time*other grain	0.48 (-0.62, 1.58)	-0.23 (-1.07, 0.61)	0.45 (-0.87, 1.78)	0.24 (-0.93, 1.41)
	Time*pasture	-0.47 (-1.73, 0.78)	0.05 (-0.88, 0.98)	-1.56 (-3.76, 0.65)	-0.23 (-1.42, 0.96)
	Time*potatoes	-1.06 (-2.52, 0.39)	0.85 (-0.18, 1.88)	-2.58 (-4.34, -0.82)	0.28 (-1.17, 1.74)
	$Time^2$	-0.16 (-0.25, -0.06)	-0.09 (-0.18, -0.01)	-0.25 (-0.35, -0.15)	-0.09 (-0.2, 0.02)
	$Time^2$*barley	0.00 (-0.1, 0.11)	-0.04 (-0.14, 0.05)	0.02 (-0.09, 0.13)	-0.07 (-0.2, 0.05)
	$Time^2$*other	0.02 (-0.13, 0.17)	-0.06 (-0.18, 0.07)	0.09 (-0.08, 0.27)	-0.16 (-0.34, 0.02)
	$Time^2$*other grain	0.01 (-0.13, 0.14)	0.03 (-0.09, 0.14)	0.01 (-0.14, 0.16)	-0.02 (-0.18, 0.13)
	$Time^2$*pasture	0.08 (-0.07, 0.24)	-0.03 (-0.15, 0.1)	0.24 (0, 0.48)	0.01 (-0.15, 0.17)
	$Time^2$*potatoes	0.19 (0.02, 0.36)	-0.09 (-0.22, 0.05)	0.34 (0.14, 0.54)	-0.01 (-0.2, 0.18)
$Time^2$*roost distance + crop type	Intercept (alfalfa)	-12.87 (-14.22, -11.52)	-9.43 (-10.05, -8.8)	-14.39 (-16.2, -12.58)	-11.53 (-12.44, -10.62)
	Barley	3.68 (3.17, 4.19)	3.26 (2.91, 3.62)	2.81 (2.31, 3.31)	3.03 (2.55, 3.5)
	Other	-0.08 (-0.69, 0.52)	0.35 (-0.04, 0.74)	-0.6 (-1.26, 0.06)	0.22 (-0.33, 0.77)
	Other grain	2.16 (1.57, 2.75)	1.83 (1.45, 2.21)	1.74 (1.14, 2.35)	1.46 (0.93, 1.99)
	Pasture	-0.29 (-0.98, 0.4)	0.07 (-0.4, 0.53)	-1.11 (-1.98, -0.23)	0.19 (-0.45, 0.84)
	Potatoes	-0.36 (-1.09, 0.37)	0.83 (0.41, 1.25)	-0.93 (-1.8, -0.06)	0.3 (-0.31, 0.9)
	Roost distance	-3.22 (-4.66, -1.77)	-0.75 (-1.25, -0.25)	-3.22 (-5.23, -1.22)	-1.07 (-1.81, -0.34)
	Time	1.71 (1.22, 2.2)	1.05 (0.81, 1.3)	2.31 (1.63, 2.98)	1.29 (0.94, 1.64)
	Time*roost distance	0.60 (0, 1.19)	0.05 (-0.24, 0.34)	0.51 (-0.3, 1.33)	0.34 (-0.07, 0.75)
	$Time^2$	-0.16 (-0.21, -0.11)	-0.13 (-0.16, -0.1)	-0.23 (-0.29, -0.16)	-0.16 (-0.21, -0.12)
	$Time^2$*roost distance	-0.03 (-0.09, 0.03)	-0.02 (-0.06, 0.02)	-0.02 (-0.1, 0.06)	-0.06 (-0.12, -0.01)

Table S2.2: Coefficient estimates (with 95% confidence intervals [CI])) for the effect of covariates on the number of greater sandhill cranes on crop fields in the San Luis Valley, Colorado, 2020-2022. Roost distance is the distance (m) to the nearest potential roost. Time represents the survey week during which roadside surveys were conducted.

Model	Covariate	Autumn	Spring
$Time^2$ + crop type * roost distance	Intercept (alfalfa)	2.61 (1.81, 3.41)	3.53 (2.9, 4.17)
	Barley	1.32 (0.83, 1.82)	0.55 (0.05, 1.05)
	Number of lesser sandhill cranes	0.33 (0.2, 0.45)	0.56 (0.39, 0.73)
	Other	1.29 (0.59, 1.99)	0.41 (-0.21, 1.02)
	Other grain	0.99 (0.37, 1.60)	0.22 (-0.35, 0.79)
	Pasture	0.28 (-0.47, 1.04)	0.22 (-0.53, 0.97)
	Potatoes	1.12 (0.29, 1.95)	0.51 (-0.08, 1.1)
	Roost distance	0.09 (-0.68, 0.86)	-0.44 (-1.06, 0.17)
	Roost distance*barley	0.23 (-0.56, 1.03)	0.72 (0.09, 1.36)
	Roost distance*other	-0.10 (-0.90, 0.71)	0.85 (0.16, 1.54)
	Roost distance*other grain	-0.35 (-1.22, 0.52)	0.71 (0.03, 1.38)
	Roost distance*pasture	0.45 (-0.48, 1.38)	0.33 (-0.63, 1.29)
	Roost distance*potatoes	-0.43 (-1.34, 0.47)	0.26 (-0.46, 0.98)
	Time	0.26 (-0.06, 0.58)	0.47 (0.22, 0.71)
	$Time^2$	-0.04 (-0.07, 0.00)	-0.09 (-0.12, -0.06)
$Time^2$*crop type + roost distance	Intercept (alfalfa)	2.36 (0.48, 4.23)	3.76 (2.35, 5.17)
	Barley	1.46 (-0.58, 3.50)	0.39 (-1.14, 1.92)
	Number of lesser sandhill cranes	0.32 (0.19, 0.45)	0.57 (0.40, 0.74)
	Other	1.19 (-2.74, 5.12)	-1.19 (-3.29, 0.91)
	Other grain	-0.09 (-2.67, 2.49)	-0.87 (-2.68, 0.94)
	Pasture	2.59 (-1.41, 6.59)	1.46 (-0.46, 3.38)
	Potatoes	5.95 (1.88, 10.02)	-0.49 (-2.95, 1.98)
	Roost distance	0.14 (0.00, 0.28)	0.22 (0.09, 0.34)
	Time	0.48 (-0.56, 1.53)	0.49 (-0.34, 1.32)
	Time*barley	-0.14 (-1.25, 0.98)	0.02 (-0.88, 0.91)
	Time*other	-0.33 (-2.23, 1.57)	1.00 (-0.23, 2.23)
	Time*other grain	0.33 (-1.00, 1.66)	0.19 (-0.86, 1.25)

Model	Covariate	Autumn	Spring
	Time*pasture	-1.55 (-3.58, 0.49)	-0.73 (-1.86, 0.41)
	Time*potatoes	-2.54 (-4.55, -0.53)	0.16 (-1.17, 1.49)
	$Time^2$	-0.07 (-0.21, 0.06)	-0.09 (-0.20, 0.02)
	$Time^2$*barley	0.02 (-0.12, 0.16)	-0.01 (-0.13, 0.11)
	$Time^2$*other	0.07 (-0.15, 0.28)	-0.15 (-0.32, 0.02)
	$Time^2$*other grain	-0.02 (-0.18, 0.15)	0.00 (-0.14, 0.14)
	$Time^2$*pasture	0.20 (-0.03, 0.44)	0.08 (-0.08, 0.24)
	$Time^2$*potatoes	0.28 (0.05, 0.51)	0.00 (-0.17, 0.17)
$Time^2$*roost distance + crop type	Intercept (alfalfa)	2.39 (1.60, 3.19)	3.86 (3.30, 4.41)
	Barley	1.33 (0.88, 1.78)	0.23 (-0.18, 0.64)
	No. lessers	0.33 (0.21, 0.46)	0.56 (0.38, 0.73)
	Other	1.20 (0.53, 1.86)	0.16 (-0.37, 0.70)
	Other grain	1.01 (0.42, 1.61)	-0.15 (-0.62, 0.32)
	Pasture	0.22 (-0.52, 0.96)	0.06 (-0.51, 0.62)
	Potatoes	1.09 (0.30, 1.88)	0.21 (-0.30, 0.72)
	Roost distance	-0.22 (-1.07, 0.63)	0.27 (-0.1, 0.64)
	Time	0.33 (0.00, 0.67)	0.47 (0.23, 0.72)
	Time*roost distance	0.03 (-0.35, 0.42)	0.04 (-0.18, 0.27)
	$Time^2$	-0.04 (-0.08, -0.01)	-0.09 (-0.13, -0.06)
	$Time^2$*roost distance	0.01 (-0.03, 0.05)	-0.01 (-0.05, 0.02)