Habitat Quality and Conservation for Ferruginous Hawks Using a Cumulative Effects Approach

by

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Abstract

Human land use and climate change can contribute to cumulative effects, which are the collective impacts from environmental and anthropogenic processes over space and time. Exploring the cumulative effects of landscape and climate change together is important for identifying potential interactions, assessing their relative influence, determining the spatial extents of their influence, and understanding their potential impact on populations. Landscape alterations from human land use can improve, degrade, or leave unaffected habitat quality for species populations. Modern landscapes often have multiple land uses, creating the potential for cumulative effects, particularly for wide-ranging animals that are likely to encounter multiple land use and human infrastructure. In the Canadian prairies, grassland loss and degradation, primarily from agriculture, are thought to be responsible for the decline of many species, including grassland birds. Energy development infrastructure and sensory disturbance can further degrade habitat and negatively affect certain wildlife populations. Climate change in this region is expected to increase seasonal temperatures, decrease precipitation during the summer, and increase the frequency and severity of storms. Changing climate is also a dominant driver of populations, sometimes more so than habitat loss. My overall objective is to evaluate how the cumulative effects of landscape, seasonal weather, and climate change influence Ferruginous Hawk (*Buteo regalis*) habitat use, reproduction, and simulations of overall population demography. My study was conducted in the grassland biome located in southern Alberta and Saskatchewan where the human footprint from multiple land uses is extensive and where climate change is altering weather patterns. I found that heterogeneous landscapes with moderate amounts of cropland and grassland, and moderate edge density were predictors of higher home range habitat selection, relative nest abundance, and nest survival. Climate and seasonal weather

were also predictors of home range habitat selection and reproductive performance. High densities of active oil wells were negatively associated with nest survival, while density of active gas wells was positively associated. Seasonal weather was also a strong predictor of nest survival and brood provisioning. Seasonal weather influenced prey diversity, and hawks that delivered more diverse prey were more likely to return more biomass compared to hawks that deliver only Richardson's Ground Squirrels (*Urocitellus richardsonii*). We used our habitat and reproduction models to develop predictive maps that could be used for prioritizing conservation and identifying avoidance zones for development to reduce risk to Ferruginous Hawk. Our spatially-explicit population model demonstrated that land cover change has a greater relative influence on the Ferruginous Hawk population in Canada compared to climate change, given the scenarios we simulated. Ferruginous Hawks are a species at risk and face multiple threats. Understanding the influence of each threat, their cumulative risk, and their relative influence on the species, over space and time, is critical for developing conservation and recovery plans. My thesis contributes to the research of cumulative effects of landscape and climate change on breeding Ferruginous Hawks and demonstrates the utility of a cumulative effects approach for population conservation and recovery.

Preface

This thesis is an original work by Janet W. Ng. This project was approved by University of Alberta Animal Care (#724) and conducted under permit AUP00000018: "Foraging and Reproduction of Wild Ferruginous Hawks" from the Research Ethics Board at the University of Alberta.

Chapter 2 of this thesis has been submitted to the Journal of Wildlife Management as J. W. Ng, T. Wellicome, and E. Bayne "Predicting wind energy conflict risk for Ferruginous Hawks in Canada" and is currently in review. I was responsible for concept formation, data collection, analysis, and writing the manuscript. T. Wellicome and E. Bayne provided input and feedback throughout the concept formation, analyses, and writing of the manuscript.

Chapter 3 of this thesis is being prepared for journal submission. I was responsible for concept formation, data collection, analyses, and writing the manuscript. T. Wellicome and E. Bayne provided input and feedback throughout the concept formation, analyses, and writing of the manuscript.

Chapter 4 of this thesis is being prepared for journal submission. I was responsible for concept formation, data collection, analyses, and writing the manuscript. T. Wellicome and E. Bayne provided input and feedback throughout the concept formation, analyses, and writing of the manuscript.

Chapter 5 of this thesis is being prepared for journal submission. I was responsible for concept formation, data collection, analyses, and writing the manuscript. T. Wellicome and E. Bayne provided input and feedback throughout the concept formation, analyses, and writing of the manuscript.

This thesis is my writing, but the contributions of my supervisors Dr. Erin Bayne and Dr. Troy Wellicome are reflected with the use of plural pronouns.

Dedication

I dedicate this thesis to my big brother, David Ng (1979 – 2012). Letting me tag along on outdoor adventures set me on this path and I am very thankful.

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Table of Contents

Tables

Figures

Chapter 1: General Introduction

Cumulative effects and habitat quality

Assessing habitat quality by linking demographic variables to habitat use is fundamental to understanding species-habitat relationships, population persistence, and species conservation (Hall et al. 1997, Franklin et al. 2000, Johnson 2007). Solely focusing on species occurrence and abundance, however, can be a misleading measure of habitat quality because performance measures, such as survival and reproduction, may not be correlated to density (Van Horne 1983), particularly in systems that have undergone human-mediated landscape change (Bock and Jones 2004).

Habitat loss and degradation from human land use are often cited as leading causes of species population decline (Fahrig 1997, Hoekstra et al. 2005, Johnson 2007). Identifying the biotic and abiotic components of species' habitat, and which factors degrade its quality, are crucial steps for habitat conservation for species. Understanding factors that influence habitat quality is more urgent for species at risk in human-modified landscapes.

Wildlife can be exposed to multiple stressors that result from drivers such as human activities and climate change (Maxwell et al. 2013). Assessing cumulative effects, which are the collective impacts that result from environmental and anthropogenic processes over space and time (Krausman 2011), is important for evaluating cumulative risk to wildlife populations. Multiple drivers can act concurrently and their effects sum to a total combined impact (i.e., additive cumulative effects). However, individual or multiple drivers can also interact, often unpredictably, and result in a total effect greater or less than their basic sum (i.e., synergistic cumulative effects). Whenever possible, wildlife studies conducted at large spatial extents or evaluating population-level research should use a cumulative effects approach to assess drivers as single and cumulative effects.

At a minimum, a cumulative effects approach can identify and control for factors that influence species' responses and improve parameter estimation for the factors of interest. Understanding how cumulative effects can interact also provides much-needed context for species' response in their variable environment. Evaluating interactive effects is particularly important for mensurative studies conducted on wide-ranging animals because the animals are likely to encounter multiple stressors that vary in level over a large spatial extent. A cumulative effects approach can also provide insight into the relative influence of each driver. In turn, this can help managers prioritize actions for conservation and recovery of species at risk. This approach can also identify interactions that are difficult to predict when drivers are studied as single factors. This field of study is relevant and urgent because human-induced rapid environmental change (Sih et al. 2011) can result in complex cumulative effects across landscapes and on wildlife populations (Theobald et al. 1997, Hodgson and Halpern 2018).

Cumulative effects can interact, resulting in unpredictable effects on wildlife populations (Darling and Côté 2008). The case of boreal woodland caribou (*Rangifer tarandus*) is an important example for the importance of taking a cumulative effects approach, as single factor studies were insufficient in identifying the multiple interacting factors that resulted in observed population declines (reviewed by Sorensen et al. 2008, Hervieux et al. 2013). Early research on caribou populations focused on the effects of habitat loss and fragmentation (Chubbs et al. 1993, Smith et al. 2000). However, studies acknowledge the synergistic relationships among linear features, predators, and co-occurring ungulate populations that influence caribou populations more than the independent effects of habitat change (Latham et al. 2011a, Latham et al. 2011b). The decline of boreal caribou is a commonly cited example of 'death by a thousand cuts' because the synergistic cumulative effect is greater than the human footprint alone. Quantifying cumulative effects is challenging, but a cumulative effects approach can improve the prediction of ecological change and ideally improving conservation outcomes (Sutherland et al. 2006, Darling and Côté 2008).

Cumulative effects can influence wildlife populations through different components of their full annual cycle. In the grasslands, a classic example of additive cumulative effects are the impacts of oil and gas development on Greater Sage-Grouse (*Centrocercus urophasianus urophasianus*) populations (reviewed by Naugle et al. 2011). Several populations of Sage-Grouse have been studied in detail at multiple spatial scales and across large portions of their range. Oil and gas development negatively affects multiple components of the Sage-Grouse's full annual cycle, including lekking, nesting, brood-rearing, and winter habitat use. The extensive, detailed study of Sage-Grouse ecology, throughout their full annual cycle, was able to identify how the combination of additive effects has contributed to the decline of sage-grouse populations (Naugle et al. 2011). Subsequent to this, other species conservation and recovery plans have also taken a cumulative effects approach across the species' full annual cycle.

Cumulative effects can manifest at multiple spatial scales, including over large spatial extents. Of greatest concern is when cumulative effects occur over a large spatial extent, as incremental effects spread over a large spatial area can collectively affect many individuals in a population or even multiple populations (Coates et al. 2014b, Gibson et al. 2018). Assessment of a driver or stressors' cumulative effects should quantify impacts to the affected population to predict overall population change. Some types of human development can occur over large spatial extents and, if associated with a negative impact to wildlife, result in a large zone of influence despite a relatively small human footprint. For example, transmission lines are positively associated with Common Raven (*Corvus corax*) occurrence (Kristan and Boarman 2007, Coates et al. 2014a, Coates et al. 2014b, Howe et al. 2014) and this association has negative impacts to Sage-Grouse (Gibson et al. 2018) and desert tortoises (*Gopherus agassizii*) (Boarman 2003). A transmission line can stretch for hundreds of kilometres and result in a large cumulative effect because its zone of influence can impact wildlife occurring along its entire length. Similarly, natural gas development in Wyoming has a potentially large cumulative effect on pronghorn (*Antilocapra americana*) because pronghorn avoid the associated footprint (Beckmann et al. 2012). As a result, large gas fields are a significant loss of habitat for a large number of pronghorn even though the individual wells and associated footprint are quite small. When possible, a cumulative effects approach should consider the spatial extent that is impacted because even a small effect over a large area can result in a large overall impact to wildlife populations.

Cumulative effects should be evaluated at multiple spatial and temporal scales. Short- and long-term implications may differ at the individual and population level. Climate change can potentially impact wildlife over relatively short time-periods at local regional scales because weather patterns occur at those scales (Fisher et al. 2015, Shank and Bayne 2015). Climate change can also affect species over long time-periods and large spatial extents. For example, species distributions of white-tailed deer (*Odocoileus virginianus*) (Dawe et al. 2014, Dawe and Boutin 2016) and wolverine (*Gulo gulo*) (Heim et al. 2017) are also influenced by long-term climate change. Long-distance migrants have been affected by climate change, where changing phenology has impacted the timing of food availability, and hence reproduction and survival (Both et al. 2009b, Aubry et al. 2013), or changing climate can affect habitat suitability (Culp et al. 2017). Thus, evaluating cumulative effects over large spatial extents and long-terms is critical to assessing their potential overall impact, especially in regions strongly influenced by climate change.

Species at risk can face multiple threats, and their level of endangered may be worse where the number of threats is associated is higher (Venter et al. 2006). Understanding how the influence of each threat, their cumulative risk, and their relative influence on a species over space and time is critical to developing conservation and recovery plans. Forecasting the impacts of cumulative effects is also important because drivers and stressors, such as land use or climate, are expected to change. Predictions of the impact of cumulative effects should be incorporated into threat assessments for species at risk. This poses a challenge because many studies are not designed with a cumulative effects approach in mind.

Landscape change

Human land use has caused considerable land cover change in most ecosystems (Fahrig 2003, Hoekstra et al. 2005, Haddad et al. 2015). Modern landscapes often have multiple land uses, creating the potential for additive or synergistic cumulative effects. Cultivation of native ecosystems to cropland is one of the greatest threats to wildlife populations (Johnson 2007, Pereira et al. 2010, Shackelford et al. 2017). In the Canadian prairies, grassland loss and degradation due primarily to agriculture are thought to be responsible for the decline of many species (Venter et al. 2006), including grassland birds (Herkert 1994, Peterjohn and Sauer 1999b, Murphy 2003, Bock and Jones 2004, Brennan and Kuvlesky 2005, Koper et al. 2009). Furthermore, there is increasing evidence that energy development infrastructure (e.g., oil and gas wells, compressor stations, road networks, and power lines) and sensory disturbance (e.g., industrial noise, traffic) degrades habitat and can negatively affect some wildlife populations (Sawyer et al. 2009, but see Gaudet 2013, Ludlow 2013, Rodgers 2013, Kalyn Bogard and Davis 2014, Wallace 2014).

Potential cumulative effects and their mechanisms are of concern to grassland species at risk because while grassland to cropland conversion has stabilized, energy sector development is projected to expand and intensify in Western Canada (Boyce 2011). The energy development footprint is often higher in native prairie compared to cropland due to development costs. This bias towards development in native prairie can potentially compromise the remaining prairie's quality for species that are associated with native prairie and sensitive to human disturbance (Schmutz et al. 1980a, Ng et al. 2017). Furthermore, whether land cover change and industrial development are additive in their effects on wildlife, or create novel synergistic interactions is poorly understood for most species (reviewed by Northrup and Wittemyer 2012).

Climate change

Climate change has become a dominant theme in conservation biology because it can result in ecological change across systems (Walther et al. 2002) and has been documented to be a more influential driver than habitat loss in several systems (Dawe et al. 2014, Clarke Murray et al. 2015, Dawe and Boutin 2016, Sultaire et al. 2016, Heim et al. 2017). As climate change continues in the Canadian Prairies, we expect average temperatures by 2080 to increase in winter by 3.4˚C to 4.7˚C, in spring by 2.5˚C and 3.2 ˚C, and in summer by 2.9 ˚C to 4.4 ˚C (Representative Concentration Pathway, hereafter RCP, 4.5 and RCP 8.5, respectively) (McKenney et al. 2011). Summers are predicted to become drier (Sauchyn and Kulshreshtha 2008) and storms more frequent and severe (Kharin and Zwiers 2000, 2005). These small incremental changes have potential to create large cumulative effects because the changes are long term, occur over large spatial extents, and can affect wildlife populations through multiple mechanisms (Traill et al. 2010).

Climate change has already impacted many wildlife populations (Lovejoy 2006, Staudinger et al. 2013, Iknayan and Beissinger 2018). A number of studies have documented negative impacts such as phenological mismatches (Lane et al. 2012, Aubry et al. 2013, Marrot et al. 2018), habitat loss due to shifting temperature and precipitation patterns (Morrison and Hik 2007, Jeffress et al. 2013), and shifts in predator-prey dynamics (Montevecchi and Myers 1997, Gilg et al. 2009). Some species or populations may also adapt to some effects of climate change (Heath et al. 2012, Smith et al. 2017). Changes to temperature and precipitation may alter landscape characteristics and change the suitability for a species, potentially impacting fitness or species distribution (Heim et al. 2017). Species response to climate change is highly uncertain, but predicting how climate change acts as a driver of wildlife populations is essential to wildlife management and climate change adaption plans (Mawdsley et al. 2009). This is particularly true for species at risk that may be more vulnerable to climate change.

Study species

The Ferruginous Hawk (*Buteo regalis*) is North America's largest *Buteo* species (detailed description in Ng et al. 2017). The species' distribution covers the grasslands and deserts in Canada, the United States, and Mexico. In Canada, Ferruginous Hawks breed in southern Alberta, Saskatchewan, and Manitoba, and then spend non-breeding months in the United States and northern Mexico (Watson et al. 2018a). Ferruginous Hawks rarely build their nest structures from scratch, but are more commonly secondary nest builders. They nest in trees, on the ground, on cliff sides and rock outcroppings (e.g., hoodoos and buttes), and are also known to nest on human structures such as artificial nest platforms and industrial infrastructure, such as holding tanks and sheds. Ferruginous Hawks are associated with open habitats such as grassland, shrubsteppe, badlands, farmlands, parkland, and the periphery of forests.

Previous habitat studies have found that Ferruginous Hawks breeding habitat is associated with a mix of grassland and cropland [Canada (Schmutz 1989), Oklahoma (Wiggins et al. 2014), North and South Dakota (Datta 2016)]. In Utah, nest sites and breeding home ranges were more likely to be associated with edge habitats (Antonova 2000), but nests were farther from landscapes with more edge and heterogeneity in Idaho (Coates et al. 2014b) and Utah (Antonova 2010). In Canada, Ferruginous Hawks were more likely to be near areas with higher abundance of Richardson's Ground Squirrels (*Urocitellus richardsonii*) (Schmutz and Hungle 1989b). In the United States and Mexico, Ferruginous Hawks are commonly associated with Black-tailed Prairie Dog (*Cynomys ludovicianus*) (Oklahoma (Tyler 2015), Texas (Ray et al. 2015), New Mexico (Merriman et al. 2007, Goguen 2012)) and Gunnison's Prairie Dog (*Cynomys gunnisoni*) colonies in Utah (Cook et al. 2003, Keough and Conover 2012). Not surprisingly, studies have also shown that Ferruginous Hawk reproductive performance is associated with prey abundance (Woffinden and Murphy 1977, Smith et al. 1981, Schmutz and

Hungle 1989b). These studies demonstrate the close relationship between habitat selection, prey, and hawk population dynamics.

Early behavioural studies suggested that Ferruginous Hawks are sensitive to human disturbance. Experiments involved observers approaching nests by foot or vehicle, while operating a 3.5 horsepower engine or while firing a 0.22 calibre rifle every 20 m while approaching the nest until the adult flushed (White and Thurow 1985). Nests were also exposed to chronic noise by mechanical noisemakers (White and Thurow 1985). These treatments resulted in early flight initiation distances and even nest abandonment, which supported the hypothesis that Ferruginous Hawks are highly sensitive to human disturbance (White and Thurow 1985). This study resulted in a broadly adopted hypothesis that Ferruginous Hawks are highly sensitive to human disturbance.

Oil and gas development is a dominant land use throughout portions of the Ferruginous Hawk's range. This land use could have negative impacts to nesting Ferruginous Hawks if they are sensitive to human disturbance. Subsequent studies evaluated habitat use and reproductive performance relative to human infrastructure and activity, founded on the hypothesis that Ferruginous Hawks are sensitive to human disturbance and would avoid nesting near human development. In Idaho, Ferruginous Hawks were more likely to nest farther away from roads and facilities (Coates et al. 2014b). In Wyoming, home range occupancy and re-occupancy was positively correlated with density of unimproved roads, but was not associated with oil and gas development (Wallace 2014). Re-occupancy in Wyoming was also weakly negatively associated with oil and gas road density near nest sites (Wallace 2014, Wallace et al. 2016a), and nest sites were less likely to be near oil and gas development (Fuller 2010). In North and South Dakota, nest sites were more likely to be far from ground-based disturbance (Datta 2016) and nests in

North Dakota were less likely to be reoccupied if the nest was located in areas with high density oil and gas development (Wiggins et al. 2017). Conversely, Ferruginous Hawks were more likely to select home ranges with a higher number of active wells in Utah (Keough 2006, Keough and Conover 2012, Keough et al. 2015). Ferruginous Hawk reproduction in Wyoming or Utah was not associated with the amount of oil and gas development around the nest (Keough et al. 2015, Wallace et al. 2016b). Recently, a study evaluated hawk behavioural responses with respect to landscape features and human disturbances and found that response behaviour is dependent on type of stimuli, prior experience, and the anthropogenic landscape around the nest (Nordell 2016, Nordell et al. 2017). Patterns have ranged from slightly negative to slightly positive associations with human development, such as roads and oil and gas infrastructure.

More detailed understanding of the mechanisms behind patterns of habitat associations would be useful in predicting habitat use. Also needed is a stratified study across a large spatial extent that can evaluate the influence of high and low densities of oil and gas development across a gradient of land cover types. Such an approach would help clarify how different human footprint types, such as land cover and industrial development, influence Ferruginous Hawk habitat use and reproduction. Evaluating how different densities of oil and gas development influence hawks would also identify any potential thresholds where impacts change from neutral to either positive or negative. These data would be important for informing how to potentially manage multiple land uses without negatively impacting hawks.

Ferruginous Hawks have been listed as a threatened species in Canada since 2010 (SAR Public Registry 2010) and an endangered species in Alberta since 2006 (Alberta Environment and Parks 2009). The population has decreased by approximately 50% since the mid-1990s and there is currently an estimated 1,200 pairs in Canada. Data from trend block surveys conducted by Alberta Environment and Parks (AEP) suggest that Ferruginous Hawk populations have stabilized in the last decade at approximately 865 (95% CI = 201) nests in Alberta, with a weak positive trend (Redman 2016). Breeding Bird Survey data estimates that Ferruginous Hawks are generally stable or slightly increasing, from 1966 to 2013 (range 0.29 to 1.82% by Bird Conservation Region) (Sauer et al. 2014). However, populations are declining in the Central Mixed Grass Prairie during this time period (-0.58%) and the greatest decline occurring between 2003 and 2013 (-1.09%) (Sauer et al. 2014). Potential threats to Ferruginous Hawks include habitat loss, climate change, poisoning and persecution, electrocution, wind energy conflict, vehicle mortality, decreased prey availability, and decreasing nest site availability (reviewed by Ng et al. 2017). The cumulative effects of multiple stressors on the Ferruginous Hawk population are generally unknown.

Few studies have evaluated cumulative effects of human development and climate change on Ferruginous Hawk ecology. Drawing conclusions on how these drivers act concurrently to influence hawks is difficult because previous studies have been limited in sample size or were conducted in study areas with regional spatial extent. Previous studies in Canada were generally focused on understanding the influence of land cover and did not study the effects of industrial development. In the United States, studies evaluating the effect of oil and gas development on Ferruginous Hawks were primarily conducted on public lands, where natural cover, such as grass and shrub steppe, is the dominant land cover. The influence of weather and climate change are also challenging to study when studies have small sample sizes or when nests are localized in a small study area because nests are exposed to the same weather effects. Studying a species that is relatively uncommon, wide-ranging, and found in a range of landscapes requires data collection over a large spatial extent, multiple years of data, and a large sample of nests distributed over a geographically stratified across varying land cover compositions and densities of industrial development. A specific cumulative effects approach is required to identify how land use and climate change influences Ferruginous Hawk habitat use and reproduction.

Study area

The study area encompasses most of the breeding range of Ferruginous Hawks in Canada, which is also the northern range of the species distribution (Ng et al. 2017). It is approximately 153,000 km^2 and is located from 49.0˚N to 51.8˚N latitude and -113.2˚W to -102.8˚W longitude. Average winter temperature is -7.0˚C (December to February), followed by an average spring temperature of 6.5˚C (March to May), and an average summer temperature of 18.7˚C (June to August) (Medicine Hat, Alberta, Environment Canada and Climate Change). Average winter precipitation is 32 mm and increases to 82.7 mm in spring and 135.9 mm during the summer (Medicine Hat, Alberta, Environment Canada and Climate Change). The study area encompasses several ecoregions, including fescue, mixed-moist grassland, and shortgrass ecoregions. The land cover is predominantly cropland and grassland. Grassland communities are characterized by species including blue gramma grass (*Bouteloua gracilis*), needle and thread grass (*Stipa comata*), and wheat grasses (*Elymus* spp.). The majority of grassland cover is grazed by cattle. Common crops include canola (*Brassica* spp.), cereals such as wheat and barley, clover (*Trifolium* spp. and *Meliliotus* spp.), and pulse crops (e.g., *Pisum* spp., *Lens* spp., dry beans). Oil and gas deposits are localized and density of petroleum development ranges from zero to 541 wells per township. Wind power generation is an emerging land use, with approximately 1704

MW produced in southern Alberta and Saskatchewan (Canadian Wind Energy Association 2018). The majority of the study area is low and flat, interspersed with regions of undulating uplands, river valleys, badlands, and coulees. Chernozem and solonetzic soils are the dominant soil orders throughout the study area (Soil Landscapes of Canada Working Group 2010).

The majority of historical grassland cover in southern Alberta and Saskatchewan has been cultivated for farming and approximately 37% and 20% remain, respectively (Hammermeister et al. 2001, The Alberta Biodiversity Monitoring Institute 2015). The greater part of grassland conversion to cropland was completed prior to 2000, however, conversion is ongoing and approximately 4.7 million hectares have been converted to cropland in the Northern Great Plains (including both Canada and United States) since 2009 (World Wildlife Fund 2017). An estimated annual loss rate of 0.75% occurred in 2015 and decreased slightly to 0.55% in 2016, converting approximately 283,000 hectares of grassland to crop. Primary crops grown in 2016 on converted grassland include wheat, corn, soy, and lentils. Grassland restoration is rare in southern Alberta and Saskatchewan and conservation efforts rely mostly on habitat stewardship.

Thesis overview

Multiple land uses and climate change could alter landscape characteristics and, consequently, Ferruginous Hawk habitat use and reproduction. My overall objective is to evaluate how the cumulative effects of landscape and climate change influence Ferruginous Hawk habitat use, reproduction, and overall population demography. I use a cumulative effects approach to study hawk ecology over a large spatial extent to assess how multiple stressors can affect habitat quality and how a cumulative effects approach can help managers prioritize how to positively influence breeding population conservation and recovery. Therefore, understanding how these drivers influence this species at risk is relevant and timely. My study was conducted in southern Alberta and Saskatchewan where there is an extensive human footprint from multiple land uses, such as cultivation and oil and gas development, and where climate change is expected to alter weather patterns. In Chapter 2, I evaluated how environmental and anthropogenic variables influence home range habitat selection. I then applied the resulting habitat model to identify potential overlap and conflict with wind energy development. In Chapter 3, I assessed the potential cumulative effects of land cover characteristics and oil and gas development on Ferruginous Hawk habitat quality. I developed a relative nest abundance model and several reproduction models, which I used to identify potential habitat mismatches by overlaying and comparing spatially-explicit nest abundance and reproductive performance maps. In Chapter 4, I evaluated how the potential cumulative effects of land cover and industrial development could influence prey delivery rates and prey diversity at Ferruginous Hawk nests. I assessed whether hawks nesting in different landscapes were able to provide similar amounts of food to nests. In Chapter 5, I evaluated the relative influence of land cover and climate change on Ferruginous Hawk population demography. I also evaluated how different land cover and climate change scenarios could impact future Ferruginous Hawk population conservation and recovery. In chapter 6, I summarize and synthesize the results from the preceding chapters, discuss conservation and recovery implications, and provide suggestions for future research.

Chapter 2: Predicting home range habitat selection by Ferruginous Hawks to identify potential wind energy conflict risk in Canada

Abstract

Global wind energy development has increased exponentially in recent decades and is expected to double in capacity in Canada by 2040. Wind farm development has significant implications for wildlife, particularly for raptors where mortality from turbine strikes and other cumulative effects are well documented. Minimizing conflict is particularly important for species at risk, such as the Ferruginous Hawk (*Buteo regalis*), because negative impacts from wind farms may hinder conservation and recovery actions. Understanding Ferruginous Hawk habitat selection is needed to assess the potential spatial overlap with wind farm development and make spatially-explicit predictions of conflict risk. Our objectives were to 1) develop a predictive map of habitat selection by Ferruginous Hawks at the home range scale and 2) identify areas of high and low potential conflict with current and future wind energy developments, by overlaying predictive habitat maps with wind potential within the Canadian Ferruginous Hawk range. We showed that landscape composition and configuration, industrial development, soil characteristics, and seasonal climate influenced Ferruginous Hawk home range habitat selection. Our risk analyses identified areas at medium to very high risk of conflict with wind energy, but also large areas with low development potential and high conservation value that would be valuable for species conservation and management. Our habitat model and risk assessment do not replace ground assessments, but they can be used during the pre-development phase to proactively site new wind farms away from potential risk for Ferruginous Hawks. We demonstrate the wind energy development can be prioritized alongside with wildlife conservation.

Keywords

species distribution model, resource selection function, conservation offset, on-shore wind energy, renewable energy, *Buteo regalis*.

Introduction

World-wide, electricity consumption is expected to grow another 0.9% annually through 2050 (US Energy Information Administration 2018). In an attempt to reduce carbon emissions, there is a growing move towards the use of renewable energy to create electricity. Wind energy, in particular, has grown exponentially in response to this demand. In Canada, wind energy production has increased 18% per year between 2012 and 2016 and capacity is expected to double by 2040 (Board 2016, Canadian Wind Energy Association 2016). This degree of wind energy development could have significant implications for wildlife (Fargione et al. 2012, Tack and Fedy 2015).

Impacts of wind energy on wildlife include both direct and indirect impacts. Increased mortality from turbine strikes (Pagel et al. 2013) or barotrauma (Baerwald et al. 2008), habitat loss and fragmentation, reduced reproductive success, behavioural avoidance, and acoustic masking are known issues associated with wind farms (reviewed by Drewitt and Langston 2006, Northrup and Wittemyer 2012, Zimmerling et al. 2013, Mahoney and Chalfoun 2016).

Cumulative effects can also arise from wind farms (reviewed by Zimmerling et al. 2013, Smith and Dwyer 2016) because infrastructure associated with wind energy, such as roads and wind turbines, can decrease the amount of available habitat and also fragment the landscapes (Northrup and Wittemyer 2012). Higher vehicle volume associated with a higher density of roads can increase mortality risk by vehicle collisions (Litvaitis and Tash 2008). Collision or electrocution risk can also increase with higher densities and proximity to power lines (Sergio et al. 2004, Shaw et al. 2018) that are built to support wind farms. Even the construction of wind farms can negatively impact wildlife, with potentially greater impact than the subsequent operation of the wind farm (Pearce-Higgins et al. 2012). These long term and large-scale cumulative effects can be additive and negatively affect habitat use, survival, and reproduction of wildlife. Therefore, pre-construction assessments for new wind farms should consider more than just the footprint of the wind farm and turbines, but also consider the broader spatial and temporal scales of cumulative effects on wildlife (Marques et al. 2014, Watson et al. 2018c).

Mitigation at wind farms is often used to reduce impacts post-construction, with varying degrees of success. Selective stopping programs can be effective mitigation, as evidenced in Spain where turbines were stopped when Griffon Vultures (*Gyps fulvus*) were observed near them. This simple technique reduced mortality by 50% and had minimal impact to energy production (de Lucas et al. 2012). Bat mortality was also reduced when the wind turbine cut-in speed was raised, which reduced turbine operation during periods of low wind speed and higher bat activity (Arnett et al. 2011). Mitigation should be used after wildlife-conflict occurs (Carrete et al. 2009, Baisner et al. 2010, Pagel et al. 2013), but a more prudent approach is better siting of wind farms so that potential negative impacts are minimized overall (Zimmerling et al. 2013, Balotari-Chiebao et al. 2016, Smith and Dwyer 2016, Zwart et al. 2016).

Predicting high-conflict areas prior to development is particularly important where wind energy will conflict with species at risk, such as Egyptian Vultures (*Neophron percnopterus)* (Carrete et al. 2009) or Griffon Vultures (De Lucas et al. 2008, Carrete et al. 2012). Mortality of raptors from turbine strikes, particularly large-bodied soaring birds, are well documented (Barrios and Rodríguez 2004, Hoover et al. 2005, Nygård et al. 2010, Carrete et al. 2012). Ferruginous Hawks have been observed using habitat within <50 m of wind turbines at relatively high rates compared to other birds (Smallwood et al. 2009) and Ferruginous Hawk mortality from turbine strikes have been documented in the U.S. and Canada (Watson et al. 2018b, B. Downey, Alberta Environment and Parks, pers. comm.). Furthermore, Kolar (2013) found that Ferruginous Hawk daily nest success was lower in areas with more wind turbines per home range, suggesting an additive effect of with the increasing number of turbines within a home range. Post-fledging daily survival rate increased farther away from turbines (Kolar 2013, Kolar and Bechard 2016). Reoccupancy rates of Ferruginous Hawk home ranges also decreased 50% in <5 years following wind farm construction in Washington (J. Watson, Washington Department of Fish and Wildlife, pers. comm.). Thus, siting wind energy development away from habitat with high suitability for nesting hawks can reduce risk to breeding pairs and fledglings by reducing spatial overlap of home ranges and wind turbines (Watson et al. 2018c).

Mapping Ferruginous Hawk habitat selection is required to predict spatially-explicit conflict risk. Species distribution models (SDMs) can help understand species-habitat relationships and predict distribution changes if landscape changes (Engler et al. 2017). Habitat models can also be used to develop predictive habitat selection maps. Ferruginous Hawks nest in a variety of landscapes, including landscapes with little human disturbance and landscapes with considerable land cover change and industrial development (reviewed by Ng et al. 2017). A previous study found that Ferruginous Hawk nest density is highest in landscapes with a mix of cropland and grassland (Schmutz 1989); however, they are still broadly associated with large tracts of grassland. Furthermore, Ferruginous Hawks are considered sensitive to human disturbance (White and Thurow 1985, Keeley and Bechard 2011), yet are observed nesting in landscapes with industrial development. Quantifying patterns of habitat selection is important to understanding how land use influences Ferruginous Hawks. Evaluating the influences of land cover composition and configuration, industrial development, soil characteristics, and climate on home range selection is the first step to making a predictive habitat model for Ferruginous Hawks in Canada. Developing such a habitat model identifies areas of low to high habitat selection and can be used to inform species conservation and management. In our example, these spatially-explicit models can also be used to inform land use planning, such as future wind farm development.

Our objectives were to 1) develop a predictive map of nesting habitat selection by Ferruginous Hawks at the home range scale over the extent of their breeding range in Canada and 2) identify areas of high and low potential conflict with current and future wind energy developments, by overlaying predictive habitat maps with wind potential within the Canadian Ferruginous Hawk range. Identifying areas of potential conflict between wind energy development and Ferruginous Hawk nesting habitat can inform macro-siting of wind farms and associated infrastructure, allowing the avoidance of high risk such as landscapes with high hawk density, regular flight paths such as within home ranges, and habitat from which young Ferruginous Hawks will fledge and disperse. Overlaying wind-potential scenarios, modelling turbines that are varying in height, will also illustrate the geographic change in potential risk as turbine height increases. Reducing potential risk is particularly important for Ferruginous Hawks because their population in Canada has declined by 50% in recent decades and they are listed as Threatened in Canada (SAR Public Registry 2010) and endangered in Alberta (Alberta Environment and Parks 2009). Ferruginous Hawks have also been identified as a high risk of experiencing population declines from wind energy (Beston et al. 2016); therefore this study is timely and relevant as wind energy development grows in Canada.

Study area

Our study area included the fescue, moist-mixed, and mixed-grass ecoregions of southern Alberta and Saskatchewan, ranging from the US-Canada border to 52˚50'N latitude, between longitudes of 114˚0'W and 103˚0'W. The climate was semi-arid, where temperatures averaged 14.6°C (April-September) and annual precipitation was on average 333 mm (Medicine Hat, Alberta, Environment Canada and Climate Change). Dominant land-covers reflect major land uses, which was farming and ranching. Farmland was predominately cropland and dominant crops including wheat, canola, peas, and lentils. Irrigation was common in parts of the study area, but the majority of cropland was not irrigated. Native grassland was generally used for grazing cattle and was dominated by blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*), wheat grass species (*Agropyron* spp.), and rough fescue. Petroleum development was found throughout the study area, ranging from 0 to >20 wells per section (256 ha). The study area was on the northern periphery of the Ferruginous Hawk range. Ferruginous Hawks arrived in mid-March and remained until fall migration in September/October (Ng et al. 2017).

Methods

Species Location Data

Nest location data was provided by researchers and biologists who submitted nests records to provincial (Alberta Fish and Wildlife Information Management System and Saskatchewan Conservation Data Centre) and federal (Environment and Climate Change Canada Wildspace) databases. Data were also collected by naturalists, such as hobby banders, who are required to meet a standard skill level for bird identification before being granted a banding permit. Only nests that were confirmed by observations of territorial adults, eggs, nestlings, or incubating females were included. We constrained nest data to between 2005 and 2010.

The majority of nests were recorded with a hand-held Global Positioning System (GPS) (accuracy to ± 10 m), but a minority of nests were reported with <400 m accuracy because the observer lacked landowner permission to approach the nest. A subset of nests were difficult to distinguish as unique or duplicate nests because they were reported in multiple instances, either by different agencies, at varying spatial precisions, or over several years because nests are often used multiple years. We resolved the varying spatial precision and eliminated possible duplicates by generalizing nest locations to the quarter-section (64 ha) in which they were observed and we represented each of these 'used' points by their quarter-section centroid. In addition, random quarter-sections were selected across the study area to provide a set of points to describe the available landscape.

Predictor variables

We categorized 57 predictor variables into five variable classes: geography, land cover, human development, soil, and climate (Table 13). Grouping similar variables allowed us to simplify a large number of predictor variables within broad variable classes and then evaluate their overall influence on Ferruginous Hawk home range selection. Furthermore, variable classes such as land cover and human development can be manipulated by land managers, regulatory agencies, and industry advisors and, therefore, may be important for developing management strategies for conservation and recovery. Geography, soil, and climate cannot be manipulated, but could be important factors for predicting habitat suitability and thereby useful for pre-development planning.

We used ArcGIS 10.1 (ESRI 2012) to measure predictor variables around used and random available points. Each variable was quantified at a 30-m resolution (Table 16). Variables were summarized around a centroid in each quarter-section out to a 2500 m buffer. We used a 2500 m buffer to approximate the 50% core area of a Ferruginous Hawk home range (J. L. Watson, unpublished data).We characterized available landscapes by generating 4000 random points and quantifying landscapes with a similar 2500-m buffer.

Geographic variables include elevation, standard deviation of elevation (to characterize heterogeneous terrain), latitude, and longitude. Latitude and longitude are included as a surrogate for unknown spatial gradients in environmental conditions that may exist.

Land cover variables include proportion of grassland (hereafter, grass), distance to nearest grass, and total edge. Total edge was calculated as the sum length along interfaces between grass and cropland. Variables related to composition of cropland (hereafter, crop) within the 2500 m radius buffer were not included because crop is highly inversely correlated with grass in southern Alberta.

Human development variables described oil and gas infrastructure and linear features. We quantified infrastructure that existed in 2010 and assumed that while development is ongoing, density of human development features are spatially auto-correlated within 2500 m radius buffers. Oil and gas infrastructure were grouped into surface wells (i.e., both oil and gas wells) and facilities, but were also considered separately as oil wells, gas wells, and noise-producing facilities. Linear features include roads, pipelines, and transmission lines. Distance to nearest feature was measured for all infrastructure types. Point features such as oil and gas wells were counted within each buffer distance and total line length within each buffer was summed for linear features.

Soil Landscapes of Canada v.3.2 was used to characterize soil around each nest location(Soil Landscapes of Canada Working Group 2010). Soil was characterized by regional texture, and proportions of parent materials and soil orders.

Climate variables included both spring (March through May) and summer (June through August) seasons. Climate normals were based on data from 1960 to 2000, and average precipitation and minimum, maximum, and average temperatures were extracted for each used and available point (Wang et al. 2011). Climate normals were used because our objective was to evaluate regional climate patterns associated with home range habitat selection, rather than short-term weather-related patterns related to, for example, annual reproductive performance.

Model development

We used STATA 11.0 (Statacorp 2009) for all statistical analyses. We followed a standard data exploration protocol to evaluate data for outliers, collinearity, and heterogeneity of variance (Zuur et al. 2010). Akaike Information Criterion (AIC) values (Burnham and Anderson 2002) were calculated for highly-correlated variables and the variable with the least explanatory power from these correlated pairs was removed from the variable class. We also used AIC values to evaluate whether linear or quadratic forms for each variable performed best, and then included the form with the lowest AIC value. Evaluating different forms of variables was an important component of our analyses because previous studies of Ferruginous Hawk habitat selection found conflicting results. The variable with the lowest AIC value, hence higher explanatory power, was included in subsequent models.

We used logistic regression to create a 2^{nd} order used versus available resource selection function (RSF) to develop a Ferruginous Hawk home range habitat selection model for each of the five model sets (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006) (Table 15, Equation 1). A hierarchical information theoretic approach was used to develop the best model from simplified variable classes. Global models for each variable class were simplified using a backwards stepwise elimination process, where terms were removed from the most complex model within that set (P>0.10) (Arnold 2010) if the resulting model AIC also decreased. Retained variables within model sets included only those terms that were significant at P<0.1. The combined variable classes forming the "all-inclusive" model were created by using all retained terms within the five model sets. Model performance was evaluated using receiver operating curves (ROC) (Hosmer et al. 2013) and AIC values. A predictive map was generated for the study area using the resulting RSF equation.

Model validation

We used an independent sample of Ferruginous Hawk nest locations, collected by our own field crews, to evaluate the predictive capability of our home range habitat selection model. Nest surveys were conducted in 2012 and 2013, and 119 active hawk nests were found across Alberta and Saskatchewan. Surveys were conducted using stratified random sampling, where surveys were geographically spread throughout the study area and distributed along a low to high grassland-cropland gradient and industrial development gradient.

We evaluated the area-adjusted probability of use relative to predicted selection by ranking RSF values into five equal-interval bins and then comparing the frequency of test data relative to the expected frequency. We used linear regression statistics (Johnson et al. 2006) to evaluate the fit of the model, where a high R^2, a slope not different from 1.0, and an intercept not different from zero was deemed a good model. We also evaluated the correlation between the proportion of expected and observed nests in each bin rank using Spearman's rank correlation.

Identifying risk of Ferruginous Hawk – wind conflict

To identify areas of conflict between predicted Ferruginous Hawks breeding habitat and wind turbines, we first determined the potential for future wind farm development across the study area. Spatial data for wind potential were obtained from the Canadian Wind Energy Atlas (www.windatlas.ca). Estimated mean wind power was generated from a model using over 43 years of averaged spatial wind data. The spatial resolution for the modeled data is 4.8 km by 4.8 km pixels. We classified mean wind power in each pixel into Wind Power Classes (WPC). This is the industry standard used to classify mean wind speed into seven categories, where wind speed averages 0 to >31.7 km/h (Elliott et al. 1987). Our estimates for wind potential are modeled for turbines 50 metres and 80 metres above the ground. The heights of new commercial turbines commonly range from 80 metres to 125 metres, where the most common turbine height is ~80 metres (Wiser and Bolinger 2017). Turbines in the near future may to be taller (e.g., 140 m hub height (Jose et al. 2015, Wiser et al. 2016); therefore, we likely underestimate future wind potential because wind speed increases with height above the ground. However, we argue our conservative estimates will identify which current areas of potential commercially viable wind energy development are associated with the highest likelihood of affecting Ferruginous Hawks. Furthermore, we thought it valuable to include a model for turbines at 50 metres to 1) compare how conflict risk and mapping can change with turbine height and 2) anticipate the possibility of wind farms with turbines at 50 metres. The recommended guideline for commercially viable developments is wind speeds over 6.5 m/s, which applies to both 50 m and 80 m turbine heights (Elliott et al. 1987).

Several wind farms in Alberta and Saskatchewan are located in areas classified as WPC 2, which is lower than the recommended guideline of WPC 3 for commercial development. However, wind potential is only one factor considered when siting a wind farm, and proximity to existing transmission lines is another high-priority factor. We accounted for the increase of commercial development potential near transmission lines by weighting WPC in areas that were within 25 km of a transmission line. Our additive model is termed Wind Development Potential (WDP) where WPC + 1 = WDP, where development potential is binned similarly to wind speed, except with an added component to weight areas in close proximity to transmission lines and, therefore, more easily connected to the power grid.

We included in the low WDP category areas that had low potential for wind energy development for other reasons, such as being in military bases, forested land, areas within 5 km of cities, or protected areas such as parks and National Wildlife Areas. In addition, we categorized areas designated as wind avoidance areas (Saskatchewan Ministry of Environment 2016) as having low wind development potential. This will allow these protected landscapes to be included in our analyses as low wind potential and to be assessed for suitability for Ferruginous Hawk habitat, allowing us to evaluate if the landscapes can be considered high conservation value for hawks.

We classified RSF values into five equal-interval bins, and overlaid the RSF map onto the 50-m and 80-m WDP maps to spatially identify areas with high wind-high hawk potential (high conflict risk), high wind–low hawk suitability (low environmental liability risk), and low wind-high hawk suitability (high conservation potential) (Table 1, Table 2)

Results

Habitat Selection

We collapsed historical nest data, from 2005 to 2010, to 2147 used quarter-sections, and characterized 'available' units by randomly selecting 11,841 quarter-sections. The top model evaluated for the geography variable set included the quadratic forms of latitude and longitude, predicting the approximate centre of the study area to have the highest probability of selection by hawks. Hawks selected landscapes with moderate amounts of grassland (Figure 1) and with lower densities of grassland-cropland edge (Figure 2). Home ranges were also more likely to be selected near water, fitting a natural log form (Figure 3). Hawks selected areas that were consistently warmer in the spring and summer. Hawks are more likely to select home ranges in areas where soil orders are composed of decreased proportions of vertisolic, chernozemic, regosolic, and luvisolic soil. Deposition modes were likely to be morainal till, undifferentiated mineral, undifferentiated bedrock, residual material, and eolian, glaciolacustrine, glaciofluvial, fluvioeolian soils. Selected home ranges were also characterized by soils composed of less silt and sand. Home ranges were more likely to be in landscapes with higher densities of resource roads and closer to active oil wells (Figure 4).

The all-inclusive model developed from the top models for each variable class was reduced further after variables with p-value >0.10 were removed, resulting in a model weight of 0.99 (Table 3, Table 4).

We used the logistic form to develop a resource selection map (Figure 5) using beta coefficients from each variable in the global all-inclusive model (Equation 1).

The all-inclusive model ROC was 0.81, suggesting the model is able to moderately predict relative probability of habitat selection. Model validation performed adequately, as the adjusted R^2 (0.64) is moderately high, the slope is not significantly different from 1.0 (slope was 0.70, p-value = 0.53), and the intercept (2.2) is near zero, suggesting the model was a good predictor of the independent sample of nest locations. The Spearman's rank correlation was rho = 0.76 (p-value = 0.01). The top two of five RSF variable bins accounted for 99.5% of the 2,147 locations used to build the RSF model and 90.0% of the 119 nest locations used to test the home range habitat selection model.

Risk of Ferruginous Hawk – wind conflict

Commercial development of wind power is currently high enough to be viable within much of the Ferruginous Hawk range in Alberta and Saskatchewan, leading to potential risk of direct collisions or indirect effects (Figure 6, Table 14).

Land with risk (i.e., medium, high, and very high risk) covers 61% and 67% of the range for 50-m and 80-m turbine hub height, respectively. The amount of very high conflict risk covers 2% of the Ferruginous Hawk range if wind farms were restricted to 50-m turbine hub height and 8% with 80-m turbine hub height. Land with high conservation value, where wind development potential is low and relative probability of selection by hawks is high, covers 36% and 29% of the range, for the respective turbine hub heights of 50 m and 80 m.

Discussion

Patterns of selection

We developed a predictive home range habitat selection model for Ferruginous Hawks in Canada. Our study found that Ferruginous Hawks were more likely to select home ranges characterized by heterogeneous landscapes. Ferruginous Hawks were more likely to select home ranges with land cover composed of approximately half cropland and half grassland, which is similar to previous studies (Wakeley 1978, Schmutz 1989, McConnell et al. 2008, Wiggins et al. 2014). We found that hawks select for home ranges with low to medium edge density, where relative probability of selection decreases if edge density surpasses 80 km in the surrounding 2500 m radius. Selection for mosaic landscapes with some edge may be related to foraging opportunities as foraging studies have shown that the hawks hunt in grazed grassland (Wakeley 1978), fragmented landscapes (Plumpton and Andersen 1998), and irrigated croplands (Leary et al. 1998). Grassland vegetation may provide foraging opportunities at different times than crops, as certain species of open-country raptors are more likely to hunt in bare to short vegetation, where prey is likely more accessible for capture, than in tall, dense vegetation (Wakeley 1978, Bechard 1982, Marsh et al. 2014). Moreover, Richardson's Ground Squirrels (*Urocitellus richardsonii*), an important component of the diets for Ferruginous Hawks nesting in Canada (Schmutz et al. 1980, Schmutz et al. 2008, Ng et al. 2017), are more likely to select short vegetation cover (Downey et al. 2006, Proulx et al. 2012, Fortney 2013). Ground squirrels were also most abundant in areas with moderate cropland and less abundant in extensive cropland (Schmutz 1989). These studies suggested that prey availability is highest in areas with some grasslands and cropland. Nest structure availability also varies with land cover, and low tree abundance in large tracts of grasslands may limit nest structure availability. Conversely, trees are more common in farmland, hence nesting in mosaics of grassland and cropland may provide benefits of foraging and nest site availability. Ferruginous Hawks were less likely to nest in landscapes with high proportions of cropland in Oklahoma (Wiggins et al. 2014) and North Dakota (Gilmer and Stewart 1983), but there are likely benefits to living in mosaic landscapes as Ferruginous Hawks in Montana that nested in grasslands near croplands were more likely to reproduce successfully (Zelenak and Rotella 1997).

Ferruginous Hawks were slightly more likely to select home ranges nearer to active oil wells and in areas with high resource road density. Keough and Conover (2012) found a similar relationship where Ferruginous Hawks in Utah were also more likely to nest nearer to active oil wells. Other Ferruginous Hawk studies have found positive (Van Horne 1983, Zelenak and Rotella 1997) or negative associations of roads, depending on road type, year, and spatial scale of analyses (Smith et al. 2010, Wallace et al. 2016b). Oil wells and roads are often associated with other infrastructure, such as fencing, power poles, and auxiliary buildings, which can be used as perches by hawks (Plumpton and Andersen 1998, Ng et al. 2017). Prey availability also may be increased near wells as small mammal abundance, including ground squirrels, can be higher in areas with natural gas extraction (Hethcoat and Chalfoun 2015b). Ferruginous Hawks may also select home ranges near wells and roads because it is common practice to mow vegetation along resource roads and around wells, which may increase the availability of prey to foraging Ferruginous Hawks, which select for shorter vegetation where ground squirrels are more accessible (Bechard 1982, Marsh et al. 2014). Most prior studies have been conducted in sage or juniper dominated landscapes; therefore, understanding the potential effects of nesting near oil development associated with higher amounts of human disturbance in moist-mixed and mixed grassland is important for fully understanding Ferruginous Hawks habitat use.

Soil and climate variables were also reasonable predictors of Ferruginous Hawk home range habitat selection. A similar study that examined home range selection for Burrowing Owls

(*Athene cunicularia*) found that soil and climate were the best predictors among a suite of analogous variable classes (Stevens et al. 2011). We found soils within the home range buffers were more likely to be coarse and were likely formed by glacial deposits, river or floodplain flow, and wind. Soils associated with less organic material were also associated with home ranges, which may be related to lower agricultural potential and therefore grassland land cover. Identifying the mechanisms, such as food or nest structure availability, is important to predicting effects to habitat selection and for making management recommendations. More stable soils maybe more suitable for mammalian fossorial prey, such as Richardson's Ground Squirrels (Proulx et al. 2012). Distribution and abundance of trees in the Great Plains is also influenced by soil and climate (Eckenwalder 1977, Bradley and Smith 1986) and may result in varying nest structure availability for hawks.

Implications for wind development

We developed a risk-assessment tool to identify potential conflict risk between wind energy development and Ferruginous Hawks, a threatened species at risk, nesting in Canada. We overlaid our predictive habitat model with wind development potential and found that 2-8% of the Ferruginous Hawk range in Alberta and Saskatchewan is potentially at very high risk of conflicting with wind power development. Conversely, we predict 33-39% of the Ferruginous Hawk range in Alberta and Saskatchewan has potentially low conflict risk. Our spatially-explicit models allow managers to assess and mitigate conflict with hawks at current wind farms in risk zones or pro-actively reduce the risk of conflict by siting future wind farms away from potentially high risk zones.

Our study showed that the relative probability of Ferruginous Hawk habitat selection varied across their range, meaning that there are low, medium, and high risk locations for new wind farms. We recommend avoiding siting wind farms in landscapes in heterogeneous landscapes, such as patch-mosaic landscapes with both grassland and cropland, and areas with moderate edge density, where the relative probability of home range selection is high. In addition, the general premise to site wind farms away from native grassland into cropland, regardless of surrounding land cover composition and configuration, can potentially increase risk to Ferruginous Hawks if the siting is shifted to mosaic landscapes. We recommend siting wind farms on landscapes that are dominated by cropland because they overlap with the least amount of risk for nesting Ferruginous Hawks and for biodiversity in general (Bond and Parr 2010).

Potential cumulative effects associated with wind power must also be considered when siting developments. For example, to-date, wind developments in Alberta and Saskatchewan have been located in zones below the highest wind potential, but near existing transmission lines to connect to the power grid. From a short-term perspective, there is concern because Ferruginous Hawks will nest on transmission towers (Steenhof et al. 1993) where towers are located in suitable landscapes for this species. If wind turbines are placed in the home ranges of hawks nesting in transmission towers, then the risk of turbine strikes will increase. Long term planning can pro-actively reduce this risk by siting future transmission lines away from suitable hawk habitat, thereby also directing wind farm development away from hawk habitat. Cumulative effects that reduce or fragment natural land cover should also be considered. An estimated 1.23 ha of vegetation is removed per turbine (Zimmerling et al. 2013) , which can cumulatively result in changes to land cover and edge density in a landscape. Our study results suggest that these changes could change the probability of a landscape for home range habitat selection by Ferruginous Hawks. Like most large-scale developments, potential cumulative effects should be managed to minimize unintended negative consequences.

The amount of area with risk was greater for the 80 m than the 50 m turbine hub height scenario. Therefore, we expect that with increased turbine height in the near future, areas with risk potential will likely expand because more landscapes will meet commercially viable wind potential. However, our study identified over 100,000 km^2 as low environmental liability under our current scenarios, suggesting that there will still be large low risk areas available for potential development. Smaller turbine capacity is typically associated with lower wildlife collision rates, but there is also less risk of collision associated with fewer larger turbines per unit energy output (Thaxter et al. 2017). Decisions about turbine capacity and number of turbines per farm could be prescriptive, where design and construction decisions are made relative to risk. Risk can further be mitigated if the home range habitat selection map is referenced as part of the pre-development assessment for new farms. As well, mapping can be updated as new wind development potential maps are generated under new technology scenarios. However, our maps do not preclude the need for ground assessments, such as pre-construction hawk surveys, but our models can be used as coarse-filter tools for landscape-scale planning because they identify potential high conflict, low environmental liability, and high conservation value zones.

As land use and climate continue to change, patterns of temperature, precipitation, and circulation are expected change at regional to global-scales. Changes in land cover and climate in our study area may change where our model predicts home range habitat selection. In addition, changes to wind patterns may change the wind potential map. Given expected changes to land cover and wind patterns, it would be prudent to replicate our models in the future with updated land cover and wind potential maps as they become available.

The cumulative effects of wind energy development as the wind energy sector continues to grow will likely have negative impacts to some wildlife. However, the increased use of renewable energy for electricity generation will result in a reduction in use of fossil fuels and associated emissions. Prudent siting and adaptive mitigation for cumulative effects associated with existing and new wind farms will reduce their impact.

Management implications

We demonstrate that wind energy development can be prioritized alongside wildlife conservation by identifying opportunities for prudent siting of new wind farms that minimize risk to Ferruginous Hawks. Our study found that the total area of potential high risk to Ferruginous Hawks was relatively low, especially when compared to large portions of the remaining study area that were categorized relatively low environmental liability (i.e., high wind development potential and low probability of hawk habitat selection). We have provided the wind energy industry and wildlife managers with maps that enable prioritizing landscapes for avoidance during pre-development assessments. Lastly, in cases where wind farms are located in high risk zones, we have identified areas with high Ferruginous Hawk conservation value (i.e., probability of hawk habitat selection is high and wind development potential is low) that could be considered for Ferruginous Hawk conservation offsets (Fargione et al. 2012, Dwyer et al. 2018). This is first time species at risk conservation and wind development potential has been modeled together in Canada, though similar exercises have been done in the United States (Tack and Fedy 2015), Europe (e.g., Migratory Soaring Birds Project) (Tellería 2009, de Lucas et al. 2012, Vasilakis et al. 2016), and South America (Péron et al. 2017). Our mapping products are specific for Ferruginous Hawks and we propose that next conservation steps include hotspot mapping for multiple species, in which a similar process of identifying spatial risk is conducted with species prone to negative effects from wind farm construction and operation (Bennett et al. 2014, Mahoney and Chalfoun 2016). Future risk assessment studies should also incorporate Ferruginous Hawk migration ecology, such as avoiding migration routes, topographic features frequently used during migration, or using shut-downs during peak migration seasons (Liechti et al. 2013).

Identifying potential conflict risk between wind energy development and a species at risk prior to large-scale expansion is important to minimizing long-term risk (Drewitt and Langston 2006, Carrete et al. 2012, Fargione et al. 2012, Balotari-Chiebao et al. 2016). Minimizing risk during the pre-construction phase is particularly crucial at a time when wind farm development in Canada is expected to exponentially increase, particularly in Alberta and Saskatchewan where aggressive renewable energy development goals have been set. Alberta is expected to increase wind energy production from 1500 MW to a minimum of 4000 MW by the year 2030, and Saskatchewan plans to increase its capacity from 200 MW to 2000 MW by the year 2030 (Canadian Wind Energy Association 2016). The majority of this development is expected to occur within Ferruginous Hawk range because the open flat terrain in the grasslands natural region is conducive to large-scale commercial wind development (Fargione et al. 2012). Therefore, prioritizing low conflict risk zones for development should minimize risk to this Threatened species (Kiesecker et al. 2011, Zimmerling et al. 2013) and set a high standard for balancing energy development and wildlife conservation.

TABLE 1. POTENTIAL CONFLICT RISK BETWEEN FERRUGINOUS HAWKS AND WIND FARM DEVELOPMENT, AS RANKED BY 'RELATIVE PROBABILITY OF HOME RANGE SELECTION BY HAWKS' SPATIALLY OVERLAID ONTO WIND DEVELOPMENT POTENTIAL FOR 50-M TALL TURBINES. CONFLICT RISK IS PREDICTED TO INCREASE AS RESOURCES SELECTION FUNCTION (RSF) VALUES INCREASE IN AREAS WITH MEDIUM TO HIGH WIND DEVELOPMENT POTENTIAL (WDP).

	RSF	Ferruginous Hawk habitat selection bin (1 = low, 5 = high)			
WDP[a]	1	2	3	4	5
1	Low	Low	Low	Low[b]	Low[b]
2	Low	Low	Low	Low[b]	Low[b]
3	Low	Medium	Medium	Medium	Medium
4	Low	Medium	High	High	High
5	Low	Medium	High	Very high	Very high
6	Low	Medium	High	Very high	Very high
7	Low	Medium	High	Very high	Very high

[b] Lands with high potential for conservation value to Ferruginous Hawks.

[a] No landscapes within the Ferruginous Hawk range in Alberta and Saskatchewan fall into WDP 8.

TABLE 2. POTENTIAL CONFLICT RISK BETWEEN FERRUGINOUS HAWKS AND WIND ENERGY DEVELOPMENT, AS RANKED BY 'RELATIVE PROBABILITY OF HOME RANGE SELECTION' BY HAWKS SPATIALLY OVERLAID ONTO WIND DEVELOPMENT POTENTIAL FOR 80-M TALL TURBINES. CONFLICT RISK IS PREDICTED TO INCREASE AS RESOURCES SELECTION FUNCTION (RSF) VALUES INCREASE IN AREAS WITH MEDIUM TO HIGH WIND DEVELOPMENT POTENTIAL (WDP).

	RSF	Ferruginous Hawk habitat selection bin (1 = low, 5 = high)			
WDP	1	2	3	4	5
1	Low	Low	Low	Low[b]	Low[b]
2	Low	Low	Low	Low[b]	Low[b]
3	Low	Low	Low	Low[b]	Low[b]
4	Low	Medium	Medium	Medium	Medium
5	Low	Medium	High	High	High
6	Low	Medium	High	Very high	Very high
7	Low	Medium	High	Very high	Very high

TABLE 3. RESULTS FROM THE TOP RANKED MODELS, COMPOSED OF TOP VARIABLE CLASSES, COMPARING MODEL FIT FOR HOME RANGE HABITAT SELECTION OF FERRUGINOUS HAWKS (N = 2147 USED QUARTER-SECTIONS) FROM ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010. A MODEL'S ΔAIC IMPROVES AS VARIABLE SETS ARE ADDED AND THE ADDITION OF SOIL CHARACTERISTICS RESULTED IN THE BIGGEST DIFFERENCE IN ΔAIC.

Geography	Land	Soil	Climate	Industry	k	LL	AIC	ΔAIC	w_i
x	x	x	x	x	27	-4,829.20	9,714.41	0.00*	0.99
x	x	x	x	x	34	-4,827.42	9,724.84	10.43	0.01
x	x	x		x	31	-4,849.72	9,763.43	49.02	0.00
x	x	x	x		31	-4,863.98	9,791.96	77.55	0.00
x	x	x			23	-4,889.94	9,837.88	123.47	0.00
x		x		x	26	-4,972.37	9,998.73	284.32	0.00
x		x	x		26	-5,018.76	10,091.52	377.11	0.00
x		x			23	-5,027.98	10,103.97	389.56	0.00
x	x				11	-5,203.23	10,430.47	716.06	0.00
x				x	9	-5,264.57	10,549.14	834.73	0.00
x			x		9	-5,345.71	10,711.43	997.02	0.00
x					6	-5,382.19	10,778.37	1,063.96	0.00
		x			17	-5,453.27	10,942.54	1,228.13	0.00
			x		3	-5,467.58	10,943.15	1,228.74	0.00
				x	3	-5,559.46	11,126.92	1,412.51	0.00
	x				5	-5,585.35	11,182.70	1,468.29	0.00

[a] Final all-inclusive model with variables p-value >0.10 removed.

TABLE 4. STANDARDIZED VALUES FOR THE ALL-INCLUSIVE MODEL DEVELOPED FROM GEOGRAPHY, LAND COVER, SOIL, CLIMATE, AND INDUSTRIAL VARIABLE CLASSES AS MODELED FOR FERRUGINOUS HAWK HOME RANGE HABITAT SELECTION IN SOUTHERN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010.

					95% CI	
Variable Class	Variable	β	SE	p-value	Lower	Upper
Geography	longitude	-39.350	3.172	0.000	-45.568	-33.132
	longitudeQ	-39.029	3.164	0.000	-45.231	-32.827
	latitude	33.672	4.201	0.000	25.438	41.905
	latitudeQ	-34.320	4.229	0.000	-42.608	-26.032
Land cover	grass2500	1.201	0.170	0.000	0.868	1.533
	grass2500Q	-0.958	0.150	0.000	-1.252	-0.664
	edge2500	0.457	0.124	0.000	0.214	0.700
	edge2500Q	-0.435	0.100	0.000	-0.630	-0.239
	waterdist_ln	-0.911	0.028	0.000	0.146	-0.037
Soil	ve	-0.204	0.053	0.000	-0.031	-0.100
	ch	-0.285	0.039	0.000	0.036	-0.209
	rg	-0.455	0.046	0.000	0.540	-0.370
	lu	-0.147	0.088	0.095	-0.320	0.025
	fluv	0.195	0.030	0.000	0.136	0.253
	gllc	-0.378	0.045	0.000	-0.465	-0.290
	glfl	0.180	0.029	0.000	0.123	0.236
	till	0.137	0.039	0.000	0.061	0.213

	resd	-0.216	0.046	0.000	-0.306	-0.126
	eoli	0.112	0.026	0.000	0.064	0.164
	rkud	-0.148	0.043	0.000	0.232	-0.065
	silta	-0.125	0.036	0.001	0.195	-0.054
	vfsana	-0.212	0.045	0.000	0.299	-0.124
Climate	tmxspr	0.139	0.058	0.016	0.026	0.252
	tmxsumstd	-0.242	0.036	0.000	0.313	-0.172
Industry	rdpet2500	0.163	0.024	0.000	0.115	0.211
	oildist	-0.213	0.048	0.000	0.307	-0.119
Constant		-2.296	0.038	0.000	-2.369	-2.222

Equations

EQUATION 1. RESOURCE SELECTION FUNCTION EQUATION.

RSF = $s_{(x)}$ = exp $(B_1X_1 + B_2X_2 \ldots +B_nX_n)$

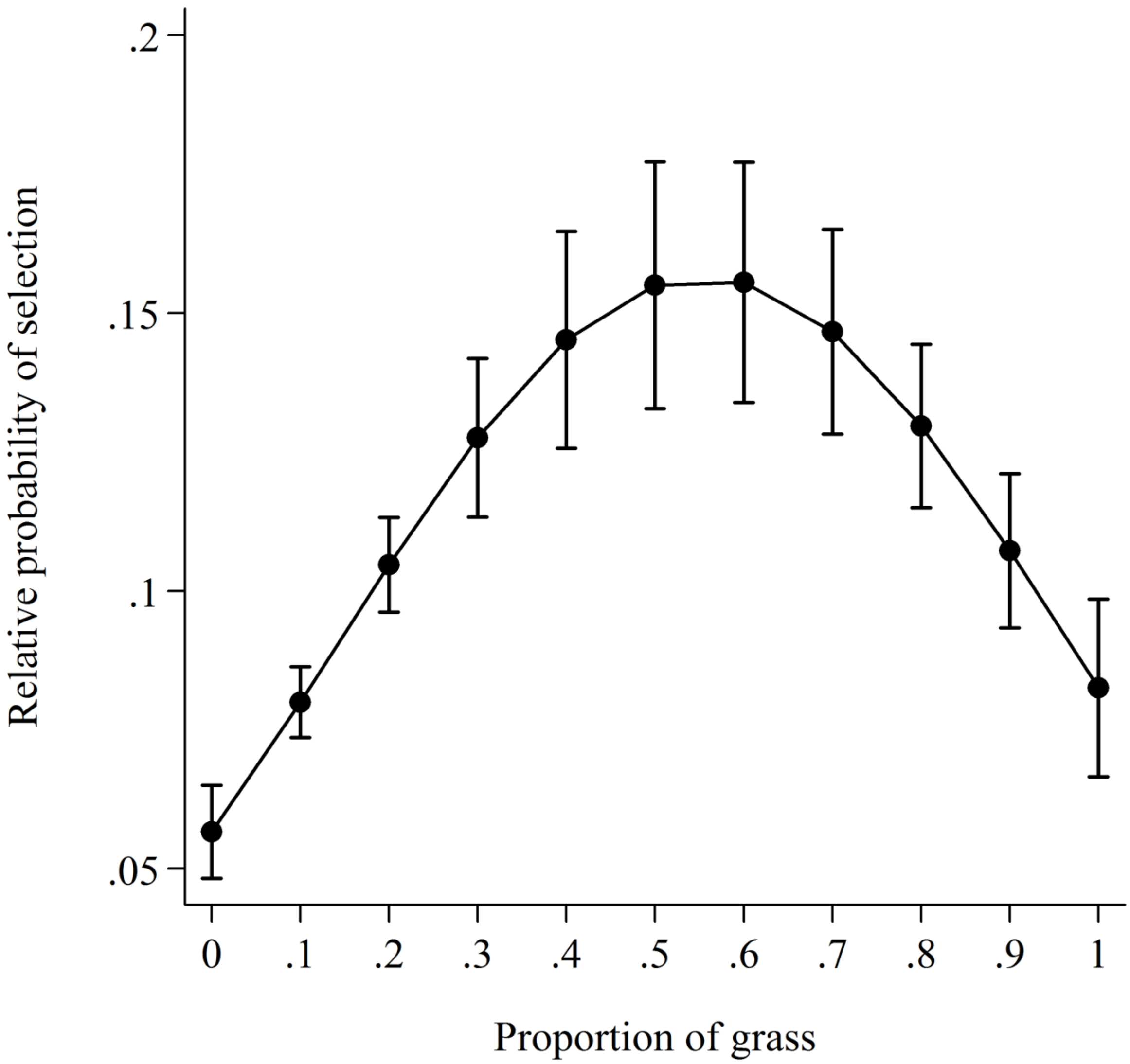


FIGURE 1. PREDICTED RELATIVE PROBABILITY OF HOME RANGE HABITAT SELECTION BY FERRUGINOUS HAWKS IN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010, RELATIVE TO PROPORTION OF NATIVE GRASSLAND WITHIN 2.5 KM OF THE NEST WHEN ALL OTHER MODEL VARIABLES ARE HELD AT THEIR MEAN VALUES.

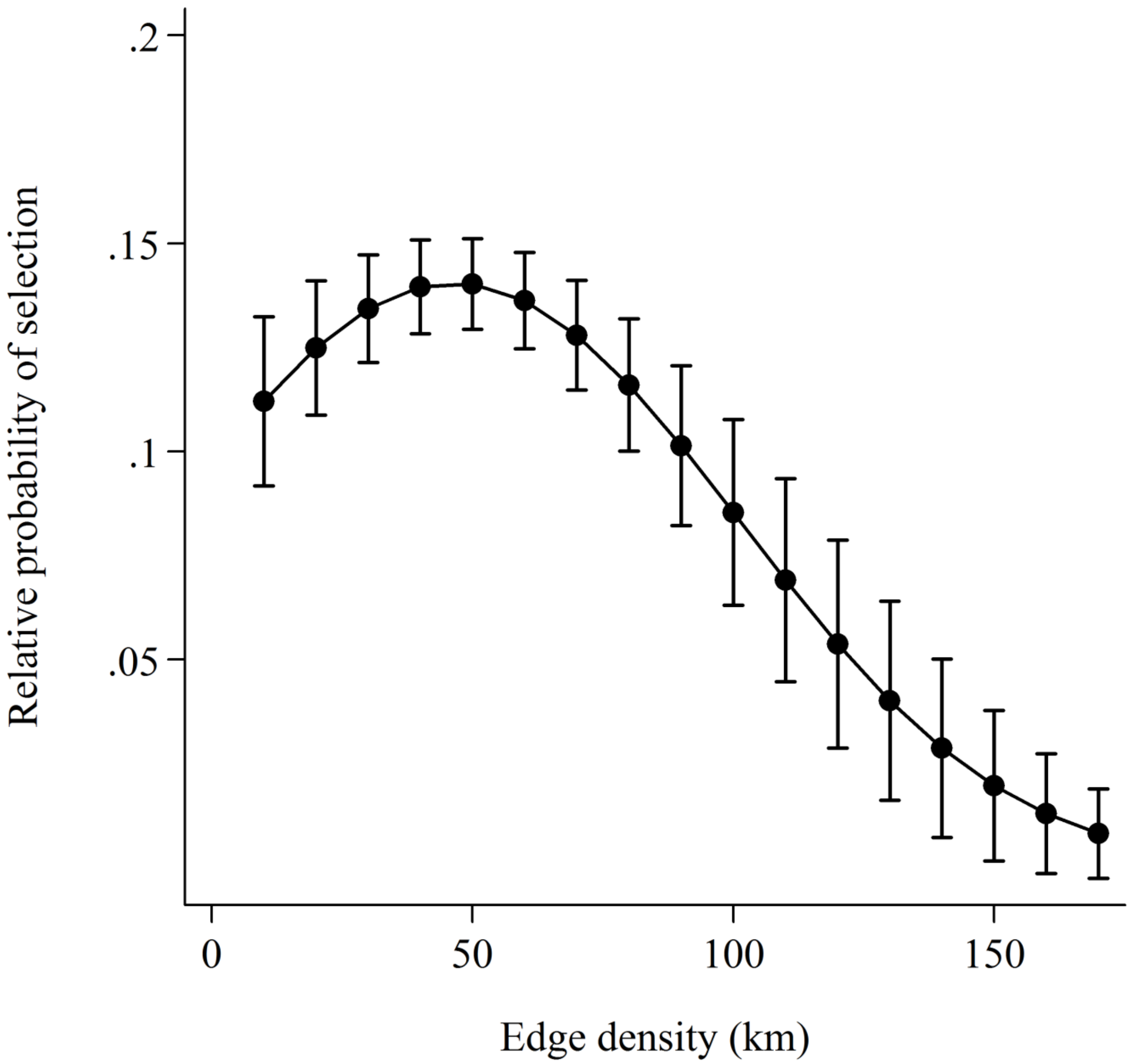


FIGURE 2. RELATIVE PREDICTED PROBABILITY OF HOME RANGE HABITAT SELECTION BY FERRUGINOUS HAWKS IN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010, RELATIVE TO GRASS-CROPLAND EDGE DENSITY THAT WAS WITHIN 2.5 KM OF THE NEST WHEN ALL OTHER MODEL VARIABLES ARE HELD AT THEIR MEAN VALUES.

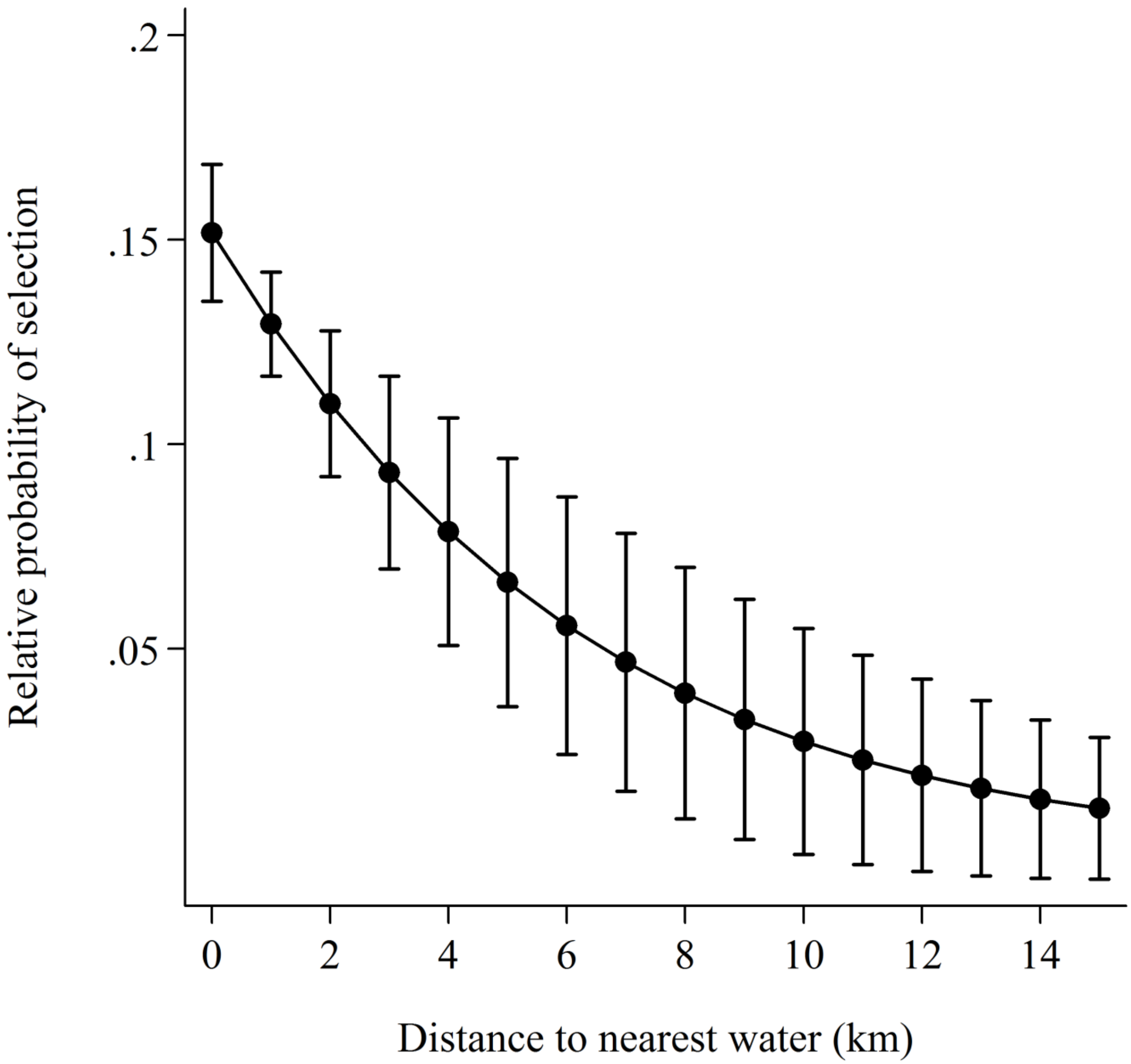


FIGURE 3. RELATIVE PREDICTED PROBABILITY OF HOME RANGE HABITAT SELECTION BY FERRUGINOUS HAWKS IN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010, RELATIVE TO THE DISTANCE TO NEAREST WATER WHEN ALL OTHER MODEL VARIABLES ARE HELD AT THEIR MEAN VALUES.

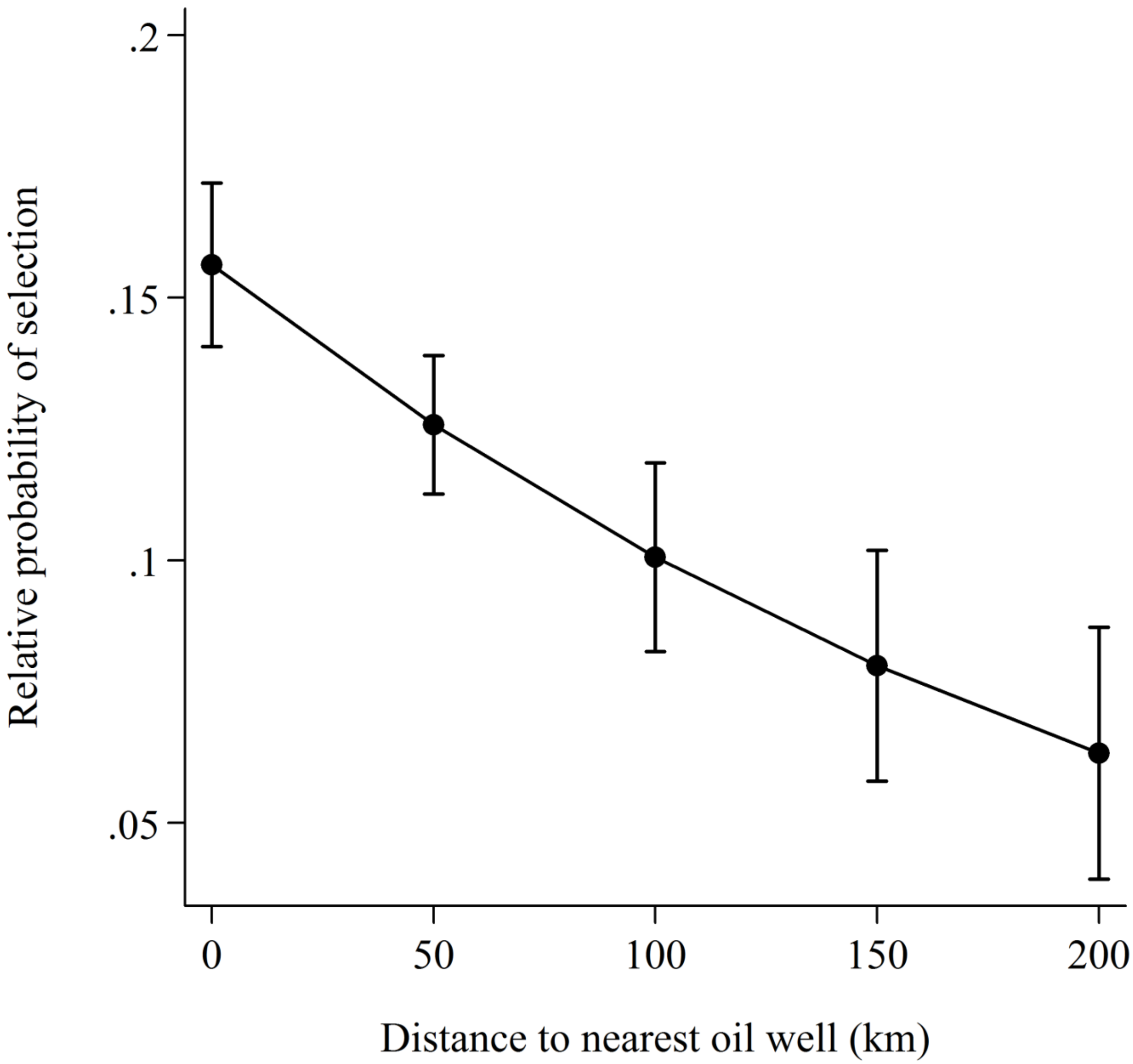


FIGURE 4. RELATIVE PREDICTED PROBABILITY OF HOME RANGE HABITAT SELECTION BY FERRUGINOUS HAWKS IN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010, RELATIVE TO DISTANCE TO NEAREST ACTIVE OIL WELL WHEN ALL OTHER MODEL VARIABLES ARE HELD AT THEIR MEAN VALUES.

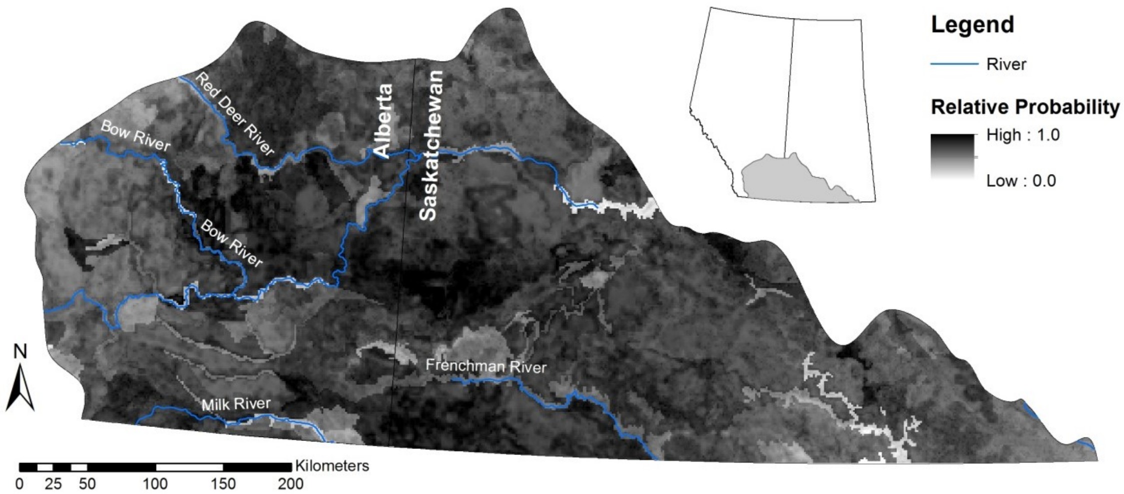
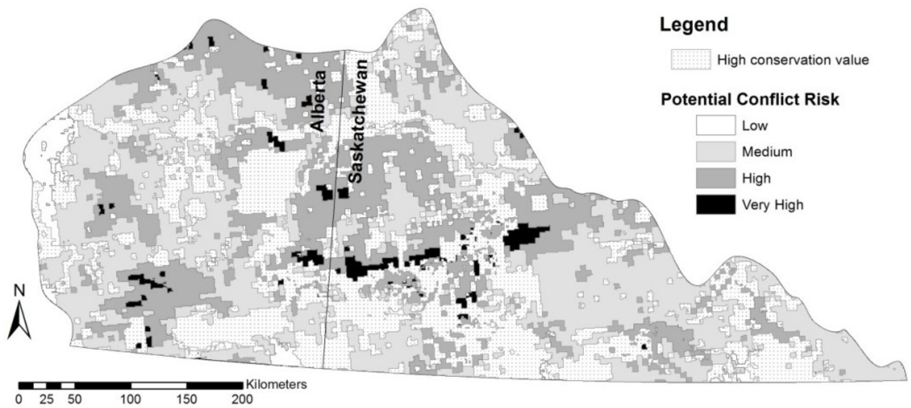
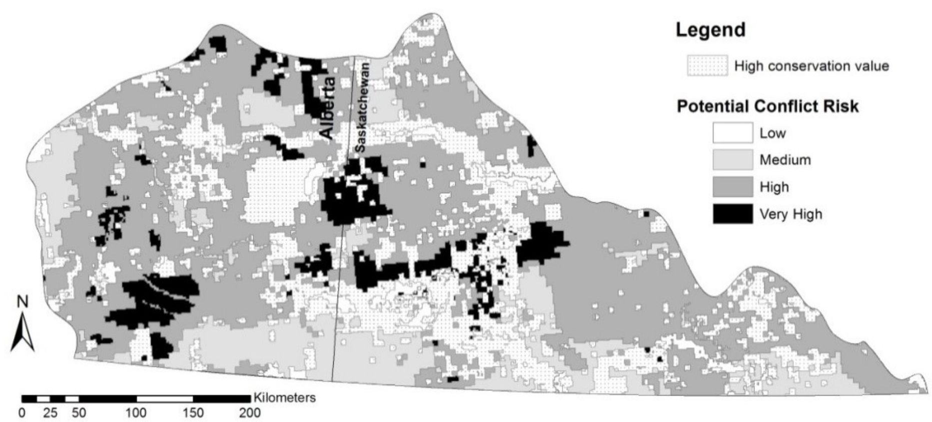


FIGURE 5. PREDICTIVE MAP OF PROBABILITY OF HOME RANGE SELECTION BY FERRUGINOUS HAWKS IN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010. GREY SHADING INDICATES RELATIVE PROBABILITY OF SELECTION, WHERE DARKER SHADING DENOTES HIGHER SELECTION COMPARED TO LIGHTER SHADING. RIVERS ARE OUTLINED IN BLUE. THIS MAP IS RESTRICTED TO CURRENT RANGE OF FERRUGINOUS HAWKS IN ALBERTA AND SASKATCHEWAN.



A)



B)

FIGURE 6. PREDICTED POTENTIAL CONFLICT RISK BETWEEN FERRUGINOUS HAWKS AND WIND ENERGY DEVELOPMENT IN SOUTHERN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010. TURBINE HUB HEIGHT SCENARIOS ARE MAPPED BY A) 50 M AND B) 80 M. BLACK SHADING INDICATES AREAS WITH HIGH ENVIRONMENTAL LIABILITY WHERE WIND DEVELOPMENT POTENTIAL IS HIGH AND RELATIVE PROBABILITY OF SELECTION BY FERRUGINOUS HAWKS IS ALSO HIGH. STIPPLED AREAS IDENTIFY AREAS WITH HIGH CONSERVATION VALUE BECAUSE THE WIND DEVELOPMENT POTENTIAL IS LIKELY LOW, BUT PROBABILITY OF SELECTION BY HAWKS IS HIGH.

Chapter 3: Managing cumulative effects for species at risk using a habitat-based framework

Abstract

Linking habitat resources and fitness is critical to understanding the effects of landscape change on wildlife populations. Landscape change from multiple land uses can result in cumulative effects, which can negatively impact habitat use and reproductive performance, even resulting in potential habitat mismatches for populations. Spatially-explicit models can be used to evaluate cumulative effects and develop habitat-based frameworks to identify, prioritize, and manage species at risk over large spatial extents. In Canada, farming, ranching, and petroleum extraction are dominant land uses within the Ferruginous Hawk (*Buteo regalis*) range and could influence on their population demography. We developed nest abundance and reproductive performance models to evaluate potential additive and synergistic cumulative effects of multiple land uses. We used these models to produce spatially-explicit maps and overlayed the maps to identify potential habitat mismatches, where nest abundance and reproduction were negatively associated. Lastly, we categorized the species range using two spatially-explicit habitat-based frameworks described by relative nest abundance and nest survival. Ferruginous Hawk relative nest abundance and nest survival were both highest in heterogeneous landscapes with moderate amounts of cropland and grassland, and moderate edge density. Density of active oil wells was negatively associated with nest survival, while density of active gas wells was positively associated. We did not find any synergistic relationships between land cover and industrial development. Mapping the Ferruginous Hawk range using a spatially-explicit habitat-based

framework was useful for categorizing landscapes. Our approach identified important landscapes for habitat conservation, which are those with high relative nest abundance and high nest survival. We also identified landscapes where additional habitat management may be needed, those with high relative nest abundance but low nest survival.

Keywords

habitat mismatch; non-ideal habitat; energy development; risk assessment

Introduction

A species' presence in a human-altered landscape does not indicate that development has a positive or even neutral influence on the species (Best 1986). Individuals may use less suitable habitat or lower quality habitat (the latter being defined as habitat characteristics associated with lowered reproductive performance) for many reasons (Pulliam 1988, Dunning et al. 1992, Battin 2004). For example, some landscapes act as ecological sinks or even attractive ecological traps (Kristan 2003, Battin 2004, Robertson and Hutto 2006). In such scenarios, landscapes provide habitat to a species, but do not contribute to overall population growth rate because of poor reproductive success or survival (Kawecki 1995, Kristan 2003). Individuals can also be displaced by conspecifics from suitable or high quality habitat and use less suitable or lower quality habitat because they are forced to (i.e., ideal despotic distribution (Fretwell and Calver 1969, Fretwell 1972)). Assuming that human-altered landscapes containing animals provide a positive or neutral contribution to animal population growth can be problematic, particularly if there are ecological thresholds where small landscape changes result in significant changes to reproductive performance or survival (Swift and Hannon 2010). Evaluating habitat quality, the link between habitat resources and fitness, is critical to understanding the effects of landscape change on wildlife populations (Aldridge and Boyce 2007).

Agriculture has resulted in habitat loss, degradation, and fragmentation of grassland ecosystems worldwide (Hoekstra et al. 2005, Krauss et al. 2010). Agriculture is responsible for the most land cover change In North American, with over 80% of native grasslands having been converted to cropland (Samson and Knopf 1994). These habitat and landscape changes have been linked to population declines and range contractions for many grassland and shrub-steppe species (Herkert 1994, Vickery and Herkert 1999, Murphy 2003, Brennan and Kuvlesky 2005, Krauss et al. 2010). However, some species historically associated with grassland are observed using landscapes with high proportions of cropland (Best et al. 1997, Murray et al. 2003), while others are found along the entire gradient of cropland cover (Murray et al. 2003). Whether these species have adapted to use agricultural landscapes or if there is a difference in the fitness of individuals between native grassland and cropland dominated areas remain poorly understood.

The human footprint in the Great Plains includes more than cropland however (Copeland et al. 2011). Human settlement features, such as roads, rural and urban residences (i.e. farms and houses), planted trees, lights, and power lines, are widespread. Extensive energy development has also resulted in more industrial infrastructure (e.g., oil and gas wells, compressor stations, road networks, and power lines) and potential disturbance (e.g., industrial noise, vehicle traffic). The additional infrastructure and human activity can negatively affect some wildlife populations in the grasslands (songbirds, (Hethcoat and Chalfoun 2015a, Bernath-Plaisted and Koper 2016); Greater Sage-Grouse (*Centrocercus urophasianus)* (Naugle et al. 2011); American pronghorn

(*Antilocapra americana*), (Beckmann et al. 2012); mule deer (*Odocoileus hemionus*), (Sawyer et al. 2009, Lendrum et al. 2012)). Cumulative negative effects of energy extraction are of particular concern in the Great Plains because energy leases currently occupy ~21% of all grassland in Western North America (Copeland et al. 2011) and may increase with market demand. Hence, consequences to wildlife populations could occur at large spatial extents, particularly if development continues.

Tracking the effects of multiple land uses, from cultivation to energy extraction, is challenging because the effects may be cumulative (Johnson et al. 2005, Sorensen et al. 2008, Sawyer et al. 2009, Johnson 2013). Cumulative effects can be additive where the total impact is the sum of each effect, but synergistic effects are also a concern because interactions among the various effects of human development can be potentially greater, less predictable, and more complex to manage (Crain et al. 2008, Côté et al. 2016). For most species, it is unknown whether anthropogenic changes to a landscape have an additive or synergistic cumulative effect. Identifying the nature of cumulative effects is critical to integrated land use planning and wildlife management because that can help predict the magnitude and rate of overall impacts to wildlife populations (Naugle et al. 2011).

Little attention has been paid to cumulative effects on habitat quality, which can potentially increase negative repercussions for wildlife populations if habitat use or animal density is not correlated with reproductive performance (Aldridge and Boyce 2007). This problem becomes even more important with species at risk. In grassland systems, few studies have shown a clear link between animal density, habitat selection, and reproductive performance in relation to area of grassland. Yet the default explanation for grassland species decline is the loss of native grassland habitat. For example, Ferruginous Hawks (*Buteo regalis*) were listed as a Threatened Species in the Species At Risk Act in Canada because of a 50% decline in population and a 50% range contraction since the 1990s (COSEWIC 2008). Habitat loss, in the form of grassland conversion to cropland, has been frequently suggested as the major driver for this decline (Schmutz 1984, Schmutz 1987a). However, Ferruginous Hawks do nest in areas with extensive cropland, and research suggests that they are most abundant in landscapes with a mixture of cropland and grassland (Schmutz 1989) (Chapter 2). Ferruginous Hawks have been observed successfully raising young in landscapes dominated by cropland, but whether the amount of cropland around a nest influences survival or reproductive performance. Ferruginous Hawk habitat use and reproduction may also be influenced by energy extraction (Keough and Conover 2012, Wallace 2014, Wallace et al. 2016a, Wallace et al. 2016b, Wiggins et al. 2017), but it is unknown if agricultural and industrial development interact to influence hawk ecology.

Another concern for species a risk is a mismatch between habitat use and reproductive performance, where habitat use is high and reproduction is low. This mismatch can result in depressed survival and productivity for the population (Kristan 2003, Nielsen et al. 2006). Habitat use or density of animals is often positively correlated with the fitness of individuals in a particular habitat. However, this positive correlation should not be assumed without demographic data (Van Horne 1983). Landscape change, such as human alteration, can result in unexpected mismatches because environmental cues used by birds to identify high-quality habitat may not be reliable if there is a mismatch with subsequent levels of reproduction and survival (Arlt and Pärt 2007, Chalfoun and Martin 2007, Gilroy et al. 2011). For example, specific habitat characteristics may be important to Ferruginous Hawks, such as short grass for increasing prey capture efficiency. However, when cropped/cultivated or tame grass (i.e., planted non-native grass) landscapes have short vegetation in the spring when Ferruginous

Hawks select home ranges and nest sites, but crop fields quickly grow tall and dense vegetation by summer, it may make it difficult for hawks to detect and capture mammalian prey. Linking reproductive performance to habitat use is required to assess habitat quality and to identify landscape characteristics or features that could be ecological sinks or traps (Kokko and Sutherland 2001, Robertson and Hutto 2006). Mapping predictive models of habitat use and reproductive performance would identify spatially-explicit areas of high and low habitat quality, as well as potential mismatches. These landscapes could be categorized into a habitat framework and help managers identify areas of high conservation value that contribute the most to population recovery, as well as areas that require action to reduce negative impacts to populations (Aldridge and Boyce 2007, Nielsen et al. 2009).

Our objectives were to 1) assess which potential cumulative effects of landscape and human development features influence Ferruginous Hawk habitat quality, 2) evaluate whether any identified cumulative effects are additive or synergistic, 3) identify potential habitat mismatches by comparing spatially-explicit relative nest abundance and reproduction performance models, and 4) produce spatially-explicit maps using habitat-based frameworks. First, we developed an abundance model to determine how environmental and anthropogenic variables influence the relative abundance of Ferruginous Hawk nests at a relatively large spatial scale. Next, we evaluated if nest survival, clutch size, or fledging rate changed across the same gradient of human-altered landscapes, and assessed whether any cumulative effects associated with multiple land uses were additive or synergistic. We hypothesized that cropland and grassland provide habitat characteristics important to Ferruginous Hawks and that home ranges are selected in landscapes with both land cover types. Therefore, we predicted that nest abundance would be highest in landscapes containing both cropland and grassland. Ferruginous

Hawk breeding density and productivity is closely tied to Richardson's Ground Squirrel (*Urocitellus richardsonii*) abundance (Schmutz and Hungle 1989b); therefore, we hypothesized that reproductive performance would be linked to landscapes with high prey abundance and availability. We also predicted that reproductive performance would be highest for nests surrounded by a high proportion of grassland and high edge densities. Grassland is associated with Richardson's Ground Squirrels (Downey et al. 2006) and edges may increase prey accessibility for hawks due to higher abundances of perches associated with edges (i.e. fence posts and power poles) or prey may be more accessible to capture due to shorter vegetation (Bechard 1982). Next, we compared our abundance model to reproductive performance models to determine if similar landscape characteristics influence both relative abundance of nests and also reproduction, thereby identifying potential habitat mismatches or non-ideal habitat selection. Lastly, we categorize landscapes into habitat states and habitat quality to identify where habitat mismatches may be occurring.

Methods

A detailed description of data collection and the model approach used to develop base models can be found in Appendix B.

Study Area

Our study area included Ferruginous Hawk nests located throughout southern Alberta and Saskatchewan (centre at 50° 10' 11.604" N, 109° 55' 39.6048" W) (Figure 7). This represents the majority of the Ferruginous Hawk northern range (Ng et al. 2017). The study area encompasses approximately 153,000 km^2 of fescue, mixed-moist grassland, and shortgrass ecoregions where land cover is predominantly cropland and grassland. Grassland is generally composed of blue gramma grass (*Bouteloua gracilis*), needle and thread grass (*Stipa comata*), and wheat grasses (*Elymus* spp.). The grasslands are often grazed by cattle. Cropland is predominantly canola (*Brassica* spp.), cereals such as wheat, clover (*Trifolium* spp. and *Meliliotus* spp.), and pulse crops (e.g., *Pisum* spp., *Lens* spp., dry beans). Other major land uses include oil and gas extraction and wind power generation. Spring temperatures (March - May) averaged 6.5˚C and summer temperatures (June - August) averaged 18.7˚C (Medicine Hat, Alberta, Environment Canada and Climate Change). On average, cumulative precipitation during spring is 82.7 mm and 135.9 mm during the summer.

Relative nest abundance

Sampling Method

In 2012 and 2013, systematic surveys were conducted throughout the study area using a stratified random sampling design. The study area was delineated into 9.6 km by 9.6 km survey blocks (hereafter block). The study area was stratified to ensure surveys were distributed geographically across the Ferruginous Hawk range in Alberta and Saskatchewan. We then randomly selected blocks within each strata so that we had a balanced randomized design (approximately equal number of blocks within high versus low levels of each landscape characteristic). The landscape was stratified by the proportion of cropland, density of transmission lines, road density, and oil & gas well density in each block using GIS layers (ESRI 2012). Survey routes were on roads, but were selected to survey through all available land cover types within each block, as well as to cover the maximum area possible within the block. Blocks were surveyed once and different blocks were sampled each year.

Model development

Predictor variables

We developed a base model to control for those variables that could potentially influence relative nest abundance but that were not related to our primary questions of how land cover and/ or industrial development influence relative abundance of hawks. See Appendix B for a detailed description of how we decided which variables to include in the base model. The variables in our best base model were latitude, longitude, and area-weighted proportion of regosolic soil.

Land cover variables were measured at the scale of a township (9.6 km by 9.6 km). We quantified the proportion of grassland and the edge density within each block. Edge density was measured as kilometres of grassland-cropland interface. We also assessed total edge density by combining the sum of grassland-cropland interface, water body and wetland edge, and road length.

Industrial features were also quantified in each survey block. Length of transmission lines, pipelines, and roads were quantified from digital spatial products (Table 16). We also counted the number of oil and gas wells. No wind turbines were located in survey blocks or near nests in this study. Density variables were assessed both in continuous and categorical forms, using natural breaks in histograms to describe density as low/medium/high, low/high, or presence/absence.

Cumulative effects model

STATA version 13.0 (StataCorp 2013) was used for statistical analyses. Data was explored for outliers, homogeneity of variances, excess zeros, collinearity, model structure, and overdispersion (Zuur et al. 2010). Prior to analysis, all predictor variables were standardized to zero mean and unit variance. This was done to allow direct comparison of the magnitude of each variable by scaling the data to the same units. Thus, variables with more extreme coefficients have a greater effect on Ferruginous Hawk abundance than those with coefficients closer to zero.

We used Poisson regression, with the count of Ferruginous Hawk nests found within blocks as the response variable. An abundance model was built using a stepwise approach and validated using an external dataset collected by Alberta Environment and Parks. We started by testing variables in univariate models and evaluated if the variable improved prediction of the external dataset. Predictive performance relative to the validation data was evaluated using Spearman's rho, and its p-value and correlation coefficient. Only variables that had a statistically significant (p-value <0.05) Spearman's rho were included in the next model. Significant variables formed a global model, that we then reduced by removing any variables with a p-value

< 0.15 in a backward stepwise procedure. As each variable was removed, we checked that the model's Spearman's rho was increasing and the associated p-value was decreasing and remained below 0.05. Lastly, the model was further reduced by removing variables if they became non-significant (p-values > 0.10) and their exclusion improved the predictive performance of the model (Arnold 2010). The final model only included statistically significant variables (p-value <0.05). For a detailed description of the model approach, please see Appendix B.

Reproduction Models

Nest monitoring

We monitored Ferruginous Hawks nests between 2010 and 2015 to collect reproductive metrics. As nests were found, we used GIS to quantify landscape and human development characteristics within a 2.5 km radius of each nest. By quantifying the landscape each home range, we were able to subsample Ferruginous Hawk nests that fit our stratified sampling design. We monitored a relatively equal number of nests across high to low levels of grassland cover and industrial intensities.

Nests were monitored weekly throughout the breeding season, with a subsample of nests monitored every two weeks or more. At each visit, we recorded nest contents (i.e., clutch size, number of live young) and whether the nest was active or inactive. Once the nest became inactive, we recorded nest fate (i.e., successful when naturally fledged at least one young), source of nest mortality when known, date of nest outcome, number of young fledged, and other reproduction parameters. See Appendix B for a detailed description of data collection.

Predictor variables

Landscape and human development variables were quantified similarly to our relative nest abundance analyses, except variables were quantified using GIS within a 2500 m radius of each nest. In addition proportion of grass and edge density, we also measured the distance to nearest water from each nest. For industrial features, transmission lines, oil and gas wells, pipelines, and roads were quantified around each nest. We categorized natural gas wells and oil wells as low (0 wells), medium (<25 wells), and high (>25 wells) (IHS Energy 2013). Distance to nearest industrial feature was also included in the reproduction analyses.

Model development

We modeled daily nest survival using logistic nest exposure (Shaffer and Burger 2004). Clutch size and fledge rate were modeled using mixed effect Poisson regression, with individual nest as random effect. In the fledge rate analyses, we excluded failed nests (i.e. nests that did not fledge any young) because nest failure was included in the nest survival analyses. The mechanisms that influence nest failure and fledge rate may be different and this analysis focused on understanding productivity.

We started our model selection procedure by creating broad variable classes: base, land cover, and energy. Similar to the relative nest abundance model, we developed a base model to account for variation not explained by landscape or human development variables. The base model included landscape ruggedness, nest structure type, nest stage, year, date of first nest visit, nest age, hatch date, and mean temperature of the previous winter, spring, and month of visit. A detailed description of our base model and the variables evaluated is included in Appendix B.

We used a forward step-wise approach to test for additive and synergistic effects of land cover and industrial development. Whole variable classes were included or excluded in each model. We tested for *a priori* interactions between land cover and industrial variable (Table 7). Each model was further simplified by removing variables that were not statistically significant (p-value >0.10) and were removed one-by-one using a backward stepwise approach, where the least significant variable was removed at each step (Arnold 2010). If the removal of the variable did not also improve the AIC, it was left in the model. AUC/ROC scores were checked after each variable was removed to assess any large decreases to model performance. This process was repeated until all variables in the model were highly predictive (p-value <0.10) or the delta AIC started to increase. This procedure ensures that each competing model remains as parsimonious as possible while only including statistically important variables. This series of stepwise procedures increases the certainty that variables influence the response variable. The best model is the model with the lowest delta AIC, the most parsimonious, and the most predictive based on receiver operating characteristic (ROC) curve. This selection procedure was used to model daily nest survival, clutch size, and fledging rate.

For a detailed description of the model approach, please see Appendix B.

Mapping

We used coefficients from the relative nest abundance and nest survival models to generate predictive maps across southern Alberta and Saskatchewan.

We used the predictive relative nest abundance and nest survival maps to generate two maps that show habitat state and habitat quality across townships in southern Albert and Saskatchewan. We adapted a previously developed framework for habitat state (Nielsen et al. 2006, Aldridge and Boyce 2007) that describes five habitat states: primary habitat (high nest abundance and high nest survival), secondary habitat (low-moderate nest abundance and high nest survival), high concern (high nest abundance and low nest survival), moderate concern (low-moderate nest abundance and low nest survival), and low concern (low nest abundance) (Table 5). Lastly, we mapped habitat quality by categorizing townships into low (areas with low to moderate abundance and low nest survival), moderate (low to moderate nest abundance and high nest survival), and high (high abundance and high nest survival) quality based on predicted relative nest abundance and nest survival (Table 5).

To create these maps, we categorized relative nest abundance by first estimating the number of nests per township. We used our model predictions, which are based on surveys that were 20 – 30 km long. We estimated that surveys covered approximately half of a township and assumed high nest detection probability within 800-m distance from a road. Using this estimated survey area, we multiplied predicted values by 1.92 to extrapolate the predicted number of nests per township. This coarse estimation allowed us to categorize townships into low (i.e., zero nests), moderate (1 nest), and high (>1 nests). We also averaged nest survival within each township and categorized predicted nest survival into low (0.0 to 0.25), moderate (0.26 to 0.50), and high (>0.51). We overlayed the predicted relative nest abundance map with the nest survival map to generate the habitat state and habitat quality.

Results

See Appendix B for a complete description of results, including results for base models of both relative nest abundance and reproductive performance analyses.

Relative abundance model

We included 223 blocks in this analysis. Of these, 63 were conducted in 2012 and 159 in 2013. The number of nests per block ranged from zero to four nests, where one nest was found in each of 42 blocks, two in 19 blocks, three in 7 blocks, and four in two blocks. Surveys were 25.84 km long on average (SE = 4.14) and were conducted between April 18 and May 16 (mean = May 6, mode = May 8).

Controlling for spatial pattern, we found that the proportion of grass and edge density were the most important land-cover predictors of Ferruginous Hawk nest abundance. There was a strong quadratic relationship with proportion grass and edge density, with Ferruginous Hawk predicted to be most abundant in blocks with 49% grass (Figure 8, Table 6). Edge density, defined as the sum of grassland-cropland interface, road density, and water body and wetland edge, predicted Ferruginous hawk nest abundance to increase until moderate edge density (~400

- 500 km in surrounding township-sized area) and then to decrease until the maximum 700 km edge density.

Nest Survival

Nests monitored any year between 2010 and 2015 were included in this analysis. In total, we included 728 nest locations, 1534 nest attempts, and 4384 nest visits in the nest survival analyses.

A higher proportion of grassland surrounding the nest was negatively associated with nest survival (Figure 10). Nest survival decreased in areas with high and low amounts of edge, including grassland-cropland interface, water body and wetland edge, and roads. Moderate amounts of these edges, between 400 and 500 km, predicted highest nest survival.

Nest survival was higher in areas with a medium density of active oil wells, but lower in areas with a high density of active oil wells. In comparison, nest survival was higher for nests surrounded by medium and high densities of active gas wells.

The additive cumulative effects model was the top model (Table 7, Table 8) because it had the lowest delta AIC with the fewest variables and a comparable area under the curve (AUC) (Figure 11). Two synergistic models had lower delta AICs, but had more parameters plus the added complexity of an interaction term that added little to their predictive power.

Validation for nest survival model

The final nest survival model had an AUC of 0.84, suggesting the nest survival model is excellent (Hosmer and Lemeshow 2005).

Clutch Size

From 2010 to 2015, we observed the nest contents during incubation at 415 Ferruginous Hawk nesting attempts for 321 individual nests across our study area. Clutch sizes ranged from 1 to 6 eggs, with a mean of 3.24 ± 1.07 SD.

Landscape and industrial development variables did not predict clutch size.

Fledge Rate

Between 2010 and 2015, we determined nest outcomes for 1,235 nesting attempts at 779 individual nests. Of these nesting attempts, 67.13% of nests successfully fledged at least one young (Table 20). Of successful nests, we observed 765 successful nesting attempts with known fledgling counts at 530 individual nests. Of successful nests, fledging rate ranged from 1 to 6 young, with a mean of 2.39 ± 1.00 SD.

There were no landscape or industrial development variables that predicted fledge rate.

Mapping

The predicted relative nest abundance ranged from 0 to 4 nests per township, where 56% of townships likely have low abundance (0 nests). Predicted average nest survival per township ranged from 0.02 to 0.62 and had a mean of 0.30 ± 0.09 SD. When relative nest abundance and nest survival were overlayed together, habitat state and habitat quality maps were generated (Figure 12). Primary habitat and high quality habitat covers 10.1% of the species range (Figure 12). Low quality habitat covers 63.7%; however, the majority is of low concern (55.8%) because predicted nest abundance is low in those areas.

Discussion

Land cover composition and edge density were important predictors of habitat quality for Ferruginous Hawks, which is consistent with our predictions. Heterogeneous landscapes predicted both relative nest abundance and nest survival, which suggests that land management approaches can be a useful tool for conservation and recovery of Ferruginous Hawks.

Relative nest abundance peaked in township-sized heterogeneous landscapes with approximately 50% grassland and 50% cropland. This pattern is similar to a previous study in Canada that found hawk nest density highest in landscapes with 70-90% grassland (Schmutz 1989). Heterogeneous land cover also predicts home range habitat selection, which in Canada is highest in areas with 45% grassland (Chapter 2). Other studies found hawks were more likely to nest in landscapes with higher amounts of grassland (Gilmer and Stewart 1983, Roth et al. 1989, McConnell et al. 2008, Wiggins et al. 2014) or lower amounts of grassland (Coates et al. 2014b). Moderate edge density predicted relative nest abundance, where hawk nests were most abundant in townships with ~5.4 km/km^2 of edge. Similarly, home range habitat selection (2500 m radius) was most likely in landscapes with ~2.3 km/km^2 of edge (Chapter 2), suggesting that hawks' habitat characteristics may differ at multiple spatial scales. A possible mechanism behind these patterns is tree availability for nesting, which may differ relative to land cover composition. Tree availability can be a predictor of Ferruginous Hawk occupancy (Kennedy et al. 2014), but did not predict nest density (Schmutz 1989). Future habitat studies should evaluate how tree availability within prairie landscapes changes with land use and how that may influence nest site selection.

Nest survival was highest in areas with moderate edge densities and more grassland. However, contrary to our predictions, landscape characteristics did not predict clutch size nor fledging rates. We expected that grassland and edges would increase foraging opportunities either by increasing prey abundance (Zelenak and Rotella 1997, Downey et al. 2006) or accessibility to prey (Bechard 1982, Marsh et al. 2014). Therefore, we expected these landscape characteristics to be positively correlated with nest abundance (Schmutz 1989, Carbone and Gittleman 2002) and productivity (Zelenak and Rotella 1997, Schmutz et al. 2008). However, it is possible that these landscape characteristics did not influence foraging success, hawks were equally successful foraging across different landscapes, or contrary to previous studies (Smith et al. 1981, Schmutz 1987b, Schmutz and Hungle 1989b, Schmutz et al. 2008), foraging and productivity were not closely associated. A more detailed study of third order and fourth order habitat selection (Johnson 1980) for foraging habitat and perch use is needed to determine where hawks are most successful hunting and whether the availability of those features influences nest productivity. Furthermore, a better understanding of home range size relative to food availability and, relatedly, the influence of conspecific density on reproductive performance would be important for understanding the apparent association between nest density and reproduction.

Industrial development in the prairies has been a concern because the consequent landscape change and increased human activity may negatively influence Ferruginous Hawk habitat use. Our study did not find industrial features to be associated with relative nest abundance, but previous studies found mixed results. Ferruginous Hawks in Alberta and Saskatchewan were more likely to select landscapes with a higher density of resource roads (Chapter 2). In Wyoming, they selected higher density of roads that were not associated with resource extraction (Wallace 2014). Nests were more likely to be in close proximity to active oil wells in Utah (Keough and Conover 2012), as well as Alberta/Saskatchewan (Chapter 2). Our study may be best situated to evaluate the influence of industrial development because it was conducted over a large spatial extent. Furthermore, our stratified study design and even sampling across a gradient of industrial development intensities allowed us to draw robust conclusions regarding the influence of oil and gas development on nest abundance.

Nest survival, but not clutch size nor fledging rate, was predicted by several industrial variables in our study. Nest survival was lowest in landscapes with high densities of oil wells and conversely, higher for nests in moderate and high densities of active gas wells. Hawks may be responding differently to different levels of human activity associated with oil and gas extraction. Areas with high densities of active oil wells (e.g., pumpjacks and screwjacks) are associated with higher traffic volume and human activity because oil wells are maintained frequently, sometimes daily, and some have oil frequently hauled from storage tanks at well sites, using large, loud trucks. In contrast, gas wells are visited infrequently, only a few times a year. Given that hawks sometimes respond to human disturbance by flushing from nests (White and Thurow 1985, Schmutz 1987a, Nordell et al. 2017), reproduction may be negatively impacted by human disturbance when nesting occurs within areas with high densities of active oil wells. In contrast, gas wells may provide hawks with perches and a foraging advantage because gas wells do not have moving parts like active oil wells and are visited much less frequently for maintenance or other operations.

Future studies should evaluate how perch availability influences hunting success. Burrowing mammals may be more abundant near well sites because of higher heat, less compact soil, or shorter vegetation from mowing (for fire-safety) or from vehicle traffic along trails or over vegetation. Any third or fourth order selection studies (Johnson 1980) of foraging habitat should also evaluate how ground squirrel abundance is influenced by industrial development. Linking patterns to mechanisms is critical for predicting how changes to landscapes will influence Ferruginous Hawk populations.

Previous studies found varying relationships between industrial development and reproduction. Hawk reproduction was not influenced by oil and gas development (Utah, Keough et al. 2015; Wyoming, Wallace et al. 2016b; North Dakota, Wiggins et al. 2017). A North Dakota study found no differences in nest density or fledging rates with increased intensity of energy extraction; however, hawks were less likely to re-use nests in areas with high intensity extraction (Wiggins et al. 2017). Conversely, hawks in Wyoming showed only weak negative relationship between territory re-occupancy and oil and gas development (Wallace et al. 2016a). Regional and annual differences among studies may account for different patterns in habitat use and reproductive performance. Next steps should evaluate reproduction over a longer period to understand how both spatial and temporal variations influence reproduction.

Additive versus synergistic cumulative effects

Our study found that additive models of landscapes and human development were better predictors of relative nest abundance and nest survival than synergistic models that we tested. We tested several models built using a priori interactions between landscape and human development and found that these interactions only increased the complexity of the models, without improving model performance. Our study did not find any synergistic relationships between landscape and human development variables, but managers should still be aware of the possibility of interactions, including both additive and synergistic effects (Côté et al. 2016). Synergistic interactions may be less common than previously thought (Côté et al. 2016), but can still occur (Crain et al. 2008) and should be examined in risk assessments for wildlife populations (Oliver and Morecroft 2014, Côté et al. 2016). Conditions outside of those included in our study may have unpredictable effects and it is still difficult to predict types of interactions when mechanisms are unknown. For example, climate change could alter landscape characteristics or other ecosystem components (Pachauri et al. 2014) important to Ferruginous Hawks. Future studies should incorporate climate change forecasts to test for synergistic effects between seasonal weather and land use, particularly because seasonal weather was an important predictor for reproductive success.

Habitat quality

We assessed the association between land cover and relative nest abundance and also reproductive performance to identify potential habitat mismatches. Land cover characteristics were consistently predictors of home range habitat selection (Chapter 2), relative nest abundance, and nest survival. Proportion of grassland and edge density each showed similar relationships with habitat use and nest survival, suggesting that they can be used as general indicators of habitat quality at a regional or home range scale. However, influences of edge densities were not consistent among scales, so caution is needed when developing indicators of Ferruginous Hawk habitat quality. This difference in edge density between spatial scales is not uncommon (Aizpurua et al. 2017), and demonstrates that habitat models should not be used as sole indicators of habitat quality (Paton and Matthiopoulos 2016).

We detected a potential habitat mismatch between relative nest abundance and reproductive performance when Ferruginous Hawks nest near or in areas with high densities of active oil wells. Relative probability of home range habitat selection was predicted to be higher nearer to oil wells (Chapter 2). However, we found that hawks nesting near high densities of oil wells had lower nest survival compared to hawks nesting away from oil wells. This mismatch is concerning because Ferruginous Hawks nest in or near areas with high densities of active oil wells in southern Alberta and Saskatchewan. In addition, artificial nest platforms are commonly installed in or near areas with high densities of active oil wells to mitigate for disturbance or to move nesting birds off of energy infrastructure. These platforms may act as an ecological trap in areas with limited nest structure availability because hawks may select these platforms and experience reduced nest survival as a consequence for nesting in areas with high densities of active oil wells. Habitat mismatches have the potential ability to suppress breeding success; therefore assessing habitat quality for species management should include both relative nest abundance and reproductive parameters to reduce risk to populations (Arlt and Pärt 2007, Gilroy et al. 2011).

Habitat state

Categorizing the Ferruginous Hawk range in Canada into habitat states was useful identifying landscapes important to the population, as well as landscapes that may require intervention to reduce negative population impacts. At a township scale, approximately 10.1% of southern Alberta and Saskatchewan that is categorized as primary habitat, where both nest abundance and nest survival is predicted to be high. The Ferruginous Hawk population could benefit if these landscapes were protected or conserved. In contrast, approximately 7.91% of the landscape is moderate to high concern. Hawks would benefit if features on these landscapes were managed to reduce their attractiveness as habitat or if features, or the underlying mechanisms, that are associated with reduced nest survival are removed. Lastly, because these landscapes of concern have been spatially identified, habitat offsets in primary or secondary habitat could also reduce the overall negative impact on hawk populations.

This habitat state framework is advantageous compared to the habitat quality framework because it parses out landscapes of low habitat quality into landscapes where habitat relative nest abundance and reproductive performance are mismatched. Landscapes with moderate to high concern may have negative impacts to a population because they could act as ecological traps (Robertson and Hutto 2006, Gilroy et al. 2011). Identifying these landscapes and the mechanisms behind these patterns is critical to intervention and reducing their negative impact. Prioritizing these landscapes for management is also important and by parsing out landscapes of low concern, where nest abundance and nest survival are expected to be low, resources can be better focused on where intervention will potentially have the most benefit.

Management implications

Conserving patches of grassland within mosaic landscapes is important for maintaining Ferruginous Hawk habitat and promoting nest survival because nest abundance and nest survival were highest in landscapes with moderate amounts of grassland and cropland, and moderate amounts of edge density. The majority of grassland conservation is focused on conserving large, contiguous tracts of grasslands, yet moderately-sized grassland patches have the potential to provide habitat to a host of species that are less area-dependent (Walk et al. 2010), are not negatively influenced by edges, and do not require habitat corridors. Conserving and restoring grassland patches in landscapes with a cropland matrix is likely to benefit Ferruginous Hawk populations in Canada.

Multiple land uses on a landscape can have cumulative effects on Ferruginous Hawk habitat quality. The identification of landscapes with multiple stressors that influence habitat suitability and reproductive performance can be used to prioritize habitat stewardship, grassland conservation and restoration, reclamation of industrial development, and limiting further industrial development within certain areas (Fedy et al. 2014). Evaluating how human development in the Great Plains, such as conversion of grassland to cropland or development for petroleum extraction, influences species at risk and is important for predicting the effect of further landscape change, prioritizing conservation initiatives, and improving recovery efforts (Rudd et al. 2011).

TABLE 5. HABITAT STATE AND HABITAT QUALITY FRAMEWORK FOR FERRUGINOUS HAWKS NESTING IN SOUTHERN ALBERTA AND SASKATCHEWAN, BASED ON PREDICTED RELATIVE NEST ABUNDANCE AND NEST SURVIVAL.

Habitat state	Habitat quality	Description
primary habitat	high quality	high abundance and moderate to high nest survival
secondary habitat	moderate quality	moderate abundance and moderate to high nest survival
high concern	low quality	high abundance and low nest survival
moderate concern	low quality	moderate abundance and low nest survival
low concern	low quality	low abundance and low-high nest survival

TABLE 6. STANDARDIZED ESTIMATED COEFFICIENTS (B) AND STANDARD ERRORS (SE) FOR THE FINAL RELATIVE NEST ABUNDANCE MODEL FOR FERRUGINOUS HAWKS IN SOUTHERN ALBERTA AND SASKATCHEWAN, FROM 2012 TO 2013.

Variable	β	SE	P	95% CI	
				Lower	Upper
latitude	53.672	20.786	0.01	12.932	94.411
latitude quadratic	-0.541	0.207	0.009	-0.947	-0.135
proportion of grass	4.914	1.715	0.004	1.552	8.276
proportion of grass quadratic	-4.600	1.703	0.007	-7.939	-1.262
edge density	0.016	0.006	0.006	0.005	0.028
edge density quadratic	0.000	0.000	0.025	0.000	0.000
area-weighted proportion of regosolic soil	-3.252	1.775	0.067	-6.731	0.228

TABLE 7. AKAIKE'S INFORMATION CRITERION (AIC) SUMMARY FOR LOGISTIC NEST EXPOSURE MODELS TESTING CUMULATIVE EFFECTS HYPOTHESES THAT PREDICT FERRUGINOUS HAWK NEST SURVIVAL IN SOUTHERN ALBERTA AND SASKATCHEWAN, FROM 2010 TO 2015. WE REPORT MODEL FRAMEWORK (MODEL), MODEL DESCRIPTION FOR INTERACTION/SYNERGISTIC MODELS, DEGREES OF FREEDOM (DF), LOG-LIKELIHOODS (LL), AIC, CHANGE IN AIC FROM LOWEST MODEL (Δ AIC), AND AKAIKE WEIGHTS(w_i), AND AREA UNDER THE CURVE (AUC).

Model	Interaction description	df	LL	AIC	Δ AIC	w_i	AUC
base + land *energy	edge*oilLMH	28	-945.851	1948.1	0	0.408	0.838
base + land *energy	grass*oilLMH	26	-948.316	1949	0.88	0.263	0.839
base + land + energy [1]		24	-950.537	1949.3	1.27	0.216	0.837
base + land *energy	grass*gasLMH	26	-949.559	1951.4	3.37	0.076	0.838
base + land		21	-955.695	1953.6	5.53	0.026	0.835
base + land *energy	edge*gasLMH	28	-949.365	1955.1	7.03	0.012	0.838
base + land		20	-967.741	1975.7	27.6	0	0.829
base		17	-971.557	1977.3	29.18	0	0.827

[1] The additive model is best because it has the fewest parameters with the lowest delta AIC and highest AUC.

TABLE 8. STANDARDIZED PARAMETER ESTIMATES (ß) AND STANDARD ERRORS FOR THE TOP NEST SURVIVAL MODEL FOR FERRUGINOUS HAWKS IN SOUTHERN ALBERTA AND SASKATCHEWAN FROM 2010 TO 2015. WE USED 728 NESTS AND 4,384 NEST VISITS TO BUILD THE MODEL. SEE TABLE 17 FOR A COMPLETE LIST OF VARIABLES AND THEIR COEFFICIENTS IN THE TOP MODEL.

				95% CI	
Variable	Estimate	SE	p-value	Lower	Upper
proportion of grass	-0.175	0.06	0.01	-0.30	-0.05
edge density	0.119	0.06	0.04	0.01	0.23
edge density quadratic	-0.063	0.04	0.13	-0.14	0.02
oil well density – low					
oil well density - medium	0.214	0.17	0.20	-0.11	0.54
oil well density - high	-1.182	0.26	0.00	-1.69	-0.67
gas well density - low					
gas well density - medium	0.422	0.15	0.01	0.13	0.72
gas well density - high	0.352	0.16	0.03	0.04	0.67
intercept	3.534	0.42	0.00	2.72	4.35

TABLE 9. SUMMARY OF SPECIES RANGE CATEGORIZED AS HABITAT STATE AND HABITAT QUALITY.

Habitat state	Proportion of study area	Habitat quality	Proportion of study area
Primary habitat	10.1	High quality	10.1
Secondary habitat	26.17	Moderate quality	26.17
High concern	2.01	Low quality	63.72
Moderate concern	5.9		
Low concern	55.81		

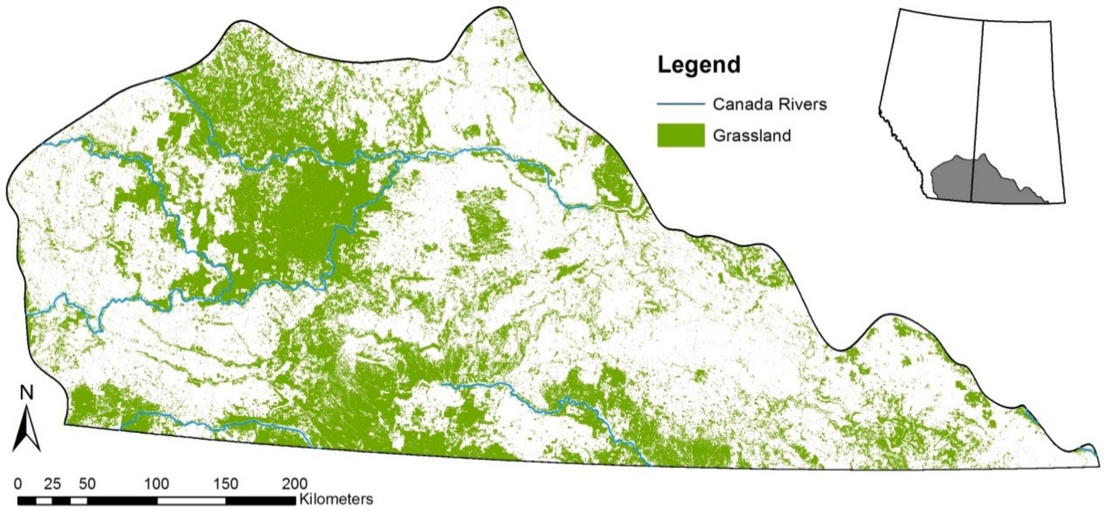
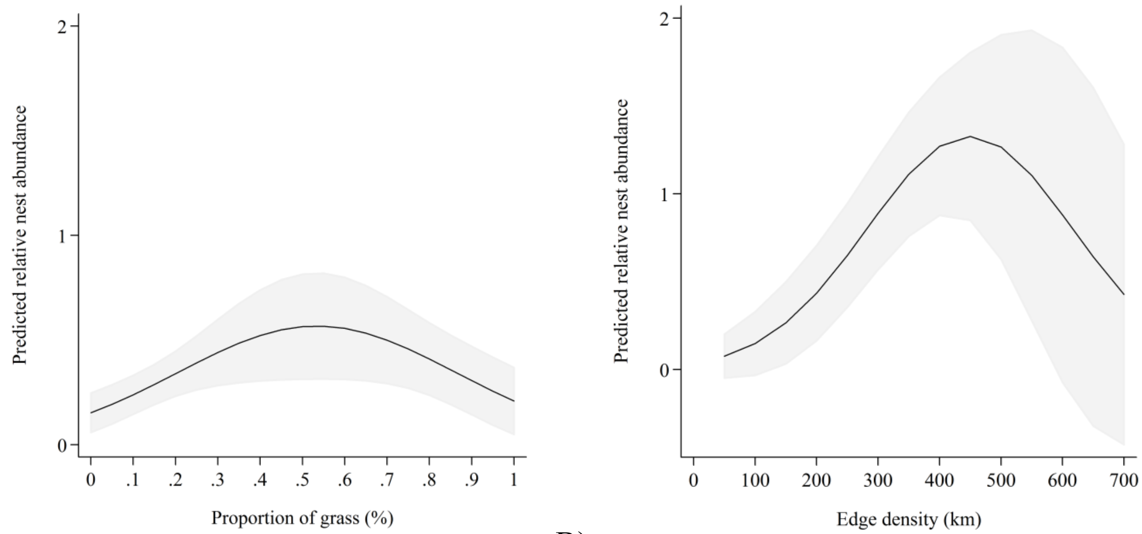


FIGURE 7. STUDY AREA IN SOUTHERN ALBERTA AND SASKATCHEWAN WHERE NEST SURVEYING AND REPRODUCTIVE MONITORING WAS CONDUCTED FROM 2010 TO 2015.



A) B)

FIGURE 8. PREDICTED RELATIVE NEST ABUNDANCE AND 95% CONFIDENCE INTERVALS FOR FERRUGINOUS HAWK NESTS IN SOUTHERN ALBERTA AND SASKATCHEWAN, AS A FUNCTION OF A) PROPORTION OF GRASS AND B) EDGE DENSITY WITHIN THE SURROUNDING TOWNSHIP.

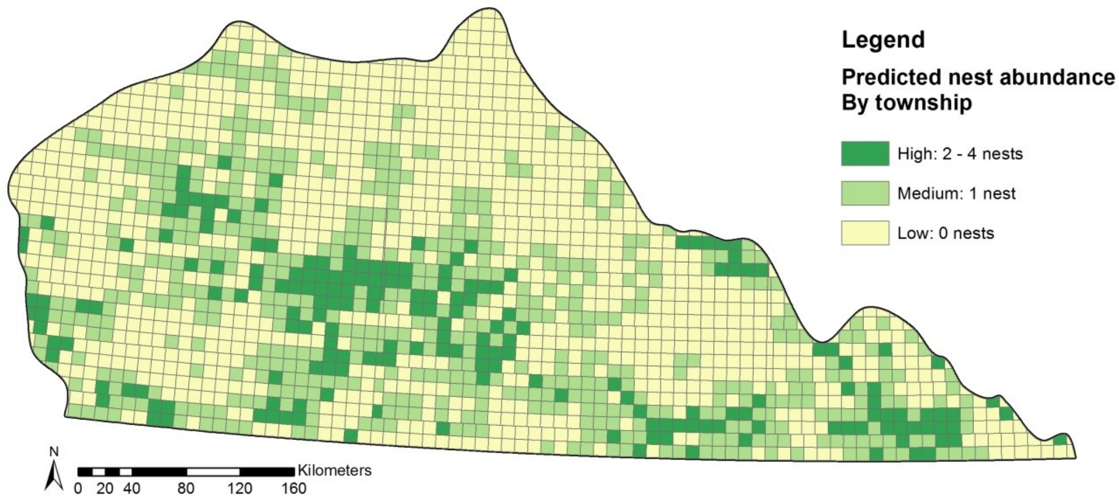


FIGURE 9. PREDICTED RELATIVE NEST ABUNDANCE PER TOWNSHIP BASED ON LANDSCAPE CHARACTERISTICS OF FERRUGINOUS HAWKS IN SOUTHERN ALBERTA AND SASKATCHEWAN, AS DETERMINED BY THE FINAL TOP ABUNDANCE MODEL.

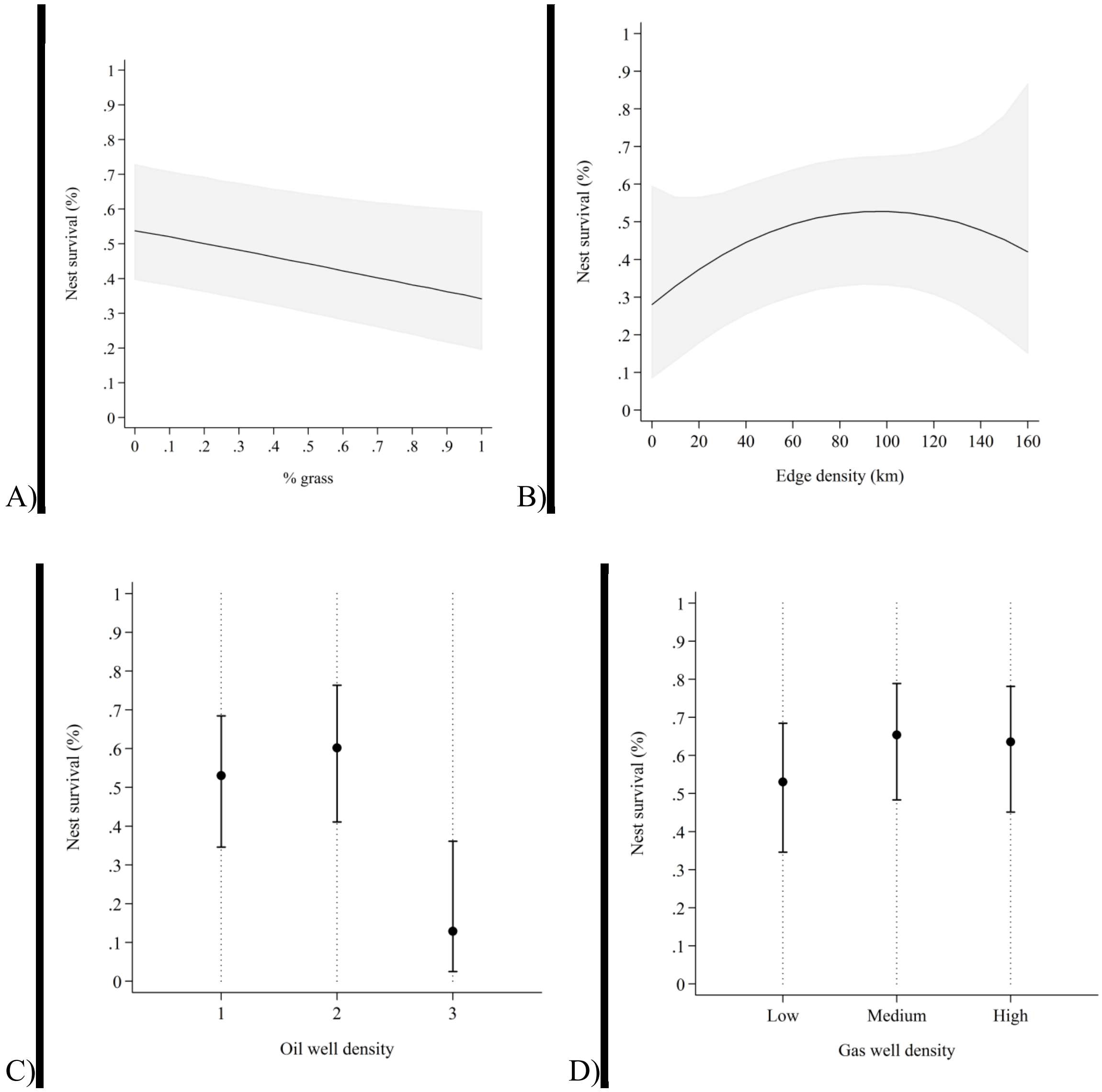


Figure 10. Predicted nest survival and 95% confidence intervals for Ferruginous Hawks in southern Alberta and Saskatchewan from 2010 to 2015, as a function of A) proportion of grass, B) edge density (km) which included grass-cropland interface, roads, and water body and wetland edges, C) active oil well density, where 0 wells = low, ≤ 25 wells = medium, and > 25 wells = high, and D) active gas well density, where 0 wells = low, ≤ 25 wells = medium, and > 25 wells = high within 2.5 km radius of the nest.

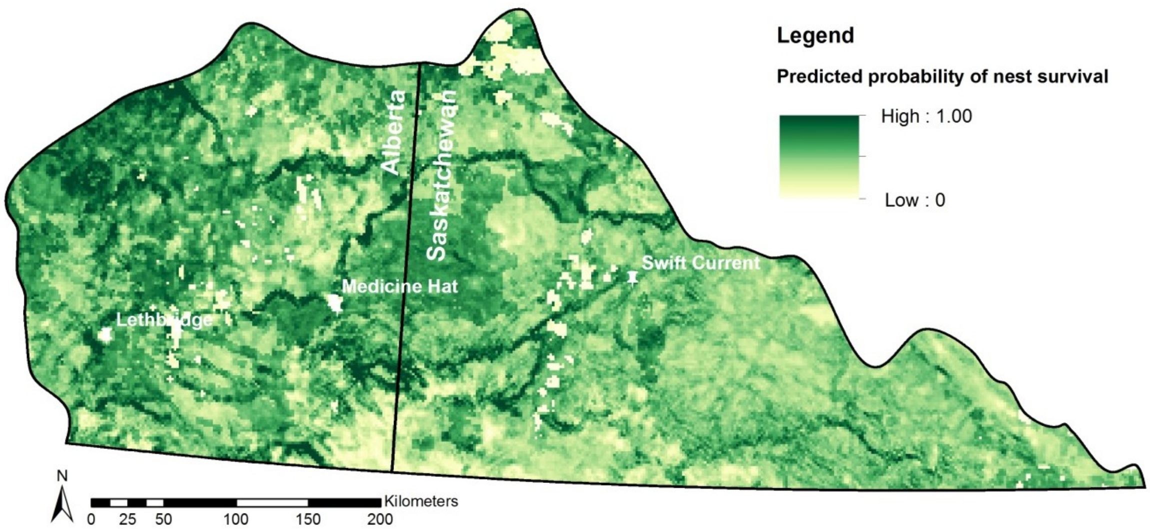
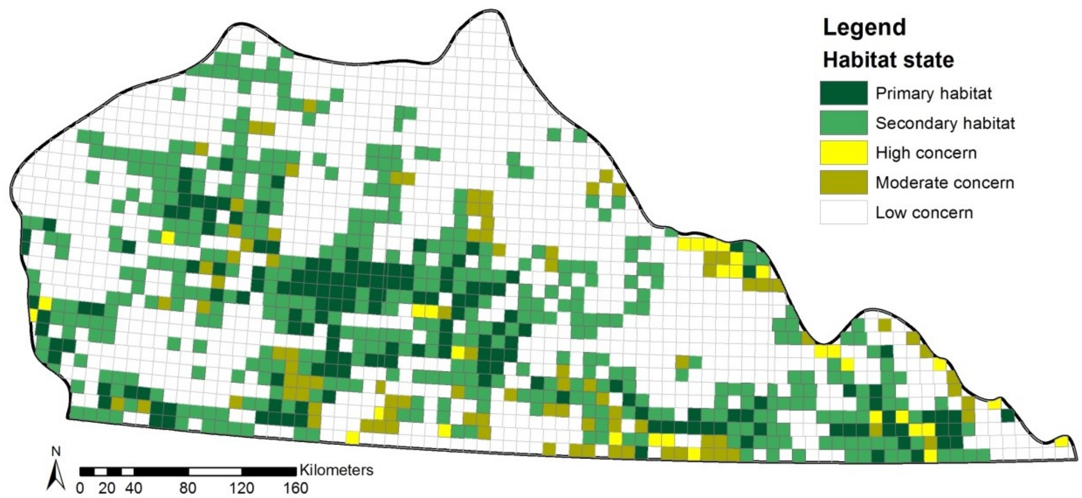


FIGURE 11. PREDICTED NEST SURVIVAL BASED ON LANDSCAPE CHARACTERISTICS OF FERRUGINOUS HAWKS IN SOUTHERN ALBERTA AND SASKATCHEWAN, AS DETERMINED BY THE FINAL TOP LOGISTIC NEST EXPOSURE MODEL. HIGHER PREDICTED PROBABILITY OF NEST SURVIVAL, AS SHOWN BY DARKER COLOURS, PREDICTS THAT FERRUGINOUS HAWK NESTS ARE MORE LIKELY TO SURVIVE UNTIL AT LEAST ONE YOUNG FLEDGES NATURALLY.

A)



B)

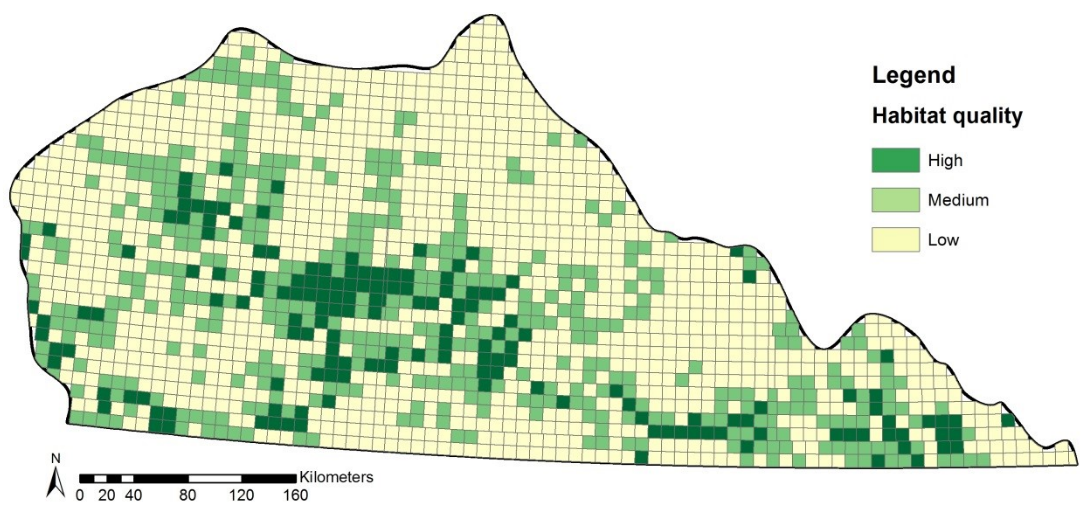


FIGURE 12. A) HABITAT STATE AND B) HABITAT QUALITY FOR FERRUGINOUS HAWKS, AS PREDICTED BY RELATIVE NEST ABUNDANCE AND AVERAGE NEST SURVIVAL PER TOWNSHIP, IN SOUTHERN ALBERTA AND SASKATCHEWAN.

Chapter 4: Landscape characteristics, industrial development, and weather influence brood provisioning by Ferruginous Hawks

Abstract

Animals should select habitat that optimizes their food intake and relatedly, brood provisioning. Understanding the linkage between landscape characteristics and weather with brood provisioning may be particularly important for predators that are central place foragers and have population dynamics closely linked to a specific prey species. Identifying these linkages has implications for quantifying habitat quality. We assessed how landscape characteristics, climate, and weather can potentially influence Ferruginous Hawk (*Buteo regalis*) brood provisioning in Canada. We quantified prey deliveries at Ferruginous Hawk nests using video footage collected at nests. We assessed how land cover composition, edge density, industrial development, and seasonal weather influenced prey delivery rates, diversity of delivered prey, and estimated prey biomass delivered to nestlings per day and by season. Our results demonstrate that the conventional hypothesis that amount of grass cover around a nest is positively associated with ground squirrel delivery to the brood was not supported, and we found no strong landscape predictors for ground squirrel delivery rate. Richardson's ground squirrels (*Urocitellus richardsonii*) are the most important prey item in the diet of Ferruginous Hawks across our broad study area in Canada because they composed the vast majority of biomass delivered to broods. However, hawks that delivered somewhat more diverse prey were also more likely to return more total estimated biomass compared to hawks that deliver mostly ground squirrels. Seasonal weather influenced prey delivery rates, but not diversity. Evaluating how the

landscape around a nest and seasonal weather influences brood provisioning will inform how landscape or climate change could potentially increase or decrease habitat quality.

Keywords

Cumulative effects; habitat quality; diet; foraging; habitat effects; habitat fragmentation; habitat loss

Introduction

Animals are hypothesized to optimally forage under given conditions (Pyke 1984) and they should, therefore, select habitat that optimizes their food intake (Fretwell and Calver 1969, Fretwell 1972, Donazar et al. 1993, Schaefer and Messier 1995, Lyons 2005). Predators may forage where food availability is higher (Lantz et al. 2010, Terraube et al. 2011, Robinson et al. 2014), which can be influenced by many factors. Climate and weather can influence prey abundance, particularly for small mammals, by affecting their phenology, habitat selection, survival, and reproduction (Merritt et al. 2001, Heisler et al. 2014, Santoro et al. 2017). Prey may be more abundant in some locations or areas compared to others because of habitat-specific availability (Morris 2005, Avila-Flores et al. 2010, Fuhlendorf et al. 2010, Heisler et al. 2013, Olson et al. 2017).

Selection of foraging habitat by predators may in part reflect prey abundance but also accessibility of that prey (Cody 1985, Morris et al. 2001). Structural characteristics of the habitat can influence a predator's ability to capture prey (Latham et al. 2011a). For example, some raptor species are able to capture small mammals more effectively in sparser vegetation, where these prey are more easily seen and captured, compared to denser vegetation where prey may be more abundant but harder to detect and capture (Swainson's Hawks (*Buteo swainsonii*) (Bechard 1982); Burrowing Owls (*Athene cunicularia*) (Marsh et al. 2014); Lesser Kestrels (*Falco naumanni*) (Rodriguez et al. 2013)). Habitat features, such as perches for predatory birds that use sit-and-wait techniques, can also improve a predator's hunting efficiencies (Hall et al. 1981, Yosef and Grubb 1993, Meunier et al. 2000). Weather can affect day-to-day foraging (Sunde et al. 2014), such as when storms impair hunting behaviour or reduce detection or activity of prey. Thus, foraging yield can be influenced by prey abundance and accessibility (Dawson and Bortolotti 2000, Ontiveros et al. 2005, Wiens et al. 2006, Robinson et al. 2017).

Identifying factors or patterns associated with foraging yield is important during the breeding season for altricial birds because energy demand is particularly high during that period, as adults must obtain food to sustain themselves and their growing young (Wellicome et al. 2013). Studies have shown that higher provisioning rates are more likely to be associated with higher nestling survival (Perrig et al. 2014, Grüebler et al. 2018), growth rates (Granbom et al. 2006), body condition (Dawson and Bortolotti 2000), and number of fledglings per brood (Wellicome et al. 2013). Habitat may influence provisioning rates and consequently, reproductive performance (Wakeley 1978, Morris and Davidson 2000, Sergio et al. 2003, Hinam and St. Clair 2008, Herring et al. 2010). If provisioning rates are related to habitat use and reproductive success, provisioning rate can be used as an indicator of habitat quality (Grüebler et al. 2018).

Understanding the linkage between landscape characteristics and prey delivery to nests may be particularly important for central place foragers and for predators that are closely linked to a specific prey species. During the breeding season, Ferruginous Hawks (*Buteo regalis*) nesting in Alberta capture mostly Richardson's ground squirrels (*Urocitellus richardsonii*), which make up 89 - 95% of the biomass consumed (Schmutz et al. 1980a, Schmutz et al. 2008). Studies have shown that Ferruginous Hawk reproductive performance is linked to the availability of their local primary prey species (Richardson's ground squirrels in Alberta (Schmutz and Hungle 1989b, Schmutz et al. 2008), black-tailed jackrabbits in Utah (Smith et al. 1981, Schmutz and Hungle 1989b). Determining if and how landscape characteristics in a Ferruginous Hawk home range influence provisioning rate may identify elements important to habitat quality. Understanding this relationship is important to predicting how landscape change could influence provisioning rate and potentially, in turn, reproductive success (Grüebler et al. 2018). For Ferruginous Hawks, this is particularly important because they are a threatened species at risk, and habitat loss is thought to be a limiting factor influencing their population decline (SAR Public Registry 2010).

Ferruginous Hawks nest in landscapes that range from low to high amounts of grassland (Schmutz 1989, Ng et al. 2017); however, it is unknown whether Ferruginous Hawks nesting in cropland-dominated landscapes have provisioning rates equal to those of hawks nesting in grassland-dominated landscapes. It is commonly hypothesized that Ferruginous Hawks with large amounts of grassland in their home ranges have highest brood provisioning rates. The hawk's main prey in Canada, the Richardson's ground squirrel, is more abundant in grassland than in cropland (Schmutz 1989, Downey et al. 2006, Fortney 2013), and ground squirrels may be more accessible to hunting hawks in shorter vegetation because prey are more visible and with less physical obstruction for prey capture (Bechard 1982). A competing hypothesis is that hawks may deliver similar amounts of biomass to their brood, either by capturing more diverse prey or catching similar numbers of ground squirrels in patches of grassland or along land cover edges, when nesting in mosaic or cropland-dominated landscapes. Evaluating how the landscape around nests influences brood provisioning should provide insight into how landscape change may alter habitat quality, in situations where food availability limits reproduction.

We investigated the ecological and anthropogenic factors that influence provisioning at Ferruginous Hawks nests in Canada. We assessed brood provisioning using digital video footage at hawk nests located along a gradient of natural to human-dominated landscapes. Our primary goal was to evaluate if hawks nesting in different landscapes were able to provide similar prey delivery rates and, using biomass as a proxy, caloric rates to their nests. We hypothesized that hawks nesting in landscapes with more grassland and higher edge density will deliver the most food to nests, predicting more specifically that the most ground squirrels and biomass will be delivered to broods in such landscapes. Second, we examined the relationship between landscape characteristics, prey delivery rates, and diversity of diet. We hypothesized that Ferruginous Hawks that nest in more heterogeneous landscapes may opportunistically capture and deliver a higher diversity of prey to the nest because a range of vegetation heights and edges, which are associated with heterogeneous landscapes, should be exploited by foraging Ferruginous Hawks. We predicted that hawks nesting in mosaic grassland-cropland landscapes with higher edge density would have higher delivery rates and a more diverse prey set. Hawks delivering a more diverse prey set may also deliver less biomass compared to hawks delivering primarily ground squirrels because we predicted that most other prey would be smaller than ground squirrels. We discuss our findings within the context of understanding how the landscape surrounding a Ferruginous Hawk nest may influence prey delivery rates and thus have potential fitness consequences.

Methods

Study Area

Ferruginous Hawk nests were monitored in southern Alberta and Saskatchewan, where the majority of Ferruginous Hawks nest in Canada and is the northern range for the species distribution (Ng et al. 2017). The study area (~153,000 km^2) and the centre of located at 50° 10' 11.604" N, 109° 55' 39.6048" W (Figure 13). It includes fescue, mixed-moist grassland, and shortgrass ecoregions where land cover is predominantly cropland and grassland. Dominant species in grassland communities include blue gramma grass (*Bouteloua gracilis*), needle and thread grass (*Stipa comata*), and wheat grasses (*Elymus* spp.). Most grassland is grazed by cattle. Common crops include canola (*Brassica* spp.), cereals such as wheat, clover (*Trifolium* spp. and *Meliliotus* spp.), and pulse crops (e.g., *Pisum* spp., *Lens* spp., dry beans). Chernozem and solonetzic soils are the dominant soil orders throughout the study area (SLC v3.2). Oil and gas extraction and wind power generation are other land uses, showing generally clustered distribution. Mean spring temperatures (March - May) were 6.5˚C and mean summer temperatures (June - August) were 18.7˚C (Medicine Hat, Alberta, Environment Canada and Climate Change). Mean cumulative precipitation during the spring is 82.7 mm and 135.9 mm during the summer.

Study Design

We monitored Ferruginous Hawk nests located along a gradient of human development, using a stratified block design. Nests were stratified first by amount of human land cover change, where nests were located in landscapes ranging from low proportions of cropland (i.e., high proportions of grassland) to high proportions of cropland (i.e., low proportions of grassland). Nests were further stratified into landscapes with low to high amounts of human development, including oil and gas infrastructure, road density, power transmission infrastructure, and human structures such as buildings.

Video footage

We used the above stratified block design to select a subset of nests to monitor using digital video cameras. Once nestlings were a minimum of 7 days old, two to three closed-circuit television (CCTV) cameras were installed near the nest and wired to a digital video recorder. One camera was mounted to provide a wide angle view so the entire nest was in view to include prey deliveries, bird behaviour, and other possible events at the nest. A second camera was mounted with a closer view, pointed towards the entrance of the nest, to capture a more detailed view of prey being delivered. Video footage was collected until the nest outcome was finalized (i.e., if the nest was predated or if the young fledged). Footage from 4 am to midnight was viewed and catalogued for prey deliveries. Date and time of delivery, prey order, prey guild, and prey species were recorded for each prey delivery.

Response variables

Prey delivery rate (hereafter referred to as PDR) was calculated as the number of prey delivered per day per nest. Unknown identifications were by classified to order and guild by assigning identities based on proportions of identified prey delivered to each nest.

We also estimated total biomass delivered to each nest for each day of watched footage. Biomass was estimated by guild, and amphibians were excluded from these analyses because they were rarely delivered to the nest (0.004% of prey deliveries were amphibian). Mass for the most commonly observed species of each guild were averaged to create a biomass proxy for each guild (Table 22).

Diversity of prey guilds was measured using the Shannon-Wiener index (Appendix C).

Predictor variables

We controlled for nuisance variables, including nest characteristics, spatial, and temporal variables that could potentially influence prey delivery rate and prey diversity. The influence of brood size, date, year, nestling age, number of days watched, hatch date, and the latitude and longitude of the nest were used to build a base model for each analysis.

Our study objectives were to evaluate the influence of landscape characteristics on prey delivery rate, but seasonal weather can also influence local small mammal abundance (Heisler et al. 2014). We controlled for these spatial and temporal patterns by including mean temperature, precipitation (mm), degree days below 0˚C, and precipitation as snow (mm) for winter (December of previous year to February), spring (March, April, and May), and summer (June, July, an August) (Wang et al. 2011). We chose to control for seasonal rather than daily weather for two reasons. First, exploring seasonal weather allowed us to examine the influence of longer term weather patterns on food availability, where prey delivery rate relative to daily weather likely stems from behavioural responses by hawks or their prey. Controlling for seasonal weather as a longer term variable suits our research objective because we are evaluating the influence of large spatial scale land cover patterns. Second, we also limited the confounding influence of daily weather by watching footage on days without inclement weather (i.e., no rain). Other weather patterns likely have little day-to-day influence on prey delivery rate because Ferruginous Hawks mainly forage during the morning and early evening, when temperatures and wind are less extreme.

Landscape and human development characteristics were quantified for each nest using geographic information system (ESRI 2012). We summarized the landscape within 1000 m buffer of each nest, which reflects the majority of a Ferruginous Hawk's core home range (J. L. Watson, unpublished data, Ng et al. 2017). We used spatial data that included ground-truthed land cover data and existing databases. Land cover was quantified as proportion of grassland cover within a 1000 m radius (AAFC 2000 Land cover). We restricted our land cover analyses to grassland cover because it is highly negatively correlated with cropland cover in southern Alberta and Saskatchewan. We also quantified the edge density around each nest by measuring the edges of water bodies and wetlands, where grassland and cropland cover interface, and roads within 1000 m radius of the nest. Industrial development was quantified as road density, active oil and gas well density. We also measured the distance to the nearest road or well feature (IHS Global Canada Ltd. 2013).

Model development

We developed a suite of models to predict prey delivery rate and prey diversity. These response variables were evaluated at both the daily and seasonal scale. Daily biomass delivered to the nest was important to measure to compare if daily prey delivery rate was similar across home ranges composed of different land covers. However, some analyses at the seasonal scale are important to understanding prey delivery over a longer time scale. For example, prey diversity was quite low on a day-to-day basis because the total numbers of prey deliveries per day were also low relative to cumulative seasonal totals. As more video was watched for the nest over the season (i.e., more days were catalogued), then prey diversity captured at each nest increased because there were more hunting opportunities analyzed. Therefore, prey diversity over the season may be more reflective of prey types captured by hawks.

We also developed prey delivery models that included only Richardson's Ground Squirrels to explore the influence of landscape on the Ferruginous Hawks' main prey source while removing the analytical noise caused by including other prey types. See Appendix C materials for a detailed description of model development.

Top models to describe 1) daily prey delivery rate, 2) daily Richardson's Ground Squirrel delivery rate, 3) Richardson's Ground Squirrel delivery over the season, 4) daily prey diversity, and 5) seasonal prey diversity were developed.

Variables were categorized into five sets: base variables, landscape, industrial development, and seasonal weather (Table 23). Variables were standardized to have a mean of zero and a standard deviation of one.

The number of days watched per nest and the total number prey items delivered were always included in seasonal models. We simplified models within variable sets by removing non-influential variables and developing parsimonious variable sets using forward stepwise selection (Burnham and Anderson 2002, Arnold 2010).

Prey delivery rate

Mixed effect negative binomial regression was used to analyze the influence of the predictor variables on daily prey delivery rate. Nest was included as a random effect because multiple days of video were catalogued for the majority of nests and this approach controlled for individual differences among pairs.

Estimated biomass delivered

Spearman's rank correlations were used to assess whether daily estimated biomass was correlated to daily prey delivery rate and daily prey diversity delivered.

Diversity

Daily prey diversity delivered to the nest was highly skewed to low diversity (H=1 for 62% of days (n=320). To overcome this left skewed distribution, we simplified the analyses to explore low versus high prey diversity. Diversity was categorized into low (H=1) and high (H>1). We used mixed effect logistic regression and with the individual nest as a random effect.

We also used t-tests to evaluate whether daily prey deliveries that had either high or low diversity prey returns had different daily prey delivery rates and estimated total biomass delivered.

Results

In 2011 to 2013, nest footage was collected for 82 nests. We watched a total of 320 days of footage, averaging 5 ± 0.15 days of video for each nest, ranging from 1 to 13 days. Age of nestlings ranged from 7 to 65 days old and the average age at camera set up was 25 ± 1.0 (mean ± SE) days old. We observed both sexes of the adults delivering prey to the nest.

The average number of items delivered to the nest per day was 5.17 ± 0.19 and ranged from one to 17 items. One nest had 27 items delivered during one day and was excluded as an outlier. The majority of nests received one to five items per day (61.25% of days).

The most common prey items were Richardson's Ground Squirrels, which composed 84% of all recorded prey deliveries at all nests (Figure 14). Mice (*Peromyscus* spp.) and voles (*Microtus* spp.) were the second most frequently delivered prey (Figure 14Figure **14.** Prey composition by frequency (light bars) and estimated total biomass (dark bars) delivered to all nests in the study.). On average of 4.36 ± 0.18 ground squirrels per day were delivered at each nest, ranging from one to 25 squirrels. On days with more than one prey items being delivered, only ground squirrels were delivered 56% (159/283 days) of days.

Ground squirrels contributed the most estimated biomass to nests (93%), averaging 1853 ± 76 grams of squirrel per day. Mammalian prey composed 94% of the estimated biomass delivered, followed by avian prey (6%) and amphibians that contributed a small estimated biomass (<0.01%).

Model 1: Daily prey delivery rate, all prey included

When all prey were included in the analysis, the daily prey delivery rate decreased with increasing nestling age (β = -0.186, SE = 0.038, p-value = <0.001) (all beta and SE values are standardized) and increased with brood size (β = 0.072, SE = 0.329, p-value = 0.028). We observed an average of 0.127 ± 0.00 deliveries/nestling/hr. Prey delivery rates were highest for nests that hatched between May 16th and June 1st (β = 3.043, SE = 1.096, p-value = 0.005; quadratic β = -3.091, SE = 1.089, p-value = 0.005) (Figure 15). Daily prey delivery rate was also negatively associated with average spring temperature (β = -0.101, SE = 0.036, p-value = 0.006). Decreased tree cover on the landscape (β = -0.963, SE = 0.392, p-value = 0.014) and increased grass cover (β = 0.098, SE = 0.038, p-value = 0.009) were also associated with daily prey delivery rate. Nests with a higher number of active oil wells (β = -0.070, SE = 0.034, p-value = 0.064) were more likely to have fewer prey items delivered (Figure 16). An interaction between spring temperature and proportion of grass predicted daily PDR, where PDR highest if the spring temperatures were cool (<3˚C) and when spring temperatures were over 3˚C, PDR increased with the proportion of grass surrounding the nest (Figure 17).

Model 2: Daily prey delivery rate, only Richardson's Ground Squirrels included

When the models were restricted to only ground squirrel deliveries, the top model was similar to the inclusive model minus any land cover predictors (Figure 18, Table 10).

Model 3: Seasonal prey delivery rate, only Richardson's Ground Squirrels included

We found that the total number of ground squirrels delivered per nest over the season (i.e., over the total number of days watched) was negatively associated with the total number of days watched per nest ($\beta = -0.056$, SE = 0.046, p-value = 0.219), positively associated with the total number of prey items delivered ($\beta = 0.648$, SE = 0.053, p-value = <0.001), and negatively associated with the total estimated summer precipitation ($\beta = -0.105$, SE = 0.040, p-value = 0.009) (Figure 19).

Prey diversity

The average Shannon Weiner Diversity Index was 1.34 ± 0.03, ranging from 1 to 3.21. From 320 days of footage, 199 days (62%) had an H index of 1. Of the days with an H index of 1, 196 days (98%) were nests that only received ground squirrels.

Model 4: Daily prey delivery diversity

Daily prey diversity was more likely to be high with decreased tree cover ($\beta = -0.397$, SE = 0.216, p-value = 0.066), increased grassland ($\beta = 0.365$, SE = 0.184, p-value = 0.047), and increased water cover (β = 0.291, SE = 0.169, p-value = 0.085). We found an interaction between the amount of grassland and water surrounding the nest, where diversity was most likely to be high in landscapes with low amounts of grass and higher water cover. The influence of water cover diminished as amounts of grassland increased (Figure 20).

Model 5: Seasonal prey delivery diversity

Prey diversity over the season at a nest was more likely to be higher as more days of video were watched per nest (β = -0.232, SE = 0.109, p-value = 0.034) and cumulative total number of observed prey were delivered (β = 0.273, SE = 0.108, p-value = 0.012). Higher diversity was associated with intermediate amounts of grassland (linear β = -0.893, SE = 0.327, p-value = 0.006, quadratic β = 0.870, SE = 0.328, p-value = 0.008) (Figure 21), higher amounts of water (β = 0.281, SE = 0.730, p-value = 0.000) (Figure 22), less shrub cover (β = -0.127, SE = 0.070, p-value = 0.068), and more active oil and gas wells (β = 0.173, SE = 0.076, p-value = 0.023).

Estimated biomass delivered

Daily prey delivery rate and daily estimated biomass delivered were highly correlated (Spearman's rho = 0.946, p-value = 0.00). We observed an average of 48.85 ± 2.39 grams of biomass delivered per nestling per hour (g/nestling/hour).

Daily diversity had little correlation with daily prey delivery rate (Spearman's rho = 0.342, p-value = 0.00) and daily estimated biomass delivered (Spearman's rho = 0.208, p-value =

0.00). However, hawks that had higher than average daily prey delivery rate (>5 items/day) delivered a more diverse set of prey ($t = -5.2814$, p-value = 0.00). Relatedly, birds that delivered $H>1$ prey diversity on any given day were more likely to deliver higher estimated biomass compared to birds that brought only one type of prey back ($t = 4.29$, p-value = <0.001) (estimated biomass on days with $H>1$ = 2395 grams, $H=1$ = 1750 grams) (Figure 23).

Discussion

Breeding Ferruginous Hawks must meet similar energetic demands for their families regardless of the particular spatial or temporal context in which they are nesting. Our prey delivery rates and diet composition by order were similar to other studies that used camera or video footage (Giovanni et al. 2007, Keeley and Bechard 2017). Our study found mammals accounted for 91% of diet by frequency and 94% of biomass delivered to nests (n=83), which is similar to Ferruginous Hawks in New Mexico [89% of diet by frequency and 98% by biomass (n = 6) and the southern Great Plains (73% of diet by frequency and 82% by biomass (n = 12)]. In the southern Great Plains, Ferruginous Hawks were documented delivering ~4.6 items/day at 670 ± 46 g/nestling/day (Giovanni et al. 2007) compared to our observed 5.17 items/day at 976.96 ± 47.72 g/nestling/day (n = 83). Hawks in New Mexico delivered 42 g/hr/nestling at 0.20 deliveries/nestling/hr (Keeley and Bechard 2017) where hawks in southern Great Plains (Giovanni et al. 2007) delivered 46 g/nestling/hr at 0.13 deliveries/nestling/hr. Our study was similar where we found an average of 48.85 ± 2.39 g/nestling/hour at 0.127 ± 0.00 deliveries/nestling/hr. Despite different prey bases, study areas, and years of studies, these three studies showed comparable delivery rates.

Similar to previous studies, we found that Richardson's ground squirrels are the major component of Ferruginous Hawk nestling diets in Alberta and Saskatchewan. However, our hypothesis that amount of grass cover around each nest is positively associated with ground squirrel delivery to the nest was not supported by our results. A weak positive relationship with coarse soil texture was included in an earlier candidate model exploring daily delivery of ground squirrels, but no landscape variables were included in the top model. Daily delivery of ground squirrels was lower for nests located near higher densities of active oil wells, but large confidence intervals suggest the relationship is weak. More research with a larger sample size and wider gradient of oil well densities may clarify this relationship. Our seasonal analyses of ground squirrel delivery did not find any landscape or industrial development predictors, suggesting that hawks are able to capture similar numbers of ground squirrels across a gradient of land covers. Ground squirrels are likely not equally available across landscapes (Downey et al. 2006, Fortney 2013, Bylo et al. 2014), and it is unknown if hawks are foraging selectively within specific land cover types (Wakeley 1979) or foraging across varying home ranges sizes (Leary et al. 1998, Santangeli et al. 2012). Future studies should evaluate third order habitat selection (Johnson 1980) by Ferruginous Hawks to understand in detail how they are able to deliver equal amounts of prey to nests located across a gradient of land cover types.

Our results show that frequency of prey delivery was positively correlated with prey diversity. Top models for prey diversity at daily and seasonal time scales varied somewhat in their set of predictor variables. On a daily basis, prey diversity was highest in landscapes with less tree cover and when nests were located in high amounts of cropland with high water cover. Over a season, prey diversity was higher at nests with more heterogeneous landscapes as characterized by moderate amounts of grassland, more water cover, less shrub cover, and more active oil and gas wells. These landscape features are often associated with higher edge density, perch density, and more heterogeneous vegetation coverage at small spatial scales, which may increase foraging yield for hawks. For example, active oil or gas wells may increase the heterogeneity of a landscape because they are often associated with roads with mowed ditches and other vegetation edges. They are also associated with infrastructure that could be used as perches by hawks. Wetlands and water bodies will have riparian vegetation and are also associated with different prey communities, including waterfowl and shorebirds. Hawks nesting in rural grasslands and grasslands near settlement in New Mexico, USA, differed in terms of the prey taxon compositions and amounts of biomass delivered to their nests, but this difference was attributed to the five-fold difference in Gunnison's prairie dog (*Cynomys gunnisoni*) abundance between the two landscape types (Keeley et al. 2016). Future studies should evaluate how prey diversity and abundance are associated with landscape characteristics and human infrastructure.

Hawks that delivered higher diversity prey generally had higher PDR, but more importantly, were likely to bring in 25% more biomass on a daily basis. This refutes our hypothesis that a more diverse diet and higher PDR is a sign of hawks compensating for lower ground squirrel delivery. Our study suggests that a more diverse diet could benefit reproductive success because Ferruginous Hawks are delivering greater biomass back for nestlings, which could result in heavier and larger young (Santangeli et al. 2012, Wellicome et al. 2013). Similarly, Verreaux's eagles (*Aquila verreauxii*) are considered a specialized predator of rock hyraxes (*Procavia capensis*), but their reproduction was highest when diet diversity was higher (Murgatroyd et al. 2016). A comparison of Golden Eagle (*Aquila chrysaetos*) diet breadth and reproduction in Spain found similar results, where more diverse diets were associated with higher productivity (Whitfield et al. 2009). Understanding the relationship between landscapes characteristics, brood provisioning, and reproductive success of Ferruginous Hawks may predict the habitat quality of a landscape. Assessing this link will also inform managers how landscape change could potentially impact hawk populations.

Richardson's ground squirrels are the most important prey item in the diet of Ferruginous Hawks in Canada because they composed the majority of biomass delivered to the nest (93%). It is unknown whether this is because they are more abundant and available compared to other prey, or whether hawks select them over other prey. However, our study has shown that hawks that delivered more diverse prey also tend to deliver more biomass compared to hawks that deliver predominantly ground squirrels. This suggests that hawks may have the ability to compensate total biomass delivery with other types of prey when ground squirrel populations are lower. Similar to Tengmalm's owls (*Aegolius funereus*), Ferruginous Hawks living in landscapes with a more diverse prey community could exploit alternative prey during years with low ground squirrel populations (Zárybnická et al. 2015). Future studies must evaluate if there are minimum thresholds for prey abundance that support successful hawk reproduction. Ground squirrels make up the majority of biomass delivered and it is possible that squirrel populations can decline to where hawks cannot compensate despite benefits associated with more diverse prey returns.

Daily prey delivery rate was associated with a suite of biotic and abiotic factors. Nestling age was negatively associated with daily prey delivery rate; though we expect food demand would increase as nestlings grow older and larger (Keeley and Bechard 2017). However, it is possible that prey abundance becomes depleted in the home range by either prey dispersal (Michener and Michener 1977) or consumption by the predator (Bonal and Aparicio 2008, McCoy et al. 2012). Our study found a linear decline in prey delivery rate with nestling age, but previous studies of Ferruginous Hawk prey provisioning found that food consumption peaked when nestlings were 22 to 28 days old (Olendorff 1974) and 21 to 25 days old (Giovanni et al. 2007). We also found that daily prey delivery rates were higher for nests that hatched around Julian day 146 (May 26th). Previous studies have shown that Ferruginous Hawk hatch date and juvenile ground squirrel emergence aboveground, which occurs late May to mid-June, is synchronized (Schmutz et al. 1980a), and our data suggest that this synchrony could result in higher prey delivery rates to nestlings. This could have survival and fitness consequences for hawks that hatch during this peak. Little Owls (*Athene noctua*) that hatched during peak rodent densities were larger than young hatched earlier (Perrig et al. 2014). Daily prey delivery rates also increased with brood size, similar to other studies, suggesting that supply must meet demand (Giovanni et al. 2007). Threshold effects with brood size should be explored, as brood provisioning could be more limited for large broods. Individual differences among pairs, such as hunting ability, should also be explored by examining age-structure of adults, third order habitat selection, and associated prey delivery rates.

Seasonal weather influenced prey delivery rates, but not diversity. Lower average spring temperatures were associated with higher daily prey delivery rates, which may be related to higher over-winter survival and/or fitness of mammals (Heisler et al. 2014, Turbill and Prior 2016), such as ground squirrels (Dobson et al. 2016). However, number of degree days below 0˚C was not a predictor in our top models. Over a season, fewer ground squirrels were delivered during summers with higher precipitation. Hunting opportunities may be fewer during wetter summers because small mammals are far less active aboveground (Neuhaus et al. 1999, Kalcounis-Rueppell et al. 2002) or because prey are less accessible when vegetation grows higher and denser. Wind and rain also likely make flying less efficient for hawks. Our study found that PDR was highest when springs were cool, regardless of the amount of grassland cover surrounding the nest. In comparison, PDR was lowest during warmer springs for hawks nesting in cropland-dominated home ranges, perhaps vegetation grew sooner and faster under these conditions reducing accessibility of prey. Spring temperature has less influence on PDR when home ranges had higher amounts of grassland cover. Hence, high amounts of grassland were associated with the most consistent PDR despite spring temperatures. This pattern could reflect higher prey accessibility or abundance in grassland. It is also possible that hawks nesting in grassland-dominated home ranges were potentially not limited by food during the study years, as evidenced by high nest success of nests included in this stuy. This pattern also reinforces the importance of cooler springs on daily PDR. Weather is a common factor influencing foraging success for many species because it has the ability to influence both predator and prey (Sergio 2003, Garcia-Heras et al. 2017).

The strongest predictors for delivery rates of ground squirrels were not landscape variables, but were hatch date and seasonal weather variables. This could be problematic for wildlife managers because unlike land cover characteristics, neither of these parameters can be directly managed. Furthermore, changes to prey phenology and seasonal weather patterns are expected under climate change forecasts (Stenseth et al. 2002, Both et al. 2009a, Both et al. 2009b). Some species have adjusted their nesting phenology with climate change (e.g., Eurasian kestrels (*Falco tinnunculus*) (Korpimäki and Wiehn 1998), American kestrels (*Falco sparverius*) (Smith et al. 2017); Pied Flycatchers (*Ficedula hypoleuca*), (Tomotani et al. 2018)), but it is unknown whether Ferruginous Hawks can adjust their lay dates or hatch dates to match changes in ground squirrel phenology. Columbian ground squirrel (*Urocitellus columbianus*) emergence dates have been delayed with climate change (Lane et al. 2012) and Richardson's ground squirrels exhibit a similar pattern emerging earlier during warmer springs (Michener 1977), potentially resulting in a timing mismatch. This mismatch could reduce the ability of hawks to exploit the abundance of naïve juvenile squirrels that would emerge during peak hatch. Climate change forecasts also predict warmer springs and wetter summers (Pachauri et al. 2014) and our results suggest that this will lead to lower daily and seasonal prey delivery rates. Studies have shown linkages between annual ground squirrel abundance and Ferruginous Hawk reproductive success (Schmutz and Hungle 1989b, Schmutz et al. 2008); therefore, long term changes to prey availability could negatively impact Ferruginous Hawk populations.

Although we did not find strong landscape predictors of prey delivery rate, we did find landscape relationships with prey diversity, which also was associated with biomass returned to the nest. Ground squirrels are important prey for Ferruginous Hawks, but our study suggests that a more diverse diet does not necessarily reflect a low caloric diet and can even result in more biomass provisioned to nestlings. Demonstrating these broad patterns will help inform how habitat relationships and climate influence brood provisioning and ultimately how reproductive success could be influenced by these factors. However, understanding the mechanisms behind these patterns will help predict how landscape and climate change could impact brood provisioning and reproduction. Ferruginous Hawks are long-lived hawks with high home range fidelity (Ng et al. 2017) and changes to prey abundance on raptors with similar life histories can result in decreased reproductive success (Steenhof et al. 1997, Moss et al. 2012, Rebollo et al. 2017) or reduced nest density (Graham et al. 199, but see, e.g., Bonelli's eagle (*Hieraaetus fasciatus*) (Ontiveros and Pleguezuelos 2000)).

Our study was not able to assess the influence of brood provisioning rate on nest survival or productivity. The nests we monitored with video cameras all successfully fledged young. This high nest success is likely a bias that resulted from selecting nests only once nestlings were a minimum of seven days old. Cameras were also only mounted near nests located in trees or platforms that could support the weight of a ladder and climber; therefore, these sturdier nests may be at lower risk from blowing out in storms and less likely to fail than trees with narrower, more flexible trunks or branches. Future brood provisioning studies should consider assessing prey remains in nests during nest visits for a wide sampler of nests across nest substrates and nestling ages (Schmutz et al. 2008).

Our analyses controlled for brood size to account for the variation in number of nestlings among nests at the time of brood provisioning. An alternate approach to understanding the relationship between landscape characteristics and seasonal weather, brood provisioning, and productivity (e.g., number of young fledged) is to analyze brood provisioning rates without controlling for brood size. This approach addresses the ability of adult hawks to provision enough food for all nestlings, given the landscape around the nest, no matter the number of nestlings. We tested the hypothesis that these two approaches (with and without controlling for brood size) would result in a different set of landscape characteristics and seasonal weather predictors. We ran identical models with and without controlling for brood size and the top models remained the same with similar beta coefficients. This suggests that brood size may already reflect conditions, such as landscape and seasonal weather, where for example, good conditions are associated with larger clutches and consequently larger broods. In years where conditions do not change through the breeding season, these good conditions can then be associated with average larger broods and higher fledge rates. The positive correlation between brood provisioning and brood size may then reflect these good conditions. Future studies should consider not controlling for brood size because it would a better reflection of the above hypothesis (i.e., brood size is associated with conditions).

Our analyses in Chapter 3 found that landscape characteristics are not associated with fledge rate. This suggests that assessing how landscape characteristics influence brood provisioning may not be a good indicator for potential nest productivity, which is unexpected given contrary results by previous studies (Schmutz et al. 1980b, Schmutz and Hungle 1989a, Schmutz et al. 2008). Our data collection took place when the population was relatively stable and potentially slightly increasing. Schmutz's work measuring the influence of food supplementation and supernumerary broods on nestling growth (Schmutz et al. 1980b) was conducted when the population was potentially increasing (Alberta Environment and Parks 2009, Redman 2016). The nuanced relationship between landscape characteristics, seasonal weather, and reproduction may be better explored when Richardson's Ground Squirrel populations are less abundant compared to during the periods of our respective studies. Continued nest monitoring during years with low ground squirrel availability will be key to understanding whether Ferruginous Hawks are able to compensate a decreased dominant prey base with a more diverse diet and whether there is a threshold in decreased ground squirrel availability that results in decreased reproductive performance or reduced fledgling body condition.

TABLE 10. STANDARDIZED VALUES FOR THE TOP MODEL DEVELOPED TO PREDICT DAILY GROUND SQUIRREL DELIVERY.

Variable	B	SE	p-value
nestling age	-0.21231	0.042621	<0.001
hatch	2.744667	1.231417	0.026
hatchJQ	-2.8264	1.223265	0.021
brood	0.148696	0.036821	<0.001
Tave_sp	-0.11671	0.041264	0.005
oil	-0.09664	0.043843	0.028
constant	1.406067	0.038371	<0.001

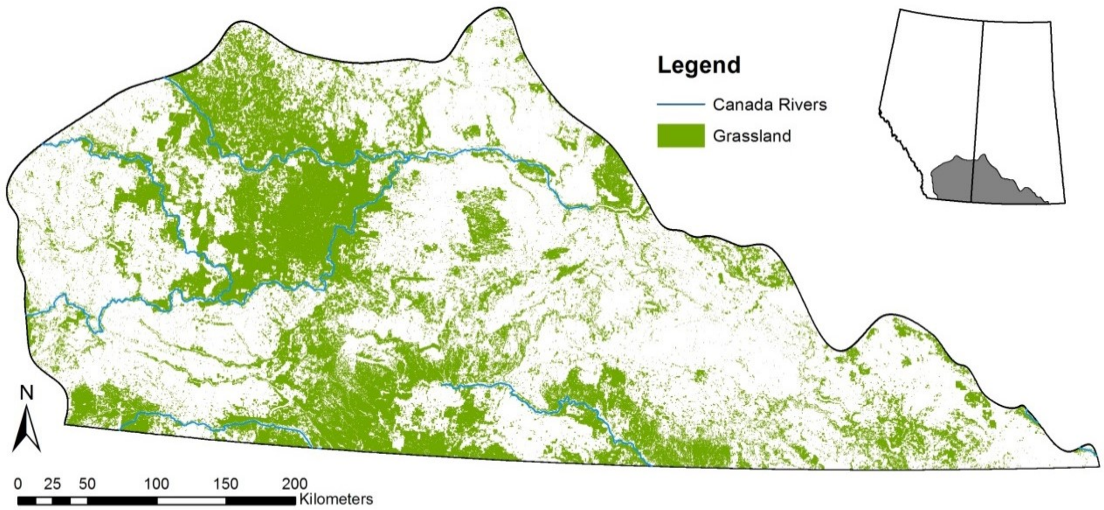


FIGURE 13. STUDY AREA IN SOUTHERN ALBERTA AND SASKATCHEWAN WHERE BROOD PROVISIONING AT A SAMPLE OF FERRUGINOUS HAWK NESTS WERE MONITORED WITH VIDEO CAMERAS IN 2011 TO 2013.

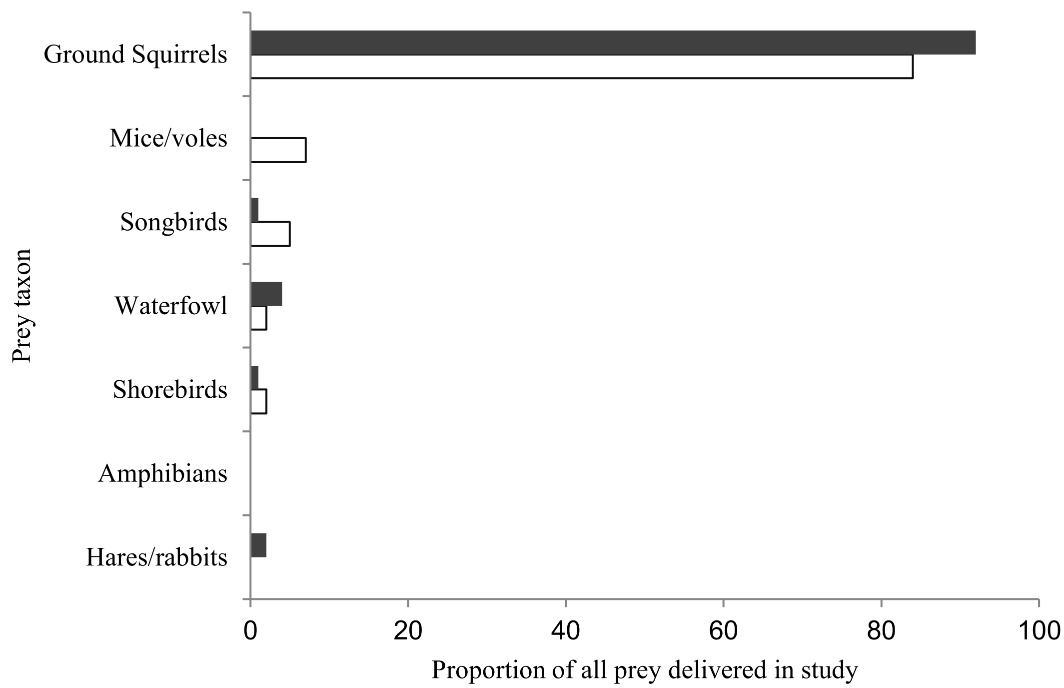


FIGURE 14. PREY COMPOSITION BY FREQUENCY (LIGHT BARS) AND ESTIMATED TOTAL BIOMASS (DARK BARS) DELIVERED TO ALL NESTS IN THE STUDY.

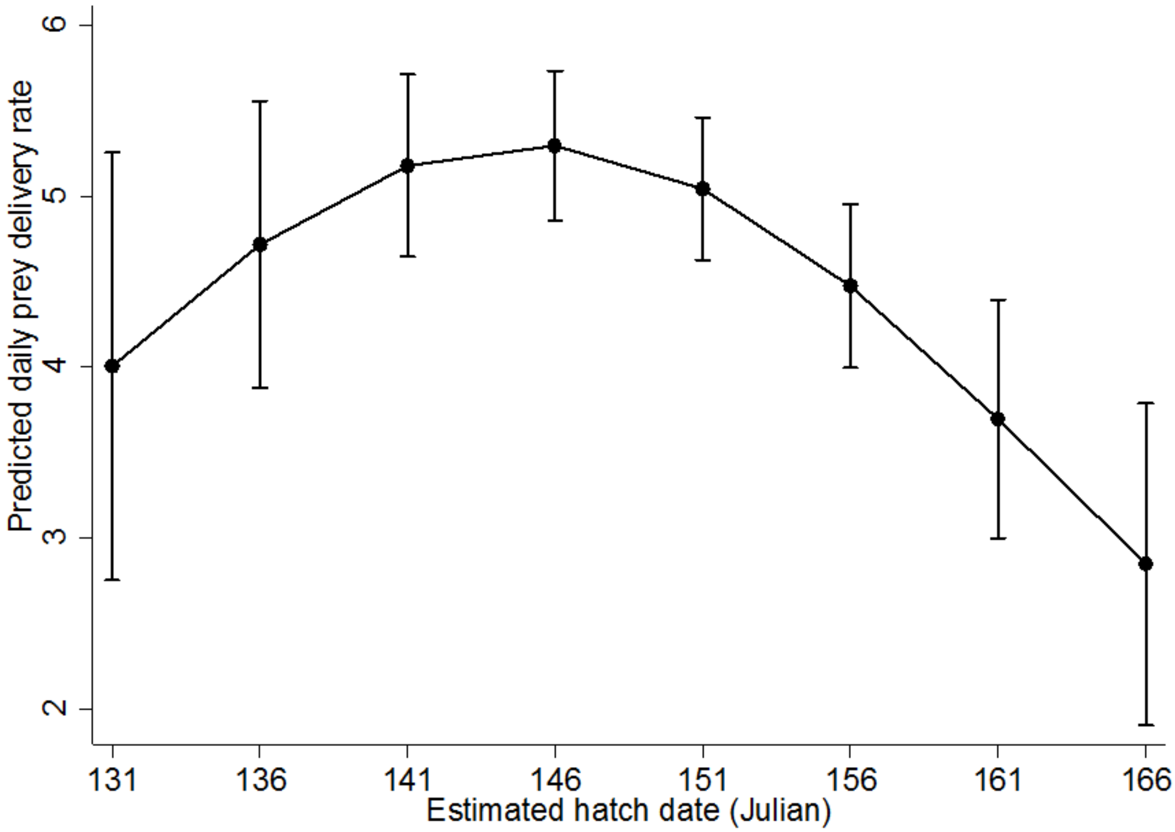


FIGURE 15. PREDICTED DAILY PREY RATE RELATIVE TO ESTIMATED HATCH DATE.

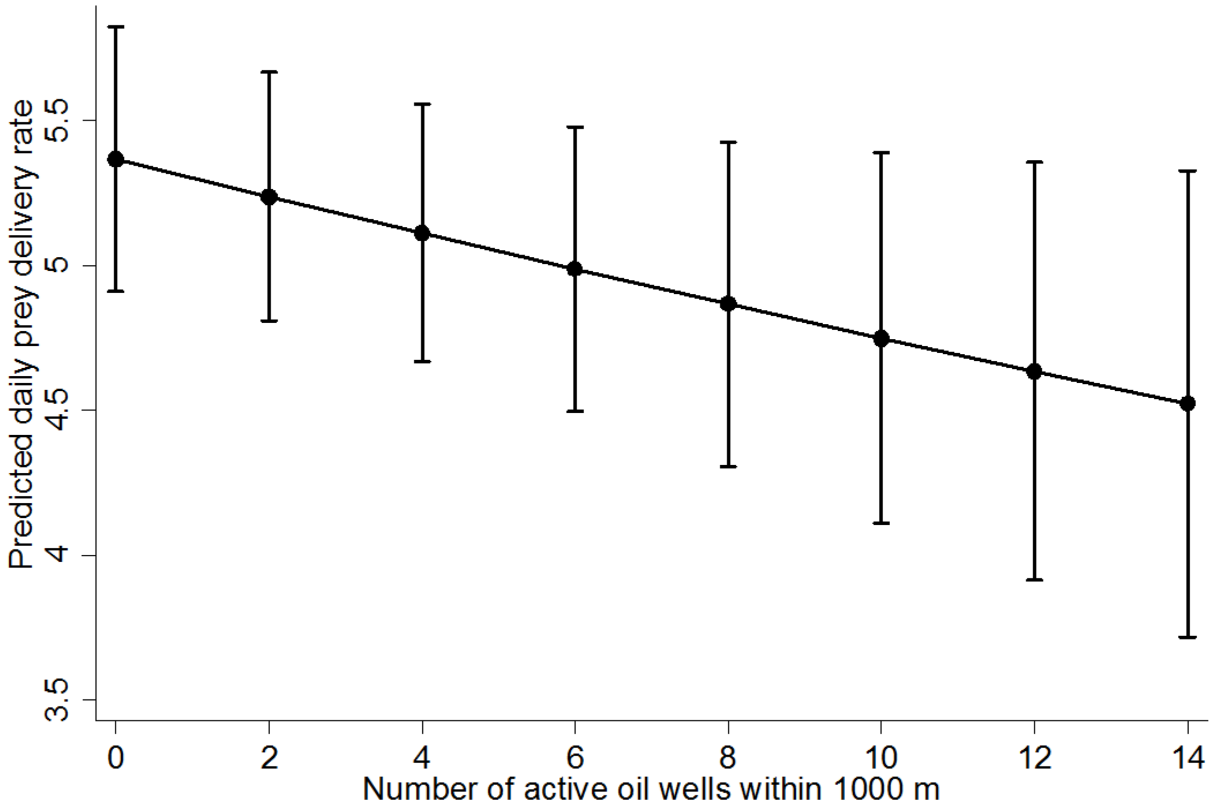


FIGURE 16. PREDICTED DAILY PREY DELIVERY RATE RELATIVE TO THE NUMBER OF ACTIVE OIL WELLS WITHIN 1000 M OF THE NEST.

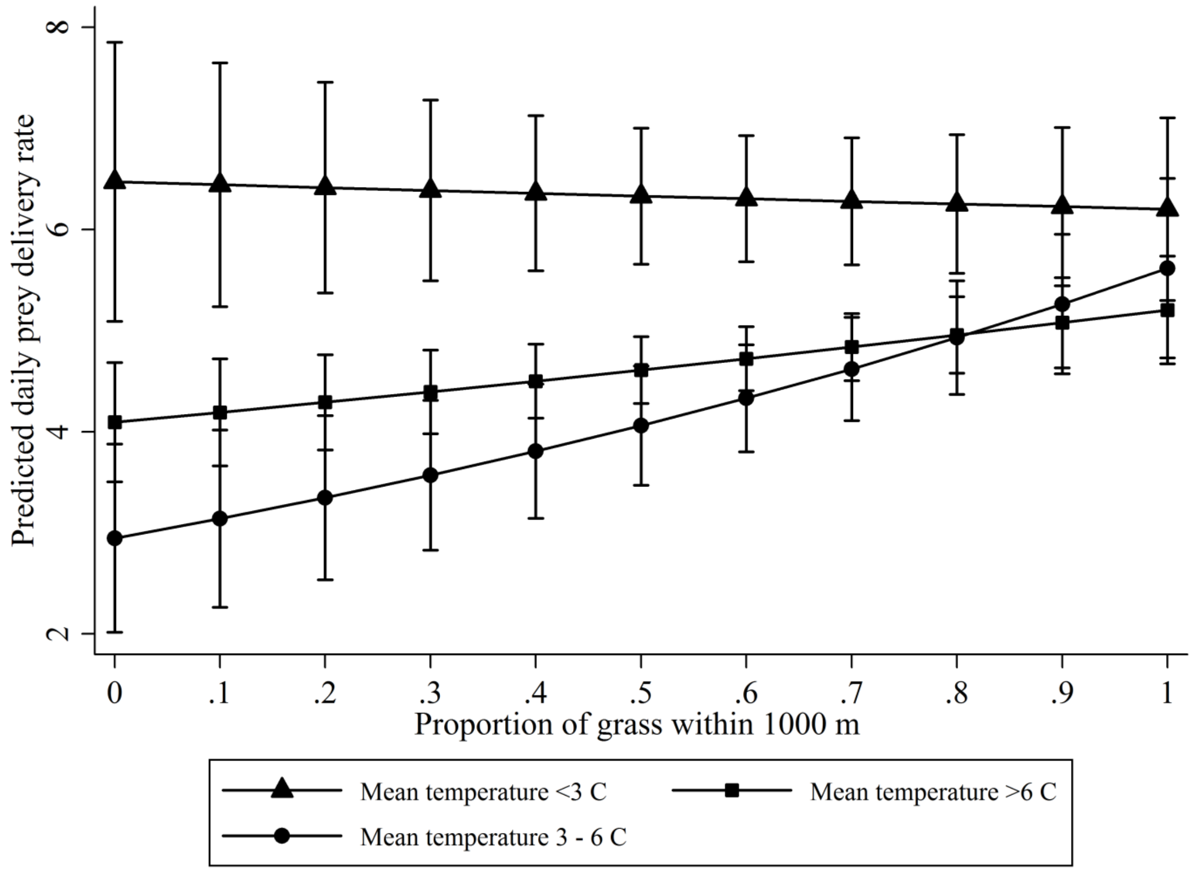


FIGURE 17. PREDICTED DAILY PREY DELIVERY RATE RELATIVE TO AVERAGE SPRING TEMPERATURE AND PROPORTION OF GRASS WITHIN 1000 M OF THE NEST.

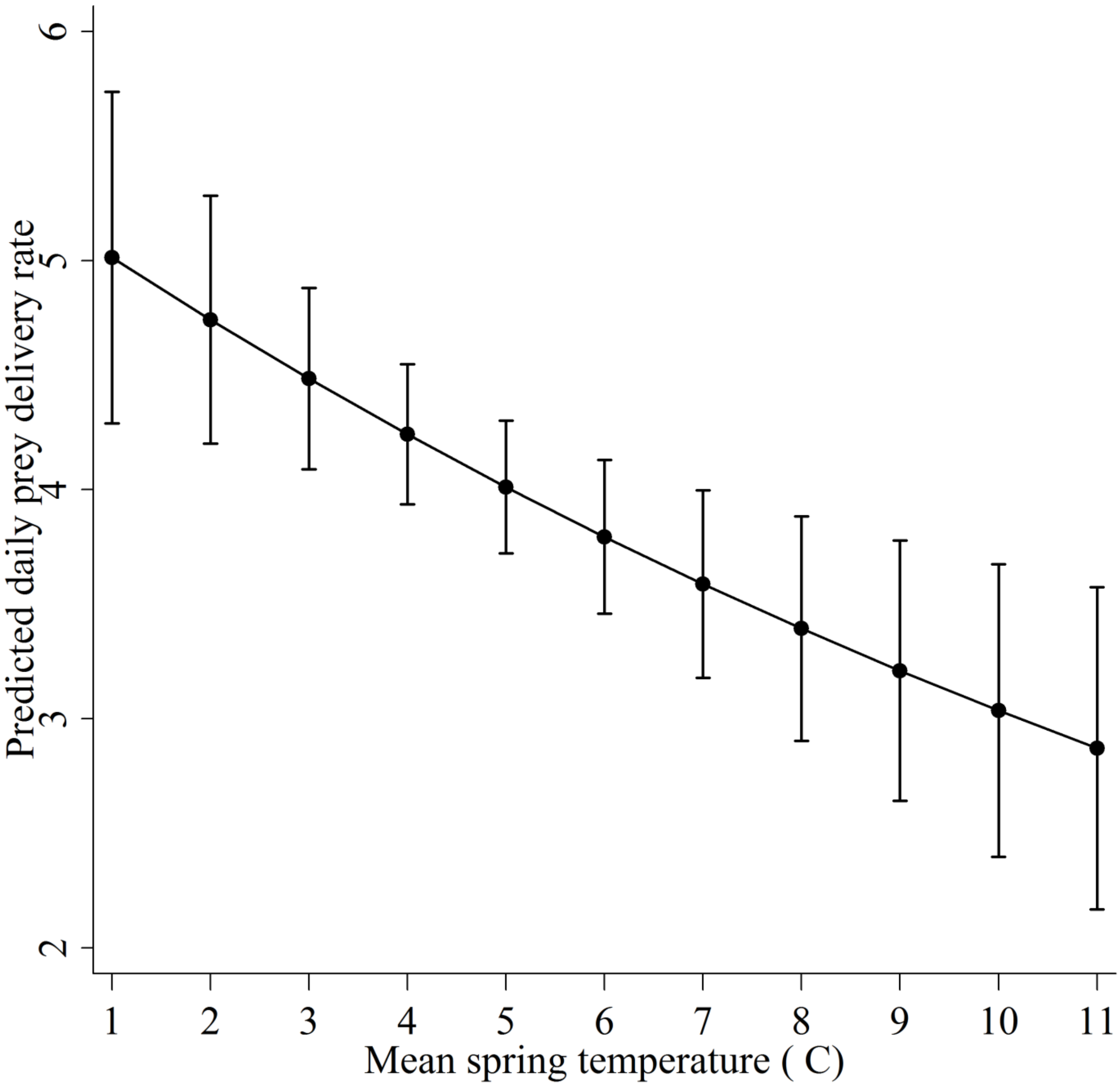


FIGURE 18. PREDICTED DAILY GROUND SQUIRREL DELIVERY RATE RELATIVE TO MEAN SPRING TEMPERATURE.

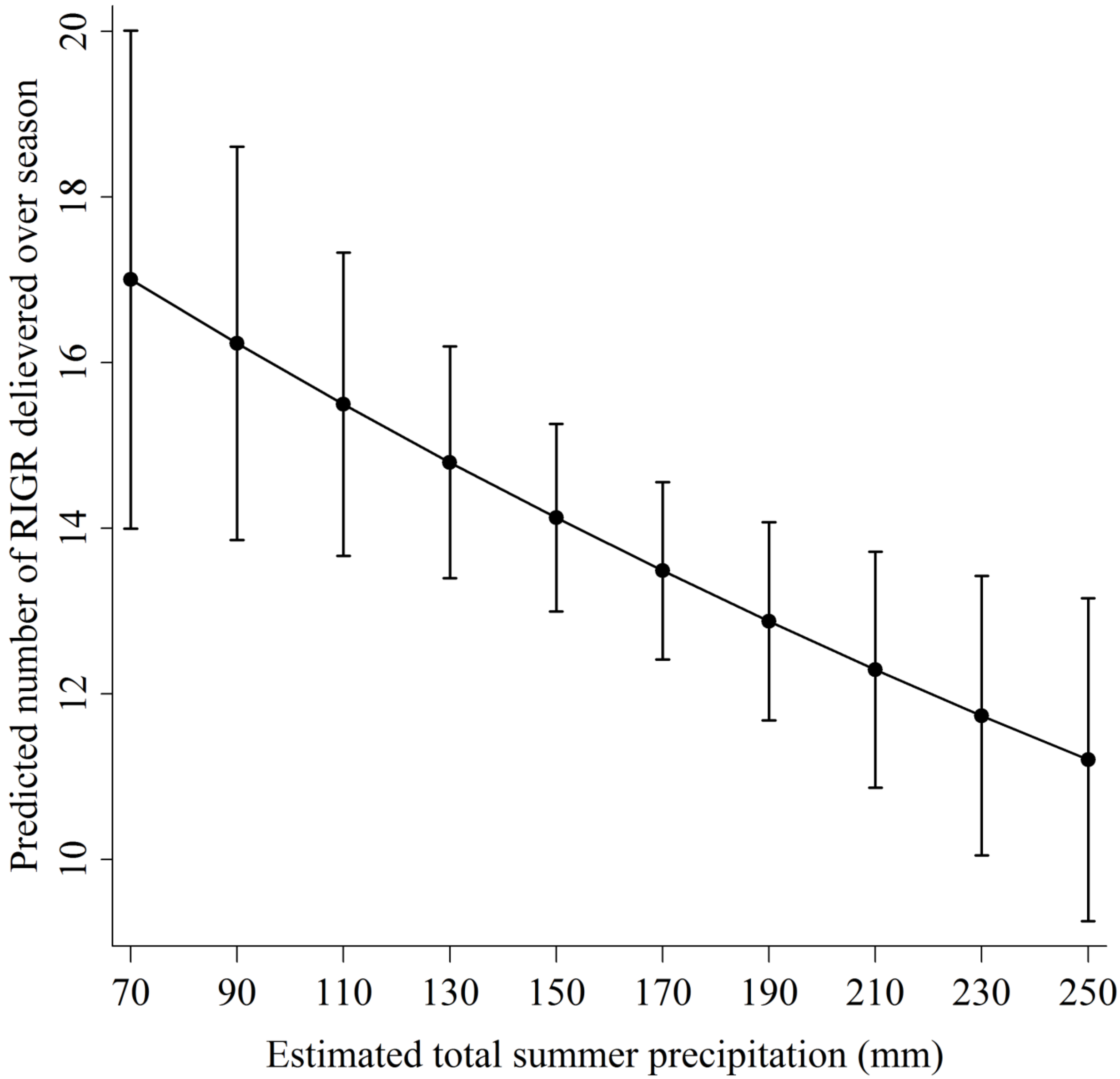


FIGURE 19. PREDICTED NUMBER OF RICHARDSON'S GROUND SQUIRRELS DELIVERED RELATIVE TO TOTAL SUMMER PRECIPITATION.

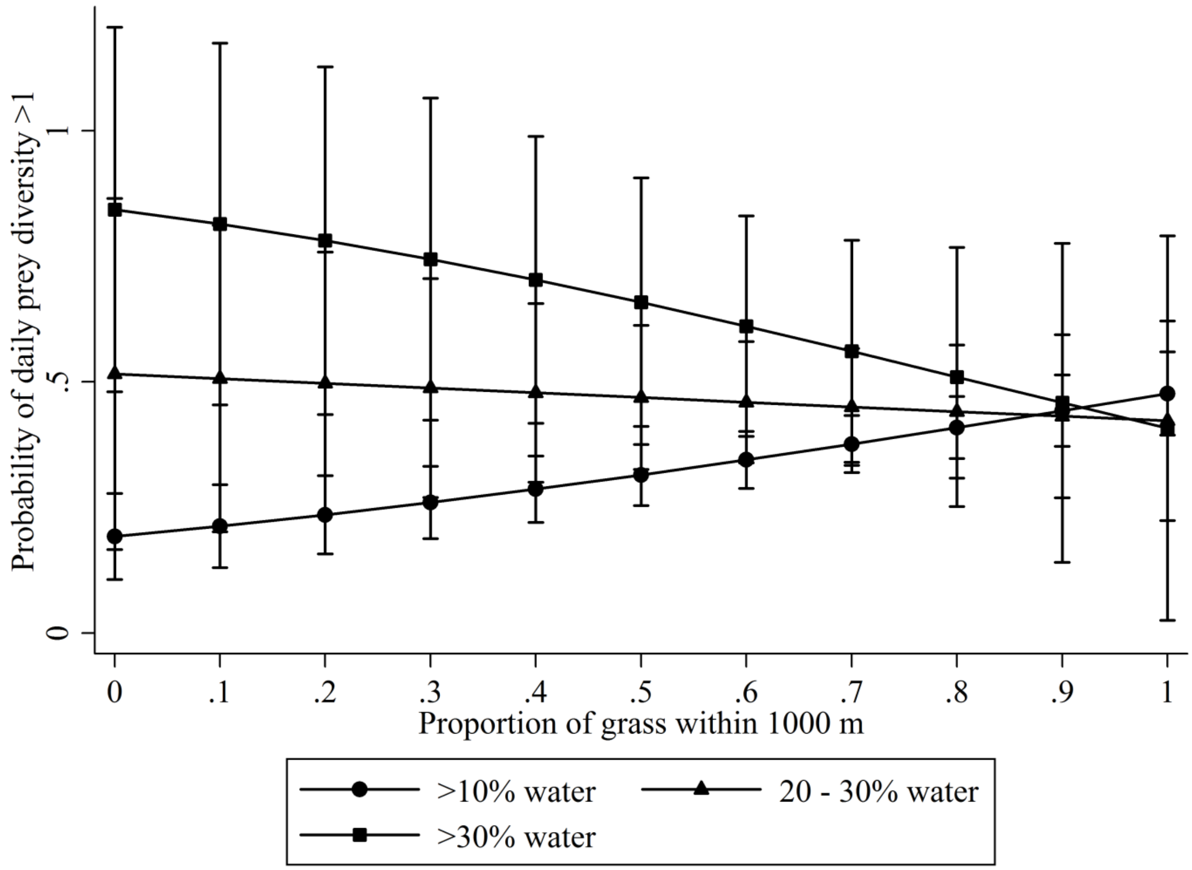


FIGURE 20. PROBABILITY OF PREY DIVERSITY TO BE H>1 RELATIVE TO PROPORTION OF GRASSLAND AND WATER SURROUNDING A NEST.

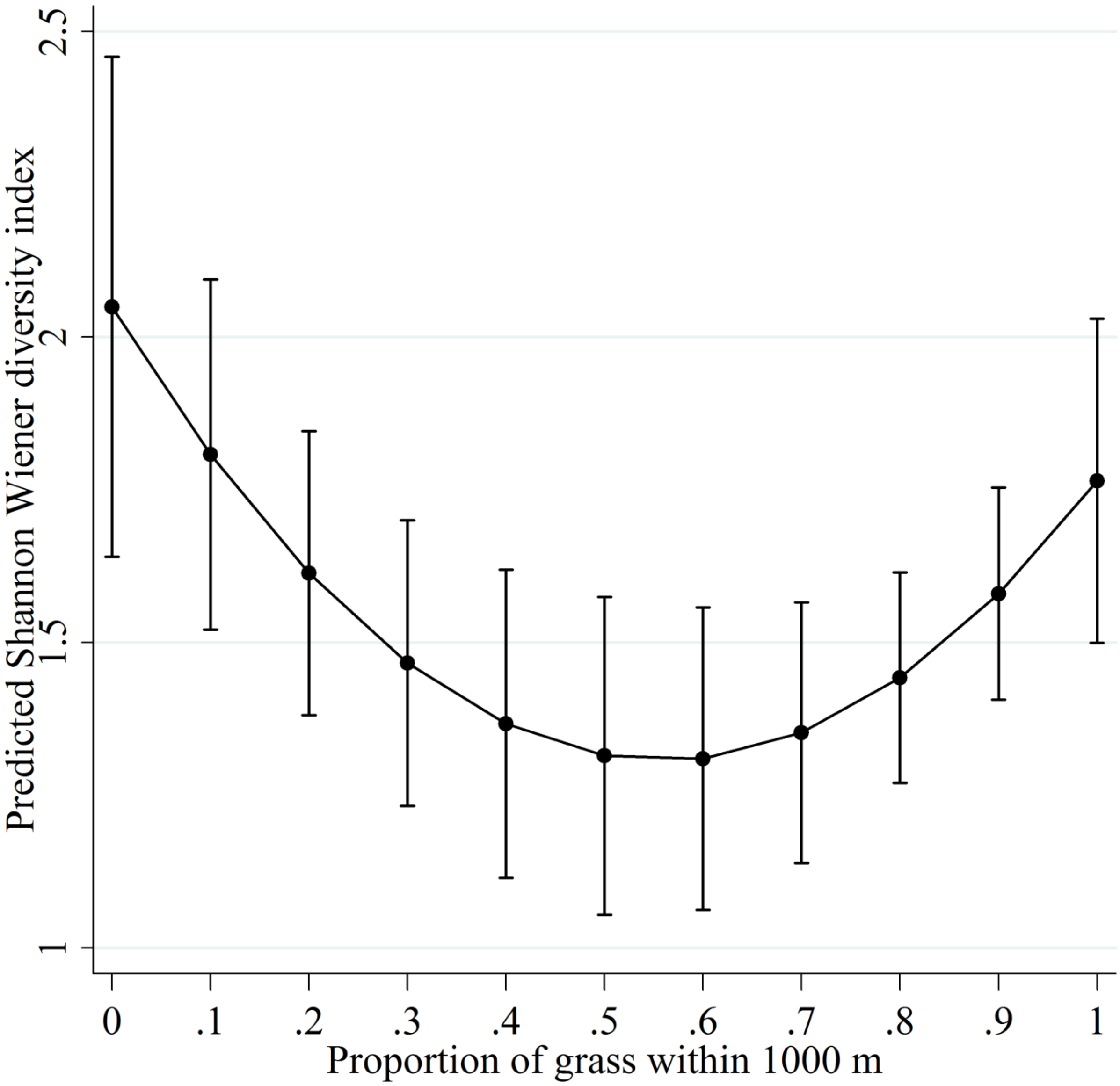


FIGURE 21. PREDICTED SEASONAL PREY DIVERSITY RELATIVE TO AMOUNT OF GRASS WITHIN 1000 M OF THE NEST.

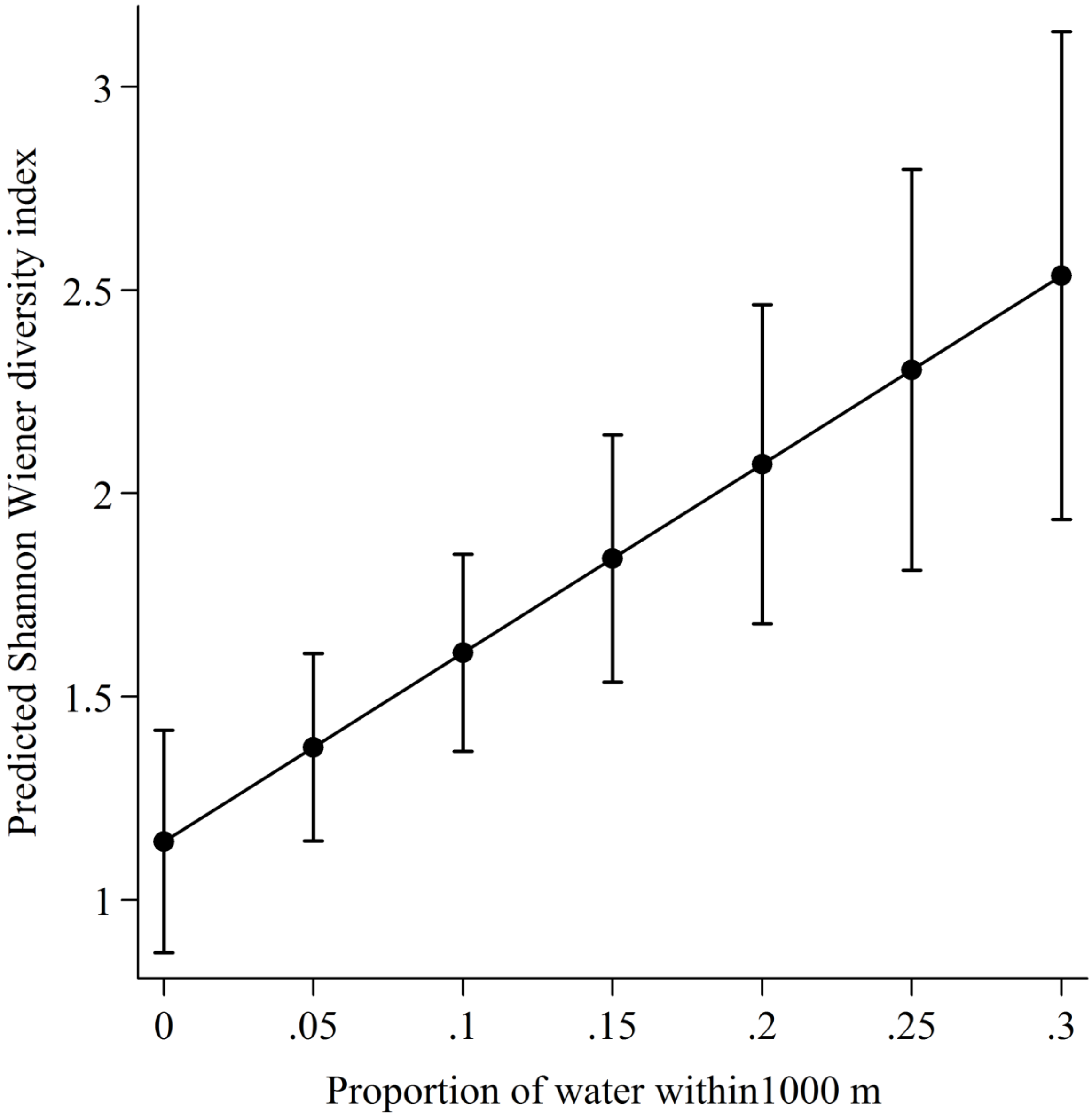


FIGURE 22. PREDICTED SEASONAL PREY DIVERSITY RELATIVE TO PROPORTION OF WATER WITHIN 1000 M OF THE NEST.

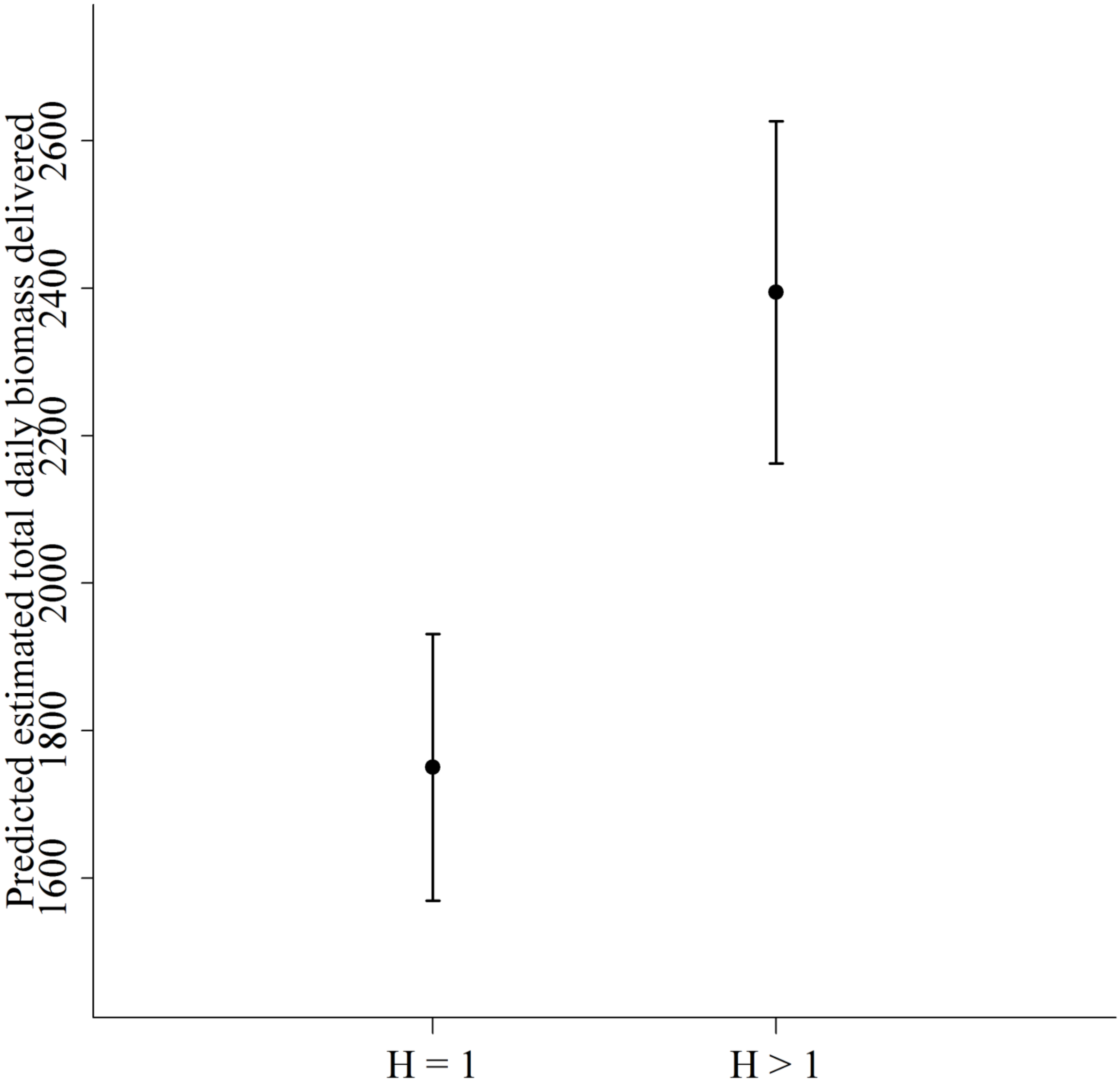


FIGURE 23. PREDICTED ESTIMATED BIOMASS DELIVERED TO NEST, RELATIVE TO DIVERSITY OF PREY DELIVERED.

Chapter 5: A spatially-explicit cumulative effects approach to forecasting relative influence of land use and climate change on Ferruginous Hawks in Canada

Abstract

Multiple environmental and anthropogenic factors can accumulate through space and time to result in cumulative effects on wildlife populations. The study of cumulative effects on wildlife species have generally focused on the influence of human land use on species; however, climate change is also expected to act concurrently with other factors, such as human land use and its footprint, to affect species. A cumulative effects approach provides context for single factors acting in an environment with multiple human activities and environmental processes. Our objectives were to evaluate 1) the relative influence of land use and climate change has on Ferruginous Hawk (*Buteo regalis*) demography in Canada over the next 50 years and 2) the potential relative influence of land use and climate change compared to status quo land use and climate change scenario. We developed a spatially-explicit population model by using a combination of previously developed models for habitat and reproduction plus vital rates estimated through our field data or published studies. We constructed a bench mark model where land cover and climate did not change. Then we manipulated land cover and climate to develop scenarios to compare outcomes to the benchmark model. When land cover and climate change scenarios were simulated individually, land cover change had the greater influence, compared to climate change, on our predictions for the Ferruginous Hawk population in Canada over a 50-year period. Our cumulative effects analyses found that simulated grassland restoration under either climate change scenario had a greater relative influence on the theoretical future

populations of Ferruginous Hawks, compared to other land cover and climate change scenarios. Our results can be used to assess relative risk when prioritizing conservation strategies for breeding Ferruginous Hawks in Canada. More broadly, results from our cumulative effects simulations can inform both grassland protection programs and climate change adaptation plans. However, extreme caution must be employed when using these models for predicting long-term population change or persistence in Ferruginous Hawks because of uncertainties in some key demographic parameters and process.

Keywords

Habitat stewardship; Single Large Several Small (SLOSS); nest survival; nest abundance; human footprint

Introduction

Multiple natural and anthropogenic factors can accumulate through space and time, resulting in cumulative effects on biodiversity (Theobald et al. 1997, Johnson et al. 2005, Hodgson and Halpern 2018). The study of cumulative effects on wildlife has generally focused on human land use impacts; however, climate change is an increasingly important driver of wildlife populations (Hunter et al. 2010, Bellard et al. 2012, Martay et al. 2017). Of growing concern is that climate change appears to be interacting with land use to yield greater effects than might be expected from land use or climate change alone (Eglington and Pearce-Higgins 2012, Dawe and Boutin 2016, Segan et al. 2016). Therefore, climate change should be considered an ever-present influence and be included in large-scale, long term population projections of cumulative effects. Studying a single factor is still informative, but the applicability of results are more limited without a cumulative effects approach, which provides context for single factors acting in an environment with multiple human activities and environmental processes. That context is critical to understanding the relative influence of each factor, and is thus important for managing cumulative effects.

Human land use is a global threat to wildlife populations because it has resulted in extensive land cover change (Song et al. 2018) and continues to reduce, degrade, and fragment wildlife habitat (Leu et al. 2008). The IUCN has identified habitat loss as a main threat to 85% of all species described in the IUCN's Red List (2015) and 60% of this land change is attributed to direct human activities (Song et al. 2018). Human footprint can directly result in habitat loss and also indirectly affect species survival, movement, and reproduction (Leu et al. 2008, Bernath-Plaisted and Koper 2016). The footprint can develop incrementally and result in landscape change over large spatial extents. An example of cumulative effects is the decline of many woodland caribou (*Rangifer tarandus*) populations. (Latham et al. 2011a, Latham et al. 2011b). Another example of habitat loss driving a species' decline is the rapid loss of the Spotted Owl's (*Strix occidentalis)* nesting habitat from logging (Bias and Gutiérrez 1992). However, other limiting factors, such as interspecific competitors, for Spotted Owl populations have been subsequently identified (Glenn et al. 2011), emphasizing the need to quantify the collective influence of cumulative effects, and the relative importance among multiple factors, when prioritizing the effectiveness of management strategies.

Climate change is becoming an increasingly important driver of wildlife populations (Lovejoy 2006, Iknayan and Beissinger 2018). Wildlife studies are increasingly focused on the future effects of climate change on species, but significant effects are already being observed (Staudinger et al. 2013). These studies have demonstrated that climate change has long term effects over large spatial extents, and can affect wildlife populations through multiple mechanisms (Traill et al. 2010). Effects can be direct, such as nest mortality from severe weather events (e.g., Burrowing Owls (*Athene cunicularia*) (Fisher et al. 2015)), or indirect through changes to phenology that later influence survival and reproduction (Lane et al. 2012, Marrot et al. 2018). Climate change may also alter landscape characteristics of an area, changing the habitat suitability for a species and ultimately its distribution (Heim et al. 2017). Several studies have demonstrated that climate change has a greater influence on wildlife populations than does land use (Dawe and Boutin 2016, Sultaire et al. 2016). Thus, assessing the relative influence of climate change on a species is critical to prioritizing conservation strategies.

The grassland ecosystem is a model system that demonstrates the need to manage cumulative effects. Cumulative effects of multiple stressors, such as land cover and climate change, occur in grassland systems and are expected to continue (World Wildlife Fund 2017). Agriculture has converted the majority of grassland to crop or tame grass, and temperate grasslands are at high risk of loss compared to other terrestrial ecosystems (Hoekstra et al. 2005). Additional land uses can add to the human footprint by way of roads, utility corridors, and industrial infrastructure, such as energy development. The increasing human footprint is a concern because habitat loss, degradation, and fragmentation are likely the cause of many grassland bird declines (Herkert 1994, Peterjohn and Sauer 1999a, Herkert et al. 2003, Walk et al. 2010, Bernath-Plaisted and Koper 2016). Furthermore, climate change is expected to change weather patterns, vegetation cover, and species interactions (Traill et al. 2010, Jonas et al. 2015, Mantyka-Pringle et al. 2015). Climate change may increase future grassland cover and species distributions may shift (Skagen and Adams 2012), but recent studies have found immediate negative effects of changing climate (Beever et al. 2011, Jarzyna et al. 2016, Ross et al. 2016). Managing for land use and climate change likely require different approaches. Understanding the relative importance and urgency of each stressor is important for prioritizing and allocating management with limited resources (Howard et al. 2015).

Wide-ranging wildlife is more likely to encounter cumulative effects because they are more likely to encounter multiple land uses, industrial infrastructure, and be exposed to varying regional weather patterns. Ferruginous Hawks (*Buteo regalis*) are one example, with breeding home ranges that average 17.59 km^2 in Alberta and Saskatchewan (Watson et al. 2014) and range between 2.30 km^2 (Colorado, (Plumpton and Andersen 1998) to 90.3 km^2 (Washington, (Leary et al. 1998)). Within their home ranges, Ferruginous Hawks are likely to encounter many types of human footprint that include crop production, ranching, oil and gas extraction, and renewable energy generation. Studies have found that moderate amounts of grass and high edge density result in greater Ferruginous Hawk habitat use, higher relative abundance, and improved reproductive performance (Chapter 2 and 3). Average climate and seasonal weather also predicted habitat use and reproduction (Chapter 2 and 3). Land cover change (World Wildlife Fund 2017), whether habitat loss or restoration, and climate change will continue to affect the grassland ecosystem in Canada (Wang et al. 2016). These changes, even in the short term of a few decades can potentially positively or negatively influence hawk populations. Understanding the relative importance of each type of change is an important first step in prioritizing management plans for this *Threatened* species at risk (SAR Public Registry 2010). Some stressors are more actionable than others, but may have relatively little impact on populations.

Our objectives were to evaluate 1) the relative influence of land use and climate change on Ferruginous Hawk demography in Canada over the next 50 years, and 2) the potential relative influence of land use and climate change compared to status quo land use and climate change scenario. We hypothesized that land cover will have a greater influence on Ferruginous Hawk populations than climate change because, in a hierarchical sense, a decrease in available nesting habitat would limit nesting opportunities before reproductive performance would be limited by climate change. We used sensitivity analyses to assess the relative magnitude of influence of land cover and climate change on the Ferruginous Hawk population through time. The population model was developed using vital rates collected from literature and from our field studies. We used models previously developed for Ferruginous Hawk habitat, survival, and reproduction to develop a bench mark model in which land cover and climate did not change. Then we simulated changes in land cover and climate to develop scenarios to compare to the benchmark model based on how current parameters are thought to respond to changes in weather and land-cover. Testing land cover and climate change in isolation allowed us to compare their relative influence on hawk populations. Next, we evaluated the relative influence of land use and of climate change on Ferruginous Hawk populations under possible future scenarios using an additive cumulative effects approach.

Methods

Study area

The study area (~153,000 km^2) (Figure 24) ranges from 49.0˚N to 51.8˚N latitude and -113.2˚W to -102.8˚W longitude. It includes most of the breeding range of Ferruginous Hawks in Canada, with the exception of approximately 25 nests (K. de Smet 2010, unpublished data) in southwest Manitoba. It is the northern range of the species distribution, with hawks returning February to March and migrating south in September to November (Ng et al. 2017).

The average winter temperature from December to February is -7.0˚C, the average spring temperature from March to May is 6.5˚C, and the average summer temperature from June to August is 18.7˚C (Medicine Hat, Alberta, Environment and Climate Change Canada 2013). Average precipitation in winter is 32 mm, spring is 82.7 mm, and 135.9 mm during the summer.

The study area is composed of fescue, mixed-moist grassland, and shortgrass ecoregions where land cover is predominantly cropland and grassland. Grassland communities are characterized by species including blue gramma grass (*Bouteloua gracilis*), needle and thread grass (*Stipa comata*), and wheat grasses (*Elymus* spp.). The majority of the study area is low and flat, interspersed with regions of undulating uplands, river valleys, badlands, and coulees. Chernozem and solonetzic soils are the dominant soil orders throughout the study area (Soil Landscapes of Canada Working Group 2010).

Land use in the study area includes agriculture, ranching, and the energy sector. Most grassland cover is grazed by cattle. Tame cover can either be grazed or hayed, depending on the cover type. Common crops include canola (*Brassica* spp.), cereals such as wheat, clover (*Trifolium* spp. and *Meliliotus* spp.), and pulse crops (e.g., *Pisum* spp., *Lens* spp., dry beans). Oil and gas deposits are localized, where oil well density ranges from zero to 541 wells per township

(0.17 oil wells/km^2) and gas wells range from zero to 534 gas wells per township (0.17 gas wells/km^2). Wind power generation is an emerging land use, with approximately 1704 MW produced in southern Alberta and Saskatchewan (Canadian Wind Energy Association 2018).

Agricultural land use to farm crops has cultivated the majority of the grassland cover in southern Alberta and Saskatchewan. Approximately 37% and 20% remain in Alberta and Saskatchewan, respectively (Hammermeister et al. 2001, The Alberta Biodiversity Monitoring Institute 2015). While the majority of the grassland conversion to cropland was completed prior to 2000, conversion is ongoing and the World Wildlife Fund estimates that 4.6 million hectares have been converted to cropland in the Northern Great Plains since 2009 (World Wildlife Fund 2017). World Wildlife Fund also estimates over 283,000 hectares of grassland was converted to cropland in the Northern Great Plains in 2016 (World Wildlife Fund 2017), which is an annual loss rate of 0.55%. This annual loss rate is slightly lower than the 2015 rate of 0.75%. Wheat, corn, soy, and lentils were the primary crops grown in 2016 on cropland that had been converted from grassland since 2009. Grassland restoration is rare in southern Alberta and Saskatchewan.

Population Simulation

We used a sensitivity analyses to evaluate the relative influence of land cover and climate change under different land use and climate change scenarios. We developed different land cover, climate change, and cumulative effect scenarios and ran 100 simulations of a demographic model. We ranked the relative influence of land cover and climate change by comparing the estimated final population size after 50 years and the average estimated lambda for each scenario. We forecasted population change over 50 years because this would include several generations of Ferruginous Hawks, and allow land use and climate to vary enough to compare relative influences.

We used a benchmark model, where land cover and average seasonal weather remained static, to estimate the relative influence of these cumulative effects as individual and additive influences on lambda for Ferruginous Hawk populations in Canada. Lastly, we used the additive model to evaluate the relative influence of land use and climate change given a benchmark scenario and different land use and climate change scenarios. Assessing the relative influence of land use and climate change using the additive model allowed us to evaluate how management approaches, such as native grassland restoration, might be used to conserve and recover Ferruginous Hawk populations in Canada.

Population model

We developed a spatially-explicit population model by using a combination of existing habitat and reproduction models, vital rates collected in our field study, and previously published vital rates from within our study area (Table 11). The spatial resolution of the population model was a township (9.6 km by 9.6 km), which is a common cadastral unit used by governments and land managers. The predicted relative nest abundance was estimated for each township for each year.

This model is spatially-explicit because models were applied to each township using the specific characteristics of that township to estimate relative nest abundance and nest survival. Landscape change was also simulated at the resolution of individual townships. Land cover and edge density at Year 0 reflect the estimates used in the model. Changes to grassland cover, such as additions (i.e., grassland restoration) or subtractions (i.e., grassland conversion to cropland) of grassland cover were applied for each township and were cumulative through years. For example, if 0.5% of grassland cover was converted to cropland each year for 50 years, then relative nest abundance would be modeled for each township with the proportion of grassland estimated for that township, minus 0.5% each year. Simulated changes to climate were represented as changes to seasonal weather. These changes were applied to all townships and used in relevant models to estimate relative nest abundance and nest survival in individual townships. A detailed description of landscape and climate change scenarios and the population model framework follows below.

Habitat

Habitat use and relative nest abundance was modeled using a spatially-explicit landscape-scale habitat model (Chapter 2 and 3). The habitat model was developed using survey data collected in 2012 and 2013, using a stratified survey design to specifically estimate relative nest abundance (Chapter 3). Land cover variables (such as proportion of grass cover and edge density), soil order, and latitude and longitude were the best predictors of relative nest abundance. We used this model to predict relative abundance in each township in the hawk range in southern Alberta and Saskatchewan in each year of our simulation. This predicted relative nest abundance only predicts abundance for the area of each township we surveyed. We surveyed approximately 52% of each township; therefore to estimate the total relative nest abundance in each township, we multiplied the estimated number of nests by a factor of 1.92 to extrapolate the estimate from our surveyed area to the entire township. For our land cover simulations, we simulated grass cover change for each township.

Reproduction

Similar to the relative nest abundance model, the nest survival component of our population model was based on an existing spatially-explicit model. We previously developed a nest survival model using nest monitoring data from 2010 to 2015. We modeled both landscape and intrinsic variables to predict nest survival (Chapter 3). In addition to intrinsic variable, such as hatch date, we found that both land cover and seasonal weather variables predicted nest survival. We applied the nest survival model to each township by down-scaling landscape characteristics at the township-scale to a smaller spatial extent used by the nest survival model (2.5 km radius). For example, the proportion of grass within the township was used as the proportion of grass around a simulated nest. Estimated total edge in the township was converted to km/km^2 and then scaled to area within a 2.5 km radius. Oil and gas variables remained the same in both township and home range analyses because they are categorized as low, medium, or high density. In our benchmark model, seasonal weather was held at mean values measured during the years data was collected. How we simulated seasonal weather is discussed below.

We previously developed fledge rate models, but did not find any landscape or weather variables that were predictive. Therefore, we used the mean fledge rate and its standard deviation in our simulations. These estimates were based on nest monitoring we conducted in our study area between 2010 and 2015. Nests that successfully fledged a minimum of one young was considered successful and only successful nests were included in the fledge rate estimate because nest failure was included in our nest survival model. The fledging rate estimate is based on 530 successful nests. In our simulation model, we limited the fledge rate to a maximum of four young per nest because nests that fledged five or six young were rarely observed. We incorporated stochasticity into the productivity component by generating a normal distribution of values using the mean and standard deviation of fledge rate. For each township and each year, we used a Monte Carlo approach to randomly draw plausible estimates for fledge rate.

Survival

We estimated juvenile recruitment using two resources. Our study estimated apparent juvenile survival using telemetry tracking data of 104 post-fledglings tracked from nests in our study area. Young were tagged with VHF telemetry tags (ATS Track) in the nest and tracked until they died or left the study area. Apparent post-fledging survival was multiplied by adult survival to reflect the remainder of the year they must survive until returning to breed. We also used a juvenile recruitment estimate from a published study (Schmutz et al. 2008), which used mark-recapture data from banded birds to estimate recruitment.

Adult survival was based on two estimates. Our study estimated apparent adult survival by tracking individuals using satellite transmitters (Microwave Telemetry Incorporated, Columbia, MD) between 2011 and 2018. We attached satellite transmitters to 50 adults from 2011 to 2018, for a combined total of 84 years of survival. Survival was defined as an adult surviving 12 months after initial tagging and for each following 12 month increment. There are likely individual differences that influence adult survival, such as age, but there is no available data to estimate survival as a function of age structure. For simplicity, we used the reported apparent adult survival estimated from our tracking data. Our second estimate of adult survival is based on Schmutz et al. (2008), which used mark-recapture models and banding data.

For both recruitment and adult survival, we had a range of plausible values based on field-collected data and published vital rates. Therefore, we used a Monte Carlo approach to randomly draw plausible estimates (Table 11) from a uniform distribution between the high and low values for each range of survival estimates. Estimates were sampled for each township and year.

Scenarios

We developed a benchmark population model where no land cover change and no seasonal weather change occurred. This model served as a comparison for the other scenarios. We began by evaluating the relative influence of land cover change and climate change in isolation. Lastly, we evaluated their relative influence on the Canadian Ferruginous Hawk population when modeled as additive cumulative effects.

Land cover

Land use and land cover has changed the Great Plains significantly in the last century (Samson and Knopf 1994). Grassland conversion to cropland is ongoing, with recent annual loss rates of 0.55% in 2016 and 0.75% in 2017 in the northern Great Plains (WWF Plow Print 2017).

In comparison, cropland conversion to grassland is rarer and while data on amount of grassland restoration was not available, it likely occurs on a very small extent.

We developed scenarios with different rates of grassland conversion to cropland (hereafter known as grassland loss) and cropland conversion to grass (hereafter referred to as grassland restoration) (Table 12). Grassland conversion to cropland scenarios increased proportion of cropland within townships and model home ranges by 0.5% (0.46 km^2 or less than one quarter-section) a year to reflect annual rates of loss based on estimates for 2016 and 2017. Our scenarios targeted townships with 25% to 50% grass cover to simulate where cultivation would most likely occur. We assumed that townships with high amounts of grassland were less likely to be cultivated because the soil has lower agricultural capability. Conversely, townships with high amounts of cropland are more likely to have high soil capability and lands with agricultural potential were historically cultivated. We assumed that townships with 25% to 50% grass cover are on the edges of productive cropland and have lands with some soil capability, and thus some possibility of cultivation. In our grassland recovery scenarios we increased proportion of grassland within townships and model home ranges by 0.5% a year in townships with 25% to 50% grass cover. These scenarios represent a deliberate grassland restoration program that uses estimates from previous habitat models, which predict that moderate amounts of grass and cropland are associated with the highest nest abundance and nest survival. Targeting restoration in townships with 25% to 50% grassland should increase the number of townships with moderate amounts of grass and crop, which models predict will have a positive effect on Ferruginous Hawk populations.

We also explored how increased edge density with land cover change could influence Ferruginous Hawk populations. We developed land cover scenarios without change in edge density to simulate land cover change on the edge of a larger contiguous tract of grassland patch, where minimal edge would be created or destroyed. We also developed land cover scenarios that created new patches of grass apart from larger tracts, where new landscape edges would be created. When edge was included in simulation, edge density was increased by 3.2 km each year in each township where grassland was lost or restored. We added 3.2 km of edge each year to reflect the land cover change of approximately one quarter-section.

Climate

Climate change is expected to alter future weather patterns, which may influence Ferruginous Hawk demographic parameters and populations (Shank and Bayne 2015). Climate change may potentially influence Ferruginous Hawk nest survival because winters are predicted to become warmer, summers drier (Sauchyn and Kulshreshtha 2008), and storms more frequent and severe (Kharin and Zwiers 2000, 2005). Our nest survival analyses (Chapter 3) found that mean winter temperature, mean spring temperature, and mean temperatures the month of a nest visit were important predictors of nest success.

We developed climate change scenarios to reflect forecasted changes in seasonal weather in our study area. Our climate change scenarios are based on the Intergovernmental Panel on Climate Change (IPCC) RCP 4.5 and RCP 8.5 scenarios (Pachauri et al. 2014). These are global climate change scenarios and we used scaled-down versions developed by Prairie Climate Centre and the Pacific Climate Impacts Consortium (McKenney et al. 2011). Delta maps predicted the change in seasonal temperature throughout different regions of our study area. For each climate change scenario, we divided the deltas by 80, which is the number of years it was projected over.

We increased the mean seasonal weather variables by these values each year to reflect climate change over time. Our climate change scenarios did not capture the mechanisms that explain the seasonal weather patterns in our nest survival model.

Cumulative effects

We also evaluated the relative importance of additive cumulative effects on Ferruginous Hawk population. We combined land cover change with climate change to evaluate how the relative influence of these variables will change population under different scenarios, the relative population trajectory under different scenarios, and how land cover management options could influence conservation and recovery.

Simulation model framework

We used these models and vital rates to construct a spatially-explicit population model for Ferruginous Hawks in Canada (Excel 2010) (Figure 25). The population model was constructed using 1643 townships that comprise the Ferruginous Hawk range in Alberta and Saskatchewan. The benchmark model and all scenario models at Year 0 used estimated land cover and seasonal weather conditions that reflected the environment during our study period. Subsequent landscape and climate change scenarios were cumulatively built on these initial models. Landscape metrics (i.e., proportion of grassland and edge density) were tracked for each township. Simulated changes were tracked cumulatively through years. For example, landscape scenarios where grassland was restored 0.5% a year would be modeled with proportion of grassland incrementally increasing by 0.5% each year, based on the previous year's value for grass cover. Climate change scenarios modeled seasonal weather changes similarly. For example, increases to winter temperature were incrementally added each year using the previous year's seasonal average as the base value. This approach resulted in a cumulative change over 50 years, based on incremental landscape or climate changes each year.

For each simulated year, we applied the relative nest abundance model to each township to estimate the number of nests in each township. We used the landscape and climate conditions present in each township to develop the model. Then we applied the daily nest survival model using the down-scaled landscape characteristics of each township and calculated the probability of nest survival for nests in that township. For each township, we estimated the number of successful nests (i.e., nests that fledged a minimum of one young) by multiplying the probability of nest survival by the estimated number of nests (Equation 1). We estimated productivity for each township by multiplying the estimated number of successful nests by a fledge rate randomly selected from a normal distribution generated from nest monitoring data (Equation 3). Recruitment in each township was estimated by multiplying productivity by an estimate of juvenile survival uniformly drawn from a range (Equation 4). Recruitment across all townships was summed. The number of breeding adults was calculated by multiplying the number of estimated nests by two (Equation 5). The number of adults that survive to the next breeding season was estimated by multiplying the number of breeding adults by a probability of adult survival randomly drawn from a uniform distribution of ranges (Equation 6). Estimated population size was the number of recruited individuals summed with the number of surviving adults (Equation 7). See model structure and equations in Figure 25.

The number of nests in each township in the next year was estimated for each time step. We estimated the number of nests per township using the landscape and seasonal weather conditions in each township. For the landscape and climate change scenarios, we would use new values of landscape and/or seasonal weather to reflect the simulated change in each township each year. We compared the number of nests estimated by the relative nest abundance model to the number of nests that would exist if adults and recruits were estimated to have survived to the next year. The higher number of nests was used in subsequent steps of the model. If the number of nests estimated by the abundance model was higher, we assumed that individuals would emigrate and fill the potential available home ranges in other townships that had not reached carrying capacity (i.e., we assumed an open population, see model assumptions). If the number of nests estimated by calculating survival of adults and recruits exceeded the estimated average abundance based on amount of grassland, we used the higher value because we assumed birds would return due to high site fidelity and natal fidelity (Gossett 1993). The maximum number of nests previously observed in a township was approximately 14 nests (Schmutz et al. 2008) and we capped each township so that the maximum number of nests that could exist was 14 (i.e., we used a hard cap to create density-dependence). Individuals and nests were then assumed to have dispersed to neighbouring townships if nest estimates exceeded 14 nests per township. The sum of the number of nests per township formed our population estimate each year.

Model assumptions

Our population model included several assumptions about Ferruginous Hawk ecology. Some assumptions were made because of knowledge gaps in hawk ecology. There is little specific information about Ferruginous Hawk nomadism, dispersal, natal site fidelity, age or stage structure, or floater ecology. Thus, components were not included in our model because parameter estimates were not available. Given these limitations, results from our models should be used with caution and should only be used to compare the relative influence of land use and climate change among simulated scenarios and to the benchmark and not used to project actual rates of population change. The values of lambda shown are predicated on some key assumptions about the age at which birds breed, rescue effects from populations in the Unites States, and density dependent territoriality and thus should not be viewed as the actual population growth rate of Ferruginous Hawk populations.

We assumed that Ferruginous Hawks in Canada are an open population, where immigration and emigration functions to occupy available home ranges. Genetic studies found that hawks on both sides of the Continental Divide had similar genetic structure, suggesting that hawks disperse over large distances and breed (Gossett 1993); though it is not known how often this dispersal occurs. Our model assumed that Ferruginous Hawks are able to breed after hatch year as some have been observed, though it is not known what proportion of first year birds breeds. Some observations suggest that hawks may be nomadic for several years before selecting a home range and breeding, but other data also suggests hawks return to near their natal range to breed (Gossett 1993). Without data on age-structure dispersal and breeding probability, we assumed that birds returned to their natal area to breed after hatch year. This assumption also predicts that recruitment compensates for adult mortality, which may obviously overestimate the number of individuals in an area. We also did not estimate the number of floater individuals, which may underestimate the number of individuals in the population.

Ferruginous Hawks are likely a density-dependent species when breeding, as observed in many territorial bird species (Newton 1998). However, data to demonstrate density-dependence or parameters to estimate its function are unknown or unavailable. Thus, we modeled the population as density-independent up to a hard limit. We set a maximum of 14 nests per township, regardless of landscape characteristics in the township. If relative abundance of nests within a township exceeded this maximum ceiling, the excess numbers of pairs were dispersed into a neighbouring township. This prevented townships from having an infinite number of nests, despite being modeled without an explicit density-dependent function applied to nest survival.

Results

We ran 100 simulations of our benchmark population model and the average population after 50 years was 983 pairs with an average lambda of 1.0004 (Table 12).

Land cover

In the grassland cultivation to cropland scenarios, grassland cover decreased from 49,398 km^2 (33%) to 41,992 km^2 (28%) in the study area over 50 years (Figure 26). In scenarios where cropland was restored to grassland, grassland cover increased from 49,398 km^2 (33%) to 56,955 km^2 (38%).

The scenario with grassland loss forecasted an average lambda greater than 1.0 and estimated 1000 nests after 50 years, which is a 2% increase from the benchmark scenario (Table

12) (Figure 27). This scenario thus had the least influence on Ferruginous Hawk populations. A similar scenario with additional edge each year forecasted an average lambda greater than 1.0 and an estimated 1125 nests after 50 years - a 14% increase from the benchmark scenario.

The scenario with grassland restoration forecasted an average lambda greater than 1.0 and resulted in an estimated 1028 nests after 50 years, which is a 5% increase over the benchmark scenario in which no land cover or climate changed. When an additional 3.2 km of edge was added in the grassland restoration scenario each year, average lambda is above 1.0 and simulations forecast an estimated 1369 nests after 50 years. This simulation forecasted a 39% increase from the benchmark scenario, which demonstrated the greatest influence on population size after 50 years.

Climate

Both high and low climate change scenarios forecasted a negative influence on the Ferruginous Hawk population (Figure 27). The low climate change scenario saw smaller annual temperature changes in average winter, spring, and monthly temperatures and resulted in a population with a lambda similar to benchmark values. Simulations forecasted an estimated 981 nests and an average lambda above 1.0, which is a less than a -1% change in population after 50 years. The high climate change scenario forecasted higher temperature change over the same time period and simulations forecasted an estimated 962 nests and an average lambda greater than 1.0, which is a -2% change in population after 50 years.

Cumulative effects

Using a status quo approach for grassland land cover change, we estimated a loss of 0.05% of grassland annually to cropland conversion. With this forecasted land cover change and under the low climate change scenario, we forecasted 997 nests and an average lambda above 1.0 after 50 years, which is a 1% increase over benchmark numbers over that period (Figure 28). The high climate change and grassland loss scenario forecasted 957 nests and an average lambda below 1.0, with a -3% decrease compared to benchmark numbers after 50 years. The high climate change scenario has the greatest influence under the additive cumulative effects scenario that included grassland loss.

Under a targeted grassland restoration scenario and expected low climate change, we forecasted 1025 nests and an average lambda greater than 1.0 after 50 years, which is a 4% increase over benchmark values. A similar scenario with expected high climate change, our model forecasted 1013 nests and an average lambda greater than 1.0 after 50 years, which is 3% higher than benchmark values.

Discussion

Overall, our scenarios demonstrated that simulated land cover change had greater influence on Ferruginous Hawk population demography than simulated climate change. In our single-factor sensitivity analyses among land cover and climate change scenarios, targeted grassland restoration that also added edge was forecasted to have the greatest positive influence on the Ferruginous Hawk population in Canada. Conversely, among the land cover and climate change scenarios we simulated, the high climate change scenario forecasted the greatest decrease in the Ferruginous Hawk population in Canada after 50 years. The difference between the relative influence of land cover and climate change is appreciable where climate change scenarios resulted in a small difference from the benchmark model (-2 to -1% difference). In comparison, land cover change scenarios resulted in larger differences from the benchmark model (5 to 14%).

However, we expect land cover and climate to change concurrently. Our simulations showed that the additive cumulative effects models had diverging forecasts, depending on the combination of land cover and climate change. Scenarios with targeted grassland restoration, with either climate change scenario, had a greater relative influence on the Ferruginous Hawk population in Canada compared to the benchmark model with no land cover or climate change. Scenarios with grassland loss and either climate change scenario were less influential compared to both grassland restoration scenarios and the benchmark model. The grassland loss scenarios also had lower average lambdas than the grassland restoration scenarios were relatively slow to change population size.

Our results suggest that targeted grassland protection and restoration could benefit the Ferruginous Hawk population in Canada. Our results from our different scenarios simulating added edge density to landscapes can be used to inform a strategic grassland restoration program. Habitat conservation or protection programs target either large continuous tracts or several small-moderate habitat patches of species' habitat (i.e., "Single Large or Several Small (SLOSS)" paradigm (Diamond 1975)). Managers often lack the data to make informed decisions regarding which strategy is more suitable for a species. For Ferruginous Hawks in Canada, our simulations suggest that increasing the amount of grassland cover in townships with approximately 25 to 50% grassland could create more high quality habitat. Our simulation models also show that adding edge with grassland restoration is predicted to have the relatively greatest positive influence on hawk populations. Therefore, among our simulated scenarios, restoring grassland cover in a patchwork design to create a mosaic landscape will likely have the greatest benefit for the population when considering only our tested options. This approach of adding patches of grass and edge contrasts with existing grassland restoration programs that generally target restoration adjacent to tracts of grassland, thus making grassland patches larger. Restoring grassland connected to larger tracts can still result in landscapes positively associated with relative nest abundance and nest survival. Assuming that restoration of grassland can achieve or provide the same mechanisms or characteristics that are positively associated with habitat quality for Ferruginous Hawks, restoring grassland connected to larger tracts has the potential to benefit both Ferruginous Hawks and grassland species associated with larger contiguous tracts. This approach would make efficient use of limited resources for conservation and recovery. Conservation approaches that protect moderately-sized grassland patches can be complementary to broader grassland protection programs because it will maintain connectivity between larger grassland patches, which will benefit many grassland-associated species at risk while also benefiting Ferruginous Hawks.

This is the first spatially-explicit demographic model for Ferruginous Hawks and has been useful for assessing the relative influence of land cover and climate change on hawk populations in Canada. However, we strongly caution against using our model and scenario results outside of this objective. Our model should not be used to assess actual population trends or predict future Ferruginous Hawk populations in Canada for several reasons.

First, our population model did not capture the full complexity of Ferruginous Hawk demography and could over or underestimate the future population size and average lambda. Our population model is missing demographic components such as how many birds become floaters, the true dispersal patterns, and other demographic parameters that vary with age-structure. Many raptor species, such as Golden Eagles (*Aquila chrysaetos*) (Wiens et al. 2017) and Black Kites (*Milvus migrans*) (Sergio et al. 2011), have vital rates that vary with age. Thus, we expect that Ferruginous Hawks exhibit ages-structured vital rates, but it has not yet been quantified. As this information becomes available for Ferruginous Hawks, it should be included in future population models because it could change recruitment and survival rates that influence demography. Our model structure also allowed for a considerable rescue effect from birds in the Unites States, the degree to which is not known. Increasing the complexity of the population model to reflect Ferruginous Hawk demography will improve the model's predictive ability.

Second, applying climate change models to predict species response is challenging and we limited the land cover and climate change scenarios to a few representative scenarios. Our scenarios simulated climate change by incrementally increasing average seasonal temperatures using climate forecasts. Our models and conclusions were limited because they did not capture the stochastic nature of extreme weather events, which are known to negatively influence Ferruginous Hawk reproduction (Chapter 3, Laux et al. 2016, Wallace et al. 2016b). Ferruginous Hawk nests are sensitive to extreme weather events, such as rain and wind storms, because nests can blow out of nest structures. Nest blowouts during the breeding season usually result in destroyed eggs or nestling mortality (Chapter 3, Laux et al. 2016). Incorporating stochasticity into the nest survival model and climate change scenarios would better represent the influence of future climate change. We also did not model how land cover change could change with climate change. We assumed that these scenarios are unlikely to occur over the short duration of our simulations (i.e., 50 years). However, including these changes into our land cover and climate change scenarios could improve our forecasting, particularly because it is has been demonstrated that climate change can changed species distribution (Rodenhouse et al. 2008).

Lastly, the relative nest abundance and nest survival models that drove the changes to population were developed using data collected between 2012 and 2013, and 2010 and 2015, respectively. The Ferruginous Hawk population in Alberta, and possibly Canada, was relatively stable or slightly declining during this time period (Redman 2016). Therefore, these models only reflect a narrow range of conditions and when the population showed little variation. It is also possible that we did not account for an unknown population driver or use suitable proxies for hypothesized drivers in our models. Our relative nest abundance and nest survival generally had high predictive performance, but they should only be used to predict within the range of environmental and anthropogenic conditions used to develop the models.

Mechanistic studies that explore why land cover change and weather impact habitat selection, nest abundance, and nest survival are needed (Oliver and Morecroft 2014). Our study is limited because we applied models that use patterns associated with habitat use and reproductive performance. We assumed that these patterns are associated with mechanisms that will hold true through change in landscapes and weather. However, our models can only predict within the range of parameters evaluated in our original habitat models. As values exceed the range previously studied, it becomes more uncertain if our models can accurately predict future relationships. This is particularly true for variables such as weather. Temperature, but also precipitation and severe weather patterns are expected to change in our study area. As average seasonal temperature exceeds the range experienced by nesting hawks during the years of our study, the predicted relationship with nest survival may change. Identifying mechanisms will help assess whether patterns hold true under future environments.

Future scenario simulations for Ferruginous Hawks should also investigate the influence of other land uses. Previous studies have shown that oil and gas development is associated with different probabilities of habitat use and reproduction. Closer proximity to active oil wells is associated with home range habitat selection (Chapter 2), but is negatively associated with nest survival (Chapter 3, Wallace et al. 2016b). At the time of our study, oil and gas development expansion had slowed. However, approximately 6163 new wells are predicted to be drilled in Alberta and Saskatchewan, including a proportion of those wells in our study area, in 2018 (PSAC 2018). With market change, oil and gas fields could be developed further. Our spatially-explicit population included existing infrastructure, but our future scenario models did not include changes in oil and gas development. Future spatially-explicit models should investigate the added cumulative effects of industrial development.

Assessing the relative influence of land cover and climate change under different scenarios provided insight potentially useful for population recovery of this species at risk in Canada. Recovery plans could prioritize actions by the relative influence of land cover and climate change. Based on our scenarios, grassland restoration may be an important conservation tool for Ferruginous Hawks in Canada.

TABLE 11. VITAL RATES FROM PUBLISHED LITERATURE WHERE FERRUGINOUS HAWK RESEARCH WAS CONDUCTED IN CANADA AND OUR FIELD STUDY CONDUCTED IN CANADA, FROM 2010 TO 2016.

Vital rate	Function of land cover or climate	Range of values	Source
relative nest abundance	land cover	0 to 13.5 nests/township	a) Chapter 3 b) Schmutz et al. 2008
probability of nest survival (ϕ_{Nest})	land cover climate	0 to 1.0	a) Chapter 3
fledge rate	neither	mean = 2.39 SD = 1.00 normal distribution	a) Chapter 3 (n = 530 successful nests)
probability of recruitment ($\phi_{Recruitment}$)	unknown	0.43 to 0.55 uniform distribution	a) field study, unpublished data b) Schmutz et al. 2008
probability of adult survival (ϕ_{Adult})	unknown	0.71 to 0.87 uniform distribution	a) field study, unpublished data b) Schmutz et al. 2008

TABLE 12. SCENARIOS, POPULATION SIZE AT 50 YEARS, AND RELATIVE INFLUENCE OF LAND COVER AND CLIMATE CHANGE ON FERRUGINOUS HAWK POPULATIONS IN CANADA. MEAN LAMBDA, POPULATION SIZE, AND EFFECT ARE RELATIVE AMONG MODELS AND SCENARIOS WE SIMULATED AND DO NOT PREDICT ACTUAL POPULATION GROWTH OF FERRUGINOUS HAWK POPULATIONS.

Objective	Scenario	Land cover conversion	Climate Change	Mean lambda	Nests at 50 yrs	Effect
	Benchmark	No change	No change	1.0004	983.36	
Sensitivity analyses	Climate change	No change	RCP 4.5	1.0004	981.29	0.998
		No change	RCP 8.5	1.00007	962.34	0.979
	Land cover change	Grassland restoration (+0.005 in townships with originally between 25 and 50% grass)	No change	1.0013	1028.16	1.046
		Cropland conversion (-0.005 in townships with originally between 25	No change	1.0008	1000.23	1.017

		and 50% grass)				
		Grassland restoration (+0.005 plus 3.2 km edge in townships with originally between 25 and 50% grass)	No change	1.007	1368.79	1.392
		Cropland conversion in patches (-0.005 plus 3.2 km edge in townships with originally between 25 and 50% grass)	No change	1.003	1124.59	1.144
Cumulative effect analyses	Cumulative effects	Cropland conversion (-0.005 in townships with originally between 25 and 50% grass)	RCP 4.5	1.00039	997	1.014
		Cropland conversion (-0.005 in townships with originally between 25 and 50% grass)	RCP 8.5	0.9999	956.57	0.973
		Grassland restoration (+0.005 in townships with originally between 25	RCP 4.5	1.001	1025.20	1.04

	and 50% grass)				
	Grassland restoration (+0.005 in townships with originally between 25 and 50% grass)	RCP 8.5	1.001	1013.37	1.03

Equations

EQUATION 2. SUCCESSFUL NESTS PER TOWNSHIP.

= Number of nests per township * ϕ_N

ϕ_N :Probability of nest survival

EQUATION 3. PRODUCTIVITY PER TOWNSHIP.

= Number of successful nests * m_a

m_a : fledge rate

EQUATION 4. RECRUITMENT PER TOWNSHIP.

= Productivity * ϕ_R

ϕ_R :Probability of recruitment

EQUATION 5. BREEDING ADULTS PER TOWNSHIP

= Number of nests per township * 2

EQUATION 6. RETURNING ADULTS PER TOWNSHIP

= Number of breeding adults * ϕ_A

ϕ_A :Probability of adult survival

EQUATION 7. POPULATION SIZE (NUMBER OF NESTS)

= (Recruitment + Adults) / 2

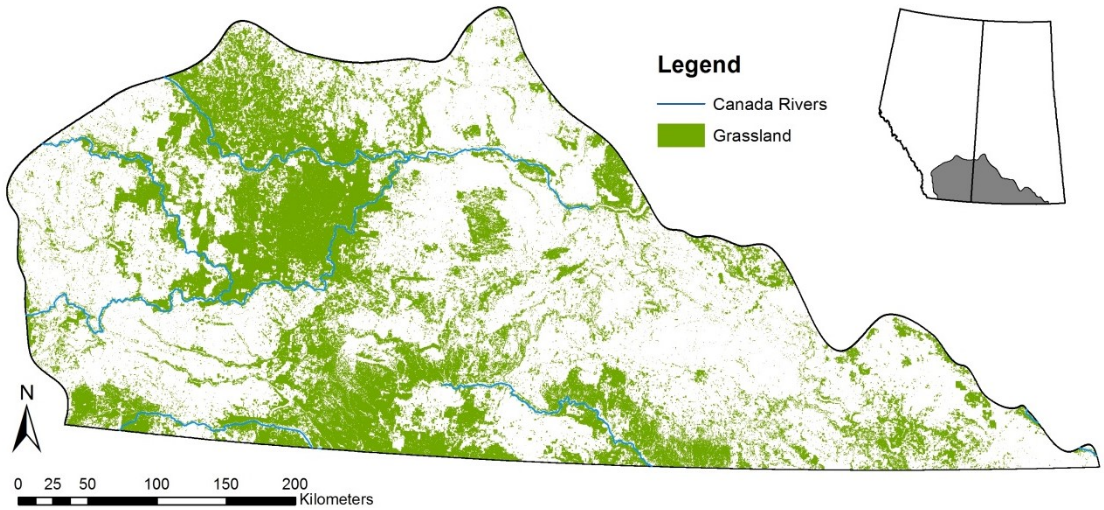
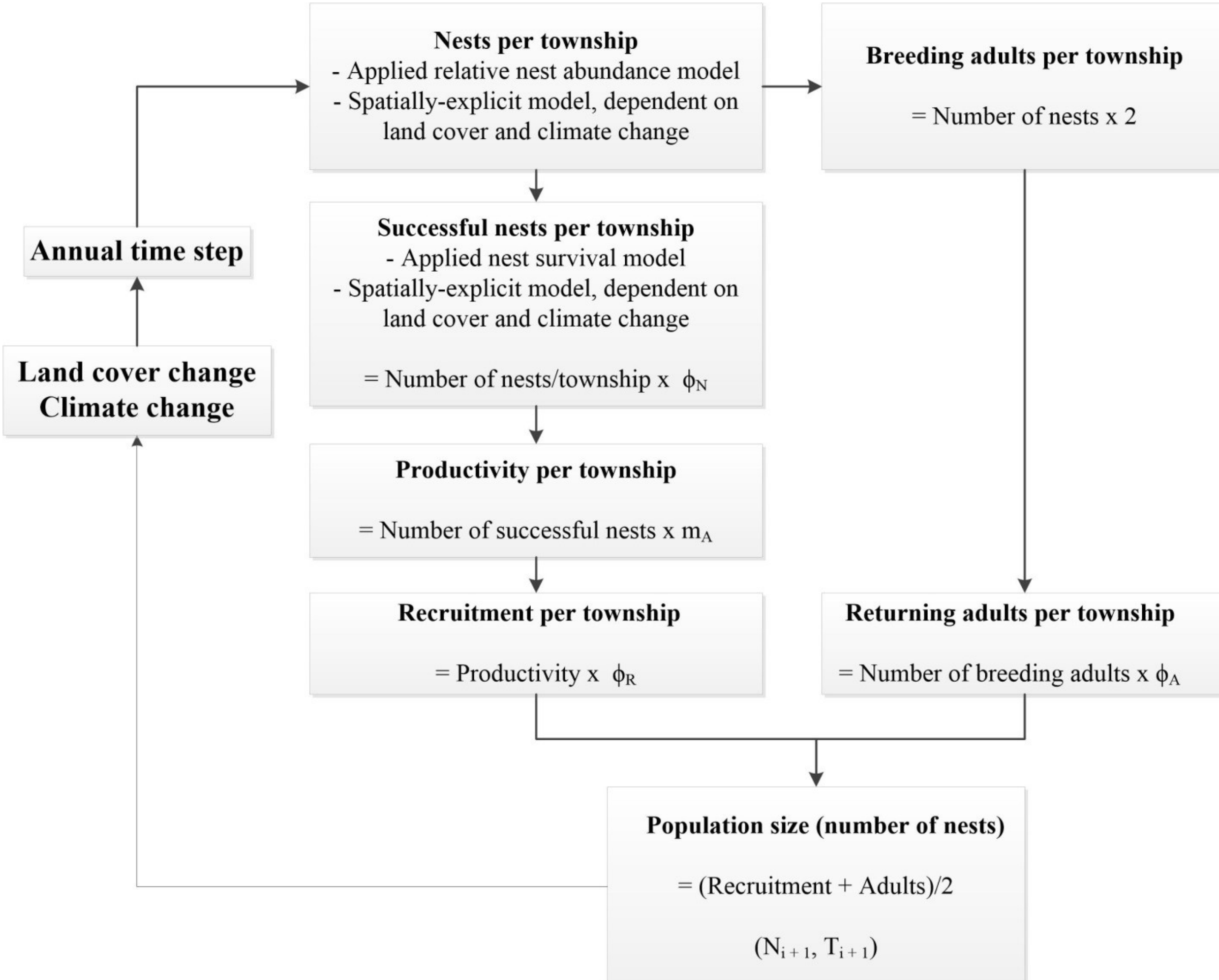


FIGURE 24. STUDY AREA IN SOUTHERN ALBERTA AND SASKATCHEWAN WHERE SURVEYS AND NEST MONITORING OF FERRUGINOUS HAWK NESTS WAS CONDUCTED.



$\phi_N = \phi_{Nest}$, probability of nest survival

$\phi_A = \phi_{Adult}$, probability of adult survival

$\phi_R = \phi_{Recruitment}$, probability of recruitment

$m_a = m_{Apparent}$, apparent fledge rate

FIGURE 25. POPULATION MODEL FOR FERRUGINOUS HAWKS UNDER CHANGING LAND COVER AND CLIMATE CHANGE.

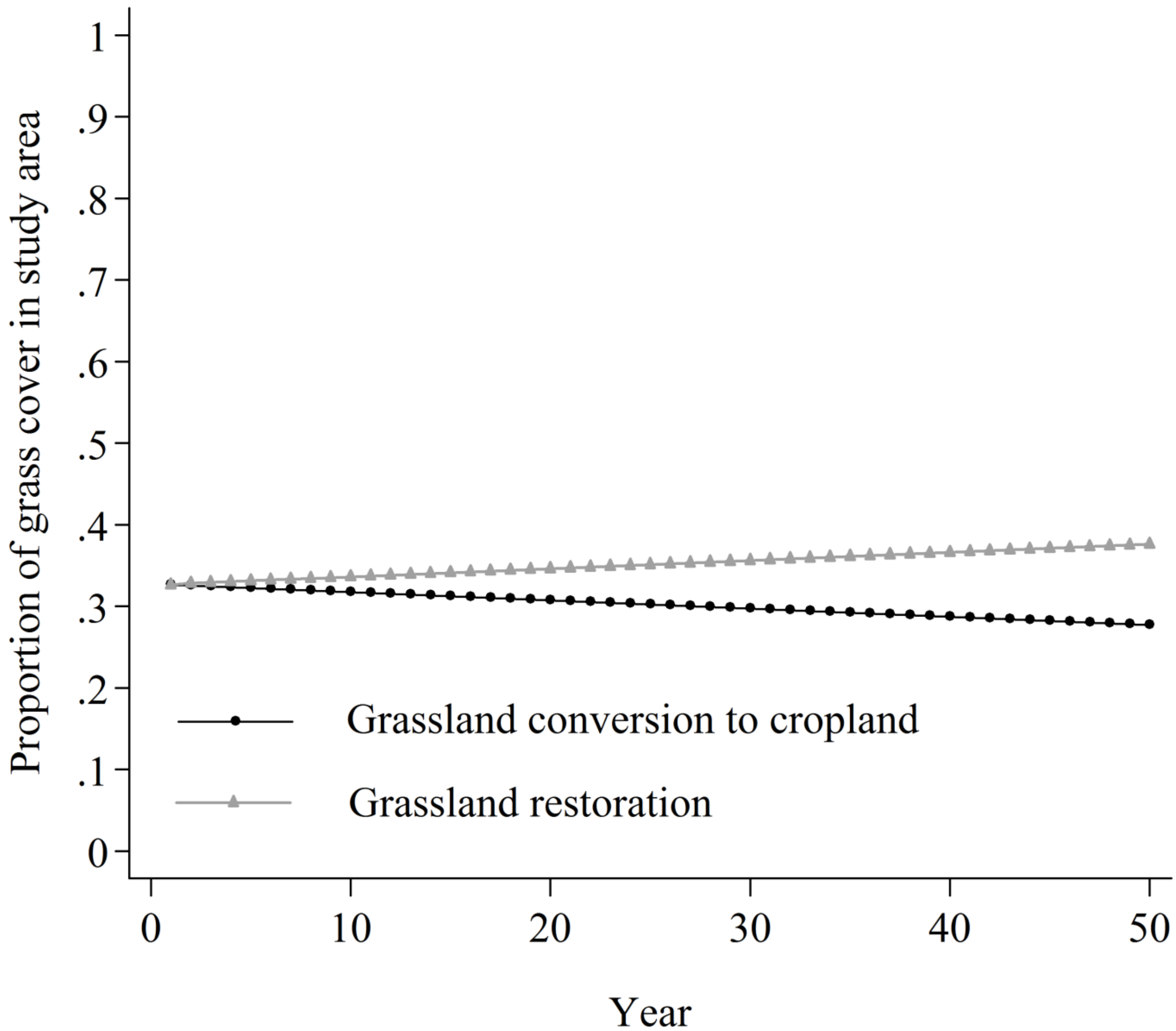
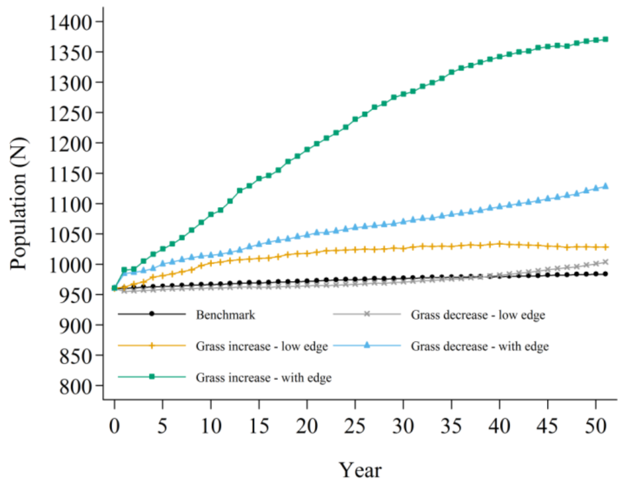


FIGURE 26. CHANGE IN TOTAL GRASSLAND COVER OVER STUDY AREA IN GRASSLAND CONVERSION AND CULTIVATION SCENARIOS.



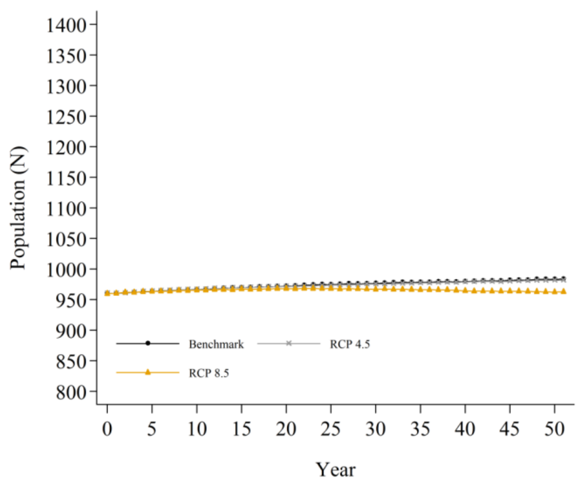


FIGURE 27. ESTIMATED POPULATION SIZE UNDER LAND COVER AND CLIMATE CHANGE SCENARIOS. A) INCREASE AND DECREASE OF GRASSLAND COVER BY 0.005% WITH AND WITHOUT ADDED EDGE. B) CLIMATE CHANGE SCENARIOS USING SEASONAL WEATHER CHANGES FORECASTED BE RCP 4.5 AND RCP 8.5 CLIMATE SCENARIOS. MEAN LAMBDA, POPULATION SIZE, AND EFFECT ARE RELATIVE AMONG MODELS AND SCENARIOS WE SIMULATED AND DO NOT PREDICT ACTUAL POPULATION GROWTH OF FERRUGINOUS HAWK POPULATIONS.

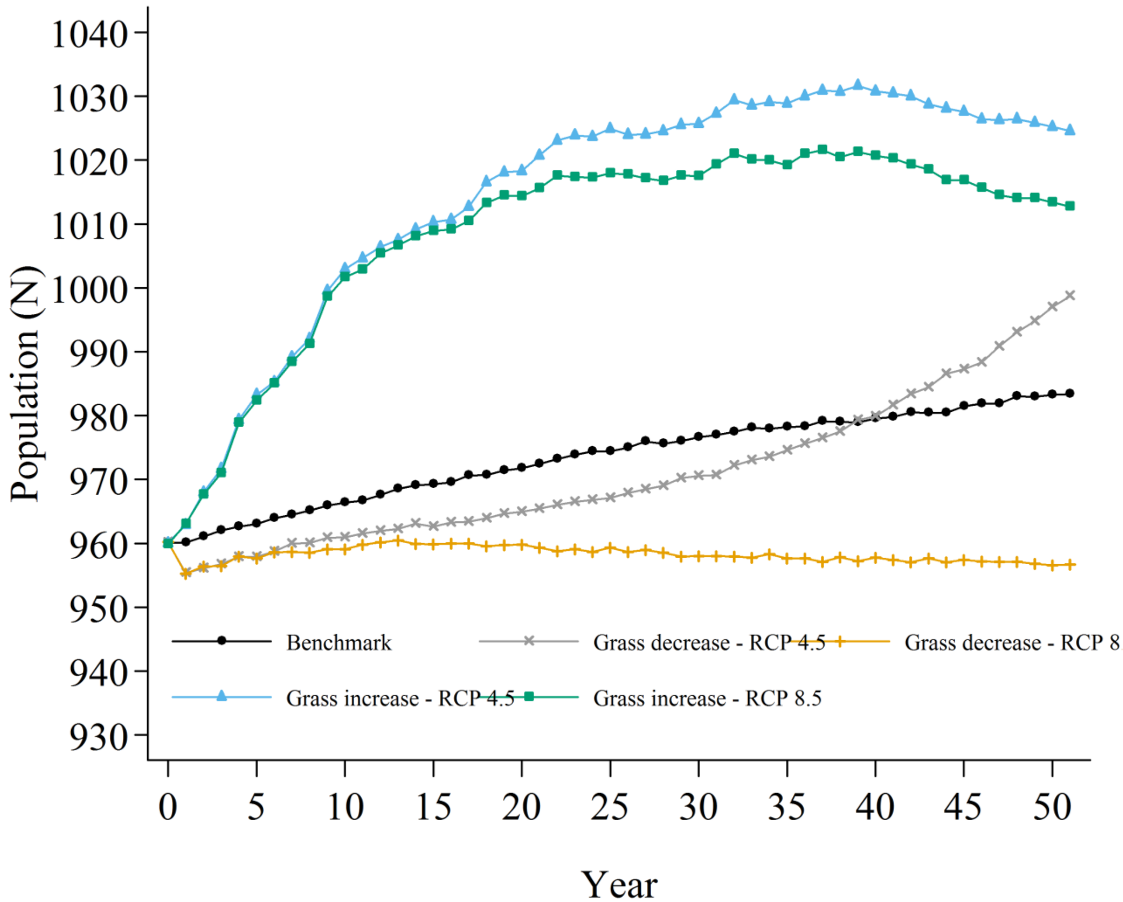


FIGURE 28. CUMULATIVE EFFECT SCENARIOS SIMULATED WITH GRASSLAND COVER AND CLIMATE CHANGE. MEAN LAMBDA, POPULATION SIZE, AND EFFECT ARE RELATIVE AMONG MODELS AND SCENARIOS WE SIMULATED AND DO NOT PREDICT ACTUAL POPULATION GROWTH OF FERRUGINOUS HAWK POPULATIONS.

Chapter 6: Synthesis

Influence of land use and climate on habitat quality

Heterogeneous landscapes composed of moderate amounts of cropland and grassland, with moderate edge densities, were associated with good habitat quality for Ferruginous Hawks. Our study found these heterogeneous landscapes were associated with home range (2.5 km radius) habitat selection, nest abundance within townships, nest survival, and prey delivery rate. Determining the mechanisms behind this common pattern is integral to understanding how landscape change can potentially influence Ferruginous Hawk populations in the future. Heterogeneous landscapes should be considered to be an important part of habitat management plans for Ferruginous Hawk population conservation and recovery in Canada.

Industrial development in southern Alberta and Saskatchewan has been a concern for this species at risk (Alberta Environment and Parks 2009), particularly for those Ferruginous Hawks observed nesting in landscapes with existing oil and gas development and where new development may occur near recently active nests. Our study found that hawks were more likely to select home ranges in areas with higher densities of resource roads and nearer to active oil wells. However, nest survival was lower in areas with high densities of active oil wells compared to areas with low or moderate densities. This pattern suggests that landscapes with high densities of active oil wells may be an ecological trap for Ferruginous Hawks. Future studies should compare overall productivity, nest survival, adult survival or condition, and post-fledging juvenile survival for nests located within and those far from areas with high densities of active oil wells to test whether areas with high densities of active oil wells are ecological traps or population sinks. In contrast to landscapes with high densities of oil wells, Ferruginous Hawks were more likely to have higher nest survival in areas with medium and high densities of active gas wells. These results suggest that there are different mechanisms for oil development than for gas development influencing Ferruginous Hawk breeding ecology. Identifying these mechanisms will be important for developing mitigation options (e.g., modified industrial site management practices) for existing development near nests, predicting impact to Ferruginous Hawk populations under different oil and gas market demand scenarios, and developing cumulative effects plans for new development to avoid negative impacts.

Prey availability is one potential mechanism that is influenced by landscape characteristics and industrial development. Studies have demonstrated that Ferruginous Hawk population dynamics are closely linked to their prey (reviewed in Chapter 4 and Ng et al. 2017); therefore, exploring the relationship between brood provisioning and the landscape around the nest could be important for understanding population dynamics. Our study found that brood provisioning could be predicted, in part, by landscape characteristics and oil well density within a 1000 m radius around the nest. Land cover types and edge surrounding the nest may provide physical structures such as perches, or vegetation structure conducive to prey capture or may be related to prey abundance (review in Chapter 4). Prey may also be related to soil characteristics, which we showed were predictive of home range habitat selection and nest abundance (Chapter 2 and 3). While Ferruginous Hawks do not generally interact directly with soil, soil may influence distribution and abundance of their main prey, the fossorial Richardson's Ground Squirrel. Our analyses found that seasonal weather was a better predictor for delivery of Richardson's Ground Squirrels than any tested landscape variable. In depth study of Richardson's Ground Squirrel habitat use, at micro and macro scales, and associated population dynamics would be valuable to improving our understanding of Ferruginous Hawk habitat use and reproductive performance.

Certain climate normals and seasonal weather were also predictors of Ferruginous Hawk habitat quality (Chapter 3). Our study found that landscapes with warmer springs and less precipitation predicted home range habitat selection and nest survival was also higher when the winter prior to the breeding season had a lower mean temperature (Chapter 2). Higher mean spring temperatures and mean monthly temperature during the breeding season also predicted higher nest survival (Chapter 3). Regardless of mechanisms, Ferruginous Hawk breeding ecology is associated with certain climate normals and seasonal weather. Under climate change, we expect temperature and precipitation patterns to change (Pachauri et al. 2014) and it is not known whether Ferruginous Hawks can adapt. We predict that changing climate normals and seasonal weather, like those included in our study, would impact future Ferruginous Hawk reproductive performance and populations (Chapter 5); however, we acknowledge that there are undoubtedly many additional factors, which we were unable to address in our study, that would vary with future climate change and likely further influence the demography of this species.

In southern Alberta and Saskatchewan, land use and climate (including seasonal weather) have cumulative effects that influence Ferruginous Hawk habitat use and reproduction (Chapters 2 and 3). Most of our habitat and reproduction models suggested effects were additive in nature, but there was an interaction between land cover and seasonal weather that influenced brood provisioning (Chapter 4). The cumulative effects approach in our study design and analyses was essential for exploring how multiple land uses and climate, including seasonal weather, may combine to impact Ferruginous Hawks.

Recommendations for conservation and management

Land cover management

Landscape ecologists often deliberate whether a "single large or several small (SLOSS)" approach to protected areas design will provide the most benefit to wildlife populations (Diamond 1975). Outside of protected areas, the same concept is important for strategic landscape conservation at large spatial extents. Often the available habitat and reproduction data is lacking to make an informed decision. Without data suggesting otherwise, many habitat conservation approaches focus on protecting large reserves because this approach is often thought to benefit many species. However, this approach may not be the most beneficial option for some species.

For Ferruginous Hawks in Canada, our study comprehensively evaluated habitat and reproduction ecology. This body of work demonstrates that heterogeneous landscapes are positively associated with habitat use at multiple scales (i.e., home range habitat selection at 2.5-km radius and relative nest abundance at the township scale, Chapters 2 and 3), reproductive performance (Chapter 3), and prey delivery rates (Chapter 4). We suggest that protecting patches of grassland in landscapes with moderate amounts of cropland should benefit Ferruginous Hawk populations more than focusing on large contiguous tracts of grassland cover.

In some landscapes in Canada, only a small proportion of native grassland remains (De Smet 1991, Hammermeister et al. 2001, The Alberta Biodiversity Monitoring Institute 2015). Therefore, grassland restoration could be an important conservation tool for Ferruginous Hawks, assuming that restoration can successfully reconstruct those grassland habitat characteristics and conditions that are beneficial for this species. Our simulations demonstrated that land cover change has the greater relative influence than the climate change variables we included (i.e., average seasonal temperatures), given the particulars of our scenarios, on Ferruginous Hawk populations in Canada (Chapter 5). Scenarios with targeted grassland restoration under either climate change scenario showed a general positive influence on the population; therefore, this should be considered for incorporation into strategies for conserving and recovering Ferruginous Hawk populations in Canada.

The majority of grassland protection and restoration programs in Canada focus on maintaining or expanding large tracts of grassland, but this approach should be re-evaluated for Ferruginous Hawks, given that the species seems to benefit from landscapes with mixed landcovers. In addition, grassland conservation and restoration is challenging and limited by resources, requiring strategic approaches to achieve goals. We propose that a conservation approach that protects and restores grassland patches can be complementary to broader grassland conservation programs that are focused on large grassland expanses. Protecting or restoring grassland patches near or connected to larger tracts of grassland is likely to benefit Ferruginous Hawks. This approach will also meet grassland conservation objectives for other species by maintaining low isolation or decreasing the degree of isolation for the target grassland patches. A high concentration of species of risk is found in Canada's grassland regions; therefore, it is crucial for species at risk recovery that efficiencies are found wherever species recovery goals and approaches overlap for aspects of grassland conservation and restoration.

Mitigation hierarchy

In the Canadian Prairies, multiple land uses on a landscape are common. Farming, ranching, oil and gas extraction, power transmission, wind and other renewable energy generation are common across the study area. A landscape may have all of these land uses occurring and some may be spatially co-occurring or overlapping. Managing and reducing their cumulative effects requires identifying their potential impact, prioritizing conservation needs, and allocating resources to create the most benefit. A mitigation hierarchy is a common approach to manage risk, where negative cumulative effects are avoided, mitigated, and lastly offset or compensated to reduce human impact.

In a mitigation hierarchy, avoiding potential impact is the first and best approach to reducing further negative effects to wildlife and landscapes. Further cultivation of grassland into cropland and high densities of oil development (>25 wells within a 2500 m radius of the nest) should be avoided in important Ferruginous Hawk habitats (see Chapters 2, 3, and 4). Landscapes with homogenous land covers and high densities of oil wells are associated with negative impacts to habitat use and reproductive performance. As well, Ferruginous Hawks are only one species at risk for which landscapes must be managed, and many species at risk in the Canadian grasslands would be negatively impacted by further grassland cover loss. Therefore, avoiding further cultivation would benefit Ferruginous Hawks in mixed landscapes, and other grassland-associated species at risk in other landscapes, within the grassland regions of Canada. Managers should also avoid adding potential cumulative effects that could impact hawk populations. For example, wind farms should be macro-sited away from important hawk habitat because turbines may reduce probability of survival and home range occupancy (J. Watson, unpublished data, reviewed in Chapter 2). Wind turbines also could be placed within cropland far from cropland-grassland edges. We recommend that our spatially-explicit risk map (Chapter 2) be used for proactively macro-siting new wind farms away from habitat important to Ferruginous Hawks and avoiding adding cumulative effects to their populations. However, we caution that macro-siting should also concurrently consider the habitat associations and distributions of other species too. Generally avoiding wind development that could negatively impact Ferruginous Hawks in the identified primary and secondary habitats (Chapter 3) would be a beneficial management practice. Our study also identified landscapes where wind development may have less impact to the Ferruginous Hawk population, thereby providing options for avoiding important habitat (Chapters 2 and 3).

If development cannot be avoided in important Ferruginous Hawk habitats, then mitigation is the next step in a mitigation hierarchy. Mitigation can be actions or strategies used to reduce the negative impact of development or disturbance. We found that nests located on human structures were strongly positively associated with nest survival (Appendix B). This result is supported by multiple studies that found similar patterns with nests located on artificial nest platforms and human structures (reviewed in Appendix B). If a nest is destroyed or at risk, installing an artificial nest platform *in situ* or nearby could be a local, immediate mitigation measure that would likely benefit individual Ferruginous Hawk pairs. The long term impact to the Ferruginous Hawk population of adding platforms to a landscape is unknown and the interactions of habitat selection, reproduction, density-dependence, and prey population dynamics are ecologically complex and unpredictable. Artificial nest platforms are often used as a 'Go To' mitigation tool for industrial disturbance, but instead should be used as a last resort for mitigation or offset. Oil well reclamation may be a broader scale mitigation option to reduce the negative impact of high density oil development to Ferruginous Hawks. Reducing the number of active oil wells in high density oil development areas near existing Ferruginous Hawk nests, or inside potentially important habitat, could decrease the potential impact to average nest survival. However, without understanding the mechanisms explaining the relationship between nest survival and oil development, it is unknown whether suspension, decommissioning, and reclamation of wells would reduce the impact, especially if more oil wells were then drilled. Within similar landscapes, future study could use an experimental approach to explore the impact of reducing densities of active oil wells (e.g., oil well suspension, decommissioning, and well site reclamation) on Ferruginous Hawk reproductive performance.

Regulators and industry may use offsets to reduce the overall impact of human development where avoidance or mitigation is not possible. In the case of wind energy development, we identified landscapes of high conservation value for Ferruginous Hawks (Chapter 2). These landscapes have high potential as important hawk habitat (i.e., high probability of home range habitat selection) and low wind potential (i.e., low likelihood of wind development projects). They would be ideal landscapes to protect or enhance to reduce overall impact of future wind development to Ferruginous Hawk populations. Our habitat state framework (Chapter 3) also identified primary and secondary habitats that would be best to target for protection or enhancement because Ferruginous Hawk nest abundance and nest survival are predicted to be relatively high in those areas. Habitat management in landscapes identified as high or moderate concern (Chapter 3) could also decrease risk to Ferruginous Hawks if limiting factors are addressed. Offsets in the form of grassland restoration in these primary or secondary habitats could benefit future hawk populations and aid in species recovery, provided that grassland restoration could be done in a fulsome way that re-creates high quality habitat for Ferruginous Hawks. Offset and compensation should be the last resort for reducing human-related negative impacts to Ferruginous Hawks, but it is important that such options are identified, in case they are needed.

Species conservation and recovery actions

Our home range habitat selection (Chapter 2) and relative nest abundance models (Chapter 3) are being used to identify important hawk habitats for the Government of Alberta (Alberta Environment and Parks) and the Government of Canada (Environment and Climate Change Canada). Our study demonstrates how spatially-explicit models can be used to understand the relative influences of potential population drivers.

Recommendations for future research

Our study was able to address the complexity of cumulative effects because our study was conducted over a large spatial extent, addressed research objectives at multiple spatial scales, and had large sample sizes for each study component. Our research was conducted over a study area approximately 153,000 km^2, covering the majority of the species' range in Canada. This large spatial extent allowed us to use a stratified design to survey for, and monitor, nests across a gradient of land cover compositions. To maximize the number of nests studied in each stratum, an immense effort went into nest searching and monitoring nests throughout the breeding season to acquire large sample sizes. Between 2010 and 2015, we found 907 unique nests, conducted over 10,000 nest visits involving more than 1533 nesting attempts, and installed video systems at over 80 nests. We were able to monitor a similar number of nests in each stratum because we deliberately focused our efforts on finding and monitoring nests within townships where landscapes suited our stratified study design. This adaptive strategy allowed us to attain relatively equal sample sizes across the strata and improved the rigour of our analyses. We also deliberately monitored nests, not only across strata, but also geographically spread throughout the study area. This large geographic extent and five years of nest monitoring allowed us to include pairs that experienced different seasonal weather patterns, compared to studies that were conducted over local or regional extents over shorter time periods. Monitoring clusters of nests would have saved time, but surveying for and monitoring nests located over a large and varied study area allowed us to reduce spatial autocorrelation. We believe that sampling over a large spatial extent was essential for addressing our research objectives.

Quantifying habitat use and reproduction for a relatively uncommon and wide-ranging species is effort-intensive. We argue that it is worth the effort to use a rigorous cumulative effects approach to gain a more thorough understanding of the influence of environmental and anthropogenic variables on wildlife populations. Cumulative effects from landscape and human development variables likely occur at small to large spatial extents. Therefore, studying their potential influence should also occur at multiple spatial scales over large spatial extents.

Predicting the influence of climate change on Ferruginous Hawk habitat use and reproduction is difficult because climate change and land use are likely interactive (Oliver and Morecroft 2014). We also did not model multiple environmental processes, such as grazing or fire, which are expected to be influenced by climate change and land use and could in turn influence habitat or prey for Ferruginous Hawks. This limits our conclusions, particularly our scenario simulations, because both grazing and fire are important ecological processes with cascading effects. We also did not assess how changing temperature and precipitation patterns are expected to influence land cover and land use, which may change the distribution of Ferruginous Hawks in Canada. In addition, we collected reproductive data during a relatively narrow window in time (between 2010 and 2015), so we were not able to assess the influence of drought periods on Ferruginous Hawk densities and reproduction. Richardson's Ground Squirrel survival and reproduction is hypothesized, and reported by local traditional knowledge, to be positively associated with drought. Forecasts of climate change in the Canadian Prairies include greater frequency and severity of drought conditions (Pachauri et al. 2014), which may interact with ground squirrel populations to positively influence future Ferruginous Hawk populations. Future study of Ferruginous Hawks and their main prey in Canada, Richardson's Ground Squirrels, would ideally include an approach that addresses the complexity of climate change and land use, and their interactions, to more accurately assess the future impact of climate change on this species at risk.

In Canada, Richardson's Ground Squirrels are an integral component of Ferruginous Hawk ecology (Schmutz and Hungle 1989a, Schmutz et al. 2008). They form the majority of the prey base (i.e., biomass) for adult, nestling, and fledgling Ferruginous Hawks. Fluctuations in Ferruginous Hawk population demography have been associated with the availability of Richardson's Ground Squirrels (Schmutz and Hungle 1989a, Schmutz et al. 2008). Given their importance to Ferruginous Hawks, including ground squirrel ecology into conservation and recovery plans for Ferruginous Hawks should be beneficial. For example, ground squirrel burrow counts were positively associated with increased grazing intensity and decreased vegetation biomass in upland habitats (Bylo et al. 2014). Other studies have also shown associations with shorter vegetation (Downey et al. 2006, Proulx et al. 2012, Fortney 2013). Managing grass cover in a heterogeneous manner, using a range of grazing intensities, may improve ground squirrel abundance for Ferruginous Hawks and could influence Ferruginous Hawk survival and reproductive performance. Our study mainly dealt with the composition of landscapes with respect to major land cover types with edge density as an additional landscape characteristic, but future studies should evaluate how varied grazing intensities in upland grassland landscapes of different grass cover composition and configuration could influence ground squirrel abundance and availability. Ferruginous Hawk nestlings, on average, hatch when juvenile ground squirrels emerge above ground (Schmutz et al. 1980b), resulting in high abundances of both adults and juveniles available for capture. Climate change may modify the phenology and fitness of Richardson's Ground Squirrels in Canada, as has been documented for Columbian Ground Squirrels (*Urocitellus columbianus*) (Lane et al. 2012). Such phenological mismatches could negatively impact Ferruginous Hawk productivity and thus future recruitment. These potential avenues of study also describe the limitations of our population demographic model and future scenario modeling (Chapter 5) because the impacts of these additional factors or processes on Ferruginous Hawk demography are not known. Future studies into Ferruginous Hawk survival and productivity should incorporate these complexities to better predict impacts to this species.

Research contributions

Our study has demonstrated how landscape characteristics and climate, including seasonal weather, are important to Ferruginous Hawks during the breeding season. We are confident in our results because we structured our study design to specifically address large spatial scale landscape, climate, and seasonal weather research objectives. Our results support an earlier, more local study that found Ferruginous Hawk nests are most abundant in landscapes containing both cropland and grassland within Alberta (Schmutz 1989). Our study also found that heterogeneous landscapes and some types of industrial infrastructure are positively associated with important components of Ferruginous Hawk ecology, including home range habitat selection, nest survival, and daily prey delivery rates. These findings may be surprising because Ferruginous Hawks were conventionally considered to be dependent on large tracts of contiguous grassland. However, our study and others (Schmutz 1989) suggest that moderately-sized patches of grassland, within a landscape mixed with cropland, are important for Ferruginous Hawk populations in Canada.

Our cumulative effects approach was essential for assessing the impacts of multiple land uses and climate on Ferruginous Hawks during the breeding season. Studies of cumulative impact often focus on the human footprint, but our study demonstrated the need to incorporate climate or weather into cumulative effects models. Climate and weather can potentially have a large impact on breeding ecology (Both et al. 2009b, Aubry et al. 2013), but the impact can also be spread over a large spatial extent and affect a large proportion of the population. The additive cumulative effects of changing climate and seasonal weather on species with large distributions, such as the Ferruginous Hawk, could be high. Our study also assessed the relative influence of multiple stressors. Mapping cumulative effects using spatially-explicit models quantified the relative influence of a stressor on a population by identifying its spatial extent of influence. This mapping with spatially-explicit data identified landscapes of conservation value for the species, as well as landscapes that may be ecological traps or population sinks. These assessments are particularly relevant for species at risk, such as the Ferruginous Hawk (SAR Public Registry 2010), because they are informative for conservation and recovery plans. Future studies of wide-ranging wildlife that may encounter multiple land uses, land cover types, and changing climate would benefit from using a cumulative effects approach to begin to disentangle potentially interacting predictors.

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Appendix A: Chapter: Predicting home range habitat selection by Ferruginous Hawks to identify potential wind energy conflict risk in Canada

TABLE 13. ALL ENVIRONMENTAL AND ANTHROPOGENIC VARIABLES INCLUDED IN THE GLOBAL HABITAT MODEL FOR FERRUGINOUS HAWKS IN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010.

Variable Name	Description and units	Data Source
Geography		
dem	elevation (m)	Climate WNA
dem_sd	standard deviation of elevation (m)	
long	longitude	
lat	latitude	
Land cover		Agriculture and
grassdist	distance to nearest grassland (km)	Agri-Food
grass2500	proportion of grassland within 2500m of the nest	Canada
edge2500	total length of edge where grass and crop interface (km)	
Human Development		
disttx	distance to nearest power transmission line (km)	IHS Energy
tx2500	total length of transmission line (km)	

	roaddist	distance to nearest road (km)	
	road2500	total length of road (km)	
	pipedist	distance to nearest pipeline (km)	
	pipe2500	total length of pipeline (km)	
	facdist	distance to nearest oil or gas facility (km)	
	fac2500	total number of oil or gas facilities	
	fnoisedist	distance to nearest sound-producing oil or gas facility (km)	
	fnoise2500	total number of sound-producing oil or gas facilities	
	welldist	distance to nearest surface oil or gas well (km)	
	well2500	total number of surface oil or gas well	
	oildist	distance to nearest oil well (km)	
	oil2500	total number of oil wells	
	gasdist	distance to nearest gas well (km)	
	gas2500	total number of gas wells	
Soil			
	eoli	proportion of eolian parent material	Soil Landscapes of Canad v3.2 Agriculture and Agri-Food Canada.
	lacu	proportion of lacustrine parent material	
	fluv	proportion of fluvial parent material	
	till	proportion of till parent material	
	coll	proportion of colluvial parent material	

fleo	proportion of fluvioeolian parent material
fllc	proportion of fluviolacustrine parent material
latl	proportion of lacustro-till parent material
resd	proportion of residual parent material
glfl	proportion of glaciofluvial parent material
gllc	proportion of glaciolacustrine parent material
rkud	proportion of undifferentiated bedrock parent material
undm	proportion of undifferentiated organic parent material
br	proportion of brunisolic order soils
lu	proportion of luvisolic order soils
ve	proportion of vertisolic order soils
ch	proportion of chernozemic order soils
gl	proportion of gleysolic order soils
rg	proportion of regosolic order soils
sz	proportion of solonetzic order soils
s_tx	categorical soil texture, from 1 (fine) to 7 (coarse)
clay	proportion of clay
silt	proportion of silt
sand	proportion of sand
carb	proportion of carbon
vfsan	proportion of very fine sand

Climate		
tmin_spr	minimum temperature in spring (°C)	Climate WNA (years = 1960-2000)
tmin_summ	minimum temperature in summer (°C)	
tmax_spr	maximum temperature in spring (°C)	
tmax_summ	maximum temperature in summer (°C)	
tav_spr	average temperature in spring (°C)	
tav_summ	average temperature in summer (°C)	
precipspr	average precipitation in spring (mm)	
precipsumm	average precipitation in summer (mm)	

TABLE 14. PROPORTION OF TOTAL RANGE AND TOTAL AREA (KM^2) OF LAND CATEGORIZED AS LEVEL OF RISK OF FERRUGINOUS HAWK –WIND CONFLICT AND LAND WITH HIGH CONSERVATION VALUE IN ALBERTA AND SASKATCHEWAN, CANADA, 2005 – 2010.

	Turbine Hub Height			
	50 m		80m	
Risk	%	km^2	%	km^2
low	39	138,648	33	115,304
medium	32	116,239	14	50,647
high	27	95,738	45	155,066
very high	2	6,708	8	27,050
high conservation value	36	129,082	29	100,316

Appendix B. Supplementary materials for Chapter 3: Managing cumulative effects for species at risk using a habitat-based framework

Objective

Develop base models for relative nest abundance and reproductive performance that evaluate the influence of geography, climate, soil characteristics, and intrinsic variables that influence habitat use and reproduction.

Methods

Relative nest abundance

Data collection

Sampling Method

We conducted surveys by vehicle, driving between 30 and 50 km/hr. A minimum of 20 km to a maximum of 30 km was surveyed in each block. We recorded the total distance surveyed and the time spent surveying. Surveys were conducted in fair to good weather conditions where visibility, and therefore detection, of Ferruginous Hawks and nests were not affected. For example, surveys could be conducted during low to high winds, but ceased during rain or snow when visibility was compromised. Nest location, status (i.e., active or empty), date, nest structure type (i.e., tree, artificial nest platform, cliff, ground, or other), and evidence of status were recorded for each Ferruginous Hawk nest. The number of Ferruginous Hawk nests was totaled for each survey. Surveys were conducted in the spring before leaves obscured tree nests.

Ideally, we would have used distance sampling to account for variation in our detection radius. However, we chose not to model these data as a distance function because of the biased spatial distribution of trees. Trees are more likely to be found near roads and farmyards, which are also near roads. The underlying assumption of distance sampling is that nests are randomly distributed relative to the transect line. As such a distance function based on roadside surveys would have artificially inflated nest abundance estimates.

Predictor variables

Grassland and cropland land cover are highly negatively correlated in the prairies and both could not be included in land cover models to avoid collinearity. We chose to analyse grasslands because it is commonly managed for by wildlife and habitat conservation agencies.

The total edge density variable was developed using features associated with different cover types, such as grassland, cropland, riparian vegetation, or tame grass associated with ditch sides, are adjacent. The change in cover type is also often associated with a change in vegetation type, height, and/or structure. These edges, while created by different features, may provide a similar function to foraging hawks or prey such as small mammals.

Human development was quantified as continuous and categorical variables. Oil and gas wells were categorized into wells (low = <150 wells, high =>150 wells), natural gas wells (low =

<100 wells, high =>100 wells), and active oil wells (low = <25 wells, high =>25 wells). Natural gas wells and oil wells were also categorized as low (<25 wells), medium (between 25 and 50 wells), and high (>50 wells). We also evaluated road density as categories of low (<100 km of roads) and high (=>100 km of roads). Roads were categorized into further distinctions, such as road class and road surface, because traffic volume and speed vary by road class and surface and may affect hawks differently. Uncommon industrial features, such as transmission lines, were described as present or absent.

A full list of variables and their data sources can be found in Table 15 and Table 16.

We used univariate models to select between collinear variables and also to test whether linear, non-linear, categorical, or presence/absence forms of a variable were the best predictor. Our analyses used an information theoretic approach (Anderson and Burnham 2004) and we compared Akaike's Information Criterion (AIC) values, coefficients, and confidence intervals for each univariate model. The functional form with the lowest AIC for each human disturbance variable was retained for subsequent models.

Model development

We developed a base model to use as a null model for our relative nest abundance model. The base model was developed to account for variation not explained by landscape or human development variables. All terms from the null model were included in the subsequent models. For example, to control for nuisance variables related to survey effort, we evaluated the importance of year, Julian date of survey, and total distance surveyed.

Spatial pattern was evaluated by evaluating the influence of latitude, longitude, elevation, and ruggedness. Their non-linear terms to the second order were also tested. Ruggedness was calculated as the standard deviation of elevation within the survey block for the abundance model and within 2.5 km of the nest for reproduction models. Controlling for spatial pattern can account for unmeasured environmental factors that vary spatially but for which we do not have data (e.g., ground squirrel abundance, tree abundance.).

We included province and the quadratic form of proportion of grass in the base model, which was included in all subsequent models. The quadratic form of grass was statistically significant and explained a large amount of variation in the data, relative to other variables (p-value = <0.001, pseudo-R^2 = 0.108), thus we included it as part of the base model to better control for its variation while evaluating for additive and synergistic effects.

Soil and climate variables were also controlled. Soil characteristics were quantified as area-weighted proportions of soil order, parent material, and texture where the proportion of each soil type was multiplied by the proportion of the survey block covered by the proportion soil type, and then summed for that soil type. Climate characteristics included minimum, average, and maximum of temperature and precipitation in spring and summer.

The base model was developed using a stepwise Poisson regression as following.

Variables to assess nest success were categorized into six classes: base, geography, land cover, industrial development, soil characteristics, and climate.

Our modeling process evaluated the influence of variables to predict nest abundance in our dataset. We used Poisson regression with the count of Ferruginous Hawk nests found within blocks as the response variable. We incorporated a validation procedure as part of the model selection process, whereby we confirmed the importance of a variable based on an external dataset. The external dataset was collected by Alberta Environment and Parks (AEP) and part of a long term monitoring program that surveyed for Ferruginous Hawk nests. AEP censuses 6.4 km by 6.4 km blocks spread throughout southern Alberta. A block is censused every five years, with a subsample of blocks surveyed every year. We used data collected between 2010 and 2015 and averaged the nest counts in each block across sampled years. These validation data were used throughout the modeling approach.

We developed models using a stepwise approach, where we predicted relative nest abundance in each block using model coefficients. We collapsed predicted values and the average number of hawk nests found on AEP survey blocks into decile bins. We started by testing variables as univariate models and evaluated if the variable improved predictive performance. Predictive performance relative to the validation data was evaluated using Spearman's rho and its p-value, and correlation coefficient. Only variables that had a statistically significant (p-value <0.05) Spearman's rho were included in the next model.

Significant variables formed a global model, that we then reduced by removing any variables that had a p-value < 0.15 in a backward stepwise procedure. As each variable was removed, we checked that the model's Spearman's rho was increasing and the associated p-value was decreasing and remained below 0.05.

Several variables were eliminated after the first suite of univariate tests despite having marginal p-values (e.g., 0.06 to 0.10). We took our reduced model and evaluated if adding each of these previously eliminated variables improved the predictive performance. If the model improved, the variable was retained. During this step, variables from the reduced model were also removed if they became non-significant (p-values > 0.10) and their exclusion improved the predictive performance of the model (Arnold 2010). The final model only included statistically significant variables (p-value <0.05).

Data collection

Nest monitoring

Nest location and type of structure supporting the nest (i.e., tree, artificial nest platform (ANP), cliff, ground, or other) were recorded. We monitored nests throughout the breeding season once a week using either a video camera mounted to a pole that could view nest contents, or by using binoculars or a spotting scope to observe the nest from afar. At each visit, we recorded nest contents (i.e., clutch size, number of live young) and whether the nest was alive or dead. At the completion of the nest, we recorded nest fate (i.e., successful when naturally fledged at least one young), source of nest mortality, date of nest outcome, number of young fledged, and other reproduction parameters. Hatching was rarely observed; therefore, almost all hatch dates were estimated from nestling age.

Model development

Base model

Similar to our relative nest abundance model, we developed a base model to control for factors that could influence nest survival, but were distinct from landscape and human development variables.

Intrinsic variables common between models include year, nest age, nest structure type (i.e., tree, artificial nest platform, cliff, or ground), and estimated hatch date. Intrinsic variables for nest survival analyses included date of visit, days since average hatch date of that year, and nest stages categorized as nest building and incubation (1), nestling age 0 to 20 days old (2), nestling age 21 to 40 days old (3), nestling age 41+ days old (4), and unknown nest stage (5). Nestlings are capable of fledging after ~40 days old, so the nest stages 2 and 3 reflect the before and after the halfway point to fledging. Days since average lay date of that breeding season was used as a proxy to nest age.

We also included survey-related variables in the base model that could potentially bias analyses. A monitoring bias can occur when nests survive further into the breeding season, they are more likely to be found compared to nests that failed early and they are more likely to survive to the next nest visit. We included date of first nest visit that year and visit number to control for the influence of monitoring bias. Furthermore, we did not have landowner permission to approach every nest; therefore, a subset of nests was monitored from the nearest road using a spotting scope. We observed these nests and assessed nest status using adult behaviour, observations of nestling, nestling age, and other indicators of nest status. Assessing the nest status from afar does not provide as detailed nest information compared to approaching the nest and assessing with a video pole. This could influence our ability to determine nest survival or nest contents. We included accuracy of nest location as a variable denoting whether we ever approached the nest or not.

Soil texture, categorized from very fine to very coarse, was evaluated (SLC version 3.2) (Soil Landscapes of Canada Working Group 2010).

Lastly, we included weather variables that were extracted from ClimateWNA version 5.40 (Wang et al. 2016). We extracted seasonal variables for the winter prior to the breeding season (December, January, and February), spring of the breeding season (March, April, and May), and summer of the breeding season (June, July, and August). Winter temperatures and snowpack have the ability to influence small mammal populations (Heisler et al. 2014), therefore we included several winter variables. Mean temperature (°C) and precipitation (mm) were extracted for winter, spring, and summer. In addition, winter degree-days below 0°C and precipitation as snow during the winter and spring were included. We also extracted monthly weather variables for each nest visit to examine the relative influence of current mean and maximum temperature (°C), and precipitation (mm) on daily nest survival. Weather data on Climate WNA was not yet available for 2016, so nest survival analyses were restricted to 2010 to 2015.

Some variables, such as visit number, days since hatch, and monthly weather prior to nest visit are suited for nest survival analyses and were not included in the clutch size and fledging rate analyses (Table 17).

Similar to our previous modeling procedure, we used AIC values to compare univariate models to select between collinear variables and also to test whether linear, non-linear, categorical, or presence/absence forms of a variable were the best predictor.

Cumulative effects model

We modeled daily nest survival using mixed effect logistic nest exposure (Shaffer and Burger 2004). A subset of randomly chosen nests were monitored weekly and the remainder of nests were monitored approximately once during incubation, once when nestlings were approximately 10 to 30 days old, and once when nestlings were close to fledging age (~40+ days old) to determine nest outcome. Only nests with exposure periods (i.e., number of days between nest visits) fewer than 15 days were included. Only nests with exposure periods (i.e., number of days between nest visits) fewer than 15 days were included after I compared models with exposure days limited to <7 days and <15 days and found that influential variables did not change, but variances decreased with a larger sample size.

Results

Relative nest abundance

Ferruginous Hawk nest abundance was predicted highest in the south central region of the study area, near Medicine Hat, Alberta (Figure 29). Low amounts of regosolic soil is associated with increased relative abundances of Ferruginous Hawk nests, decreasing in a near linear relationship as proportion of regosolic soil increases in the surrounding township-sized area.

Nest Survival

We found that 8.4% of all nesting attempts resulted in a blow out. Of all blow outs, 90.2% occurred in tree nests compared to <0.001% blow outs that occurred on platforms, where 22.7% resulted in nest failure and only 7.6% of blown out nests successfully fledged at least one young generally.

The base model included intrinsic, geographic, and seasonal weather predicators (Table 18). Compared to artificial nest platforms, nests in trees had lower nest survival. Ground and cliff nests were excluded from the analyses because of low survival variation, where every ground nest (n = 9) failed and every cliff nest (n= 4) successfully fledge a minimum of one young. Relative to the incubation stage, nests with nestlings 0 to 20 day old and 21 to 40 days old were more likely to survive. Nests with nestlings 41+ days old were the most likely to survive and this stage was removed from the analyses because of low survival variation. In comparison, when nest stage was unknown, the nest was less likely to survive. Hatch date was negatively associated with nest survival. The date of first nest visit was positively associated with nest survival. Geographic space variables were not predictive, but ruggedness was positively associated with nest survival. Weather variables in the final variable set included both a seasonal and monthly metric. Increased average winter temperature, decreased average spring temperature, and the average temperature of the month when visited were associated with decreased nest survival (Figure 30).

Clutch Size

Year was not included in the final model, but 2011 had the highest average clutch size (3.83 ± 1.02 SD) compared to other years (Table 19). The median clutch size was 3 for each year, except for 2011 when the median clutch size was 4.

Clutch size was positive associated with average spring temperature (standardized B = 0.109, p-value = 0.00). While only marginally significant, the amount of spring precipitation as snow (B = 0.053, p-value = 0.07) is also positive associated with clutch size (Figure 31).

Fledge Rate

The average spring temperature was positively associated with fledge rate (standardized B = 0.077, p-value = 0.002) (Figure 32) and generalized hatch date was negatively associated with fledge rate (B = -0.048, p-value = 0.016).

Discussion

Geographic variables predicted hawk nest abundance, but not reproductive success. Hawk nest abundance was highest near the south central region of the study area, which may reflect the high abundances of Richardson's Ground Squirrels in that region (Proulx et al. 2012). Nest abundance was lowest on the northern periphery of the study area, which coincides with the northern limit of their range. We might not have evaluated some landscape, soil, or climate variables that restrict the Ferruginous Hawk range and also reduces their nest abundance near the range edge.

The type of nest structure was an important predictor of nest survival. Nests located on nest platforms and cliffs were more likely to survive compared to nests in trees or on the ground. Platforms and cliffs may provide a more stable nest structure compared to trees. Almost all blown out nests failed to fledge young and very few were successful when young were at fledging or near-fledging age when the event occurred. We propose that nest blow outs are an important cause of nest failure as almost 8% of all nest attempts ended in a collapsed nest. Previous studies have also documented summer storms are an important source of nest failure (Gilmer and Stewart 1983, Wallace et al. 2016b). Furthermore, platform and cliff nests are less accessible by terrestrial predators, such as coyotes, compared to ground nests, which experienced 100% nest failure (n = 4, ground nests with known outcome). Previous studies also found higher nest success when nests were on cliffs, power line towers, platforms, and other anthropogenic structures (Gilmer and Stewart 1983, Steenhof et al. 1993, Wallace et al. 2016b). Nest platforms may be useful for mitigation plans or important for recovery plans where elevated nest structure availability is low.

Nest survival varied depending on nesting stage. Nests were less likely to survive early in the breeding season compared when nestlings were at fledging or near-fledging age. Nests at an unknown nest stage were also associated with low nest survival in my model, but this is likely because the nest stage is difficult to determine when the nest contents are missing (i.e., from predation), particularly when the eggs have not hatched and the nest is difficult to age. Furthermore, general nest age (number of days since hatch) was negatively associated with nest survival, suggesting that nests earlier in the breeding season were more likely to fail. Years with earlier average hatch dates were also associated with lower nest survival. Spring storms, associated with cooler temperatures and precipitation, may be the mechanism behind the decreased nest survival during early nest stages. Conversely, Ward and Conover (2013) found that survival was highest during the early nestling period and lowest during the late nestling and fledging period (Ward and Conover 2013). Specific mechanisms, such as extreme weather or predation, which result in nest failure must be determined to understand why survival varies by nest stage and between studies.

Soil is often an important driver of species distribution because it can dictate land cover type, drainage, and other landscape characteristics (Stevens et al. 2011). Relative abundance of hawk nests was negatively associated with the amount of regosolic soil in a landscape. In the prairies, regosolic soil is found along large river systems which are lined with trees and shrubs (Soil Landscapes of Canada Working Group 2010), but Ferruginous Hawks are generally not found in heavily wooded areas (Blair and F. Schitoskey 1982) and likely do not nest in these riparian areas. Soil texture was not correlated with nest abundance (Schmutz 1987a), but soil was an important predictor of home range habitat selection (Chapter 2). Further exploration to understand the mechanisms behind the association of soil characteristics and Ferruginous Hawk ecology should assess the relationship between soil and land cover, small mammal and ground squirrel abundance, and tree cover.

Climate variables did not predict hawk nest abundance, but seasonal weather and weather preceding a nest visit were good predictors of reproductive performance. Colder winters, which may benefit small mammal and therefore prey abundance (Heisler et al. 2014), were associated with high nest survival the following breeding season. Warmer average spring temperatures were also associated with larger clutch sizes and higher fledging rates. Lower average temperature of the month preceding a nest visit was also associated with lower nest survival. These patterns may reflect how severe weather, which is correlated to cooler average temperatures, impacts nest. Severe weather such as rain or wind storms can result in a nest blow out, exposure of vulnerable young to inclement weather, or reduce foraging success and provisioning by parents. Mild weather may result in better condition adults, perhaps being less energetically stressed by cool or inclement weather, who are able to lay larger clutches and fledge more young. Prey activity may also increase in mild weather, such as ground squirrels foraging aboveground, and result in increased prey availability and better adult body condition. Similarly, Wallace et al. (2016b) found higher fledging rates when there were fewer severe storms in June (Wallace et al. 2016b). Understanding if spring storms are specifically the mechanism for lower nest survival and lower productivity will be important for predicting the future effects of climate change.

TABLE 15. VARIABLES INCLUDED IN THE MODEL SELECTION PROCEDURE EVALUATING FACTORS THAT INFLUENCE FERRUGINOUS HAWK NEST ABUNDANCE.

Variable Name	Description and units
Geography	
long	longitude
lat	latitude
Land cover	
grass	proportion of grass
edge	total length of edge including where grass and crop interface, water body and wetland edge, and roads (km)
Human Development	
disttx	distance to nearest transmission line (km)
tx	total length of transmission line (km)
road	total length of road (km)
pipe	total length of pipeline (km)
fac	total number of oil and gas facilities
fnoise	total number of sound-producing oil and gas facilities
well	total number of surface oil and gas well
oil	total number of oil wells
gas	total number of gas wells
Soil	
eoli	area-weighted proportion of eolian parent material
lacu	area -weighted proportion of lacustrine parent material

fluv	area -weighted proportion of fluvial parent material
till	area -weighted proportion of till parent material
coll	area -weighted proportion of colluvial parent material
fleo	area -weighted proportion of fluvioeolian parent material
fllc	area -weighted proportion of fluviolacustrine parent material
latl	area -weighted proportion of lacustro-till parent material
resd	area -weighted proportion of residual parent material
glfl	area -weighted proportion of glaciofluvial parent material
gllc	area -weighted proportion of glaciolacustrine parent material
rkud	area -weighted proportion of undifferentiated bedrock parent material
undm	area -weighted proportion of undifferentiated organic parent material
br	area -weighted proportion of brunisolic order soils
lu	area -weighted proportion of luvisolic order soils
ve	area -weighted proportion of vertisolic order soils
ch	area -weighted proportion of chernozemic order soils
gl	area-weighted proportion of gleysolic order soils
rg	area -weighted proportion of regosolic order soils
sz	area -weighted proportion of solonetzic order soils
s_tx	categorical soil texture, from 1 (fine) to 7 (coarse)
clay	area -weighted proportion of clay
silt	area -weighted proportion of silt

sand	area -weighted proportion of sand
carb	area -weighted proportion of carbon
Climate	
tmin_spr	minimum temperature in spring (°C)
tmin_summ	minimum temperature in summer (°C)
tmax_spr	maximum temperature in spring (°C)
tmax_summ	maximum temperature in summer (°C)
tav_spr	average temperature in spring (°C)
tav_summ	average temperature in summer (°C)
precipspr	average precipitation in spring (mm)
precipsumm	average precipitation in summer (mm)

TABLE 16. SOURCE, UNIT OF MEASUREMENT, AND SPATIAL RESOLUTION OF LAND COVER FEATURES USED TO DESCRIBE LANDSCAPE CHARACTERISTICS OF FERRUGINOUS HAWKS.

Attribute Type	Spatial Resolution	Year	Source
Land cover	30 m	2000	Agriculture and Agri-Food Canada
Industrial	30 m	2013	IHS Energy
Climate	1 km	2016	Climate WNA version 5.40
Soil	500 m	2010	Soil Landscapes of Canada v3.2

TABLE 17. LIST OF VARIABLES INCLUDED IN NEST SURVIVAL, CLUTCH SIZE, AND FLEDGING RATE ANALYSES.

Variable name		Description and units
Base model variables		
	year	year of breeding attempt
	dateJ	date of visit, Julian
	visit	visit number to the nest (e.g., 1st visit, 2nd visit, etc)
	interval	number of exposure days between visits
	visitStartD	first day of monitoring for the breeding season, Julian
	hatchJ	hatchDate, Julian
	hatchDateJGen	actual hatch data if available, otherwise average hatch date for that year
	daysSinceHatch	estimated age of nest, number of days since average hatch date of that breeding season
	nestAgeGen	estimated age of nest, number of days since HatchDateJGen
	long	longitude
	lat	latitude
	accuracy	coordinate take from nest (1) or from nearest road (0)
	nestTypeID	tree(1), human-made platform (2), cliff(3), ground(4)
	nestStage	nest building/incubation, 0 – 20 day old nestlings, 21 – 40

		day old nestlings, 41+ day old nestlings/>=1 young fledged, unknown
	soiltxt	soil texture
	elevation	elevation
	ruggedness	ruggedness
Seasonal weather		
	tave_wt	winter mean temperature (°C)
	tave_sp	spring mean temperature (°C)
	tave_sm	summer mean temperature (°C)
	ppt_wt	winter precipitation (mm)
	ppt_sp	spring precipitation (mm)
	ppt_sm	summer precipitation (mm)
	dd_0_wt	winter degree-days below 0°C
	pas_wt	winter precipitation as snow (mm)
	pas_sp	spring precipitation as snow (mm)
	Tave04#	mean temperatures (°C) by month of visit
	TMX04#	maximum mean temperatures (°C) by month of visit
	PPT04#	precipitation (mm) by month of visit
Landscape		
	grass	grass, proportion of
	grassq	grass quadratic, proportion of
	edgegrass	edge density, grass/crop (km)
	wateredge	edge density, water/wetland (km)

edgeall	edge density, all (grass/water/road)
water	water, proportion of
waterdist	water, distance to (km)
waterdist	water, distance to (km)

Industrial Development

txline	transmission line density (km)
txdist	transmission line distance (m)
road	road density, all (km)
roadhard	road density, hard surface (m)
roadloose	road density, loose surface (m)
roadhwyart	road density, hwys & arterials (m)
roadres	road density, resource (m)
distroad	road distance (m)
distrdhard	road distance, hard surface (m)
distrdloose	road distance, loose surface (m)
distrdres	road distance, resource (m)
distrdhwyart	road distance, hwys & arterials (m)
pipe	pipeline density, superpipes (m)
distpipe	pipeline distance
wells	well density
welldist	well distance
oil	oil well density

oildist	oil well distance
oilLMH	oil well density (low = 0, medium = 1 to 25, high = 26+)
gas	gas well density
gasdist	gas well distance
gasLMH	gas well density (low = 0, medium = 1 to 25, high = 26+)

TABLE 18. STANDARDIZED PARAMETER ESTIMATES (ß) AND STANDARD ERRORS FOR THE TOP NEST SURVIVAL MODEL FOR FERRUGINOUS HAWKS IN SOUTHERN ALBERTA AND SASKATCHEWAN FROM 2010 TO 2015. WE USED 728 NESTS AND 4,384 NEST VISITS TO BUILD THE MODEL.

				95% CI	
Variable	Estimate	SE	p-value	Lower	Upper
Platform nest					
Tree nest	-0.524	0.17	0.00	-0.85	-0.20
Nest stage - Incubation					
Nest stage - 0 - 20 day old nestlings	0.758	0.21	0.00	0.34	1.17
Nest stage - 21 - 40 day old nestlings	1.711	0.27	0.00	1.18	2.24
Nest stage - Unknown	-2.245	0.20	0.00	-2.64	-1.85
Year2010					
Year2011	1.304	0.43	0.00	0.46	2.15
Year2012	0.685	0.43	0.11	-0.16	1.53
Year 2013	0.671	0.50	0.18	-0.32	1.66
Year2014	1.215	0.51	0.02	0.21	2.22
Year2015	1.481	0.52	0.00	0.47	2.49
Nest age	-0.509	0.15	0.00	-0.80	-0.22
Visit start date	0.271	0.06	0.00	0.15	0.39

Hatch date general (Julian)	-0.233	0.10	0.03	-0.44	-0.03
Mean temperature spring	0.362	0.14	0.01	0.08	0.64
Mean temperature previous winter	-0.555	0.17	0.00	-0.90	-0.21
Mean temperature month of visit	-0.199	0.11	0.07	-0.41	0.01
Proportion of grass	-0.175	0.06	0.01	-0.30	-0.05
Edge density	0.119	0.06	0.04	0.01	0.23
Edge density quadratic	-0.063	0.04	0.13	-0.14	0.02
Oil well density – low					
Oil well density - medium	0.214	0.17	0.20	-0.11	0.54
Oil well density - high	-1.182	0.26	0.00	-1.69	-0.67
Gas well density - low					
Gas well density - medium	0.422	0.15	0.01	0.13	0.72
Gas well density - high	0.352	0.16	0.03	0.04	0.67
Ruggedness	0.161	0.06	0.00	0.05	0.27
Intercept	3.534	0.42	0.00	2.72	4.35

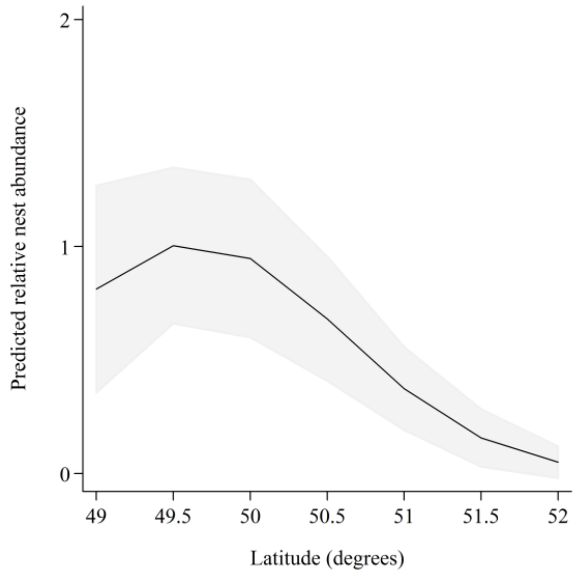
TABLE 19. MEAN AND STANDARD DEVIATION CLUTCH SIZE OF FERRUGINOUS HAWKS BY YEAR. YEARS AFTER 2013 WERE EXCLUDED FROM THE SUMMARY STATISTICS BECAUSE OF LOW SAMPLE SIZES (N<5).

Year	Mean	SD	n
2010	2.93	1.08	106
2011	3.83	1.01	142
2012	3.09	0.97	83
2013	2.74	0.75	81

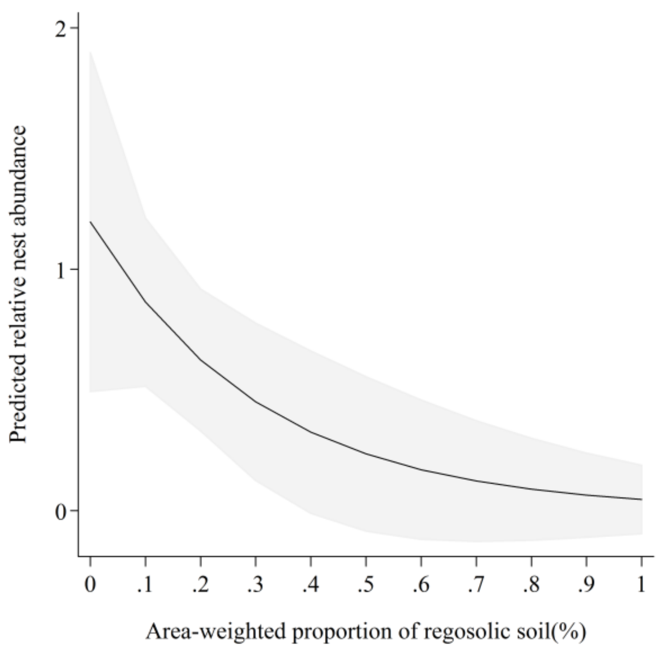
TABLE 20. SUMMARY STATISTICS FOR NEST SUCCESS METRICS INCLUDING APPARENT NEST SUCCESS, FLEDGING RATE FOR ALL NESTS WITH KNOWN NEST OUTCOME (INCLUDING FAILED NESTS), AND FLEDGING RATE FOR ONLY NESTS THAT SUCCESSFULLY FLEDGED AT LEAST ONE YOUNG.

Year	n	Number Successful	Apparent nest success	Fledging rate including failed nests	SD	Fledging rate successful nests only	SD	n[1]
2010	130	79	0.61	1.35	1.29	2.22	0.90	79
2011	240	174	0.73	2.10	1.57	2.90	1.05	174
2012	286	195	0.68	1.57	1.30	2.31	0.89	195
2013	329	191	0.58	1.19	1.22	2.06	0.88	190
2014	73	49	0.67	1.40	1.45	2.43	1.06	42
2015	92	75	0.82	2.10	1.45	2.64	1.08	73
2016	85	66	0.78	1.99	1.41	2.60	1.00	65
Total	1,235	829	0.67	1.67	1.38	2.45	0.98	818

[1] Number of successful nests included in the fledging rate for successful nests only differ from the total number of successful nests. We could not get an accurate fledging rate estimate for all successful nests.

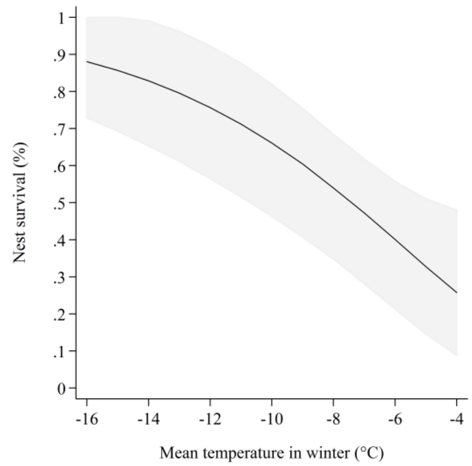


A)

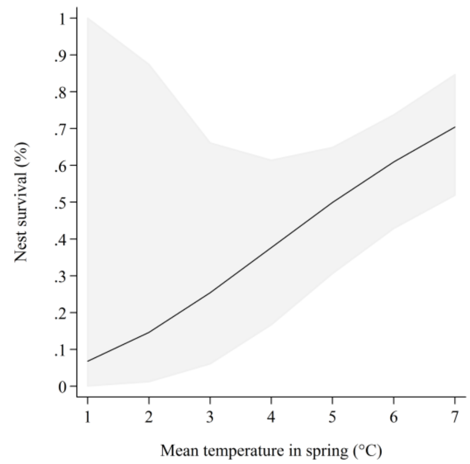


B)

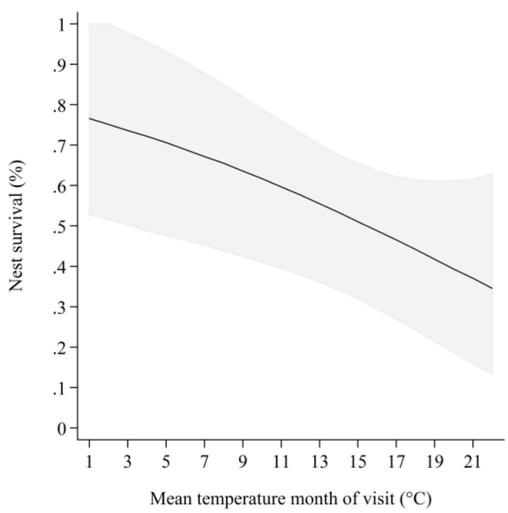
FIGURE 29. PREDICTED RELATIVE NEST ABUNDANCE AND 95% CONFIDENCE INTERVALS FOR FERRUGINOUS HAWK NESTS IN SOUTHERN ALBERTA AND SASKATCHEWAN, AS A FUNCTION OF A) LATITUDE, AND B) AREA-WEIGHTED PROPORTION OF REGOSOLIC SOIL WITHIN THE SURROUNDING TOWNSHIP.



A)

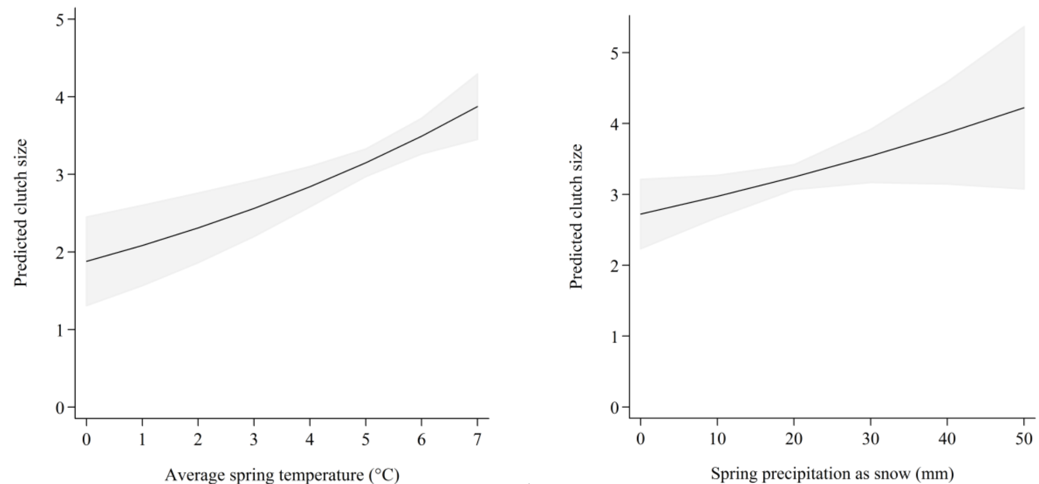


B)



C)

FIGURE 30. PREDICTED NEST SURVIVAL AND 95% CONFIDENCE INTERVALS FOR FERRUGINOUS HAWKS IN SOUTHERN ALBERTA AND SASKATCHEWAN FROM 2010 TO 2015, AS A FUNCTION OF A) MEAN TEMPERATURE IN WINTER (°C , DECEMBER, JANUARY, AND FEBRUARY), B) MEAN TEMPERATURE IN SPRING (°C MARCH, APRIL, AND MAY), AND C) MEAN TEMPERATURE DURING THE MONTH OF VISIT(°C).



A) B)

FIGURE 31. PREDICTED CLUTCH SIZE AND 95% CONFIDENCE INTERVALS RELATIVE FOR FERRUGINOUS HAWK NESTS IN SOUTHERN ALBERTA AND SASKATCHEWAN BETWEEN 2010 AND 2013, RELATIVE TO A) AVERAGE SPRING TEMPERATURE AND B) SPRING PRECIPITATION AS SNOW (SPRING = MARCH, APRIL, AND MAY).

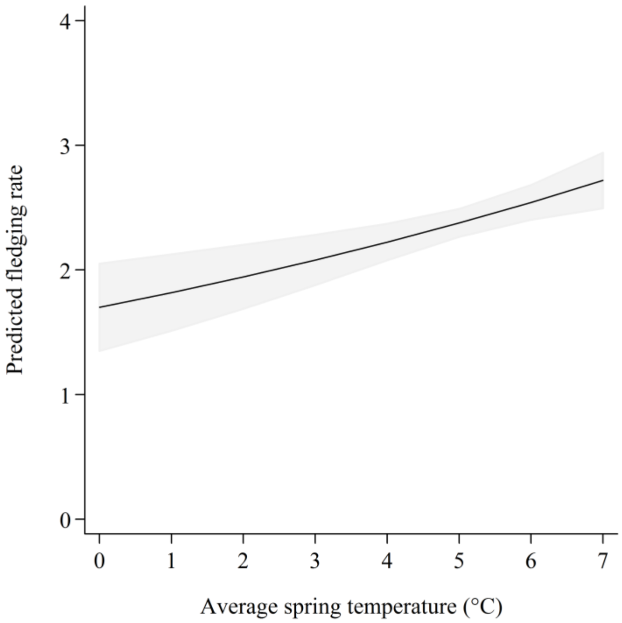


FIGURE 32. PREDICTED FLEDGING RATE AND 95% CONFIDENCE INTERVALS RELATIVE FOR FERRUGINOUS HAWK NESTS IN SOUTHERN ALBERTA AND SASKATCHEWAN BETWEEN 2010 AND 2013, RELATIVE TO A) AVERAGE SPRING TEMPERATURE (SPRING = MARCH, APRIL, AND MAY).

Appendix C: Supplementary material for Chapter 4: Landscape characteristics, industrial development, and weather influence brood provisioning by Ferruginous Hawks

Methods

Model selection

We explored the data for outliers, homogeneity of variances, normality, excess zeros, collinearity, model structure, and overdispersion (Zuur et al. 2010). We also standardized all predictor variables to zero mean and unit variance prior to analyses. This allowed direct comparison of the magnitude of each variable as the data is scaled the same.

Univariate models tested a priori hypotheses for variables that could have linear or non-linear relationships. Between the linear and quadratic models, the model with a lower delta AIC was compared to the null model and included in the next model selection procedure if the variable improved model performance.

We simplified models within variable sets by removing non-influential variables and developing parsimonious variable sets using forward stepwise selection (Burnham and Anderson 2002, Arnold 2010). This reduces the number of variables included in the final model selection process and reduces the likelihood of including spurious predictor variables. Once variable sets were developed, we built an all-inclusive model by using a forward step-wise approach that included or excluded whole variable sets at each step. The all-inclusive model was further simplified by using a backward step-wise approach to remove variables that were not statistically significant (p-value >0.10), where the least significant variable was removed at each step

(Arnold 2010). The variable was left in the model if its removal did not improve the delta AIC. Variables were removed until all variables in the model were highly predictive (p-value <0.10) or until the delta AIC started to increase. This elimination process builds the most parsimonious model as possible, while only including statistically important variables. Model weights were used as additional evidence for top models.

Results

Out of 1665 prey deliveries, only 142 were not identified to order. They were assigned an order proportionally by the prey items identified.

$$H' = \exp(-\Sigma p_i \ln (p_i))$$

EQUATION 8. SHANNON WIENER DIVERSITY INDEX, DOUBLING METHOD.

TABLE 21. SUMMARY OF PREY DELIVERED ON VIDEO TO FERRUGINOUS HAWKS NESTS INCLUDED IN OUR VIDEO FOOTAGE STUDY.

Guild	Count	Proportion	Total Estimated Biomass (kg)	Proportion
Lagomorph	5	0.00	11.5	0.02
RIGR*	1395	0.84	592.9	0.92
Mice/vole	111	0.07	3.4	0.01
Shorebird	34	0.02	8.3	0.01
Waterfowl	31	0.02	22.6	0.04
Songbird	82	0.05	3.7	0.01
Frog/toad	6	0.00	0	0.00
Total	1664	1	642.38	1

*Richardson's Ground Squirrel

Table 22. Mass of common species observed in study area used to generate an estimate for biomass delivered to Ferruginous Hawk nestlings.

Group	Species	Mass (g)	Mean mass (g)	Median mass (g)	Mass used for study	Source
Ground Squirrels	Richardson`s Ground Squirrel	Juvenile 275 Females 450 Males 550	425		425	Dobson, F. S., & Michener, G. R. (1995). Maternal traits and reproduction in Richardson's ground squirrels. *Ecology, 76*(3), 851-862.

Lagomorphs	Mountain cottontail	1200	1200		2300	http://aep.alberta.ca/fish-wildlife/wild-species/mammals/rabbits-rodents/mountain-cottontail.aspx
	White-tailed jackrabbit	3400	3400			http://aep.alberta.ca/fish-wildlife/wild-species/mammals/rabbits-rodents/whitetailed-jack-rabbit.aspx
Mouse/voles	Deer mouse	10-24		17	30.5	http://animaldiversity.org/accounts/Peromyscus_maniculatus/
	Meadow vole	44	44			http://animaldiversity.org/accounts/Microtus_pennsylvanicus/
Shorebirds	Willet	200–330		265	245.3	Lowther, Peter E., Hector D. Douglas III and Cheri L. Gratto-Trevor. 2001. Willet (*Tringa semipalmata*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.579
	Killdeer	75-128		101.5		https://www.allaboutbirds.org/guide/Killdeer/lifehistory
	Marbled Godwit	285–454		369.5		Gratto-Trevor, Cheri L. 2000. Marbled Godwit (*Limosa fedoa*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York,

					USA. https://doi.org/10.2173/bna.492
Waterfowl	Mallard	967-1300	1133.5	728.9	Drilling, Nancy, Rodger D. Titman and Frank McKinney. 2002. Mallard (*Anas platyrhynchos*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.658
	Northern Pintail	709-1110	909.5		Clark, Robert G., Joseph P. Fleskes, Karla L. Guyn, David A. Haukos, Jane E. Austin and Michael R. Miller. 2014. Northern Pintail (*Anas acuta*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA.https://doi.org/10.2173/bna.163
	Northern Shoveler	400-800	600		Dubowy, Paul J. 1996. Northern Shoveler (*Spatula clypeata*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.217
	Blue-winged	325-403	364		Rohwer, Frank C., William P. Johnson and Elizabeth R.

	teal					Loos. 2002. Blue-winged Teal (*Spatula discors*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.625
	American Coot	427–848		637.5		Brisbin Jr., I. Lehr and Thomas B. Mowbray. 2002. American Coot (*Fulica americana*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.697a
Songbird	Western Meadowlark	M 106 F 89.4 M 115.3 F 93	100.9		44.9	Davis, Stephen K. and Wesley E. Lanyon. 2008. Western Meadowlark (*Sturnella neglecta*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.104
	Horned Lark	28–40		34		Beason, Robert C. 1995. Horned Lark (*Eremophila alpestris*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York,

						USA. https://doi.org/10.2173/bna.195
	Vesper Sparrow	24.7	24.7			Jones, Stephanie L. and John E. Cornely. 2002. Vesper Sparrow (*Pooecetes gramineus*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.624
	Chestnut-collared Longspur	17–23		20		Bleho, Barbara, Kevin Ellison, Dorothy P. Hill and Lorne K. Gould. 2015. Chestnut-collared Longspur (*Calcarius ornatus*), version 2.0. In The Birds of North America (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.288
Frog/toad	Great Plains Toad	negligible			0	
	Boreal Chorus Frog	negligible			0	

TABLE 23. LIST OF VARIABLES EVALUATED IN PREY DELIVERY, PREY DIVERSITY, AND BIOMASS MODELS.

Variable name		Description and units
Base model variables		
	year	year of breeding attempt
	dateJ	date of visit, Julian
	hatchJ	estimated hatch date, Julian
	days	days of video watched per nest
	nestlingAge	estimated age of nest, number of days since hatch date
	long	longitude
	lat	latitude
	soiltxt	soil texture
Seasonal weather		
	tave_wt	winter mean temperature (°C)
	tave_sp	spring mean temperature (°C)
	tave_sm	summer mean temperature (°C)
	ppt_wt	winter precipitation (mm)
	ppt_sp	spring precipitation (mm)
	ppt_sm	summer precipitation (mm)
	dd_0_wt	winter degree-days below 0°C
	pas_wt	winter precipitation as snow (mm)
	pas_sp	spring precipitation as snow (mm)

Landscape

ng	Native grass, proportion of
cr	cropland, proportion of
tamehay	tame grass and hay, proportion of
tamenggra	native and tame grass, proportion of
crth	Cropland, tame grass, and hay, proportion of
th	tame hay, proportion of
tg	tame grass, proportion of
if	idle field
shrub	Shrub cover, proportion of
tree	tree cover, proportion of
hedge	hedge cover, proportion of
edgeland	edge density, grassland/cropland (km)
edgeall	edge density, all (grass/water/road)
water	water, proportion of

Industrial Development

hs	human structure, proportion of
ogfoot	oil and gas footprint, proportion of
og	oil and gas structure, proportion
road	road, proportion of
power	power, proportion of

well	wells, proportion of
gas	gas wells, proportion of
oil	oil wells, proportion of