Ferruginous Hawk (*Buteo regalis*) responses to human disturbance during the breeding season

by

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Abstract

The expansion of the human footprint across the world is increasing the number of interactions between humans and wildlife. Many studies have quantified wildlife behavioural responses to humans, as this is an active area of research with practical implications for species conservation. Animal behaviour may be influenced by the properties of the human disturbance itself, the environment in which the interaction occurs, and the individual's past experience, but these potentially important factors have rarely been evaluated. Furthermore, it is unclear how individuals behave through time after a human disturbance. In southern Alberta and Saskatchewan, I quantified flight initiation from the nest by Ferruginous Hawks (*Buteo regalis*) in response to approaching investigators and used digital video systems to quantify their behaviour following investigator departure.

In Chapter 2 I studied the flight initiation distance (FID), the distance at which flight is initiated from the nest in response to an approaching threat, by adult Ferruginous Hawks. We used FID to quantify the relative probability of flight during a given approach. Probability of flight was related to the type of approach by investigators, the anthropogenic landscape around the nest, and the number of previous visits by investigators. Approaches by humans on foot resulted in a greater probability of flight than those in a vehicle. Approaches while driving on private access roads, which are roads used infrequently by vehicles, were associated with increased probability of flight relative to other road types. Probability of flight was negatively related to an index for the number of vehicles passing near the nest, and increased as the number of previous investigator approaches to the nest increased. Chapter 2 highlights the dynamic and complex nature of the decision to initiate flight from the nest and provides insight as to why probability of flight varies within a species.

Having explored factors influencing the Ferruginous Hawk's decision to initiate flight in response to human disturbance in Chapter 2, Chapter 3 focused on the behavioural consequence through time after being disturbed by humans. Here, I used digital video footage of Ferruginous Hawk nests to document behaviour at the nest of adult males and females up to 12 hrs following an investigator disturbance, and test two non-exclusive hypotheses that may explain differences in behaviour relative to undisturbed control periods. On average, across the 12-hr sample period, female Ferruginous Hawks spent significantly less time on the nest following investigator disturbance compared to controls, but individual variation was high. Delivery of prey items to the nest was not significantly different between disturbed and control sample periods for the same nests. Time on nest was initially lower for disturbed females than for controls but became more similar over the span of the 12-hr sample. Age of nestlings and number of nestlings were important, as female time on the nest returned to control-levels more quickly for individuals with young nestlings or larger broods. Thus, I found support for both the harm-to-offspring and reproductive value hypotheses. This was among the first studies to identify that disturbed animals demonstrate behavioural differences up to 12 hrs following disturbance.

The ability to adjust flight initiation behaviour in response to types of human approaches and the consistent delivery of prey when disturbed suggested that Ferruginous Hawks nesting in the highly anthropogenic regions of southern Alberta and Saskatchewan demonstrated the behaviours that should allow them to coexist with some human disturbance at the nest site. However, I also found instances of Ferruginous Hawk flight initiation at large distances, and that some individuals reduced time on nest for lengthy durations following a human disturbance. Understanding how these extreme behaviours relate to reproductive success of Ferruginous Hawks is likely essential to understanding human impacts on the population in Canada. My research was intended to contribute to the ongoing conservation effort for this species, and I discuss potential implications for management in Chapter 4. I suggest that management policies should vary the size of protective setbacks according to the apparent degree of sensitivity of adults during different nesting stages and for different types of disturbance. For example, after nearly all clutches have hatched (by mid-June), 500-m setbacks should effectively prevent Ferruginous Hawks from being disturbed by low-level disturbances, such as passing vehicles.

Preface

This thesis is an original work by Cameron J. Nordell and no part of this thesis has been previously published. The research for this thesis was conducted with the Raptor Ecology and Conservation Team (REACT), a collection of graduate students and post-doctoral fellows working to generate a comprehensive dataset of Ferruginous Hawk biology to inform conservation efforts for the species. This group is supervised by Dr. Erin Bayne at the University of Alberta and Dr. Troy Wellicome with the Canadian Wildlife Services (University of Alberta Adjunct Professor). I present Chapters 1 & 4, primarily my own writing, in the first person. Chapters 2 & 3 were written by myself and modified by my co-authors Dr. Erin Bayne and Dr. Troy Wellicome, and are presented in plural.

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.

"This splendid bird is undoubtedly the most powerful hawk met with"
- E. S. Cameron (1914)

"Studying such a shy, easily disturbed hawk soon instilled within me a near reverence for the sanctity of hawk nests--they were to be regarded as a sacred trust of sorts.
My every move around these nests was cautiously planned"
- Leon R. Powers (2003)

Acknowledgements

This research would not have been possible without support from more people than I can possibly name. First and foremost, I would like to thank my supervisors Dr. Erin Bayne and Dr. Troy Wellicome. Erin maintained lofty expectations while also giving me an incredible amount of freedom, which I believe has made me a better prepared researcher for any challenge that lies ahead. I'd also like to thank my co-supervisor with the Canadian Wildlife Service, Dr. Troy Wellicome, who never shied away from late night logistical discussions to help me survive the field season. I thank my final committee member, Dr. Colleen Cassaday St. Clair, for pushing me to improve the theoretical aspects of my project at every turn. Thank you to my arm's length examiner Dr. Andrew Derocher. To my entire committee, the experience has been rewarding, and I have learned something from every high and low that came with it.

I was fortunate to have financial and in-kind support for this project from the Canadian Wildlife Service, Alberta Upstream Petroleum Research Fund, Altalink, The Alberta Conservation Association, Suffield Canadian Forces Base, Alberta Sport, Recreation, Parks and Wildlife, and the University of Alberta. I was part of a very ambitious research project that would not have been possible without all of these resources.

Thank you to the Bayne Lab and fellow students and researchers at the University of Alberta. My time at the UofA was enriched by your presence, I wish you all the best of luck with your own research. I thank especially Dr. Samuel Haché and Dr. Ryan Fisher, without their support I would not have made it far enough to write this acknowledgements section. Many thanks to the hundreds of public and private landowners across Alberta and Saskatchewan that graciously (or begrudgingly) granted us permission to work on their property. This project would not be what it was without them.

Thank you to the countless field assistants, students, and volunteers associated with a project of this size. I have valued all of your companionship and dedication these past three years, and have included everyone's names at the end of my presentations -- there is not enough space on the powerpoint slides anymore. I'd like to acknowledge specifically my field technicians Mike Sveen, who taught me the difference between clockwise and counter-clockwise, and Ricky Kong for carrying batteries heavier than he is for a species that he didn't think was as cool as the plants on the side of the road.

Thank you to my graduate student family within the Raptor Ecology and Conservation Team: Janet Ng, Melynda Johnson and Jesse Watson. Janet knew just when to offer chocolate covered coffee beans, Melynda supplied fireworks for the team, and Jesse was there with me from start to finish. I most certainly would have quit by now without Jesse.

Finally, I’d like to thank my (actual) family and friends who played a huge role helping me through. A special thank you to Jonathan Sears, who was my official Petroleum Industry Consultant. Greg Bosse, my roommate who tolerated an antisocial hermit living with him for most of this degree. To all the friends to which I have said "I can't right now", "maybe next month" or "when I am done my thesis". I hope you agree that my hard work paid off. My parents, Clint and Pam, and brother, Graeme, have supported me in more ways than I can name, and will always be a huge part of my life. But, undoubtedly the most support came from Sonya Widen, who was officially designated "in charge of morale", and continues to be an incredibly positive force in my life. I hope I can repay her with the same level of support in the future.

Thank you.

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Chapter 1: Introduction

Anthropogenic alteration of natural landscapes is ubiquitous and continues to accelerate globally. Sala et al. (2000) suggest that alteration of landscapes by humans through land-use change may be the single greatest threat to global biodiversity in this century. As much as one half of the earth's land has been altered by humans (Vitousek et al. 1997). In the mixed grasslands ecoregion of Canada, the energy sector is currently responsible for a large amount of habitat alteration. Given energy use worldwide is projected to increase by more than 50% within 30 years (International Energy Agency 2013) increased pressure on the mixed grasslands is expected. Oil and gas exploration, development, and extraction are major contributors to land-use changes depending on the resources, companies, countries, and ecosystems involved (Leu et al. 2008). The agricultural sector, another major contributor to habitat alteration in the mixed grasslands, has been forecast to increase production dramatically in the near future to meet global dietary need (Foley et al. 2005). Furthermore, residential, recreational, and commercial development all contribute to an increasingly anthropogenic world (Miller and Hobbs 2002). Ultimately, human expansion in its many forms, increases the frequency, diversity, and magnitude of interactions between humans and wildlife (Sanderson et al. 2002).

As the pervasiveness of human-wildlife interactions increase, so too does the need to understand these interactions. Animal behaviour in response to *human disturbance* -- a human presence, sound, or other stimulus (defined by Frid and Dill 2002) -- is an active field of research. An animal that demonstrates a change in behaviour in the presence of a human disturbance is said to be *disturbed* (Frid and Dill 2002). Quantification of disturbed behaviour has been used to understand the potential for human impacts on animal populations (Blanc et al. 2006, Beale 2007, Houston et al. 2012), which is important to create and implement management strategies that promote species conservation. In some cases, frequent or substantial human disturbance may change animal behaviour enough to result in fitness consequences, such as decreased reproductive success or increased mortality (White and Thurow 1985, Blackmer et al. 2004, Shively et al. 2005, Arroyo and Razin 2006, Krüger et al. 2015). A review of the impacts of human disturbance for wildlife (Boyle and Samson 1985) found that 81% of studies reported negative effects for animal body condition or populations, though more recent studies suggest more conservative estimates (Stankowich 2008, Martínez-Abraín et al. 2010). Understanding the types of human activities that cause animals to change their behaviours and how these behaviours differ from normal is important for protection of wildlife populations and conservation of threatened species (Blumstein et al. 2005, Fernández-Juricic et al. 2005, Stankowich and Blumstein 2005).

1.1.1 Study Area

Prairie and grassland ecosystems are among the most altered habitats on earth (Hoekstra et al. 2005) with as little as 30% of the Great Plains Bioregion remaining undisturbed in North America (Samson et al. 2004). Early hunting and trapping resulted in elimination of many large vertebrates including the bison (*Bison bison*), plains wolf (*Canis lupus*), and plains grizzly bear (*Ursus arctos*) in this region (Atkinson 2009). Starting in the late 19th century, the native grasslands were segmented for agricultural purposes. Agriculture changed the natural vegetation community through introduction of non-native cereals (e.g. wheat; *Triticum aestivum*), forage (crested wheatgrass; *Agropyron cristatum*) and irrigated crops. Fire suppression after human settlement has favoured the establishment of trees and shrubs which further altered the vegetation community. Through the 20th century, accelerating agricultural conversion and livestock production (Hayes and Holl 2003), industrial exploration and construction (Braun et al. 2002), and development of roads and residences, have further contributed to the considerable human footprint in the mixed and moist-mixed grasslands of southern Alberta and Saskatchewan that we see today (Atkinson 2009, Kissinger and Rees 2009, Wellicome et al. 2014).

Data collection for this study was conducted across the mixed grasslands ecoregion from southwestern Alberta to southeastern Saskatchewan from Pincher Creek (49.49° N, 113.95° W) situated in the Rocky Mountain foothills to moist-mixed grassland in Weyburn (49.66° N, 103.85° W) with an area > 250 000 km^2 (Figure 1.1). The native mixed grasslands remaining are dominated by spear grass (*Heteropogon contortus*), blue grama (*Bouteloua gracilis*), wheat grasses (*Agropyron* spp.), and sagebrush (*Artemisia* spp.), though vegetation can vary regionally across the study area. The region is typically flat grassland with minimal topography. The mean summer temperature is 16˚C and mean annual precipitation varies from 250-350 mm (Environment Canada 2014). Dominant tree species include aspen / cottonwood (*Populus* spp.) and willow (*Salix* spp.).

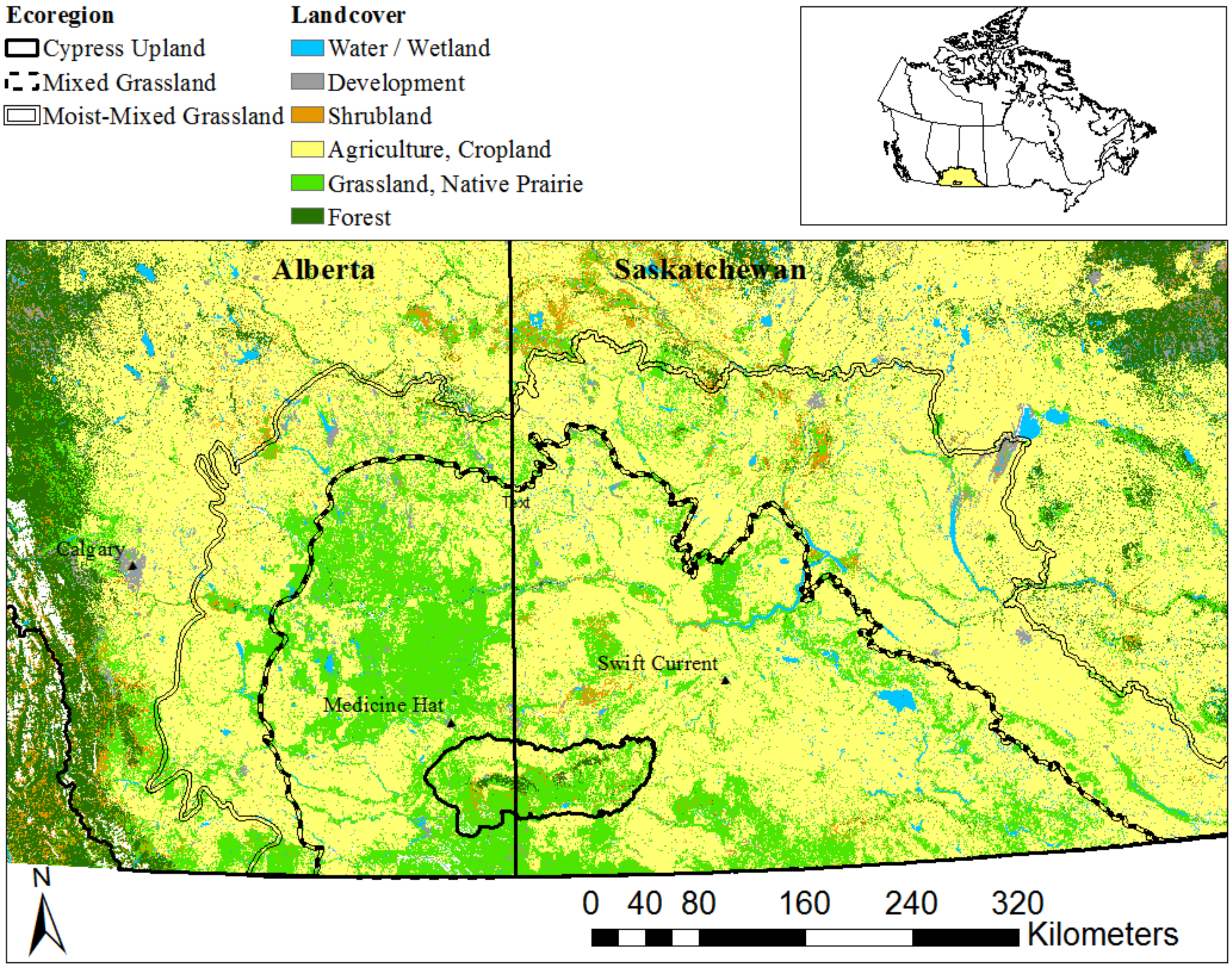

Figure 1.1: Landcover in the mixed and moist-mixed grassland ecoregions of southern Alberta and Saskatchewan, Canada.

1.1.2 Study Species

Ferruginous Hawks (*Buteo regalis*) are migratory raptors that typically arrive at their breeding grounds in Canada in March (Bechard and Schmutz 1995). They occupy flat or rolling, open-country environments, such as grasslands and shrub-steppes with few, isolated trees and tree stands (Bechard and Schmutz 1995). In Canada, the Ferruginous Hawk range encompasses the entirety of the mixed and moist-mixed grassland ecoregions. Historically a ground-nesting species (Bechard and Schmutz 1995), Ferruginous Hawks now most commonly nest on elevated structures such as trees and man-made artificial nest platforms (ANPs). In Canada, the most common prey item is Richardson's ground squirrel (*Spermophilus richardsonii*), but also includes other mammals (voles [*Microtus* spp.], thirteen-lined ground squirrel [*Ictidomys tridecemlineatus*]), birds (C. Nordell unpubl. Data), amphibians, reptiles, and insects (Schmutz et al. 1980). Males do the majority of the hunting and survey for prey by perching on elevated structures (Palmer 1988), such as trees, fence posts, distribution poles, and transmission poles. Males are also the primary territorial member of a breeding pair, deterring potential competitors and predators that enter their territory. Females exclusively brood and feed the nestlings and spend much of their time on or near the nest, especially early in nestling development.

The Ferruginous Hawk population appears to be decreasing in Canada (Moltzahn 2010), and as a result the species has been designated *threatened* federally since 2010 (Canada 2002), *threatened* in Manitoba since 1994 (Manitoba 1989), and *endangered* in Alberta since 2006 (Alberta 2000). There is evidence to suggest that human disturbance around Ferruginous Hawk nests during early nesting stages can cause them to abandon their breeding attempt (White and Thurow 1985), potentially to use alternate nest sites (Smith and Murphy 1978), which may ultimately result in reduced reproductive success (Snow 1974, Blair 1978, White and Thurow 1985). The work of White and Thurow (1985), who found experimentally disturbed nests were less successful and fledged fewer young than undisturbed nests, has strongly influenced the notion that Ferruginous Hawks are sensitive to human disturbance. However, these disturbance treatments were extreme and included discharging firearms and operating motors at nest sites. Blair (1978) found reduced nest success and fledge rates in Ferruginous Hawks nesting nearer to human activity, but the mechanism behind this reduction was unclear. In other studies, the evidence concerning sensitivity to disturbance is anecdotal, such as the incidents of nest abandonment in response to disturbance reported by Olendorff (1972) and Powers (1981). It is broadly accepted that adults sometimes abandon their nests when disturbed during the nest building or incubation periods, but

Olendorff (1994) acknowledges the controversy and uncertainty surrounding their sensitivity to human disturbance. It remains unclear whether this response to humans in a way that decreases reproductive success might contribute to documented population declines. More recently, studies of nesting Ferruginous Hawks reported no adverse effects of investigator or other human activity for breeding success (Holmes et al. 1993, Van Horn 1993, Keeley and Bechard 2011, Keough et al. 2015, Wallace et al. 2016), perhaps owing partly to observation outside of the sensitive early nesting period.

In Canada, human disturbances of Ferruginous Hawks are avoided using government-mandated setback distances (Environment Canada 2009) such that industrial activities are restricted during the breeding season from March 15 to July 15 each year (Table 1-1). These restrictions are implemented with the goal of preventing disturbance or harm to individual animals and their dwellings. This legislation differentiates between different levels of disturbance by categorizing them as either low (passing nest, fewer than one disturbance per week), medium (one disturbance per day from 15 min - 2 hr in duration), or high (permanent structures, human disturbance > 2 hr in duration; Environment Canada 2009). However, this framework offers little flexibility regarding the timing of disturbance within the breeding season. Furthermore, the low, medium, and high disturbance categories are not specific to Ferruginous Hawks. These criteria are subjective generalizations meant to encompass all species of concern (Environment Canada 2009). The study of behavioural responses to different types of human disturbances, and how responses change across the breeding season may improve the efficiency of setback distances around Ferruginous Hawk nests while maintaining sufficient protection. For example, Ferruginous Hawks FID appears to differ depending disturbances are on foot or by vehicle (Holmes et al. 1993), and the apparent sensitivity to human disturbance may decrease after the end of the incubation period.

Table 1-1: Provincial setback distances for Ferruginous Hawks adapted from the Petroleum Industry Activity Guidelines for Wildlife Species at Risk (Environment Canada 2009).

Level of	Alberta		Saskatchewan	Manitoba
Disturbance	Mar. 15 - Jul. 15	Jul 16. - Mar. 14	Mar. 15 - Jul. 15	Mar. 15 - Jul. 31
Low	1000 m	50 m	500 m	500 m
Medium	1000 m	50 m	750 m	750 m
High	1000 m	1000 m	1000 m	1000 m

Much of the rationale for setback distances have used data from flight initiation distances (hereafter FID), the distances at which an animal initiates flight from the nest in response to an approaching stimulus. In New Mexico, Keeley and Bechard (2011) documented mean FID of 486 m in rural Ferruginous Hawk adults, and 340 m in adults near urban centers. However, on the wintering grounds in Colorado, Holmes et al. (1993) found maximum FIDs of 165 and 280 m when Ferruginous Hawks were approached by humans on foot and by vehicle, respectively; whereas Hansen (1994) documented a mean FID of 100 m in Idaho and Van Horn (1993) found mean FID of 205 m in Montana. These studies are the basis for the creation of setback distances despite the lack of agreement on FID across studies and the lack of FID quantification for individuals nesting in Canada.

1.1.3 Objectives and Thesis Outline

The objective of my study was to improve the current understanding of the effects of human disturbances on wildlife behaviour by studying the Ferruginous Hawk. Specifically, I explore (1) what causes Ferruginous Hawks to change their behaviour, and (2) what behavioural differences are demonstrated by disturbed hawks compared to controls. To fulfill these objectives, I collected FID during nest monitoring at 420 nests, and sampled behaviour using digital video recordings of 58 nests. In Chapter 2, I examine specific hypotheses that could explain variation in probability of flight from the nest in response to human disturbance. I monitored nests across a spectrum of landscape types, from highly developed (anthropogenic) to pristine native grassland, and used different types of investigator approaches to the nest to test how different types of disturbance influence probability of flight. Thus, I explore whether Ferruginous Hawk probability of flight changed based on the anthropogenic landscape, the actions of the investigator, or previous experience with investigator approaches. In Chapter 3, I assessed the behaviour of Ferruginous Hawk adults using nest video footage and quantified behaviours following human disturbances relative to control periods. Specifically, I documented male and female arrival and departure from the nest and delivery of prey to the nest. Chapter 4 summarizes my conclusions and discusses management implications and future work necessary for creating effective setback distances for this Species At Risk.

Chapter 2: The probability of flight initiation by nesting adult Ferruginous Hawks depends on distance from nest, characteristics of the disturbance, individual experience, and the anthropogenic landscape

2.1 Introduction

Anthropogenic habitat alteration is a primary driver of wildlife population declines globally (Sala et al. 2000). In landscapes where habitat has been altered by humans, there is often an associated increase in the frequency of human-wildlife interactions (Knight and Gutzwiller 1995, Leu et al. 2008). Animal responses to human interactions are poorly quantified for many species, but in theory they should resemble those to potential predators (Frid and Dill 2002). There is a conservation concern when these interactions occur because they may result in potentially preventable increases in energetically costly behaviours for wildlife. For example, individuals may increase defence, aggression, or vigilance behaviours, thus decreasing time and energy available for other activities such as foraging, offspring care, maintenance, and rest (Ydenberg and Dill 1986, Steidl and Anthony 2000, Houston et al. 2012, Northrup et al. 2012). Understanding when and how wildlife respond to human stimuli, the types of human activities that cause disturbances, and whether unnecessary behavioural changes can be mitigated are important components of human-wildlife coexistence (Blumstein et al. 2005, Fernández-Juricic et al. 2005, Stankowich and Blumstein 2005).

The decision to initiate flight in response to a disturbance stimulus is determined by a cost / benefit trade-off whereby the perceived risk (cost) associated with an approaching threat becomes greater than the benefit of maintaining regular activity (Trivers 1972, Ydenberg and Dill 1986). Animals continually assess risk when interacting with a human or predator, ultimately responding behaviourally when it is optimal to do so based on their perception of risk to themselves or their young (Bouskila and Blumstein 1992). Thus an animal's flight initiation distance (FID), the distance at which an animal initiates flight in response to human stimulus, should change with the perceived costs and benefits associated with responding to stimuli. FID provides an unambiguous and easily quantifiable change in animal behaviour (Beale 2007). To understand animal FIDs, the study of inter-individual differences among them is essential. However, Herrero et al. (2005) stressed that how individuals respond to disturbance stimuli is driven not only by inter-individual biological differences, but by the properties of the stimulus itself and the environment in which the interaction occurred.

FID is known to change with the presence of young (Stankowich 2008), distance to refuge (Camp et al. 2012), group size (Ydenberg and Dill 1986), concealment, visibility (Camp et al. 2012, Miller et al. 2013), and weather (Fisher et al. 2004). However, controlling for these factors, FID still varies considerably within a species (Blumstein et al. 2005). An increasing number of studies demonstrate that differences between approaching stimuli can change FID. It has been suggested that relatively faster moving, noisier, and larger stimuli (Stankowich and Blumstein 2005, Cooper et al. 2007, Tyack et al. 2011), should be perceived as greater risks. This dangerous stimulus hypothesis predicts that vehicles should result in greater FID than humans on foot. However, FIDs in response to vehicles have been shown to be shorter than those in response to humans on foot (Stalmaster and Kaiser 1998, Cooper Jr and Frederick 2007, Wolf and Croft 2010, McLeod et al. 2013), perhaps owing to habituation to vehicles. In addition to the stimuli itself, an animal's past experiences with stimuli (Fraker 2009), leading to habituation (Thompson and Spencer 1966, Rankin et al. 2009) or sensitization (Klein and Kandel 1978, Bejder et al. 2009), are potentially important components of FID. However, few studies have quantified FID using repeated stimulation (but see Wam et al. 2014), and for many species it remains unclear how FIDs change in response to repeated human disturbance. FID tends to decrease as the level of anthropogenic disturbance in a region increases (McCleery 2009, Tao et al. 2012, Díaz et al. 2013, McGiffin et al. 2013, Gravolin et al. 2014, Møller and Tryjanowski 2014, Price et al. 2014, Bjørvik et al. 2015), potentially owing to habituation by animals in increasingly anthropogenic regions. A recent study by Mikula (2014) found a negative relationship between the number of pedestrians and FIDs in urban birds. However, given the difficulty of quantifying human-wildlife interactions at large scales, quantitative links between the number of human-wildlife interactions in anthropogenic landscapes and FID are deficient (Price et al. 2014). Furthermore, no studies have simultaneously examined the effects of stimulus type and animal experience in different landscapes.

Our objective was to quantify flight initiations in Ferruginous Hawks in response to investigator approaches with different modes (vehicle vs on foot) and road classes (highway, range roads, and access roads) of travel, while simultaneously taking into account the individual's previous experience, and anthropogenic landscape. Ferruginous Hawks breed across southern Alberta and Saskatchewan and are reportedly sensitivity to human disturbance (White and Thurow 1985, Olendorff 1994). Nesting in isolated trees in open grassland habitat, most nests are relatively poorly concealed and adults likely detect humans and initiate flight at great distances, presumably to deter potential threats from approaching the nest and young (Holmes et al. 1993, Keeley and Bechard 2011). Given the potential for frequent initiation of flight at large distances from the nest in Ferruginous Hawks, we aimed to improve existing analytical approaches and statistical power to test a wider breadth of potential factors influencing FID.

Specifically, while controlling for other important sources of variation, we tested the relative importance of stimulus in the form of investigator approach characteristics, individual experience from repeated approaches to nests, and the number of human-wildlife interactions around nests (vehicular traffic). Based on the habituation to vehicles hypothesis, we predicted that Ferruginous Hawks would be more likely to initiate flight in response to humans on foot. Alternatively, based on the dangerous stimulus hypothesis, we predicted that the probability of initiating flight should be greater for larger, noisier, faster moving vehicles compared to humans on foot. Based on the only study to show a change in FID with repeated stimulation (Wam et al. 2014), we predicted that Ferruginous Hawks should demonstrate decreased probability of flight initiation in response to repeated approaches. Alternatively, Knight and Temple (1986) suggest animals may interpret departure from the home range by humans as a successful defence of the nest, reinforcing the behavioural decision to defend (positive reinforcement hypothesis) which would lead to increased probability of flight initiation in our study. Finally, we predict that as vehicular traffic encountered by Ferruginous Hawks increases they will demonstrate reduced probability of flight in response to our approaches, presumably a result of habituation to anthropogenic disturbances around their nests.

2.2 Materials and Methods

2.2.1 Study Area

Data collection for this study was conducted across the mixed and moist-mixed grasslands ecoregion from southwestern Alberta to southeastern Saskatchewan. This area spans ~900 km east to west and ~300 km north south, with a total area > 250 000 km^2. Ferruginous Hawk habitat is typified by grassland with minimal topography and few hills between 600 and 1300 m above sea level. In this region the species generally nests in lone trees (but occasionally in tree stands), free standing artificial nesting platforms (Migaj et al. 2011), and occasionally electrical transmission infrastructure towers. Dominant nest tree species are aspen and cottonwood (*Populus* spp.). The region has undergone considerable landscape transformation since it was first settled in the 1900s (Rowe and Coupland 1984, Samson et al. 2004, Kissinger and Rees 2009). Ferruginous Hawks nest exclusively in non-urban regions (Schmutz 1984), but do so across a gradient of human activity. Active oil and gas well densities range from 0-15 wells per km^2. Landcover conversion around nest sites has resulted in local vegetation that ranges from 0 to 100% agriculture, a mix of cropland and rangeland pasture (Kissinger and Rees 2009). A network of roads with varying traffic volumes permeates the study region, including variable densities of highways, range roads along most township gridlines (1.6 km separation), and industrial access roads, right of way, and private access roads (henceforth access roads) which allow vehicular access near many nests. Highways and some range roads are paved, most range roads are gravel, and access roads are gravel, graded dirt, or vehicle tracks worn into the ground. Anthropogenic features in Alberta (e.g. industrial infrastructure, crop fields, and houses) are accompanied by increases in roads and traffic (Wellicome et al. 2014), so we used traffic as a surrogate index for total level of anthropogenic activity around nests.

2.2.2 Data Collection

Measuring Flight Initiations

We documented FID beginning in 2012 as part of a large scale Ferruginous Hawk nest monitoring project across the Canadian mixed and moist-mixed grasslands. Nests were monitored during the breeding season (May - August) from 2012 through 2014 for at least one full breeding attempt. Some nests were monitored for multiple breeding attempts across the 3 years of study. However, it was unknown whether the same breeding pair returned to a given nest between years. Before approaching the nest (~ 1000 m away), we conducted a scan of the nest and the surrounding area for adult Ferruginous Hawks. The sex of individuals on the nest was unknown but males spent very little time on the nest, so the vast majority of flight initiations were likely by females. We moved toward the nest (dependent upon road access and permission from landowners) and documented FID using handheld GPS and electronic rangefinders. Occasionally, only distant observations using spotting telescopes were possible, and no flight initiations were observed. Our approach consisted of three stages: (1) researchers drove as close to a nest as possible using public roads before (2) parking and exiting the vehicle, and (3) walking the remaining distance to the nest (Figure 2-1). The distance from the nest at which these events occurred was calculated in ArcGIS 10.2 (ESRI 2013). We also calculated the number of previous approaches to the nest and mean approach rate (approaches / day) at each nest. To avoid harming eggs or young, we did not approach the nest in cold (< 10 ºC) or rainy conditions, or if we suspected egg laying had recently occurred. Mean temperature (^{o}C) and wind speed (km/h) were recorded over 60-second intervals using hand held devices (Kestrel $^©$; www.kestrelmeters.com) before each approach, at distances > 1 km from the nest. Nest structure was recorded including, trees, ANPs, transmission tower nests, and few ground nests or buildings (other).

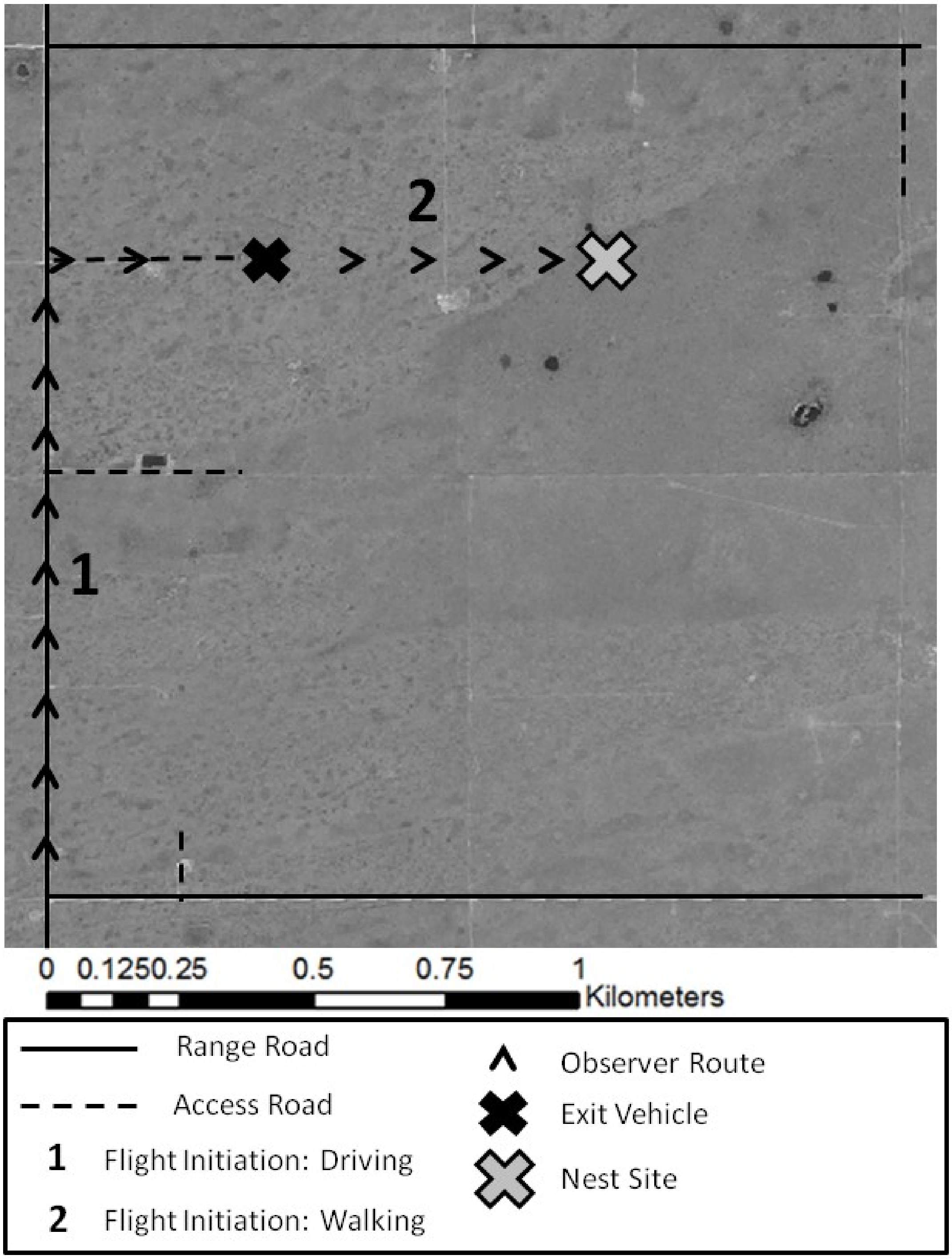

Figure 2.1: A visual representation of a typical investigator approach to a Ferruginous Hawk nest in southern Alberta and Saskatchewan during the breeding season in 2012, 2013 or 2014.Investigators travelled in a vehicle via publicly available roads before exiting the vehicle and proceeding the remainder of the distance to the nest on foot, when granted permission to access the land. (1) and (2)

indicate separate approaches in which Ferruginous Hawks initiated flight from the nest while the investigator was driving or walking, respectively.

Environmental Covariates

Using ArcGIS 10.2 (ESRI 2013) we mapped all roads (using Alberta Transportation (http://www.transportation.alberta.ca/), Saskatchewan Transportation (http://www.highways.gov.sk.ca/) and IHS Road Layers (2012; www.ihs.com) in a 2500-m radius (approximately the average homerange size; Watson 2014) around each study nest. Our road layer included road classes (highways, range roads and access roads) and surface substrates (hard surface, loose, gravel and dirt), and we used these classes and substrates to create road categories. To determine the number of vehicles using these roads categories, we used data from 178 MetroCount ® 5600 Vehicle Classification Systems (traffic counters) to collect daily traffic volumes (vehicles / day) between the months of May and August from 2008 through 2013, some of which came from a companion Burrowing Owl (*Athene cunicularia*) study (Scobie 2015).

2.2.3 Statistical Analysis

Probability of Flight Initiation from the Nest

We used a modified time to event (survival) analysis (Cleves et al. 2004) to model FID, in which the event was flight initiation from the nest by an adult Ferruginous Hawk. Rather than the conventional analysis interval, time (Miller 2011), we used investigator distance from nest. The largest observed FID was 950 m and we used 1000 m as our subject entry distance. We assume that we were able to detect Ferruginous Hawks present on the nest with perfect accuracy and assume no left censoring (flight initiation occurred before observation began) of subjects from the analysis. However, we did not always approach nests closely enough to cause flight initiation, thus our data were right censored and our analytical approach allowed us to use information from right censored approaches to understand flight initiation behaviour. We binned our flight initiation data into 25-m subsets as a conservative estimate of FID measurement accuracy of GPSs, rangefinders and investigators.

We used the Cox proportional hazards regression model (Cox 1972), a semiparametric analysis that estimates hazard ratios. Hazard ratios estimate the relative effect of covariates on the hazard function, which is the probability of an event occurring over some interval (Cleves et al. 2004). In biological terms, we estimated the effect of covariates (hazard ratios) on the relative probability that an adult Ferruginous Hawk (a subject) initiated flight (an event or failure) as we approached the nest. We estimated a shared frailty for each nesting attempt, the Cox regression equivalent of a random intercept model (Cleves et al. 2004), to control for non-independence when repeatedly sampling at the same nesting attempt. The random intercept model serves as our null model for human approaches to Ferruginous Hawk nests before fitting covariates. We used the Efron method for handling tied events, flights that occur at identical distances from the nest, to minimizes bias when estimating coefficients for datasets with heavily tied failures (Hertz-Picciotto and Rockhill 1997). Discrete time-varying covariates, those that changed as we approached the nest, were used to test for an effect of investigator approach type (driving on highways, range roads and access roads, walking and exiting the vehicle) on the probability of flight. We present coefficients generated by the Cox proportional hazard model as hazard ratios ($\exp[\beta_i]$) and standard errors. The dependent variable resulting from this analysis is the probability of flight from the nest at a given investigator distance from the nest, henceforth probability of flight. Probability of flight is analogous to the more commonly measured FID and these metrics should be interpreted similarly. When our models estimate a greater probability of flight this is equivalent to the mean FID being higher in a linear regression model often used in FID analyses.

Traffic

We estimated the daily traffic volume for road class (highway, range road and access roads) and substrate (hard surface, loose, gravel and dirt) combinations using data from traffic counters. Not all class-substrate combinations had significantly different traffic volumes and we combined them to six different types of roads (Table 2-2). We then extrapolated the estimated traffic volumes for each road type around all Ferruginous Hawk nests in our study. This extrapolation is an estimate of traffic volume on each road, and we did not know the actual traffic volumes at each nest. We assigned estimated traffic volume to each road type within 400-m and 2500-m radii around our study nests (henceforth: traffic indices). The 400 m scale was the 95th percentile of our FID data, while the 2500 m scale was based on the average Ferruginous Hawk home range in Canada (Watson 2014). Thus, 400 and 2500 m represented the distances at which Ferruginous Hawks would likely respond to, and encounter vehicles in their home range, respectively. We applied an inverse weighting to the traffic indices using distance to each road from the nest, such that a weight of 1 was applied to roads adjacent to nests and decreased proportionately to 0 at 400 or 2500 m, respectively. The resulting values were an index of traffic volume at two scales at each nest that gives more importance to vehicular traffic near the Ferruginous Hawk nest (henceforth: near-traffic indices).

Model Building

We considered covariates for inclusion using forward stepwise model construction with an AIC selection framework (Akaike 1998). Highly related covariates ($r>0.7$) were selected for inclusion in our analysis based on the lowest AIC scores when compared. Covariates improving our model fit ($\Delta AIC>2$) were included in sequential model-building steps. Some covariates, such as structure type, wind speed, temperature, year, and ordinal date (Table 2-1) were potentially important sources of variation in the response variable, but were unrelated to our objectives. Thus, we generated a base model to control for these covariates before testing for effects of stimulus, experience, and landscape context. To construct our stimulus, experience, and landscape models, we used a forward stepwise approach to determine if our variable(s) explained variation in FID, using the base model as a starting point (Table 2-1). To test for potential interactive relationships, we constructed a final model using stimulus, experience and landscape combinations. To assess fit and robustness of our full model and to identify leverage points in our independent variables we used approaches discussed in chapter 11 of Cleves et al. (2004). The Cox-Snell residuals increase linearly with time, suggesting good fit of the final model to the data. High leverage points (± 0.02 β) were uncommon, and their removal did not change covariate significance. All analyses were carried out using Stata v 13 (StataCorp 2013).

Table 2-1: Covariates considered for inclusion in a Cox proportional hazards regression model of adult Ferruginous Hawk flight initiation distances when approached by investigators.

Model	Covariate	Abbreviation
Base Model	Nest Structure	struc
	Temperature	temp
	Temperature, quadratic	temp2
	Wind speed	wind
	Wind speed, quadratic	wind2
	Ordinal Date	date
	Ordinal Date, quadratic	date2
	Year	yr
Stimulus	Approach Type[1]	apptype
Experience	Approach Number	appnum
	Approach Rate	apprate
Landscape	Traffic Index 400[†]	ti4
	Traffic Index 2500[†]	ti25
	Near-Traffic Index 400[‡]	nti4
	Near-Traffic Index 2500[‡]	nti25

[1] walking / exiting vehicle / drive highway / drive rangeroad / drive access road, a discrete time-varying covariate (see Cleves et al. 2004)

[‡ / †] Traffic volume on each road within 400 and 2500 m from the nest, each given no weighting (†) and inverse-weighted by distance from nest (‡)

2.3 Results

At least one adult hawk was present on the nest for 1378 observations, which represented 623 unique nesting attempts, at 420 different nest sites. We observed an adult on their nest between one and eight instances for each nesting attempt. We recorded flight initiation by adult Ferruginous Hawks in 721 instances, from 406 unique nesting attempts, at 324 different nests. Flight initiation distances were highly right-skewed ($\bar{x}$ = 130 m, median = 74 m, 95th percentile = 450 m) and ranged from 0 m to 950 m from the nest (Figure 2-4).

Table 2-2: Daily traffic volume (vehicles / day) as recorded by 178 traffic counters installed on roads throughout the range of Ferruginous Hawks in Alberta and Saskatchewan. We present the means (x̄), standard errors (SE), and numbers of roads (n).

Road Type	x̄	SE	n
Hard surface highways	415.2	79.8	22
Loose surface highways	100.2	17.2	8
Hard surface range roads	45.7	20.8	5
Gravel range roads	44.2	4.7	47
Dirt range roads	21.2	3.0	62
Access roads	9.4	2.5	34

The relationship between flight initiation and both wind speed (ΔAIC =0.2) and ordinal date (ΔAIC =1.5) was linear rather than quadratic, so quadratic terms for these variables were not used in subsequent analyses. Flight initiation was related to quadratic temperature (ΔAIC=5.3), but temperature was highly correlated with linear ordinal date, which received more support (ΔAIC=47.5). Thus, temperature was not considered in subsequent analyses. Flight initiation was related to nest structure (ΔAIC=403.2), ordinal date (ΔAIC=68.5), and year (ΔAIC=33.6), as identified in steps 1-3, respectively. Neither wind nor number of young were identified as important for flight initiation in the fourth step (ΔAIC>=1.1). Our model building then created the best fitting stimulus model, learning model, and landscape model (Table 2-1). We found evidence that approach type (ΔAIC=261.1) did improve fit for the stimulus model. Approach number (ΔAIC=6.4), but not approach rate (ΔAIC=1.1) improved fit for the experience model. The weighted traffic index within 400 m (ΔAIC=12.3) improved fit for the landscape model, but not all remaining landscape quantifications (ΔAIC>=-1.8). Our full model included approach type (ΔAIC=261.1), approach number (ΔAIC=9.4), and the near-traffic (within 400 m) index (ΔAIC=4.2) in sequential steps. Our power to predict flight initiation was not improved by the inclusion of interactive effects (ΔAIC>=-0.9).

Table 2-3: Null, base, stimulus, experience, landscape, and full models created using forward-stepwise model building. We used Cox proportional hazards regression to model the probability of flight by adult Ferruginous Hawks from the nest when approached by an investigator. AIC indicates Akaike's Information Criterion Score (Akaike 1998) used to select for covariates that best fit our data. $h_{ij}(t)$ is the relative hazard at distance from the nest (d) given the value of x for the j^{th} nest approach in the i^{th} nesting attempt (the random effect). α_i parameterizes the latent variation between nesting attempts.

Model Name	AIC	Model
Null Model	9345.7	$h_{ij}(d) = h_0(d) + \alpha_i \exp(x_{ij}\beta)$
Base Model	8840.4	$h_{ij}(d) = h_0(d) + \exp \alpha_i (x_{ij}\,\text{struc}^{a}) + \exp \alpha_i (x_{ij}\,\text{date}^{b}) + \exp \alpha_i (x_{ij}\,\text{yr}^{c})$
Stimulus Model	8569.9	$h_{ij}(d) = h_0(d) + \exp \alpha_i (x_{ij}\,\text{struc}^{a}) + \exp \alpha_i (x_{ij}\,\text{date}^{b}) + \exp \alpha_i (x_{ij}\,\text{yr}^{c}) + \exp \alpha_i (x_j\beta\text{apptype}^{d})$
Experience Model	8834.0	$h_{ij}(d) = h_0(d) + \exp \alpha_i (x_{ij}\,\text{struc}^{a}) + \exp \alpha_i (x_{ij}\,\text{date}^{b}) + \exp \alpha_i (x_{ij}\,\text{yr}^{c}) + \exp \alpha_i (x_j\beta\text{appnum}^{e})$
Landscape Model	8828.2	$h_{ij}(d) = h_0(d) + \exp \alpha_i (x_{ij}\,\text{struc}^{a}) + \exp \alpha_i (x_{ij}\,\text{date}^{b}) + \exp \alpha_i (x_{ij}\,\text{yr}^{c}) + \exp \alpha_i (x_j\beta\text{nti4}^{f})$
Final Model	8565.7	$h_{ij}(d) = h_0(d) + \exp \alpha_i (x_j\beta\text{struc}^{a}) + \exp \alpha_i (x_j\beta\text{date}^{b}) + \exp \alpha_i (x_j\beta\text{yr}^{c}) + \exp \alpha_i (x_j\beta\text{apptype}^{d}) + \exp \alpha_i (x_j\beta\text{appnum}^{e}) + \exp \alpha_i (x_j\beta\text{nti4}^{f})$

[a] nest structure, [b] ordinal date, [c] year, [d] approach type, [e] approach number, [f] 400 m near-traffic Index

Probability of flight initiation by an adult Ferruginous Hawk at a given distance was positively related to ordinal date (1.011 ± 0.003), increasing about 1% per day. Probability of flight was more than double (2.7 ± 0.3) for hawks nesting on platforms than for hawks nesting on trees. Probability of flight also differed across years, and was lower in 2013 (0.61 ± 0.06) and 2014 (0.53 ± 0.08) compared to 2012. Approaches by vehicles on range roads resulted in probability of flight about equal to highways (0.70 ± 0.15), but approaches by vehicles on access roads had a probability of flight greater than those on highways (1.3 ± 0.3). Approaches on foot represent a probability of flight nearly four times as great (3.9 ± 0.8) as those on highways, while exiting the vehicle resulted in a probability of flight over five times as great (5.3 ± 1.2) compared to approaches on highways (Figure 2-2). We exited the vehicle at only one distance intervals for a given nest approach, thus this coefficient was estimated based on a smaller number of distances than other approach types (Table 2-7). Probability of flight increased by about 18% with each subsequent visit to the nest (1.18 ± 0.06) and decreased as the near-traffic (within 400 m) index increased (0.98 ± 0.01). The largest changes in relative hazards occurred across different approach types and different nest structure types; whereas, the smallest changes were in the near-traffic index and across years (Figure 2-3). Our shared frailty (random effect; θ) for nesting attempt explained a significant proportion of latent variation in our null and base models ($\theta = 0.15 \pm 0.06$, $P<0.001$).

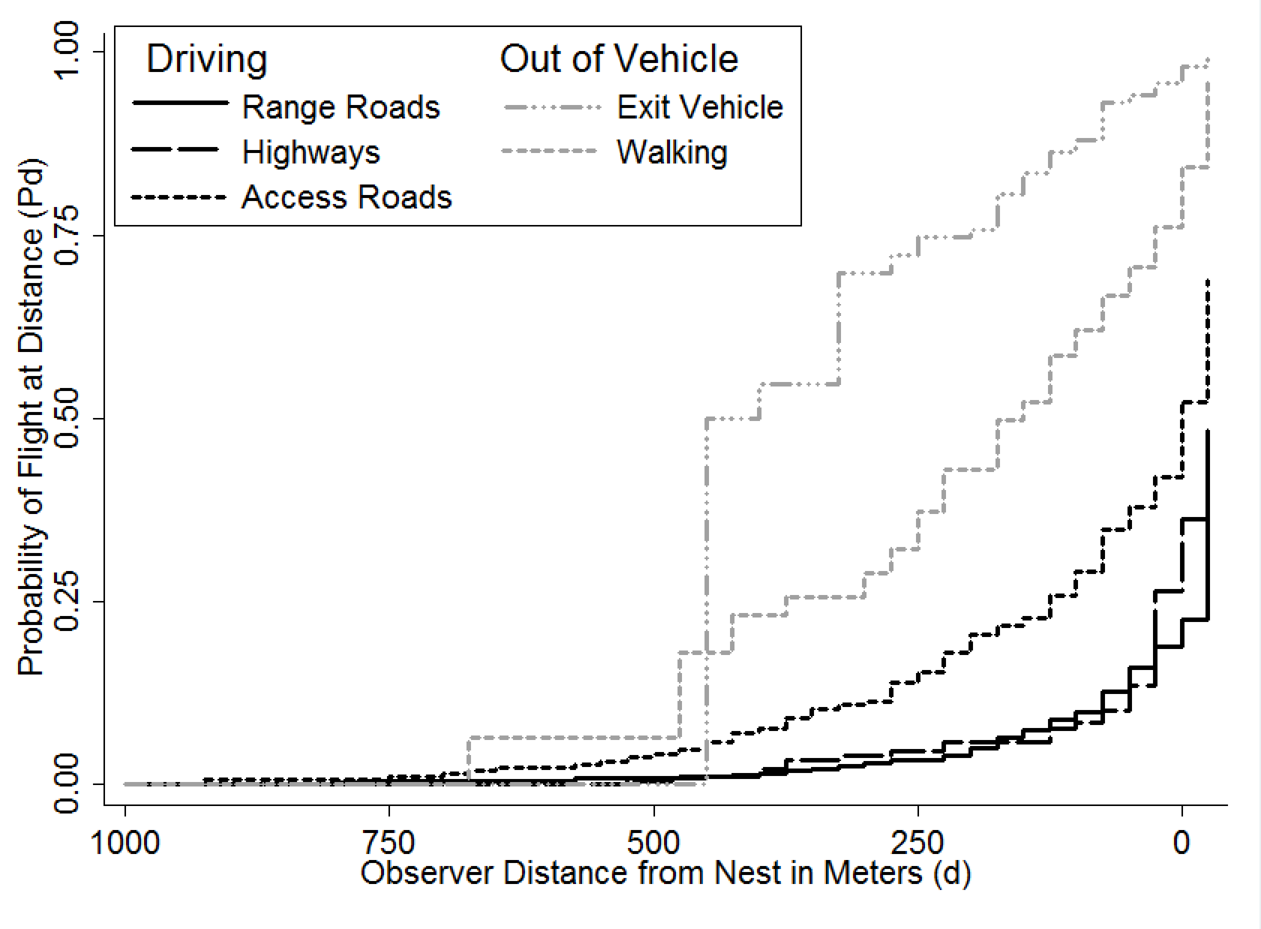

Figure 2.2: Kaplan-Meier (KM) failure estimator (Kaplan and Meier 1958) used to plot the probability of flight by adult Ferruginous Hawks from the nest at a given distance, specifying that they were exposed to investigators at those distances and had not previously initiated flight during the approach. Separate failure plots are shown for highways, range roads and access roads for investigator approaches

driven along different road classes. Walking describes approaches on foot and exit vehicle describes the act of investigators parking and exiting their vehicle.

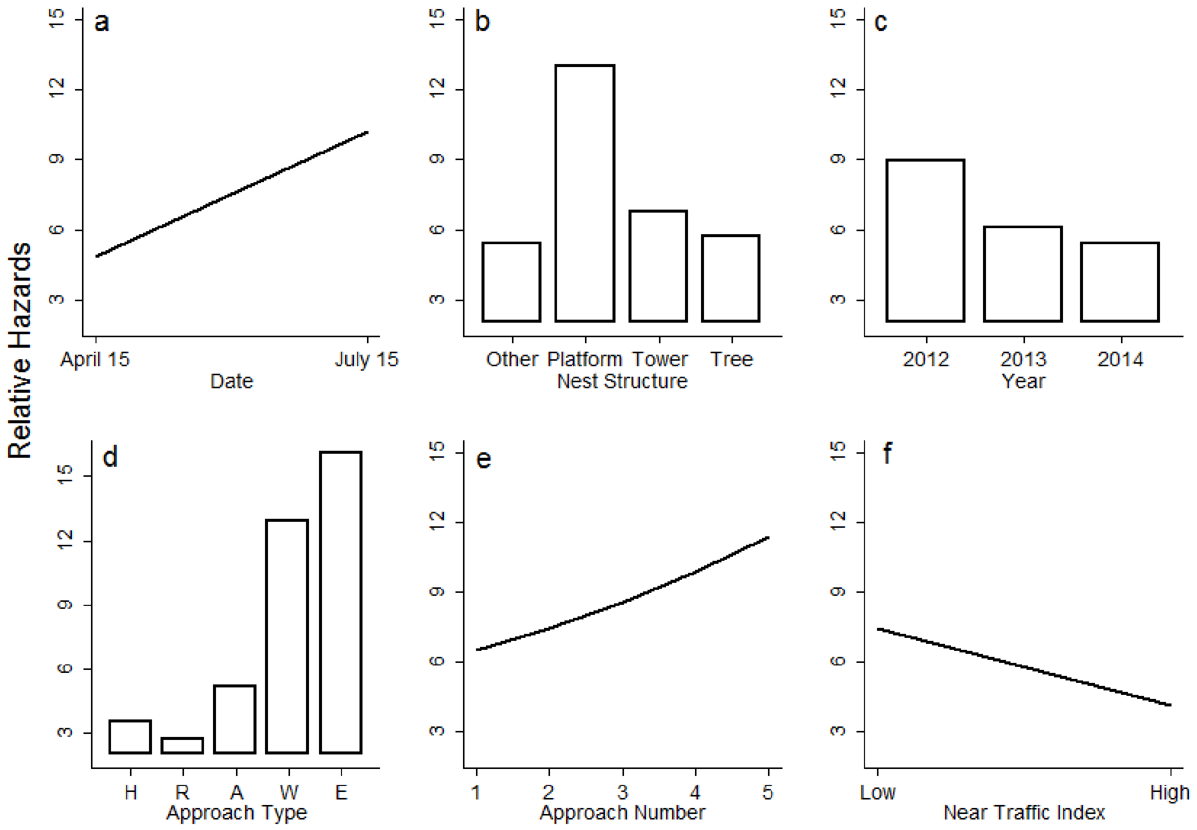

Figure 2.3: Marginal effects plots demonstrating the effect size, or change to the relative hazards (exp[βi]), defined as relative changes to the probability of flight by adult Ferruginous Hawk from the nest at varying distances from the nest, for each covariate in our full model. Each subplot: a, b, c, d, e, and f describes one of six covariates in our full model: ordinal date, nest structure, year, approach type, approach number, and near-traffic index within 400 m, respectively. H, R, A, W, and E (d) represent driving on highways, range roads, access roads, walking, and exiting the truck, respectively.

2.4 Discussion

Mean Ferruginous Hawk FIDs in our study (130 m) were most similar to those in Holmes et al. (1993) in Colorado, and were shorter on average than all other previous studies, including Keeley and Bechard (2011) and Van Horn (1993), where mean FIDs were 393 m and 205 m, respectively. Holmes et al. (1993) measured FID during the non-breeding season, potentially changing the costs and benefits of flight initiation compared to studies during the breeding season. Also, Ferruginous Hawks nested on ground and cliff sites in 96% of nests in Van Horn (1993), and the perception of risk by those individuals may differ from our study. Our data agrees with Holmes et al. (1993) who found that Ferruginous Hawks approached on foot were more likely to initiate flight than those approached by vehicles and agree with the importance of distinct types of stimuli for explaining variation in FID, as stimulus type had the largest effect size and best relative performance among competing models in our study.

We found that, similar to Van Horn (1993), Wolf and Croft (2010), and McLeod et al. (2013), the Ferruginous Hawks in our study demonstrated significantly reduced probability of flight in response to vehicles compared to humans on foot. Humans on foot, in the form of recreational and agricultural activity are likely infrequent compared to vehicle activity which permeates our study area, with some nests exceeding 5000 vehicles passing/day (http://www.highways.gov.sk.ca/sask-maps). Thus, we suggest that Ferruginous Hawks in our study are more likely to have habituated to vehicles than to humans on foot, and find support for the habituation to vehicles hypothesis, but not the dangerous stimulus hypothesis. Alternatively, FID in response to humans on foot are more likely to be associated by the disturbed individual with targeted harassment, such as hunting, evoking a stronger behavioural response (Stankowich 2008). Historically, shooting of adults has been an important and common source of mortality for Ferruginous Hawks (Fisher 1894, Weston and Ellis 1968, Olendorff 1994) which may have resulted in an increased aversion to humans on foot, through selection for fearful individuals or behavioural transmission from parents.

Importantly, we found that approaches on roads with lower traffic volumes were more likely to result in flight initiation than those on roads with greater average traffic volumes. Rather than faster moving and noisier approaches on highways and range roads, being perceived as higher risk (Cooper et al. 2007, Tyack et al. 2011), the likelihood of flight initiation in adult Ferruginous Hawks decreased when approached on highways and range roads; roads that had greater traffic volumes. These results provide additional support for the habituation hypothesis, as vehicles rarely travel on access roads and Ferruginous Hawks are less habituated to vehicle approaches on this road type. Other studies have found that approaches that are atypical relative to what animals usually encounter are related to increased behavioural responses. For example, American Robins (*Turdus migratorius*) were more likely to respond to humans walking off paths than those on paths (Eason et al. 2006), and red kangaroos (*Macropus rufus*) responded with greater FIDs when approached off-trail where humans do not normally walk (Wolf and Croft 2010).

Unexpectedly, the act of exiting the vehicle increased the probability of initiating flight at a given distance more than either humans on foot or driving. This response likely arises from a combination of unmeasured characteristics associated with exiting the vehicle, resulting in an increase in perceived risk. This increasing risk could be related to the time spent in the home range, changing from tangential to direct approach (Burger and Gochfeld 1990), or increasing group size (Geist et al. 2005) as investigators exit the vehicle. Alternatively, humans likely behave and appear more similar to a predator than does a vehicle, and could be perceived as a predator emerging from hiding. Animals should respond strongly to unfamiliarity, because underestimating risks could result in injury or mortality (Frid and Dill 2002).

Though we propose habituation as the dominant mechanism driving differential Ferruginous Hawk FIDs to stimulus type, we also found evidence for sensitization, which is the increased behavioural response to repeated stimulation (Klein and Kandel 1978, Knight and Temple 1986). Each successive visit to nests by investigators increased the likelihood that the Ferruginous Hawk would initiate flight from the nest at a given distance. If we interpret greater FIDs as an increased willingness to defend the nest from intruders, this result supports the positive reinforcement hypothesis (Knight and Temple 1986). Alternatively, Ferruginous Hawks may have perceived approaches to the nest by investigators as threatening compared to the more common, relatively non-threatening vehicles or humans that did not move directly toward or interact with the nest. Other studies of Ferruginous Hawks showed defending adults increased call rate with repeated visitation to the nest (Keeley and Bechard 2011). It is unclear to what extent the Ferruginous Hawks in our study were able to recognize individual vehicles or researchers and subsequently alter their behaviour, but this possibility has been demonstrated in other species (Lee et al. 2011, Vincze et al. 2015).

Similar to Keeley and Bechard (2011), who showed that Ferruginous Hawks nesting in exurban landscapes demonstrate 43% shorter FIDs than in rural landscapes, we found evidence that individuals nesting in landscapes with greater vehicular traffic near to the nest had a lower probability of flight. The negative relationship between FID and human activity on a landscape has been previously demonstrated in other species (McCleery 2009, Tao et al. 2012, Díaz et al. 2013). Our study is the first non-urban study to use a quantification of the anthropogenic landscape context around an animal and relate it to flight distance. The decreased probability of flight by Ferruginous Hawks with more traffic near to the nest may reflect habituation to humans around the nest site. Alternatively, individuals with specific personalities (the consistency of individual behaviour across time and context), may choose to build nests where near-traffic index values are greater and could explain the decreased probability of flight observed in such areas. For example, in other species, individuals with more tolerant personalities in other species nested in regions with more humans (Evans et al. 2010, Carrete and Tella 2013)

Theoretically, defence should increase with brood value (Redondo 1989). However, in agreement with flight initiation and nest defence studies (Regelmann and Curio 1986, Breitwisch 1988, Redondo and Carranza 1989, Galeotti et al. 2000, Kazama et al. 2010), we found no evidence that the probability of flight changed with number of young. There are a number of possible explanations. For example, current brood size may not be a good indicator of the reproductive value of the current brood relative to the residual reproductive output of the adult (Møller and Tryjanowski 2014). The maximization of parental effort on a given breeding attempt or year does not necessarily maximize lifetime fitness, especially in long-lived species (Møller and Nielsen 2014). Further, defending adults may be unable to assess the value of their current brood without breeding experience (Curio et al. 1984). We suggest date is a proxy for age of young and we found that Ferruginous Hawks were more likely to initiate flight from the nest at a given distance as date increased. Avian nest defence increases across the nesting cycle (Knight and Temple 1986, Redondo and Carranza 1989), likely due to increasing value of the young to the parents (Knight and Temple 1986) and increasing offspring survival probabilities with age (Redondo 1989). The increased likelihood of flight initiation from ANPs compared to transmission tower or tree nests may be due to the unvegetated, exposed structure of ANPs. Ferruginous Hawks on platform nests may perceive themselves or their young at higher risk of detection by a predator or threat (Camp et al. 2012), resulting in great probability of flight than concealed nests (Burhans and Thompson III 2001). Although transmission tower and ANP nests may be similarly exposed, adult hawks may perceive less risk because of the greater height of the transmission tower nests (Watson 2004). Nest height presumably decreases nest accessibility by non-avian predators.

Some of the variance in probability of flight was explained by the random intercept in our model, likely owing to unmeasured differences among individuals and nest sites. These differences may include personality (Sloan Wilson et al. 1994), body condition (Beale and Monaghan 2004) stress (Möstl and Palme 2002), concealment (Camp et al. 2012), experience (Fraker 2009, Møller and Nielsen 2014), and/or predation risk (Elliot 1985). Many studies report high inter-individual variation in behavioural responses to humans (Knight and Temple 1986, Regelmann and Curio 1986, Runyan et al. 2004, Carrete and Tella 2013), and delineating sources of inter-individual variation is an area of active study (de Jong et al. 2013, Roche and Brown 2013, Williams 2013, Cooper Jr 2015).

Our study highlighted the complex and dynamic interactions between costs and benefits comprising a decision to react to an approaching human. FID has been quantified previously in Ferruginous Hawks (Keeley and Bechard 2011), other raptors (Holmes et al. 1993), and other species (Stankowich 2008). FID has been used by government regulators to establish setback distances (Knight and Gutzwiller 1995, Richardson and Miller 1997, Jotikapukkana et al. 2010), which are used to limit industrial activity near Ferruginous Hawks nests in Canada (Environment Canada 2009) to minimize human-wildlife conflicts. A powerful approach for future studies would be the use of FID or probability of flight in conjunction with fitness or population level information to understand how animal decision making may influence long term viability of the population. In agreement with Herrero et al. (2005), we suggest that, when attempting to reduce the incidence of wildlife flight initiation, consideration should be given to the stimulus, the individual, and the environmental (in this case anthropogenic) context.

2.5 Appendices

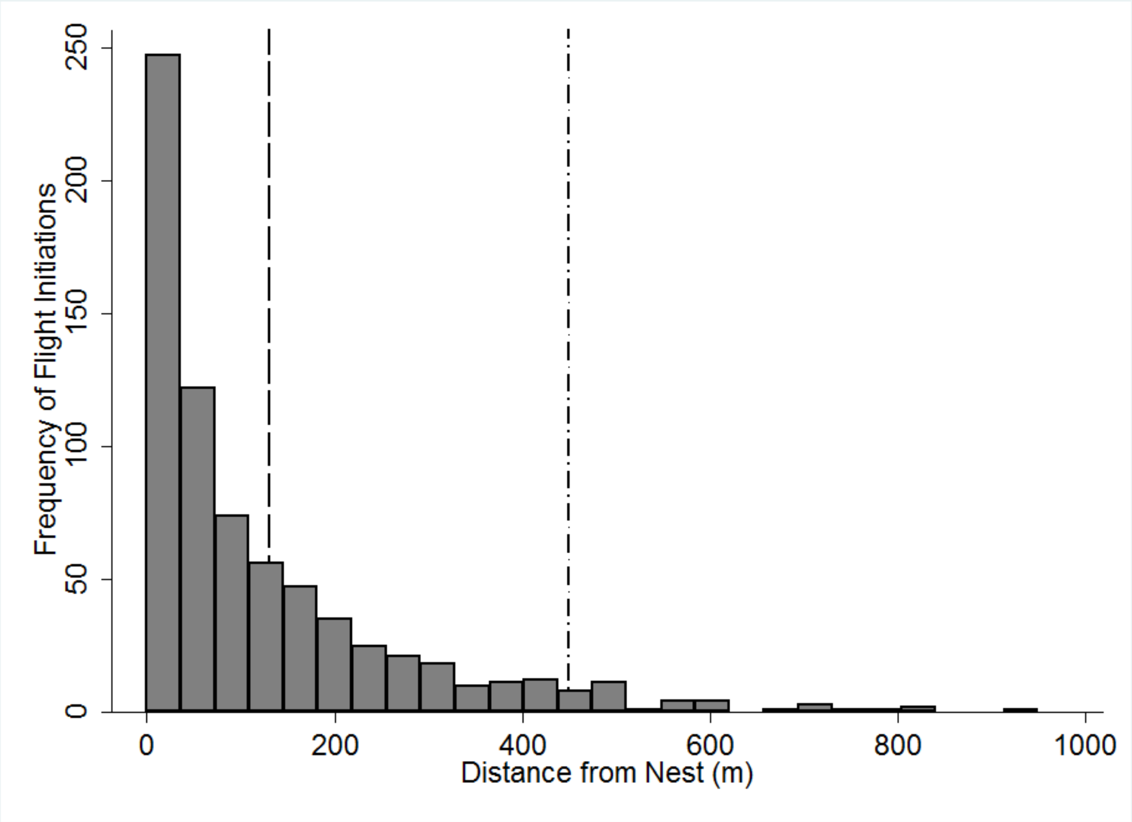

Figure 2.4: Histogram showing the frequency distribution of Ferruginous Hawk flight initiation distances during investigator nest approaches.Flight initiations were documented in southern Alberta and Saskatchewan from 2012-2014. The dashed and dash-dot vertical lines indicate the mean (130 m) and the 95th percentile (450 m) flight initiation distances, respectively.

Table 2-4: Mean (x̄) flight initiation distances documented at Ferruginous Hawk nests in southern Alberta and Saskatchewan from 2012-2014 across structure (struc) and year (yr) categories with standard errors (SE) and sample sizes (n) presented.

		x̄	SE	n
struc	Other	77.9	15.3	26
	Platform	208.9	16.5	161
	Transmission tower	116.2	23.7	24
	Tree	101.3	4.4	516
year	2012	138.2	7.8	314
	2013	102.5	5.5	343
	2014	173.6	20.7	70

Table 2-5: Model coefficients and standard errors for our final model used to explain variation in probability of flight in Ferruginous Hawk adults nesting across Alberta and Saskatchewan from 2012-2014. *P* values indicate the significance of each term. Model coefficients are relative hazards (the exponetiated beta-coefficients; exp[β_i]), or relative change in the probability of flight. *Italics* indicate categorical variables with baseline category indicated in brackets. H, R, A, W and E represent driving on highways, range roads, access roads, walking and exiting the truck, respectively.

	Hazard Ratio	SE	P
struc (tree)			
Other	0.87	0.21	0.56
Platform	2.75	0.33	< 0.001
Transmission tower	1.17	0.29	0.54
date	1.01	0.00	< 0.001
yr (2012)			
2013	0.61	0.06	< 0.001
2014	0.53	0.08	< 0.001
apptype (H)			
R	0.70	0.15	0.1
A	1.33	0.29	0.01
W	3.91	0.84	< 0.001
E	5.30	1.16	< 0.001
appnum	1.18	0.06	< 0.001
nti4	0.98	0.01	0.02

Table 2-6: Raw data summarized in a failure table demonstrating the failures (flight initiation) and censoring (approach stopped) of adult Ferruginous Hawks at various distances from the nest.

Distance Interval	Start	Failures	Censors	Probability of Flight
1000-975	1377	0	2	0
950-925	1375	1	1	0.0007
925-900	1373	0	1	0.0007
875-850	1372	0	5	0.0007
850-825	1367	0	2	0.0007
825-800	1365	1	0	0.0015
800-775	1364	2	3	0.0029
775-750	1359	1	1	0.0037
725-700	1357	1	3	0.0044
700-675	1353	3	6	0.0066
675-650	1344	1	4	0.0073
650-625	1339	0	3	0.0073
625-600	1336	0	2	0.0073
600-575	1334	4	2	0.0103
575-550	1328	1	2	0.0111
550-525	1325	3	2	0.0133
525-500	1320	1	1	0.014
500-475	1318	5	6	0.0178
475-450	1307	6	0	0.0223
450-425	1301	7	7	0.0276
425-400	1287	6	5	0.0321
400-375	1276	11	19	0.0404
375-350	1246	5	15	0.0443
350-325	1226	7	9	0.0497
325-300	1210	6	9	0.0545
300-275	1195	16	7	0.0671
275-250	1172	11	11	0.0759
250-225	1150	20	19	0.0919
225-200	1111	16	12	0.105
200-175	1083	24	26	0.1249
175-150	1033	16	31	0.1384
150-125	986	38	43	0.1716
125-100	905	29	35	0.1982
100-75	841	58	43	0.2535
75-50	740	46	40	0.2999
50-25	654	67	67	0.3716
25-0	520	117	88	0.513

Table 2-7: Raw data summarized in failure tables demonstrating the number of instances (start) and number of failures (flight initiations) for each different type of approach (exiting the vehicle, walking, highway, range road, and access roads)

	Exit Vehicle		Walking		Highway		Range road		Access Road	
Distance Interval	Start	Failures	Start	Failures	Start	Failures	Start	Failures	Start	Failures
1000-975	0	0	0	0	228	0	979	0	170	0
975-950	3	0	3	0	228	0	961	0	180	1
950-925	2	0	6	0	227	0	953	0	185	0
925-900	0	0	6	0	227	0	951	0	204	0
900-875	0	0	9	0	224	0	935	0	206	0
875-850	0	0	7	0	223	0	933	0	212	0
850-825	4	0	7	0	223	0	925	1	217	1
825-800	0	0	11	0	223	0	918	2	218	0
800-775	5	0	11	0	223	0	903	0	219	1
775-750	0	0	16	0	223	0	900	0	230	1
750-725	0	0	16	0	223	0	899	0	240	1
725-700	0	0	16	1	213	0	894	1	253	0
700-675	1	0	15	0	213	0	875	0	260	0
675-650	0	0	16	0	213	0	857	0	264	1
650-625	0	0	16	0	213	0	847	0	269	1
625-600	0	0	16	0	209	0	845	3	276	2
600-575	1	0	15	0	209	0	834	0	287	1
575-550	0	0	16	0	207	1	826	0	286	2
550-525	0	0	16	0	199	0	826	0	298	3
525-500	0	0	16	2	198	1	818	0	301	4
500-475	2	1	14	0	195	0	798	2	296	2
475-450	3	0	16	1	186	0	795	2	307	5
450-425	11	1	20	0	179	2	781	1	301	4
425-400	4	0	30	1	173	2	762	3	296	2
400-375	15	0	31	0	167	0	732	1	306	1
375-350	3	1	45	0	164	1	718	3	301	9
350-325	1	0	46	2	163	0	694	3	289	5
325-300	12	1	44	2	163	1	675	3	296	9
300-275	11	1	52	4	157	0	663	1	284	9
275-250	7	0	56	5	155	2	636	4	269	4
250-225	24	1	60	0	151	0	592	6	259	3
225-200	10	2	84	10	150	0	570	8	249	10
200-175	20	3	82	4	148	0	524	6	216	10

175-150	23	4	105	14	141	3	468	7	178	14
150-125	33	4	108	9	124	1	424	5	149	7
125-100	33	14	131	16	115	2	384	12	137	9
100-75	52	8	126	15	78	3	335	13	84	15
75-50	41	11	157	29	60	9	259	9	26	9
50-25	66	36	158	55	30	4	182	7	158	55
25-0	81	75	116	88	10	2	82	23	116	88

Chapter 3: Ferruginous hawks demonstrate latency to resume typical time on nest following human disturbance

3.1 Introduction

As humans encroach on wildlife habitat, human-animal interactions are expected to increase (Mikula 2014). Accordingly, an increasing number of studies examine animal behavioural responses to human presence or activity (Ciuti et al. 2012, Houston et al. 2012, McLeod et al. 2013, Lima et al. 2015), referred to hereafter as human disturbance. We use the term disturbed to refer to animal behaviour that differs from undisturbed or typical behaviour when responding to human disturbance (Frid and Dill 2002). Understanding disturbed behaviour is particularly important when it has deleterious effects on fitness, reproduction, or survival. The study of disturbed behaviour, and its potential impact to individual animals (White and Thurow 1985, Ruhlen et al. 2003, Krüger et al. 2015) is necessary to inform management activity performed with the goal of minimizing negative effects on wildlife caused by human disturbance.

Behavioural changes in response to human stimuli derive from the same fight or flight processes that drive behaviours in response to predators (Frid and Dill 2002). Selection may favour disturbed behaviours that persist following an interaction with a stimulus if that behaviour minimizes the risk to adults or young in the future. Thus, animals may demonstrate disturbed behaviour not only during, but for some period after, an interaction with a human stimulus. For some breeding birds, nest return times (Yasué 2006, Yasué and Dearden 2006) and time to resume feeding (Dale et al. 1996) following a disturbance have been quantified. However, most studies have quantified animal behaviour for only seconds (Yasué 2006, Yasué and Dearden 2006) or minutes (Trimper et al. 1998, Ghalambor and Martin 2000, Zimmer et al. 2011), following a human disturbance. Importantly, changes in behaviour following a disturbance may reveal increases in, or offsets to, energetic costs incurred during the human disturbance itself. For example, woodland caribou (*Rangifer tarandus*) disturbed by tourists reduced bouts of rest in favour of vigilance, but increased rest after the departure of the humans, potentially offsetting negative impacts caused by the disturbance (Duchesne et al. 2000). Female Hooded Warbler (*Setophaga citrina*) reduced the duration of incubation bouts for one hour following an experimentally induced predation treatment, potentially at a cost to nestlings (Schaef and Mumme 2012). Because of the challenges of quantifying behaviour at the nest (Cutler and Swann 1999), the occurrence, magnitude, and duration of behavioural changes following the departure of a disturbance are less well understood over longer periods for most bird species.

In breeding birds, one potential response to human disturbance (Strasser et al. 2013, Krüger et al. 2015) or predators (Ackerman et al. 2003) is the cessation of time or energy investment in a reproductive attempt by parents, referred to as an abandonment. Abandonment is a trade-off made by adults between current and future reproduction (Trivers 1972), which occurs when the adult perceives a likely cost to reproductive success now and in the future (for example: the potential for injury or mortality) that is greater than the benefit of continued investment in their current brood (Coleman and Gross 1991, Gross 2005). A parent that chooses to abandon a reproductive attempt in response to a disturbance, rather than remain at the nest and minimize harm to offspring, likely perceives that maintenance of typical nesting behaviour following the disturbance puts them at too great a risk. However, when birds encounter a disturbance and do not abandon the breeding attempt, it is unclear what subsequent behaviours are expected. We propose that, similar to instances of abandonment, changes in nesting behaviours following a human disturbance likely reflect a change in the perceived risk to the parents. Under this assumption, disturbed parents may be unwilling maintain regular nest attendance, prey provisioning, or both for some time after a disturbance, if there is a perceived increase in risk to the adults by doing so.

To explore the potential for behavioural changes through time, we examine the occurrence, duration, and magnitude of Ferruginous Hawk behaviours following human disturbance when the likelihood of abandonment is low. Having demonstrated reproductive impacts, such as nest abandonment (White and Thurow 1985), and fewer fledged young when experimentally disturbed early in the breeding season (White and Thurow 1985), this species in considered sensitive to human disturbance (White and Thurow 1985, Olendorff 1994). White and Thurow (1985) qualitatively described Ferruginous Hawks at disturbed nests (those that did not abandon) exhibiting prolonged periods during which they did not return to the nest. Powers (2003) describes the absence of a female from the nest that lasted most of the day when disturbed, leading to the death of a nestling. These observed reproductive decreases and the potential for extreme behaviour in response to humans have resulted in concern regarding the impacts of human disturbance for Ferruginous Hawk populations. However, no studies have quantified changes in behaviour over longer periods (hours) following the departure of a human disturbance for Ferruginous Hawks, or for any raptor.

Given the history of abandonment by Ferruginous Hawk adults and importance of the risk to parents in other species (Yasué and Dearden 2006, Schaef and Mumme 2012), we assume that adult Ferruginous Hawk will behave to minimize risk to themselves following a disturbance. However, we expect that there should be variability in the level of perceived risk adult Ferruginous Hawks will tolerate. Based on the reproductive value hypothesis (Trivers 1972, Dawkins and Carlisle 1976), which suggests that parents should tolerate greater risk to themselves when their nestlings are more valuable in terms of the parent's residual reproductive success, we predict adults should resume typical nesting behaviour sooner when broods are larger and older, representing greater value than smaller, younger broods (Redondo 1989). Alternatively, the harm-to-offspring hypothesis (Dale et al. 1996) suggests parents will tolerate greater risk to themselves when the marginal benefit of engaging in risky behaviours is greatest. We predict, based on the harm-to-offspring hypothesis, that Ferruginous Hawks should resume typical behaviours sooner when nestlings are young and vulnerable, or risk of nest predation is high. Nestling predation risk likely changes throughout the day (Lima and Bednekoff 1999, Low et al. 2008), and for Ferruginous Hawks is highest during the night and crepuscular periods, when raccoons (*Procyon lotor*) and Great-Horned Owls (*Bubo virginianus*) depredate Ferruginous Hawk nestlings (C. Nordell unpubl. Data).

After hatch, female Ferruginous Hawk adults attend their nest for bouts lasting several hours, during which they brood and feed nestlings, while likely deterring potential predators and competitors from approaching the nest (Swanson et al. 2012). At this time the adult male provides prey (> 80% Richardson's ground squirrel [*Spermophilus richardsonii*] in our study area; C. Nordell unpubl. Data) for the nestlings and female, and rarely returns to the nest except to deliver prey. As the nesting season progresses and nestlings are able to autothermoregulate and dismember prey more effectively (Powers 1981), the female increases contribution to prey capture, spending less time on the nest (Smith and Murphy 1978). Using digital video footage of nests, we examined whether behaviours at the nest, specifically female returns to, female time on, and total prey delivered (male and female) to the nest, were different following a human disturbance than during control periods. Our objectives were to (1) determine the occurrence, magnitude, and duration of changes in behaviour following a human disturbance and (2) test the reproductive value and harm-to-offspring hypotheses for explaining disturbed behaviours relative to control behaviours.

3.2 Methods

3.2.1 Video Recording and Data Collection

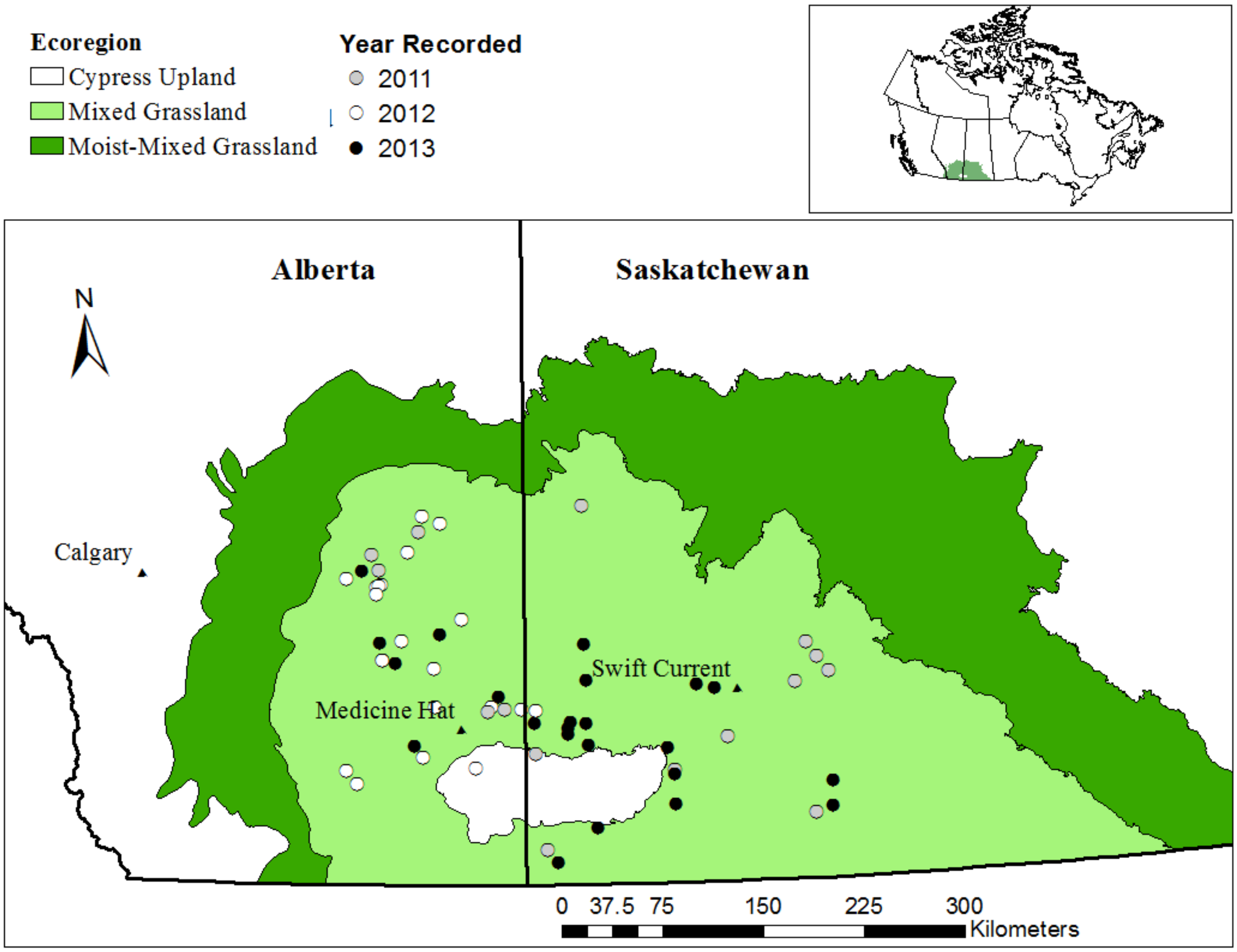

Figure 3.1: Map showing the extent of the mixed and moist-mixed grassland ecoregions in Canada where Ferruginous Hawks typically nest. Indicated are 58 video monitored Ferruginous Hawk nests across Alberta and Saskatchewan used in this study in each of three field seasons (2011-2013).

Data for this study were collected across the mixed grasslands ecoregion (Figure 3-1). Ferruginous Hawks in this ecoregion nest in trees and artificial nesting platforms (ANPs; Schmutz et al.

1984, Migaj et al. 2011), with few exceptions. Digital video recorder (DVR) systems connected to small standard CCTV security cameras were installed near 58 Ferruginous Hawk nests from May 29 to July 18 in 2011, 2012, or 2013, at tree nests and ANPs. We installed video systems when nestlings were > 10 days old, as required by our research permits to minimize the risk of adult abandonment. Each nest was filmed continuously from two camera angles using infrared illumination (wavelength > 700 nm, outside the visible spectrum for most vertebrates) during low-light periods to improve visibility of adults and nestlings. We ascended to nest height using personal climbing equipment or ladders, and cameras were installed at various distances from the nest based on the availability of attachments (e.g. branches). Cameras ranged from 1-20 m away. Batteries and DVRs, camouflaged with tarps and burlap to minimize conspicuousness, were located on the ground at the base of the nest structure and were maintained every 5–7 days. This maintenance visit represented the human disturbance in our study. Typical maintenance required installation of newly charged batteries and verification of camera angles. Ferruginous Hawk adults did not deliver prey or return to the nest during maintenance. Instead, they tended to fly or perch nearby and give alarm calls. Sometimes one or both adults left our sight. The demands of system maintenance prevented us from quantifying adult behaviour while we were at the nest. Nestlings were aged based on size and plumage growth with reference to an aging guide by Moritsch (1985). Lay date (the estimated date of first egg was laid) was calculated by back-calculating from estimated hatch dates (based on age of oldest nestling), assuming 30 days of incubation and two days per nestling to account for asynchronous egg laying (Bendire 1892, Bechard and Schmutz 1995). Maintenance activities by investigators were not conducted in extreme hot or cool temperatures, or during precipitation to reduce thermoregulatory stress to nestlings.

Frequently, maintenance required CCTV cable, camera, or DVR repair, or adjustment of camera locations. Thus, in some instances, we ascended to nest level. Ascending to nest level may be perceived as a greater threat than human disturbance on the ground (as suggested by White and Thurow 1985), and we tested for an effect of investigators ascending the nests as a factor influencing adult hawk behaviour. We documented the duration of each maintenance event (ranging from 16 to 120 minutes). Thus costs (decreased time on nest and foraging time) or perceived risk during disturbance may have varied with disturbance duration, and we tested for an effect of disturbance duration on behaviour. Finally, we studied behaviour following disturbance in individuals that varied in the number of previous exposures to researchers, and tested for potential increased or decreased behavioural response (Fraker 2009, Rankin et al. 2009) with past exposure. Maintenance events took place at 09:00 HR at the earliest and 19:00 HR at the latest.

3.2.2 Behaviour Sampling and Statistical Analysis

We analyzed the effect of human disturbance stimuli for Ferruginous Hawk behaviour using a paired treatment-control sampling design. We sampled video recordings directly following a system maintenance event (disturbed period) and paired these with a sample at the same nest ±2 days, at the same time of day (control period). This sampling design allowed us to control for latent inter-individual differences, and variation in behaviours across the nesting season or time of day. We began quantifying adult Ferruginous Hawk behaviour, including the timing of prey delivery and the arrival and departure of adults from the nest, when the investigators departed from the home range (t_0). Adult females and males were distinguished primarily by size, supplemented by observation of distinct color markings and the presence of leg bands and GSM transmitters on males at some nests (Watson 2014). Behaviours were summarized in 1-hr intervals for up to 12 hrs (t_0 - t_{11}), a time range that extended into the evening when hawks were expected to return to the nest; we therefore expected to capture all remaining diurnal activity. In some sample periods, video systems failed before the 12-hr sample period was completed so the duration of sampling ranged from 2-12 hrs (median = 12) for each disturbance-control pair.

To test for changes in focal behaviours over the entire observation period (disturbance vs control), we performed paired t-tests for disturbance-control sample pairs to test for differences in the number of returns to the nest by the female, time on nest by the female, and total number of prey delivered by the male and female. To compare mean behaviours in a given hour we used mixed effects general linear models with random effects for nesting attempt and sample period to adjust standard errors for non-independence for repeated sampling at a given nest through time. General linear models also generated appropriate confidence intervals for counts (returns to the nest and prey delivered) and proportions (time on nest by the female).

To examine behaviour differences between disturbed periods and control periods through time we subtracted behaviours observed in a given hour during control periods from those during disturbed periods (for each hour from t_0 to t_{11}) to create response variables that indicated the change in disturbed behaviour relative to control in each hour. Negative and positive values indicated a decrease or increase, respectively, in a behaviour relative to the matched control period. Importantly, by subtracting control periods from disturbed periods, we modelled the change in behaviour specifically for each sample pair, rather than the population on average. We created a mixed-effects generalized linear model with a longitudinal data structure using hour as a distinct observation for a given individual. Two random effects were used: for nest and disturbed-control period pairs, thus adjusting standard errors for non-independence when repeatedly sampling at a given nest and through time during a given sample period, respectively. We included time since maintenance event (i.e. disturbance) as a covariate in all models as change in behaviour through time was of primary interest. Focal behaviours included female time on nest and total prey delivered. We used forward-stepwise model building, using a set of potential predictor variables (Table 3-1), to model disturbed adult behaviour differences relative to controls through time. Thus our baseline model (base model), against which we tested for inclusion of predictors variables, included time since maintenance event and random effects for nest and sample period. We used Akaike's Information Criterion (AIC; Akaike 1998) to assess whether addition of a given predictor improved our model at each step. ΔAIC scores>2 were considered significant improvements. We tested for quadratic relationships in continuous predictors and interactive relationships with time since maintenance event for all predictors. Outliers, leverage points, homoskedasticity, and colinearity were assessed for our final model to ensure we met the assumptions of linear regression.

Using our full dataset we compare distributions and skewness of behaviours exhibited in control and disturbed periods. Using only sample periods 12 hrs in duration, we identified outliers in behaviours by calculating the 95th percentiles of time on nest and disturbed time on nest relative to controls. We also performed a linear regression to explore whether time on nest in control periods explained time on nest in disturbed periods. All analyses were conducted using Stata 13 (StataCorp 2013).

3.3 Results

We quantified Ferruginous Hawk behaviour for 89 disturbance-control period pairs, at 58 nests, for a total of 1850 hrs of footage. 925 hrs were sampled during disturbance sample periods, and we recorded a total of 300 nest returns and 306 hours on the nest by females, and a total of 192 prey items delivered to the nest. For 925 hrs during control sample periods, we documented 451 nest returns, 388.5 hrs on the nest, and 207 total prey items delivered.

The number of returns to the nest, as well as time on the nest by the females ($P < 0.001$) differed significantly, but not total prey delivered ($P = 0.45$), between disturbed and control periods. On average, females returned to the nest 1.7 fewer times, and spent 55 fewer minutes on the nest during disturbance periods than during control periods. The mean number of prey delivered was 2.2 (± 0.21 SE) and 2.3 (± 0.21 SE) for disturbance periods and control periods, respectively. The mean number of returns to the nest by the female was significantly lower one hour following disturbance, but not in any other hours. The mean number of minutes on the nest and mean total prey delivered in a given hour after a maintenance event was not significantly different between disturbed and control periods (Figure 3-2). However, the number of returns and total time on nest was lower on average for the first 10 hrs following a disturbance (t_0 - t_9). The total time spent on the nest and number of arrivals by females was highly correlated (r = 0.92), so we considered only total time on nest in our next analysis step.

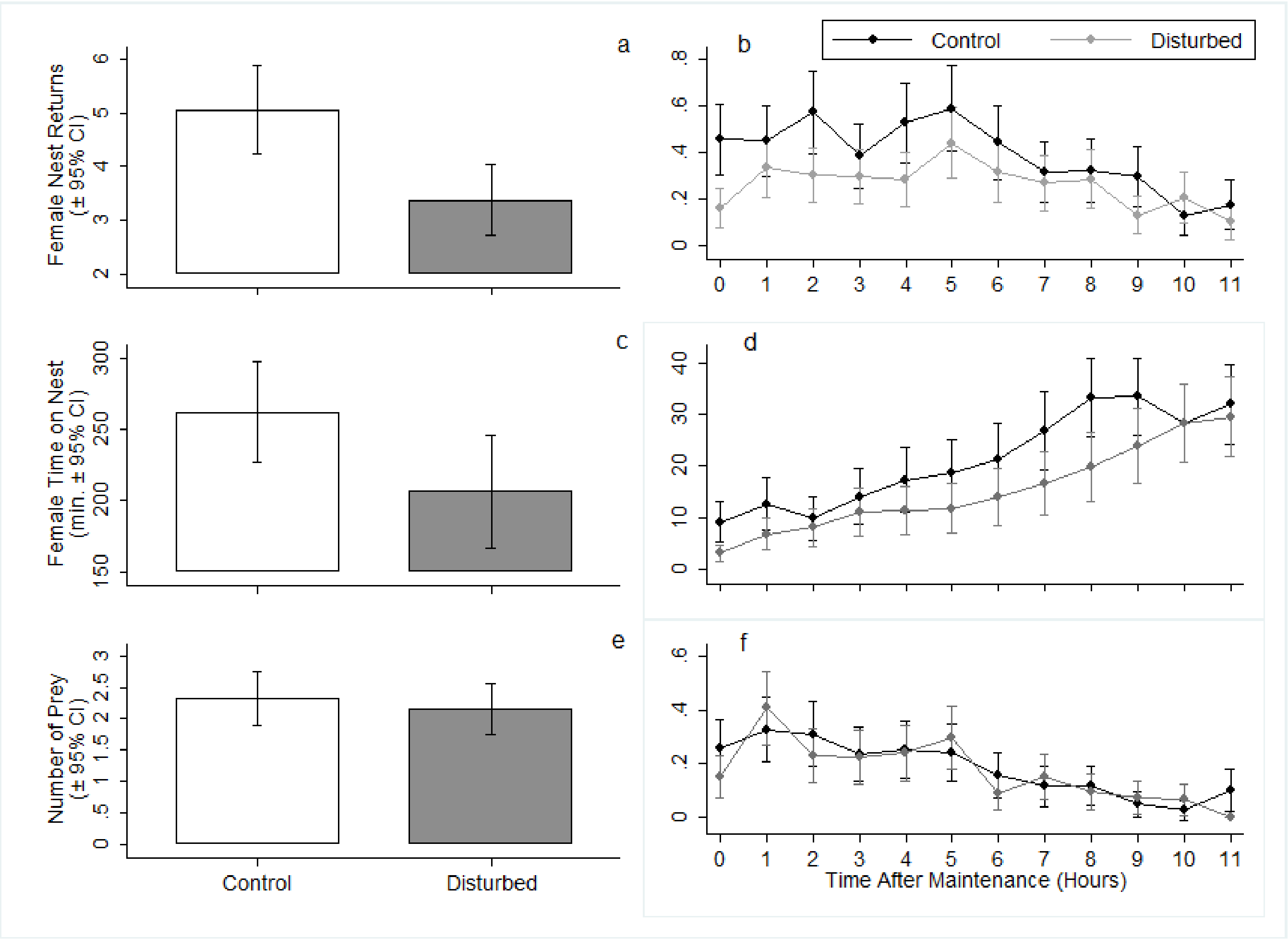

Figure 3.2: Ferruginous Hawk behaviour at the nest following a human disturbance compared to controls.Behaviour data were collected using digital video monitoring of nests in southern Alberta and

Saskatchewan between 2011 and 2013. Bar plots (left) indicate means for entire sample periods with 95% confidence intervals. Line plots (right) indicate means in a given hour with 95% confidence intervals adjusted for repeated sampling at nests through time. The mean number of returns to the nest was significantly lower for disturbed periods compared to control periods ($P < 0.001$; a), and was significantly lower for hour 0, and remained lower on average to hour 9 (b). Total time on nest by the female was significantly lower on disturbed periods compared to control periods ($P < 0.001$; c) and though not significant for each hour, was consistently lower on average through time up to hour 9 (d). Total prey was not statistically different between disturbed periods and control periods ($P = 0.45$; e) and showed no pattern through time on average after a human disturbance (f).

To quantify disturbed behaviour relative to controls through time we used 925 hrs during which we quantified, and calculated differences between, disturbed and control behaviour observations. The final model included two interactive effects (age X time since disturbance, number of young X time since disturbance), and four linear terms (time since disturbance, nest structure, age and number of young; Table 3-1). On average, females spent 10 fewer minutes on the nest relative to controls immediately following a maintenance event (Figure 3.3). As time since disturbance increased, the difference in minutes on the nest relative to controls approached zero. When nestlings were young, the adult female initially spent fewer minutes on the nest relative to controls and increased as time since maintenance event increased, eventually reaching a greater amount of time on the nest relative to control periods (t_6 - t_{11}). However, as nestling age increased, the slope became increasingly negative and females spent less time on the nest compared to controls as time from maintenance event increased (Figure 3.3). Females with small broods initially spent fewer minutes on the nest relative to control periods, and continued to spend fewer minutes on the nest as time since disturbance increased, with a slightly negative slope. As brood size increased, the slope became increasingly positive and the females spent more time on the nest relative to control in the final hours of the sample period (t_9 - t_{11}; Figure

3.3). Females whose lay dates were estimated to be early in the season initially spent less time on the nest soon after being disturbed relative to control periods, but returned to control-levels as time since disturbance increased. However, for late lay dates, the difference between time on nest for disturbed treatments compared to control were close to zero (Figure 3.3). We were unable to explain variation in prey deliveries to the nest through time, as no predictors were selected by our model building to explain variation in the difference in prey deliveries delivered to the nest on maintenance days relative to controls (Table 3-1).

Table 3-1: Predictor variables considered to explain the relative hourly female time on the nest and total prey delivered to the nest compared to controls by Ferruginous Hawk adults.Indicated are β coefficients from our model building ± standard errors. ~ indicates that the predictor was not included by our model building approach.

Covariate		Hourly Female Time On Nest	Hourly Total Prey
t (hrs Since Maintenance Event)	Linear	8.3 ± 2.9	~
Age of Nestlings	Linear	0.34 ± 0.22	~
Age of Nestlings	Quadratic	~	~
Age of Nestlings X t	Interaction	-0.11 ± 0.03	~
Number of Nestlings	Linear	-2.6 ± 1.7	~
Number of Nestlings	Quadratic	~	~
Number of Nestlings X t	Interaction	0.86 ± 0.22	~
Year	Categorical	~	~
Year X t	Interaction	~	~
Number of Previous Disturbances	Linear	~	~
Number of Previous Disturbances	Quadratic	~	~
Number of Previous Disturbances X t	Interaction	~	~
Duration of Disturbance	Linear	~	~
Duration of Disturbance	Quadratic	~	~
Duration of Disturbance X t	Interaction	~	~
Ascend to Nest	Binary	~	~
Ascend to Nest X t	Interaction	~	~
Tree / ANP	Binary	~	~
Tree / ANP X t	Interaction	~	~
Time of Day	Linear	~	~
Time of Day	Quadratic	~	~
Time of Day X t	Interaction	~	~
Lay Date	Linear	0.49 ± 0.18	~
Lay Date	Quadratic	~	~
Lay Date X t	Interaction	0.06 ± 0.02	~

X = indicates interaction, t = indicates time since disturbance, ANP indicates artificial nest platform

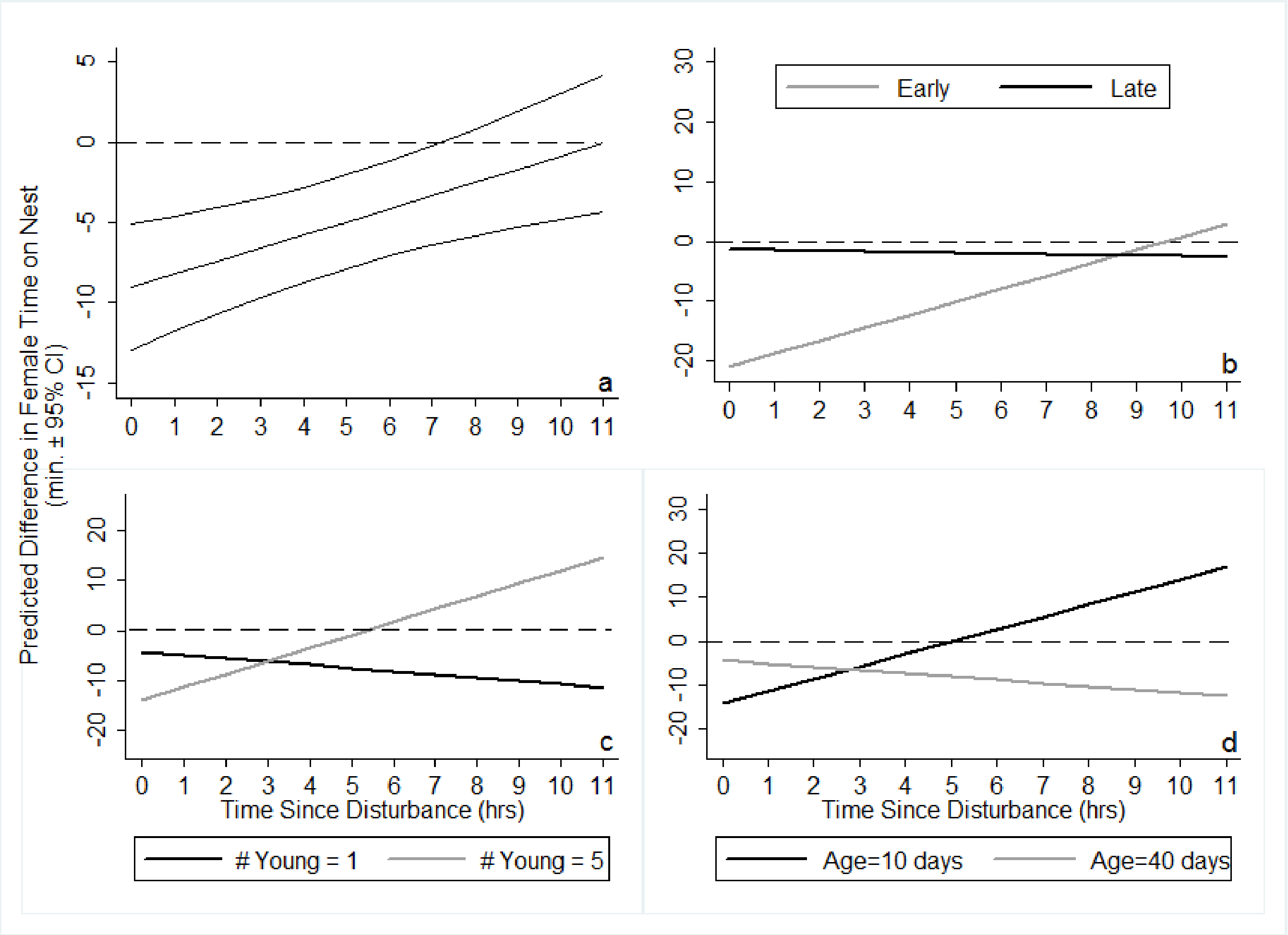

Figure 3.3: Marginal effects plots showing the predicted mean for the response variable, the difference in time on the nest by the female Ferruginous Hawk between disturbance and control sample periods, with all other covariates held at their mean. The panels demonstrate the effect of time since disturbance (a), estimated lay date (b), number of nestlings (c), and nestling age (d). The outer lines in (a) indicate 95% confidence intervals, dashed black lines in all 4 figures indicate a value of zero, or no difference between disturbed and control sample periods. In (d) early and late indicate early and late estimated lay dates, respectively.

Finally, we assessed the occurrence of large behavioural changes between the entire disturbed and control sample periods. The distribution of female time on nest was more skewed during disturbance sample periods (mean = 19.9, median = 0, skew = 0.71) compared to control periods (mean

= 25.2, median = 16, skew = 0.33; Figure 3.4). For sample periods receiving the full 12-hr behaviour quantification (n = 64), females did not return to the nest for 12 hrs, in 6 and 13 instances for control and disturbance periods, respectively. 5 of these 12-hr absences occurred in both the disturbed and control periods for a given paired sample (Figure 3.4). Female time on nest during the disturbed sample was significantly positively related to female time on nest during control periods ($P < 0.001$, $R^2 = 0.51$). The distribution of total prey delivered was equally skewed during disturbance sample periods (mean = 2.2, median = 2, skew = 1.27) and control periods (mean = 2.3, median = 2, skew = 1.29). For sample periods receiving the full 12-hr behaviour quantification, no prey was delivered to the nest for 12 hrs, in 7 and 10 instances for control and disturbance periods, respectively. In 1 sample pair, no prey was delivered in either the disturbed or control periods. Total prey delivered to the nest during the disturbed period was significantly positively related to total prey delivered during control periods ($P < 0.001$, $R^2 = 0.22$).

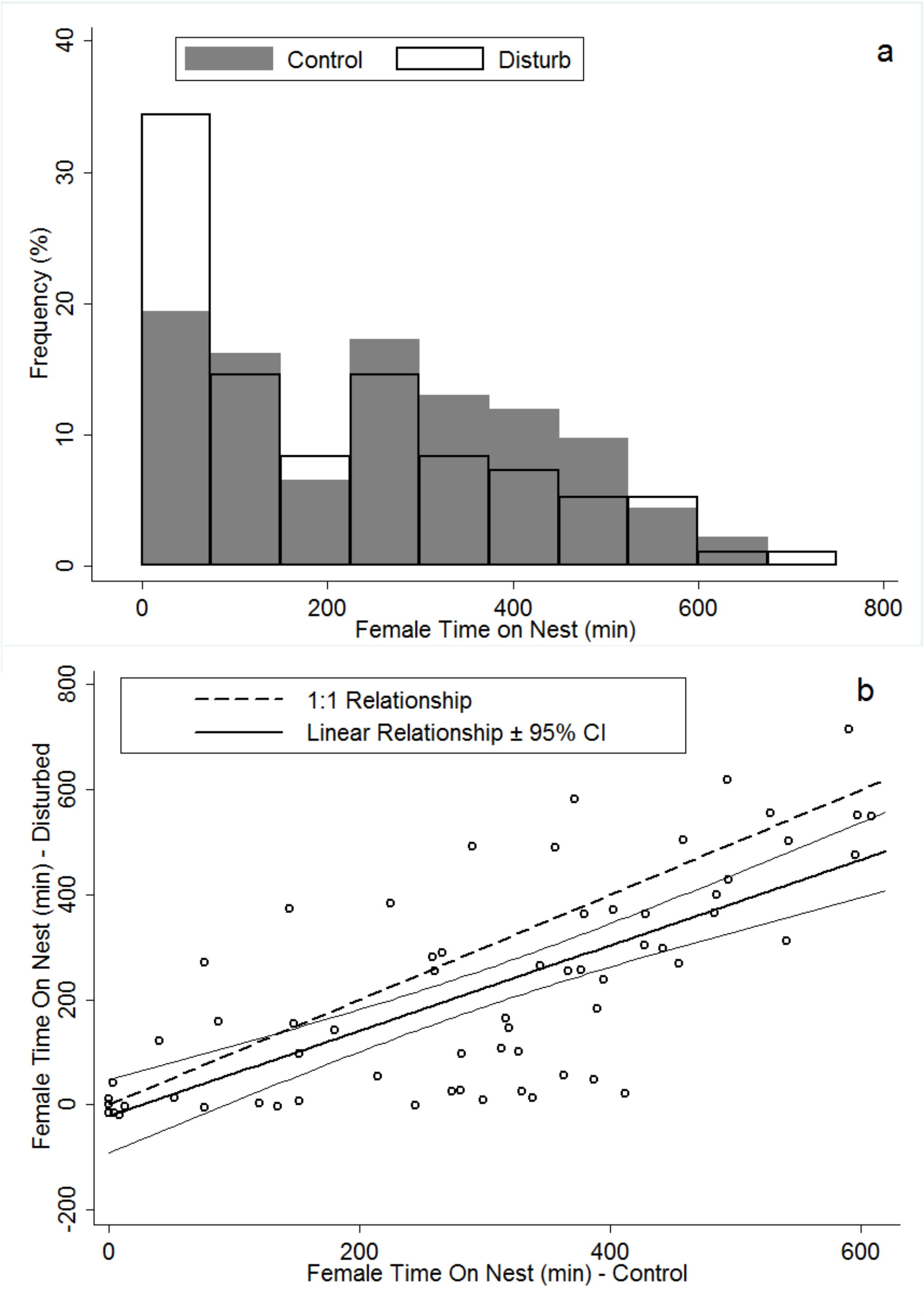

Figure 3.4: Changes in prevalence of extreme behaviour in Ferruginous Hawk adults. (a) superimposed histograms demonstrate the shift in distribution of female time on nest for disturbance periods compared to control for 89 disturbance-control sample pairs, and (b) a scatter plot illustrating that female time on nest is related between control and disturbed periods for 64 disturb-control sample pairs with 12-hr periods of behaviour quantification (*P* <0.001, $R^2 = 0.51$). Points are jittered 5% to display overlapping values near the origin.

Discussion:

Ferruginous Hawk females spent less time on the nest following a disturbance relative to control periods, and on average disturbed behaviours returned to control-levels over the 12-hr sample period. Generally, our results agree with other studies that demonstrated nesting birds were less likely to return to the nest following an interaction with a threat (Yasué and Dearden 2006, Weston et al. 2011, Schaef and Mumme 2012). We found some support for both the reproductive value and harm-to-offspring hypotheses. As predicted by the reproductive value hypothesis, females resumed control-level behaviours sooner when broods were larger, perhaps because females were willing to accept more risk to themselves for larger broods, which are more valuable in terms of total lifetime fitness (Redondo 1989). Alternatively, larger broods may be at a greater risk of predation because they are noisier or more conspicuous (Harvey and Greenwood 1978), supporting the harm-to-offspring hypothesis. However, we observed Ferruginous Hawk nestlings to be largely non-vocal and their large nests in open habitats are likely highly conspicuous regardless of the number of nestlings. We also found that, in support of the harm-to-offspring hypothesis and contrary to the reproductive value hypothesis, female Ferruginous Hawks returned to control-level behaviour sooner when nestlings were young, when they were relatively defenceless against predators and more vulnerable to thermoregulatory stress (Powers 1981). Tests of the harm-to-offspring hypothesis have been conducted for songbirds and shorebirds during or immediately following a predation, event and generally studies have found support for the hypothesis (Bures and Pavel 1997, Bures and Horackova 1998, Listøen et al. 2000). However, the harm-to-offspring and reproductive value hypotheses are not mutually exclusive (Fernandez and Llambías 2013), and the relative importance of each hypothesis for the level of risk parents will tolerate likely differs across species.

Delivery of prey by Ferruginous Hawks was similar between disturbed and control sample periods. The cost to nestlings that receive fewer prey items is potentially considerable (Brinkhof and Cavé 1997, Wellicome et al. 2013). It is unclear whether the adults consumed food at similar rates during disturbed periods relative to controls, as most food consumed by adults was away from the nest. Given the assumption that behavioural changes in the 12-hr sample period following a disturbance are due to a perceived increase in risk to the adult, we conclude that the Ferruginous Hawks adults do not perceive an increase in risk associated with maintaining typical prey delivery behaviour following a disturbance by an investigator. Female adults that are off their nest may be able to survey for prey with equal or greater effectiveness compared to when they are on the nest.

A key uncertainty in our study is the relative importance of the risk to adults and the risk to nestlings in explaining the behaviours observed at the nest. We assume, based on the occurrence of abandonment in Ferruginous Hawks (White and Thurow 1985), that the reduced time on the nest by Ferruginous Hawk females is related to a perceived increase in risk to the female following a disturbance. Similarly, shorebird (Yasué and Dearden 2006) and songbird (Schaef and Mumme 2012) adults, reduced time on nest following a disturbance, likely due to the perception of increased risk to themselves. In shorebirds and songbirds, adults will often minimize risk to the nestlings by remaining on the nest to defend (Swanson et al. 2012) or minimize the chance of detection by threats (Bures and Pavel 2003). In contrast, Ferruginous Hawks, may minimize the risk to nestlings by actively deterring threats through aggressive displays or attacks (Keeley and Bechard 2011), rather than discreet behaviours (Bures and Pavel 2003). Thus, the decrease in time spent on the nest following a disturbance by Ferruginous Hawk females may minimize not only risk to themselves, but also the risk to their nestlings, potentially by increasing vigilance for, or aggression toward, intruders in their territory. More carefully designed studies will be necessary to delineate the relative contributions of risk to nestlings and risk to parents to the decrease in time on nest following disturbance. Regardless, the absence from the nest by an adult females is associated with a decrease in nesting behaviours, such as brooding, nestling grooming, or prey evisceration, all of which are avoided by minimizing unnecessary human disturbance at the nest site.

Importantly, we found evidence for considerable inter-individual variation in female time on nest. Differences in responses may result from many sources of inter-individual variation, including body condition (Koivula et al. 1995), temperament / personality (Vrublevska et al. 2014), social rank (Koivula et al. 1995, Rajala et al. 2012), predator density (Frid and Dill 2002), and experience (Rajala et al. 2012), changing the costs and benefits underlying behavioural responses. Some individuals in our study did not return to the nest for the entire sample period following the disturbance, but these large absences from nests were documented during control periods as well. Ferruginous Hawk nestlings may be able to tolerate receiving little care in the form of female parents on the nest for long periods, as we documented no nestling mortality directly attributable to our disturbances. Additionally, nest success remained high in our study despite our intermittent disturbance of nests. The documented sources of nestling mortality in our nests included predation (n = 1 nest), inclement weather (n = 1 nest) and 2 unknown sources of mortality. None of these mortalities occurred in the 12-hr period following our disturbances. However, potentially avoidable human-induced absences from the nest by female adults when nestlings are in poor condition (Bures and Pavel 1997), during inclement weather (Katzenberger et al. 2015), or when potential predators are present (Stout et al. 2007, Sergio and Hiraldo 2008), could influence nest success.

Our findings highlight that, in studies of wildlife disturbance behaviour, consideration of behaviour through time following a disturbance is warranted. As nest predation is the primary cause of reproductive failure for most bird species (Ricklefs 1969), many breeding birds adjust aspects of their reproductive strategy in relation to perceived risk of predation (Zimmer et al. 2011, Schneider and Griesser 2013, Sorato et al. 2015). This is consistent with our observations of behavioural changes following disturbance. Over evolutionary time scales, changes in behaviour following an encounter with a threat may be optimal behaviour, but when responding to humans that pose no real threat to adults or young, disturbed behaviours likely represent a waste of time and energy (Houston et al. 2012). On average, behavioural changes were not extreme in our study. Instead, extreme absences from the nest by some female adults are more likely to explain decreases in Ferruginous Hawk reproductive success resulting from disturbances, like those in Blair (1978) and White and Thurow (1985). However, uncertainty remains regarding the importance of disturbance for Ferruginous Hawk reproductive success during early nesting stages (nest building, egg laying and incubation). Additional studies of their behaviour are needed (perhaps where populations are not threatened, for ethical reasons) to better understand potential impacts during these earlier nesting stages.

3.5 Appendices

Table 3-2: 58 Ferruginous Hawk nests in southern Alberta and Saskatchewan showing the duration of behaviour sampling periods(multiple sample periods separated by commas). Each sample period represents the duration in hrs for Ferruginous Hawk adult behaviour sampling following a disturbance, equal in length to the control period. Also shown are counts of nestlings (Nestling Number), estimated egg laying dates (Julian Lay Date) and the structure on which the nest was built (Nest Structure).

NestID Number	Sample Period Duration	Nestling Number	Julian Lay Date	Nest Structure
1	12,12,12	2	114	Tree
2	10	4	118	Tree
3	12	1	118	Tree
4	12,12	1	102	Tree
5	12	4	121	Tree
6	12,10	1	129	Tree
7	4	1	129	Tree
8	7	3	112	ANP
9	12	1	136	Tree
10	12	1	122	Tree
11	11	3	110	Tree
12	12	3	113	Tree
13	6,6	4	104	ANP
14	12	4	123	ANP
15	12	3	113	Tree
16	12	3	119	Tree
17	12,12	3	99	ANP
18	10	2	120	ANP
19	11,12	2	117	Tree
20	8	2	124	Tree
21	12	1	126	Tree
22	12	3	115	Tree
23	9	1	122	ANP
24	10,12	2	127	Tree
25	12,11,12,12	1	81	ANP
26	11	3	110	ANP
27	12	1	130	Tree
28	2,12	4	105	Tree
29	12,12	3	119	Tree

30	12	2	123	Tree
31	12	1	125	Tree
32	12,3	4	114	Tree
33	12,12	3	125	Tree
34	12,12,12,12	4	120	Tree
35	12	2	127	Tree
36	11	1	116	ANP
37	12,11	3	118	Tree
38	12	1	126	Tree
39	12,12,9	5	121	Tree
40	12	2	123	Tree
41	10	2	131	Tree
42	7,11	3	116	Tree
43	10,8	3	115	Tree
44	9	5	117	ANP
45	12	3	123	Tree
46	12,12	2	117	Tree
47	5	2	119	ANP
48	12	3	120	Tree
49	5,12	3	113	Tree
50	10	2	118	Tree
51	12	2	115	Tree
52	12	4	120	ANP
53	12	4	126	Tree
54	12	4	110	Tree
55	12	2	114	Tree
56	12	3	117	Tree
57	12,6,6	4	101	ANP
58	12,6,6,6	3	113	Tree

ANP = Artificial Nest Platform

Table 3-3: Covariates considered for inclusion in our models of adult Ferruginous Hawk behaviour data for each of the 89 disturbance - control period pairs.Covariates include nestling age, number of previous disturbances (#), duration of disturbance (Time at Nest), whether we ascended the nest tree or not (Ascend), and the time of day. Also shown are the raw counts of female arrivals and prey deliveries and the number of minutes spent on the nest during Control and Disturbance periods, respectively.

						Control			Disturbance		
ID	Nestling Age	#	Time at Nest (min)	Ascend	Time of Day (hr)	Female Arrivals	Female Time on Nest	Total Prey	Female Arrivals	Female Time on Nest	Total Prey
1-1	28	1	84	Y	15	4	393	2	3	364	2
2-3	36	3	24	N	13	4	354	3	5	63	4
3-4	40	4	18	N	14	3	273	1	2	23	1
4-1	17	1	23	N	13	7	268	6	3	184	3
5-1	24	1	120	Y	13	3	346	1	3	286	2
6-2	30	2	23	Y	10	3	224	1	3	71	3
7-3	33	3	31	Y	15	3	146	1	2	17	2
8-1	25	1	30	Y	13	4	598	2	6	526	5
9-1	12	1	19	N	19	11	620	4	5	550	2
10-2	15	2	64	Y	10	18	390	3	5	441	1
11-1	20	1	16	N	19	2	200	0	2	143	0
12-5	47	5	28	N	16	1	114	0	1	14	2
13-1	29	1	25	N	15	5	130	1	1	15	0
14-3	39	3	14	N	10	3	262	1	2	10	1
15-2	25	2	32	N	13	14	361	1	8	574	2
16-1	14	1	69	Y	10	7	451	3	2	271	2
17-2	16	2	35	N	15	13	231	3	4	159	1
18-3	30	3	33	N	11	8	133	2	2	35	2
19-2	31	2	45	Y	12	4	63	4	0	0	1
20-2	34	2	29	Y	10	6	325	4	1	24	1
21-2	30	2	22	N	13	5	365	2	5	272	3
22-1	13	1	32	Y	13	12	461	5	13	525	4
23-2	21	2	32	Y	13	8	535	3	14	301	6
24-1	28	1	36	N	19	2	226	1	2	227	1
25-1	38	1	28	N	14	0	0	0	0	0	0
26-1	22	1	32	N	13	4	446	2	7	285	2
27-5	43	5	22	N	10	2	14	5	0	0	1
28-2	21	2	98	Y	14	1	140	0	5	433	2
29-1	33	1	29	Y	12	0	0	1	0	0	0
30-1	30	1	64	Y	10	7	307	5	2	138	1

31-1	21	1	50	Y	15	5	451	1	4	508	2
32-1	17	1	90	Y	11	2	148	1	0	0	0
33-2	26	2	42	Y	15	0	0	0	0	0	0
34-2	19	2	21	N	12	10	389	3	4	257	3
35-3	23	3	24	N	13	9	393	0	3	176	3
36-4	28	4	19	N	13	10	390	0	6	372	1
37-5	32	5	58	N	14	2	327	1	0	0	1
38-4	42	4	27	N	13	0	0	0	5	25	3
39-3	34	1	17	N	16	0	0	2	0	0	3
40-2	28	2	90	Y	14	0	76	0	0	0	0
41-5	42	5	35	Y	11	8	96	1	4	162	2
42-1	27	1	11	Y	15	7	406	4	0	0	2
43-2	30	2	25	N	15	7	380	3	1	26	1
44-1	24	1	24	N	18	4	518	0	5	576	1
45-t	34	1	41	Y	11	0	0	1	0	0	0
46-1	22	1	18	N	11	11	310	6	4	141	3
47-4	27	4	28	N	13	0	0	0	1	118	2
48-2	19	2	34	Y	12	6	214	3	5	377	2
49-6	44	6	50	Y	10	1	254	4	0	0	0
50-2	13	1	22	N	9	18	140	9	13	173	9
51-2	20	2	9	N	9	4	66	3	12	271	6
52-2	25	3	46	N	13	7	147	3	4	343	3
53-2	29	4	26	N	13	8	407	2	6	244	5
54-4	40	5	5	N	13	0	0	1	0	0	0
55-1	27	1	19	Y	13	9	304	5	0	0	0
56-1	13	1	20	Y	15	6	605	3	3	470	1
57-2	18	2	31	Y	13	5	367	3	8	473	5
58-1	34	1	35	N	9	4	314	4	6	107	7
59-1	24	1	32	Y	13	3	273	2	5	251	3
60-3	26	3	22	Y	17	3	473	2	2	400	1
61-4	29	4	25	Y	14	4	234	0	1	142	1
62-1	21	1	29	N	12	7	472	3	10	362	7
63-1	37	1	9	N	14	4	40	1	0	0	0
64-1	36	1	52	Y	17	2	290	0	1	278	0
65-2	41	2	39	N	13	2	431	0	0	307	3
66-1	24	1	43	Y	18	2	240	1	1	123	1
67-2	33	2	12	N	16	4	145	2	4	431	3
68-1	33	1	16	N	15	3	48	2	5	35	3
69-1	29	1	40	N	12	6	193	5	6	143	5
70-1	35	1	33	N	14	4	147	2	1	67	2
71-3	40	3	33	N	13	2	50	3	1	106	1
72-4	48	4	30	N	18	0	0	1	0	0	0
73-1	24	1	28	N	9	7	282	10	4	72	7
74-3	24	3	28	N	19	4	149	0	2	143	1
75-4	28	4	31	Y	18	4	428	2	2	387	1

76-1	32	1	20	N	14	6	177	3	3	243	2
77-2	31	2	29	N	18	4	587	1	2	717	0
78-2	29	2	39	Y	14	14	281	8	8	484	2
79-1	20	1	7	N	16	1	485	2	5	608	3
80-1	33	1	16	N	14	4	277	0	4	282	4
81-2	34	2	21	N	12	4	256	2	3	303	2
82-2	19	2	16	N	11	6	322	3	6	91	3
83-1	22	1	25	N	15	11	537	1	5	489	1
84-4	39	4	17	N	16	6	281	5	1	2	1
85-5	45	5	18	N	16	5	233	3	4	154	2
86-1	11	1	16	N	9	11	499	6	6	400	7
87-2	17	2	26	N	14	4	189	3	3	229	3
88-4	22	4	16	N	14	5	92	3	2	274	1
89-7	33	7	32	N	11	2	124	1	1	95	0

Table 3-4: AIC scores and β coefficients for each step of stepwise model building to model the effect of covariates on relative time on nest by disturbed female Ferruginous Hawks compared to controls.

	β(t)	β(a)	β(y)	β(l)	β(aXt)	β(yXt)	β(lXt)	β(0)	n	K	AIC
Base Model	0.66	-	-	-	-	-	-	-8.3	925	4	8760.3
Step 1	4.5	0.39	-	-	-1.3	-	-	-19.2	925	6	8742.2
Step 2	1.8	0.32	-2.5	-	-0.12	0.8	-	-10.7	925	8	8731.7
Step 3	8.3	0.33	-2.6	0.49	-0.11	0.9	-0.1	-67	925	10	8725.6

t = time in hrs since disturbance, a = age of nestlings, y = number of nestlings, l = lay date

β = model coefficient

X indicates interactive effect

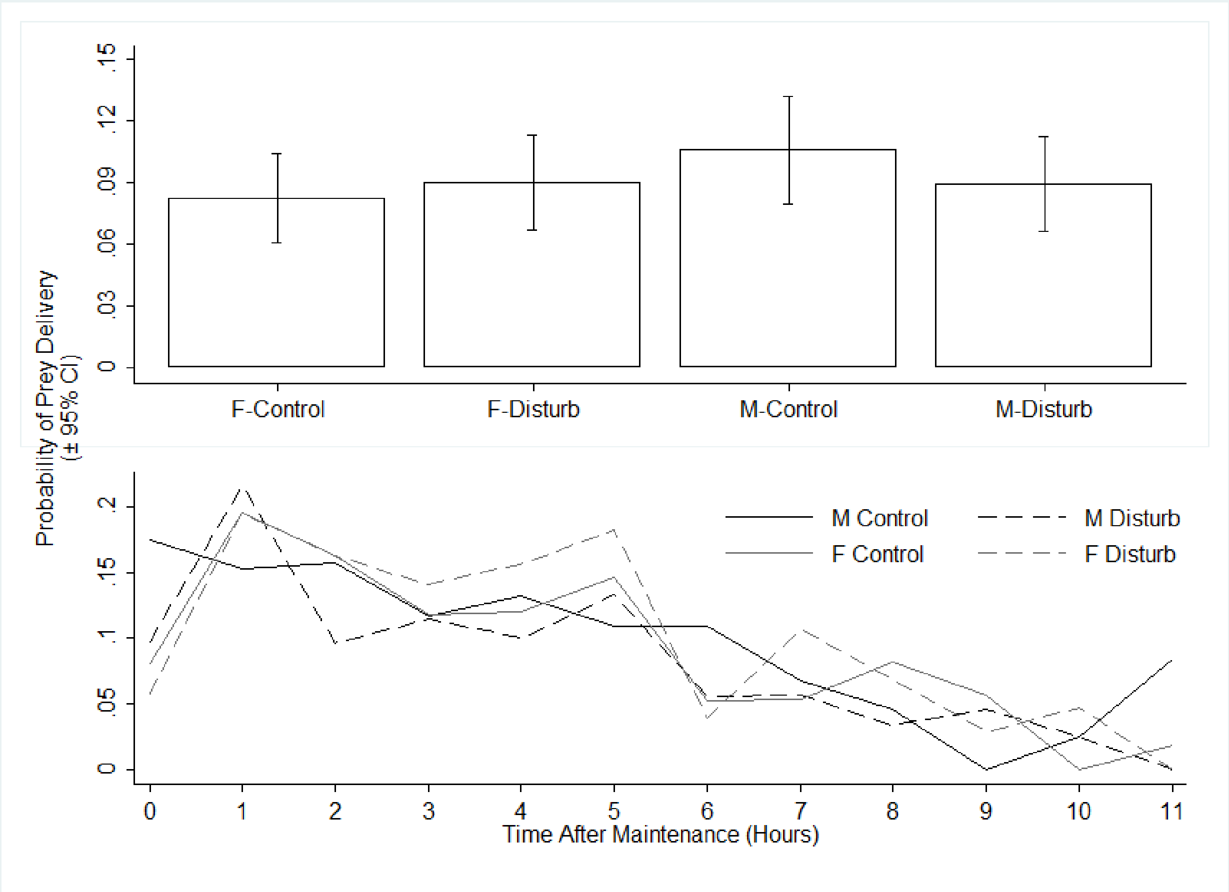

Figure 3.5: Mean prey delivered by Ferruginous Hawk females (F) and males (M) across our 12 hour sample periods (top) and within each hr since disturbance (bottom). Male and female prey deliveries were compared across control and disturbed periods at 58 nests in southern Alberta and Saskatchewan using video to monitor nest behaviour between 2011 and 2013.

Chapter 4: Conclusion and Management Implications

4.1.1 Summary of Findings

Chapter 2 demonstrated that adult Ferruginous Hawks across southern Alberta and Saskatchewan initiated flight from the nest in response to human approaches closer than 400 m in 95% of instances. Of the 1378 distinct observations of adults on the nest, no flight initiation distances (FID) were documented at distances greater than 950 m. Probability of flight was related to the approach path of the investigator, categorized by the mode (vehicle vs on foot) and road class (highway, range roads and access roads) of travel, the number of past investigator approaches, and the number of vehicles expected to travel near the nest. The lowest probability of flight initiation was for approaches on highways and range roads, and probability of flight increased significantly when investigators drove on access roads (a 50% increase in likelihood of flight initiation), walked (3.9 times more likely), or exited the vehicle (5.3 times more likely). Probability of flight increased as the number of previous approaches increased (an 18% increase per approach), and decreased when more roads that are typically associated with greater volumes of vehicular traffic were present near the nest.

Past work on FID has focussed on how individuals vary with respect to flight distances in response to an investigator (Blumstein et al. 2003, Runyan et al. 2004). However, in agreement with Herrero et al. (2005), my study demonstrated that while FIDs likely vary among individual animals, they also differ depending on the stimulus and the context in which an interaction occurs. FID studies have generally followed restrictive procedures for data collection in which investigators move from set starting points towards an animal at a constant speed and angle until flight occurs (Blumstein 2003, McCleery 2009). In contrast, my statistical methodology allowed modification of the properties of the approach, and modelled the effects of these properties on flight initiation. This statistical method may benefit studies with the goal of delineating specific actions by human disturbances to which animals respond. The demonstration of a quantitative relationship between of the anthropogenic landscape and probability of flight is unique, as other studies have typically relied on qualitative observation of landscape differences (but see Mikula 2014).

Chapter 3 demonstrated that female Ferruginous Hawks decreased time on nest following a disturbance, with 2 fewer returns to the nest and 55 fewer minutes on the nest compared to controls over a 12-hr period. I found no difference in total prey delivered to nests during this same period of time following a disturbance compared to paired control periods. There was no evidence to suggest males behaved differently after disturbance than during paired controls periods, but more accurate quantification of male behaviour not captured in nest footage is desirable. Females resumed control-level time on nest over the 12-hr sample period. The decrease in time on nest was driven, at least partially, by the occurrence of individuals that demonstrated extreme decreases, as females did not return to the nest for 12 hrs in 20% of disturbance trials, and decreased time on nest ≥ 3 hrs relative to controls in 23% of disturbances. However, the fitness consequences of these behavioural changes remain unclear.

Human disturbance can cause animals to distract (Pavel et al. 2000), conceal themselves or their nest (Bures and Pavel 2003), flee, seek refuge (Koivula et al. 1995) or behave aggressively. The latter is common for raptors and includes behaviours such as vocalization, stooping, and attacks (Andersen 1990, Sergio et al. 2001, Keeley and Bechard 2011). Chapter 3 demonstrates that certain behavioural changes may be evident, not only immediately after a disturbance occurs, but also when monitored over a longer period of time. I found evidence that number and age of nestlings, and estimated lay dates, influenced how soon post-disturbance female behaviour resumed to control-levels, providing support for both the harm-to-offspring and reproductive value hypotheses. The ubiquity of this type of behavioural change among species is unknown, as no studies have quantified behaviours for several hours after a disturbance. My findings provide a starting point to understand when and why breeding birds exhibit changes in nesting behaviour following a disturbance.

4.1.2 Management Implications

Legislation for nationally listed species, *The Species at Risk Act* (Canada 2002) dictates that "no person shall kill, harm, harass, capture or take an individual of a wildlife species that is listed"; an objective mirrored by the provincial *Wildlife Acts* (Manitoba 1987, Saskatchewan 1998, Alberta 2000). Founded on these Acts, activity setbacks of various distances have been implemented to protect individuals (rather than populations or critical habitat) of listed wildlife, including Ferruginous Hawks (Environment Canada 2009). Here, I discuss how Chapters 2 and 3 can inform regulators and managers regarding harassment and harm of individual Ferruginous Hawks.

The investigator disturbances in Chapter 2, being infrequent and short in duration, likely fall within the low- or medium-disturbance levels for current setback distance recommendations (Environment Canada 2009). Investigators also likely resemble the most common types of disturbances Ferruginous Hawks are likely to encounter, such as private or industrial vehicular traffic, recreationists, and private landowners passing by nests. My results suggest that the 1000-m setback during the breeding season in Alberta is overly precautionary, at least for low- or medium-level disturbances during the brood rearing period, as only 3% (n=21) of flight initiations occurred when humans were > 500 m from the nest (Chapter 2). The 500-m setback implemented in Saskatchewan and Manitoba is likely sufficient to prevent most flight initiations by Ferruginous Hawks. A 1-km setback is also highly precautionary given my findings in Chapter 3, that fairly intense disturbance during brood rearing (i.e., approaching, and sometimes climbing, nest trees) did result in a quantifiable behavioural response, but there was no evidence to suggest that it caused nest abandonments or nestling mortality, or that prey delivery or nest success decreased.

I did not engage in intense disturbances Ferruginous Hawk during the potentially more sensitive nest-building, egg laying, or incubation stages, so I am unable to make recommendations with respect to current guidelines during those periods. Negative effects of disturbance for Ferruginous Hawks appear minimal during the stage that I studied, based on the criteria I measured. However, strict setback enforcement may be crucial during the earlier nesting stages with the goal of preventing nest abandonment. On average, in our study region Ferruginous Hawk nestlings hatched in late-May (Bayne et al. 2014) and current precautionary setbacks (1-km) may be warranted until mid-June when we expect > 95 % ($\bar{x}$ + 2 standard deviations) of clutches to have hatched; after which time shorter setbacks (500 m) are likely warranted until migration south.

The different protection afforded by Saskatchewan and Manitoba for low, medium, and high disturbances is a reasonable strategy, given that I found evidence that different types of stimuli resulted in changes to flight probabilities. However, my study indicated that present categorizations of disturbance can be improved. For example, more frequent and faster moving disturbances are currently given higher disturbance level designations, and greater setback distances. In contrast, I found evidence that more frequent disturbances and approaches at higher speeds do not result in higher probability of flight. Overall, my study suggests instead that atypical types of disturbances that Ferruginous Hawks are less likely to encounter, such as humans on foot or vehicles travelling where traffic is infrequent, are better candidates for medium- or high-disturbance designations.

As Ferruginous Hawks with greater anthropogenic traffic near their nest sites had lower probabilities of flight in response to investigator approaches, policy makers may also consider the anthropogenic level of the landscape as a tool to adjust setback distances regionally or for given nests on a case-by-case basis. However, this effect size was small, with a 30% decrease from lowest to highest near-traffic index (Chapter 2). Changes to setbacks based on the anthropogenic landscape could potentially allow human activities closer to Ferruginous Hawk nests in some instances. However, in these scenarios consideration should be given to the unpredictable and undesirable large flight initiations by certain individual females, which setbacks are implemented to prevent. The use of on-site biologists (or "nest monitors") in situations where relaxation of setbacks is considered appropriate would be important to avoid flight initiation by particularly sensitive individuals.

Construction of artificial nest platforms (ANPs) has been implemented as a strategy to promote Ferruginous Hawk nesting, especially in Alberta. These platforms have been successful in terms of attracting Ferruginous Hawks, and many have been used as successful nesting substrates for several years (Schmutz et al. 1984, Migaj et al. 2011, Wallace et al. 2016). Potentially relevant for use of ANPs for Ferruginous Hawks, flight initiations from ANPs were at greater distances (209.0 m ± 16.4 SE) than for those individuals nesting in trees (101.3 m ± 4.5 SE). To mitigate large FIDs for hawks nesting on ANP's, and to limit the potential stress incurred if individuals on these nests perceive themselves as more exposed to humans, placement of ANPs away from areas of high human activity may be the best strategy to prevent disturbing Ferruginous Hawks using these structures. For example, ANP's should not be placed within active petroleum well leases.

As part of the upcoming *Recovery Strategy for the Ferruginous Hawk in Canada* (Environment Canada In preparation) recovery planners perform a Threat Assessment which rates the severity and scope of potential threats to Ferruginous Hawks at the population level. Currently the draft severity rating for human activity and its potential to harm Ferruginous Hawk populations has been rated between negligible and moderate depending on the type of activity. The scope, the proportion of the population likely to be affected, is rated as small for most human activities. I suggest instead that cumulatively the pervasiveness and variety of potential human disturbances influence a large portion of the Ferruginous Hawk population in Canada. If the decreased time on nest by Ferruginous Hawks (Chapter 3), especially the extreme instances observed in some individuals, resulted in reduced reproductive success then there could be negative consequences for Ferruginous Hawk populations.

However, in my study nest success was high and departures from control-level time on nest did not have obvious effects for Ferruginous Hawk nestling condition or survival. Further, considering Ferruginous Hawks maintained prey delivery rates similar to controls when disturbed, there is little evidence to suggest the types of disturbance we caused had direct energetic consequences for nestlings. Specific management consideration may be given to disturbances that occur when the nestlings would be exposed to inclement weather (Laux et al. 2015) or high nest predator densities, as reproductive consequences may be more apparent in these scenarios. Ultimately, the occasional disturbance to nesting activity after nestlings reach 10 days of age did not appear to have quantifiable detrimental effects for reproductive success. Thus, my findings agree with the Environment Canada (In preparation) draft assessment that severity of human disturbances is likely low, but I emphasize the need to better understand the timing of the disturbance for Ferruginous Hawk behaviour and reproductive success, such as those early in the breeding season or during periods of inclement weather.

Chapter 2 suggests probability of flight is highly variable among individuals. There is potential to use my results to improve the efficiency of setback distances for Ferruginous Hawks and other species if regulators can implement management strategies that utilize information about the stimulus and anthropogenic context to optimize setback distances to prevent flight initiation. However, the implementation of such strategies will be challenging, and I recommend on-site monitoring by biologists as an important component to mitigate the unpredictable impacts of different types of human activities. Ferruginous Hawk behaviour through time in Chapter 3 indicated that behavioural responses to disturbances may represent a conservation concern, but direct effects to survival and reproduction during brood-rearing. Future work exploring reproductive consequences in scenarios where egg or nestling vulnerability is high will be important.

4.1.3 Future Research

A more in-depth exploration of the types of stimuli that influence FID is warranted. For Ferruginous Hawks in particular, there is still considerable uncertainty as to FIDs when disturbance levels are "high" (Environment Canada 2009). Some agricultural equipment, for example, is large, loud and may approach close to nests that are in agricultural land. Further, higher impact industrial activities, such as construction of transmission lines, or oil and gas well drilling, may involve crews of people, large equipment, and high noise levels (Environment Canada 2009). Importantly, these activities may be perceived differently by Ferruginous Hawks than an approach by a single, small vehicle or people on foot, but these types of high-impact disturbances are comparatively rare, and have been investigated for few species. Although we found evidence that Ferruginous Hawks may habituate to traffic around their nest sites, it is unclear whether they would eventually habituate to other types of disturbance that may be perceived differently by adults. Considerable uncertainty remains as to how FID might change when disturbances are present for longer durations. For example, our results indicate individuals are unlikely to initiate flight when a disturbance comes within a certain distance of the nest, but individuals may initiate flight eventually if the disturbance lasts for longer periods of time at a given distance. Using similar approaches to those presented here (Chapter 2), additional research on various stimuli that illicit behavioural responses, and how these responses are related to the landscape in which wildlife are found (Price et al. 2014, Bjørvik et al. 2015), could improve our understanding of disturbance behaviour in many other species.

A variety of human activities occur in my study region, and it is challenging to apply my study of Ferruginous Hawk behaviour to all of these activities. The video system maintenance disturbances are likely closer in proximity to nests than almost all other activities occurring in the region, and may represent one of the more extreme disturbances encountered by Ferruginous Hawks. Future work could consider how behaviours change in response to potentially high impact disturbance activities, longer duration disturbances, or those that occur frequently throughout the day (Environment Canada 2009), especially if sensitization to repeated approach by investigators can also occur in response to other types of repeated disturbances. Additionally, given that my study took place when nestlings were at least 10 days post-hatch, key uncertainties exist with regards to Ferruginous Hawk perception of, and responses to, human disturbance in the first 8-10 weeks on the breeding grounds, while acquiring territories, nest building, incubating, and hatching (Bechard and Schmutz 1995). These early periods may be crucial for protection of individual Ferruginous Hawks from harm or harassment (White and Thurow 1985). A fundamental challenge to studying extreme instances of disturbance, or during early nesting stages, is that the researchers themselves risk causing reproductive failure for the species of conservation interest. The study of behaviour in analogous species with populations not considered At Risk, for example the Swainson's Hawk (*Buteo swainsonii*), or the study of Ferruginous Hawks in other regions where populations are not considered At Risk, may be viable approaches for future work.

Potentially the most critical goal for future disturbance research in Ferruginous Hawks, and undoubtedly for many species, is to understand how animal behavioural responses to human disturbances are related (or unrelated) to the reproductive consequences of disturbing those individuals. Behavioural changes do not necessarily influence fitness (Gill et al. 2001) and behavioural changes may fall within the norms that animals typically encounter, thus incurring few reproductive costs (Beale 2007). Without fitness or demographic metrics, the assessment of the importance of human disturbances for a population's viability are subjective.

Finally, further research is needed to understand the applicability of these findings for other species. Ferruginous Hawks spent much of their evolutionary history as ground-nesters on hills, mounds, or rocky outcrops, and this nesting habit has been associated with passive nest defence among raptors (Morrison et al. 2006). It is unclear whether this nesting preference may give Ferruginous Hawks a predisposition to extreme behaviour in response to threats, but in the past a number of now extirpated land-based predators and grazers may have threatened their nests and nestlings (Atkinson 2009), potentially resulting in behavioural effects that linger today.

4.1.4 Concluding Remarks

The motivation for this study was the historical perception that Ferruginous Hawks are a species particularly susceptible to disturbance, but the role of human disturbance for reported population declines in Canada was unclear. The prevailing view of human disturbance for Ferruginous Hawks appears to have been dominated by reports of negative effects of disturbance for reproductive success (Snow 1974, Blair 1978, Powers 1981, White and Thurow 1985), potentially related to predominant reports of negative reproductive impacts of human disturbance for raptors in general (Voous 1977, Swenson 1979, Craighead Jr and Mindell 1981). For example, in a report summarizing raptor management programs across the USA, LeFranc and Millsap (1984) emphasized human disturbance as a principle threat to raptor populations. However, more recently, Keeley (2009) found few effects on Ferruginous Hawk nesting or foraging success related to human disturbance. Wallace et al. (2016) found few effects of industry on Ferruginous Hawk territory occupancy or nest success, and Keough et al. (2015) found nest productivity was unaffected by proximity to nearest active oil or gas structure. Perhaps owing to an increased emphasis on larger, more statistically-powerful sampling designs, reporting negative results, or selection over time for more tolerant individuals, the effects of human disturbance for Ferruginous Hawk reproductive success now appears to be more moderate than previous studies indicate, and my study provides additional evidence in support of this view.

My study presents insight into previously unexplored areas of wildlife behavioural change in response to humans. Context-specific decisions when initiating flight, and the maintenance of regular prey deliveries when disturbed, are potential mechanisms by which Ferruginous Hawks may be able to coexist with moderate human disturbances around their nests. My results contribute to (1) the discipline of behavioural ecology, specifically when and how animals respond to human disturbances, and (2) the conservation of sensitive species now and in the future as human expansion increases.

Figure 4.1: An un-disturbed female Ferruginous Hawk and her nestlings at 07:00 HR on June 06, 2013, captured by digital video recorder (DVR) on an artificial nest platform (ANP), in Southwestern Alberta.

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