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Autumn Foraging and Staging Ecology of Eastern Population Sandhill Cranes (Antigone canadensis tabida)

Everett E. Hanna, *The University of Western Ontario*

Supervisor: Drs. Scott Petrie, *The University of Western Ontario*
Joint Supervisor: Beth MacDougall-Shackleton, *The University of Western Ontario*
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Abstract

Spatial and temporal variation in the density and distribution of waste agricultural grain (grain herein) during staging can affect the carrying capacity of habitats that support avian populations. Such variation in food resources can also have proximate effects on behavioural ecology (e.g., influence optimal behaviour). The Eastern Population of Greater Sandhill Cranes (*Antigone canadensis tabida*; EP herein) likely began to recolonize Ontario and its historic range starting in the early 1900s and now relies on agricultural grain during migration. Accordingly, ecologists possess little knowledge of how EP crane behavioural ecology may be affected by grain. Thus, my study focused on grain effects on the following topics: 1) age-specific foraging scale and numerical response, 2) age-specific foraging efficiency, and 3) roost use. I used field observation and experimentation, GPS tracking, and GIS analysis to investigate these topics at a key staging area on Manitoulin Island, Ontario, Canada. Although adult cranes remain with offspring during autumn staging and juveniles continue to grow and learn, juveniles did not appear to affect family group field use. Relative food density at a scale of 5 km from feeding fields had the strongest effect on field use, approximately aligning with mean foraging flight distance (6.4 ± 0.15 km) calculated from GPS tracking data. Adult cranes did not forage more efficiently than juveniles; if anything, juveniles may have foraged more efficiently than adults. Alternatively, the social contexts of foragers (e.g., small family flocks or larger mixed flocks) may have obscured age differences in foraging efficiency, grain may not have been sufficiently novel to affect behaviour, or juvenile cranes may learn to forage for grain relatively quickly. Both anthropogenic disturbance and grain affected roost use. Distance to primary paved roads had the most important

effect on roost use, although grain density within 12 km of roosts also had an effect. However, road type (e.g., paved, gravel) may not be an accurate index of nighttime traffic when cranes typically use roost wetlands. Thus, I conclude that grain affects crane foraging and roosting behaviour during staging, but effects vary in nature between field use, foraging efficiency, and roost use contexts.

Key Words: agricultural grain, Eastern Population, foraging efficiency, foraging scale, numerical response, giving-up density, *Antigone canadensis tabida*, habitat use, Manitoulin Island, migration, Ontario, roost, sandhill crane, staging.

Co-Authorship Statement

Dr. Scott Petrie provided technical guidance, including conceptualization of this study, and facilitated funding for my research. He will be included as second author on all related publications where I am lead author. Dr. Ben Rubin provided technical guidance for data analysis in Chapter 2 and will be included as a co-author on publications resulting from the research presented therein.

Acknowledgements

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Table of Contents

List of Tables

List of Figures

xvii

List of Appendices

1 Foraging and staging ecology in Sandhill Cranes

1.1 Foraging Ecology

1.1.1 Optimizing Foraging Behaviour

Behaviour is governed by trade-offs as they affect fitness and it was established in the

1960s that animals might use foraging as a means to maximize fitness (Emlen 1966,

MacArthur & Pianka 1966). In the context of foraging behaviour, the long-held thought

(~40 years; Pyke *et al*. 1977) has been that natural selection favours an optimal balance

between the amount of energy expended attaining food (i.e., locating, capturing,

consuming, and digesting) and the amount of energy gained via digesting and

metabolizing that food such that fitness is maximized (i.e., optimal foraging theory, OFT;

Werner & Hall 1974). The study of animal behaviour strictly related to foraging with an

implicit connection to fitness is a common approach (e.g., Halsey *et al*. 2003, Svanback

& Bolnick 2005, Mitchell & Powell 2012). However, interpreting the effects of foraging

behaviour on fitness in isolation of other behavioural considerations (e.g., predator

avoidance) has been considered misguided and overly simplistic in certain instances (e.g.,

Pyke 1984, Pierce & Ollason 1987). For example, in some ecological contexts (e.g.,

periods of increased predation risk; Krebs 1980), animals may face pressures beyond

maximizing food intake.

The concept of optimality in foraging has become so contentious at times that

researchers (e.g., Pierce & Ollason 1987) have developed extensive arguments against the

use of the theory. However, defences of OFT have been quick to follow (e.g., Stearns &

Schmid-Hempel 1987, Parker & Smith 1990). Of particular importance in the historic

contention of OFT was the establishment (reaffirmation) of the true meaning of optimality in the context of behavioural ecology. OFT and other theories invoking behavioural optima are careful not to refer to behaviours as categorically optimal, but instead as the *most optimal* given a set of environmental, experiential, and genetic conditions by which behavioural variation is limited. Thus, OFT appropriately maintains a prominent role in modern studies of foraging ecology (Sauter *et al*. 2007, Doniol-Valcroze *et al*. 2011).

Though OFT is applied widely to studies of behavioural ecology, it is imperative for researchers to consider the assumptions of alternative experimental designs, especially when making explicit links to fitness. Within the OFT framework, Pyke (1984) proposed six key assumptions, namely: 1) fitness is linked to foraging behaviour, 2) foraging behaviour is heritable, 3) there is an established relationship between foraging behaviour and fitness, 4) there are no effects on evolution from genetic constraints (e.g., single genes affecting multiple traits), 5) existing knowledge of the functional constraints on the evolution of foraging behaviour, and 6) foraging behaviour evolves faster than the conditions implicated in the behaviour thereby allowing animals to actually forage optimally. While it is understood that making inference to measurable characters of fitness is not the goal in all studies of foraging ecology, and often not practical (Stearns & Schmid-Hempel 1987), the implications of these assumptions remain critical nonetheless to the ecological context in which the resulting data are interpreted (Krebs *et al*. 1983).

In general, OFT involves the integration of some currency and one or more constraints to yield an optimal decision rule. **Currency** is the variable that the organism attempts to maximize in each ecological context and is assumed to contribute to

maximizing fitness. ***Constraints*** are those factors that the organism is weighing against

the currency. Constraints are often grouped into temporal (e.g., handling time;

Richardson & Verbeek 1987), energetic (e.g., prey size; Meire & Ervynck 1986; foraging

cost; Chakravarti & Cotton 2014; digestibility; Verlinden & Wiley 1989), and cognitive

categories (e.g., memory and learning; Gould & Lewontin 1979, Sinervo 1997, Nachev &

Winter 2012), though other factors also interact with these general categories (e.g.,

intraspecific competition; Chakravarti & Cotton 2014). Finally, the ***optimal decision***

rule is the relationship between the currency and constraints that yields the greatest net

fitness benefit (e.g., optimal food intake, optimal time spent feeding, etc.). Given the

nature of this framework, clearly developing appropriate and precise definitions for these

factors, specific to each system in which optimal foraging is being studied, is critical

(Hainsworth & Wolf 1976, Montgomerie *et al*. 1984).

   Most often, animals must decide which prey item to target from a variety of options.

Assuming the goal is to maximize energy intake to secure some positive effect on fitness,

the profitability of prey must be computed (i.e., the optimal diet model, AKA the

contingency model; Belovsky 1984). This computation involves three primary elements:

the energy (and nutrients) gained from a prey item, the cost of acquiring the prey item,

and the time taken to acquire the prey item. The theoretical equation following (Krebs

1978) demonstrates the mathematical relationship between those elements:

$$Profitability\ of\ Prey = \frac{Energy\ per\ prey\ item - Cost\ of\ acquiring\ prey}{Time\ taken\ to\ acquire\ prey\ item}$$

In this equation, the estimated energy per prey item is adjusted by the cost of acquisition (energetic constraint) before being divided by the time cost (temporal constraint). It is in this exact context that animals forage. As such, even the most apparently straightforward foraging decisions in nature are governed by this theoretical relationship. For example, brown bears (*Ursus arctos*) follow this principle when deciding where to find the most berries and which berry species to consume during bouts of pre-hibernation hyperphagia (Hertel *et al*. 2016) while Australian fur seals (*Arctocephalus pusillus doriferus*) optimize the duration of their dives according to the probability of encountering and profitability of prey (Foo *et al*. 2016). Some more modern variations on the optimal diet model have been adapted to allow for simultaneous searching and handling, as is the case in grazing and browsing large herbivores (Farnsworth & Illius 1998, Courant & Fortin 2012); however, the essence of the original relationship remains.

In the context of predatory animals, certain species' foraging behaviour appears to be better described by alternative OFT models. These alternative OFT models do not simply assume that predation rates are determined by the aggregate prey handling and processing cost, but instead by the larger of the two factors. For example, Jeschke *et al*. (2002) grouped predatory species into one of two categories: handling-limited predators and digestion-limited predators. In the former case, maximum predation rate is limited by handling time whereas in the latter case it is limited by digestion time. Jeschke *et al*. (2002) noted that most predators in their study were digestion-limited, contrary to the more typical handling time-centered OFT framework.

Animals can employ various strategies to optimize the foraging energy equation. For instance, Schoener (1971) proposed four key aspects of optimal foraging strategies as follows: 1) the optimal diet, 2) the optimal foraging space, 3) the optimal foraging period, and 4) the optimal foraging-group size. The relationships between behavioural optimization and these key aspects were conceptualized to represent the optimization of the entire suite of interactions an animal has with its environment. The development of more complex optimization models ultimately assists in better representing the lifetime behavioural decision-making space in which animals must survive and reproduce (Holt & Jorgensen 2015).

1.1.2 *Ecological Implications of Marginal Value Theorem*

When studying behaviour over increasing spatial scales, focus shifts from individual prey items to groups, or patches of prey. Animals must decide not only how to feed but also how long to feed in each location. The marginal value theorem (MVT) was developed to treat this relationship (Krebs 1974, Charnov 1976). In essence, MVT introduces the depletion of food resources, or learned evasion in cryptic or motile animal prey, to the OFT framework (Davies *et al*. 2012). This relationship functions by the law of diminishing returns whereby the profitability of a prey item can decrease through time as it either becomes less abundant or harder to catch, such that it eventually becomes more profitable to forage elsewhere (Stephens 2008). Thus, animals face pressure to decide when to continue or terminate foraging in each patch (i.e., giving-up time (GUT); Krebs 1974, McNair 1982). To distinguish between the process of optimization in energy-limited contexts from that of time-limited contexts, an alternate form of GUT is

often used; giving-up density (GUD; Brown 1988, Vickery *et al*. 2011, Gyimesi *et al*. 2012, Carthey & Banks 2015). GUD is defined as the threshold density of a prey item below which the predator decides to forage elsewhere. Thus, GUD incorporates perceived costs associated with predation, reduced feeding opportunities, and energetic expenditure associated with increased search times (Brown 1988, Vickery *et al*. 2011).

The concept of GUD, like GUT, has been tested and applied extensively in the field of behavioural and social ecology. As was the case when optimization first emerged (e.g., Pyke 1984), Bedoya-Perez *et al*. (2013) proposed seven points that require consideration in the application of GUD, namely: 1) the curvilinear relationship between harvest rate and energy, 2) the forager's energetic context, 3) the effects of group foraging, 4) food quality and forage substrate properties, 5) the forager's ability to predict patchiness, 6) the forager's complete set of behavioural traits, and, 7) incidental species affecting the system. These considerations permit obtaining a more accurate representation of the forager's decision framework in the context of a given set of environmental conditions (e.g., habitat selection in voles; Morris 2014, predation risk in herbivores; McArthur *et al*. 2014).

1.2 Study System

1.2.1 Sandhill Crane Ecology & Distribution

My research focused on the portion of the Eastern Population (EP) of Sandhill Cranes (*Antigone canadensis*; crane herein) that stages and, to a lesser extent, breeds along the North Shore of Lake Huron, Ontario, Canada (see Section 1.2.2 below for further

description of crane populations in North America). The Sandhill Crane is an avian species belonging to the family, *Gruidae*. Adult cranes stand 0.8-1.2 m tall and typically weigh 3-6.5 kg (Gerber *et al*. 2014), though there is considerable variation in height and mass between subspecies (e.g., Ivey *et al*. 2015). Cranes are socially monogamous with shared long-term parental care (extending from incubation through the first 8 - 10 months after hatching; Nesbitt *et al*. 2008), though more recent observational (Hayes 2007) and genetic studies (Hayes *et al*. 2006) have reported extra-pair copulations. Although diet varies seasonally, cranes are typically considered generalists, capitalizing on available food resources ranging from animal matter to native plants and seeds to planted grain crops (Ballard & Thompson 2000).

Of the six subspecies of cranes in North America, three are non-migratory (Cuban, *A. c. nesiotes*; Florida, *A. c. pratensis*; Mississippi, *A. c. pulla*) and three are seasonally migratory (Lesser, *A. c. rowani*; Canadian, *A. c. canadensis*; Greater, *A. c. tabida*). The treatment of *A. c. canadensi*s as a subspecies remains somewhat contentious to date (Glenn *et al*. 2002, Jones *et al*. 2005). There are six migratory populations in North America, including the Pacific Coast, Central Valley, Lower Colorado River Valley, Eastern, Rocky Mountain, and Mid-Continent Populations (Figure 1.1). The Mid-Continent Population is comprised of all three migratory subspecies whereas the remaining populations are thought to be comprised of almost exclusively either *A. c. rowani* or *A. c. tabida*.
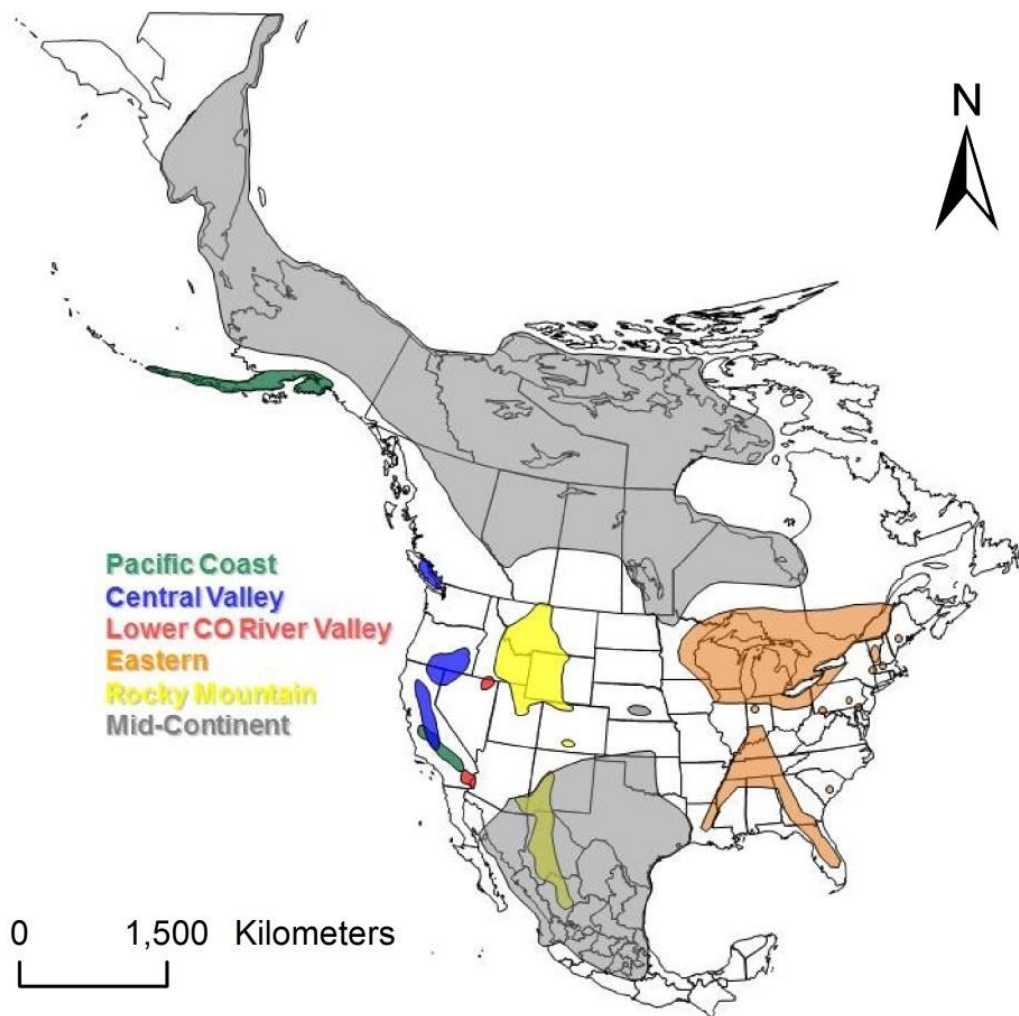
Figure 1.1 Map of Sandhill Crane (*Antigone canadensis*) migratory population winter and

summer ranges in North America (adapted from Kruse *et al.* 2014 and Collins *et al.* 2016). The

present study focused solely on individuals from the Eastern Population (shown here in orange).

1.2.2   Focal Population

My study is focused solely on individuals belonging to the EP. The EP ranges from central Florida, USA in the winter to northern Ontario and Quebec, Canada (and likely into Atlantic Canada) during the breeding season. Wintering occurs as far north as Long Point on the Canadian side of Lake Erie (unpub. data) whereas breeding occurs as far south as southwestern Ontario, Canada and northcentral Ohio, USA. Though portions of the EP breeding range encompass agricultural landscapes, as a species, Sandhill Cranes generally nest in natural or semi-natural wetland settings (Ivey *et al*. 2008, McWethy *et al*. 2009). When available, agricultural grains are often consumed as carbohydrate-rich food sources by adult and recently fledged juvenile cranes (hatched during the current calendar year or "hatch year", HY herein), especially leading up to and during autumn migration (Clark & Sugden 1990).

These carbohydrate-rich foods are typically converted to lipid reserves, which can be used as energy during migration (McWilliams *et al*. 2004). However, as with all migratory birds, cranes must secure various other nutrients from their environment in addition to carbohydrates. This consideration is likely especially important for HY cranes during autumn as they continue to grow long bones and muscles leading up to migratory departure (Krapu & Johnson 1990, Curro *et al.* 1996). For example, in migratory songbirds, switching from a primarily insect-based diet (relatively high protein-to-calorie ratio) to a fruit-based diet (relatively low protein-to-calorie ratio) coincides with migratory departure because high dietary protein can reduce lipid deposition rates (Bairlein 1998). In this way, it is admittedly an oversimplification to consider only effects from carbohydrate-rich food sources on crane behavioural ecology

during staging. Especially for HY cranes, various other nutrients likely affect how cranes interact with their nutritional environment.

The ecological gradient (in terms of types of available food resources) that EP cranes encounter along their latitudinal range is noteworthy in that individuals hatched north of central Ontario, Canada do not likely encounter agricultural habitats prior to migrating south to the Great Lakes basin where the cultivation of modern small grain crops (e.g., barley, *Hordeum vulgare* Linnaeus, wheat, *Triticum* sp. Linnaeus, and oats, *Avena sativa* Linnaeus) is more common. As part of the Great Lakes basin, Manitoulin Island (Manitoulin herein) is located at the north edge of Lake Huron and represents a relatively important patch of habitat for migrating cranes. Approximately 200-300 cranes inhabit Manitoulin during summer whereas >6,000 individuals stage there during autumn, typically arriving in late August and departing in late September/early October (Hanna *et al*. 2014). Thus, most of the cranes present during autumn have arrived from locations further north (no evidence of northerly migration during autumn to date). Beyond a relatively narrow strip of agricultural land along the mainland North Shore, the landscape to the north is primarily mixed-wood forest extending to the coniferous boreal forest several hundred kilometres north. For juvenile cranes arriving at Manitoulin in late summer and early autumn, agricultural grain fields represent a novel yet apparently important nutritional landscape. The relationship between juvenile growth and development and agricultural grain is critical to portions of my study and will be discussed more extensively in Chapters 2 and 3.

1.2.3 Manitoulin Island Study Site

All field components of my study were conducted at Manitoulin Island, Ontario, Canada (UTM Zone 17 E 0394968 N 5065491; Figure 1.2). Manitoulin is located at the northern end of Lake Huron and is the largest freshwater island in the world at 2,766 km^2 (Chapman & Putnam 1973, Kraus *et al*. 2009). Furthermore, Lake Huron has the largest collection of freshwater islands in the world. This landscape feature is thought to contribute significantly to the region's biodiversity (Kraus *et al*. 2009). The underlying geological formation is primarily limestone and dolostone, which is locally unique, at least in contrast to the dominant Precambrian Shield that comprises much of the mainland to the north (Bergström *et al*. 2011). Manitoulin has relatively fertile soil, primarily because limestone introduces calcium carbonate into the soil which neutralizes soil pH, in turn increasing agricultural yields (e.g., Asio *et al*. 2006). The northern reaches of the Niagara Escarpment extend to the southeastern region of Manitoulin. For a more extensive description of the local geology see Sanford (1978).

Manitoulin has several permanent and ephemeral wetlands, ranging from treed bogs to shallow limestone marshes to coastal alvars (personal obs.). There are also several smaller lakes on Manitoulin (mean surface area = 90.2 ha, mean maximum depth = 5.4 m; Jackson & Harvey 1989; Ridgway *et al*. 2012) with extensive emergent aquatic vegetation.

Land cover on Manitoulin ranges from intact deciduous and mixed forest to bog and fen wetlands to globally significant alvars (Catling & Brownell 1995) to cleared agricultural land for grazing and crop production (i.e., hay, soybean, *Glycine max* Linnaeus, and other small grain crops). As of 2006, there were 258 farms on Manitoulin,

spanning >70,800 ha with an average farm area of 279.2 ha (HCA 2009). Approximately

13,760 ha of the farmland were in crops while 6,070 ha were in tame or seeded pasture,

33,994 ha were classified as natural land for pasture, and the remaining 17,806 ha were

classified as other (HCA 2009). As of 2006, the 258 farms located on Manitoulin were

categorized as follows: eight dairy cattle, 152 beef cattle, two poultry and egg, four sheep

and goat, 17 other animal production, one oilseed and grain, one fruit, five greenhouse,

nursery, or floriculture, 64 other crops, and four vegetable (HCA 2009). Finally,

Manitoulin's agricultural area (hectares) was categorized as follows in 2006: 83.8 wheat,

342.8 oats, 855.1 barley, and 522 mixed grains (HCA 2009). Farmers who grow barley,

oats, and/or wheat on Manitoulin typically allow cut crops to dry laying in swaths before

being combined later (personal obs.). Variation in such harvesting practices may have

implications for waste grain availability (Pearse *et al*. 2010).

Figure 1.2 Map of Manitoulin Island, Ontario, Canada.

1.3   Logical Overview

1.3.1   Thesis

The central aim of my research was to investigate the extent to which spatial and temporal variation in food (grain) affects EP crane behaviour during autumn staging. I sought to test if changes in grain density and distribution play a central role in determining foraging behaviour in general, but also specifically as they relate to age/social status (i.e., adult vs. juvenile and parental adult/offspring vs. non-parental adult), foraging scale/giving-up density, foraging efficiency, and roost site use. Because of their shift to carbohydrate-rich diets (i.e., agricultural grain) during migration and the apparent relative importance of such food resources to migration (Krapu *et al*. 2004, Anteau *et al*. 2011), I hypothesized that cranes modulate behaviour (searching for food and wetland roost site selection) to exploit spatial and temporal variation in food resource abundance. Using the approach outlined in the following two sections, my research sought to test for a grain food resource effect by asking if spatial and temporal variation in grain density and distribution were important determinants of crane behaviour during autumn staging.

1.3.2   Research Objectives

To ensure the data I collected could be used to evaluate my central hypothesis, I established the following objectives to guide my research:

1.   Quantify spatial and temporal variation in grain during autumn staging.

2. Collect observational data describing the age-specific numerical response (i.e., aggregational behaviour of field-feeding cranes) to spatial and temporal variation in grain in fields studied as part of Objective 1 above.

3. Collect observational data describing the age-specific foraging behaviour response to spatial and temporal variation in grain in fields studied as part of Objective 1 above.

4. Experimentally manipulate grain density and distribution in experimental fields to: a) quantify temporal depletion of agricultural grain, and b) collect numerical response and foraging behaviour data specific to experimental grain density treatments.

5. Quantify temporal changes in roost site (wetland) use during the autumn staging period as they relate to spatial and temporal variation in grain.

If my central hypothesis regarding grain food resource effects on behaviour is correct, I predicted the following outcomes: 1) spatial and temporal variation in grain density and distribution are important factors in determining age-specific numerical response; 2) spatial and temporal variation in grain density and distribution are important factors in determining age-specific foraging efficiency (i.e., behaviourally-naïve juvenile (hatch-year, HY) cranes are less efficient at foraging as compared to adult (after-hatch-year, AHY) conspecifics); and, 3) spatial and temporal variation in grain density is an important factor in determining roost site use (i.e., if grain food resources affect behaviour, cranes should roost in closer proximity to better feeding sites).

1.3.3 Dissertation Structure

In Chapter 2 (*Numerical response and foraging scale of Greater Sandhill Cranes (Antigone canadensis tabida) feeding in harvested agricultural grain fields during autumn staging*), I tested my first prediction related to the age-specific effects of spatial and temporal variation in grain density and distribution on numerical response. I collected data on spatial and temporal changes in food resources, and age-specific field use by cranes, to elucidate foraging scale (the level at which the species interprets food resources) and giving-up density in this system. I used a systematic design with manual sampling to collect grain density and distribution data and employed road-based transects and GPS tracking to collect behavioural data.

In Chapter 3 (*Age-specific foraging efficiency of Greater Sandhill Cranes (Antigone canadensis tabida) in harvested agricultural grain fields during autumn staging*), I tested my second prediction relating to the age-specific effects of spatial and temporal variation in grain on foraging behaviour. I collected observational data on spatial and temporal variation in grain as described above for Chapter 2 while quantifying age-specific foraging behaviour. I used these data to examine the relationship between grain food resources and foraging behaviour, including age-specific effects, and interpreted the results in the context of optimal foraging theory. Moreover, to provide an experimental test of the relationship between foraging behaviour and grain food resources in this system, I conducted a landscape-level experiment wherein I manipulated grain density and distribution in experimental plots placed in natural feeding locations. I collected grain food resource data as specified above and employed vehicle-based observations to collect behavioural data.

In Chapter 4 (*Roost site use by Eastern Population Greater Sandhill Cranes (Antigone canadensis tabida) during autumn staging*), I tested my final prediction relating to the effects of grain food resources on roost site use. I compared levels of use between roost sites at my study site and modelled the effects of grain density and anthropogenic disturbance to determine if they were important factors in crane roost site use. I employed field observation and GPS tracking data to collect roost site use data.

In Chapter 5 (*General Discussion*), I synthesize my overall findings by linking my primary conclusions back to my original hypothesis and associated predictions. This chapter provides a thorough interpretation of crane behaviour at my study site, integrating the various datasets that I collected in the field (i.e., grain food resources, direct observation of behaviour, and GPS tracking data), to develop a better understanding of grain food resource effects on crane foraging ecology during autumn staging. I also provide guidance for related future research and summarize the key findings of my study.

1.4   Management Implications

While the hypotheses and associated predictions presented and tested here will advance current ecological knowledge of a novel species and system, my study also has important implications to the field of wildlife management.

The EP was reduced to an estimated one to two dozen breeding pairs and extirpated from Ontario within the last 100 years (Walkinshaw & Wing 1955, Lumsden 1971, Hunt *et al.* 1976). After receiving protection under the Migratory Bird Treaty Act of 1916, the EP grew relatively quickly to an estimated 83,479 individuals in 2014 (Kruse &

Dubovsky 2015) with a three-year average from 2012-2014 of 78,500 (Fronczak *et al*., In press, Figure 1.3). This growth has mostly been due to the cessation of commercial crane harvest. However, in recent years, limited modern recreational harvest has been introduced in Kentucky and Tennessee (2011 and 2013, respectively). In 2014, a total of 401 cranes were reported harvested between Kentucky and Tennessee (Kruse & Dubovsky 2015), representing 0.05% of the 2014 population estimate.

Following recent population growth, my study was in part proposed by the Canadian Wildlife Service (CWS) and developed in collaboration with a project in the United States led by David Fronczak from the US Fish and Wildlife Service (USFWS) and University of Minnesota at St. Paul. Collectively, these projects aimed to collect contemporary population biology data for the EP to inform managers charged with decision-making related to the species (i.e., USFWS in the USA and CWS in Canada).
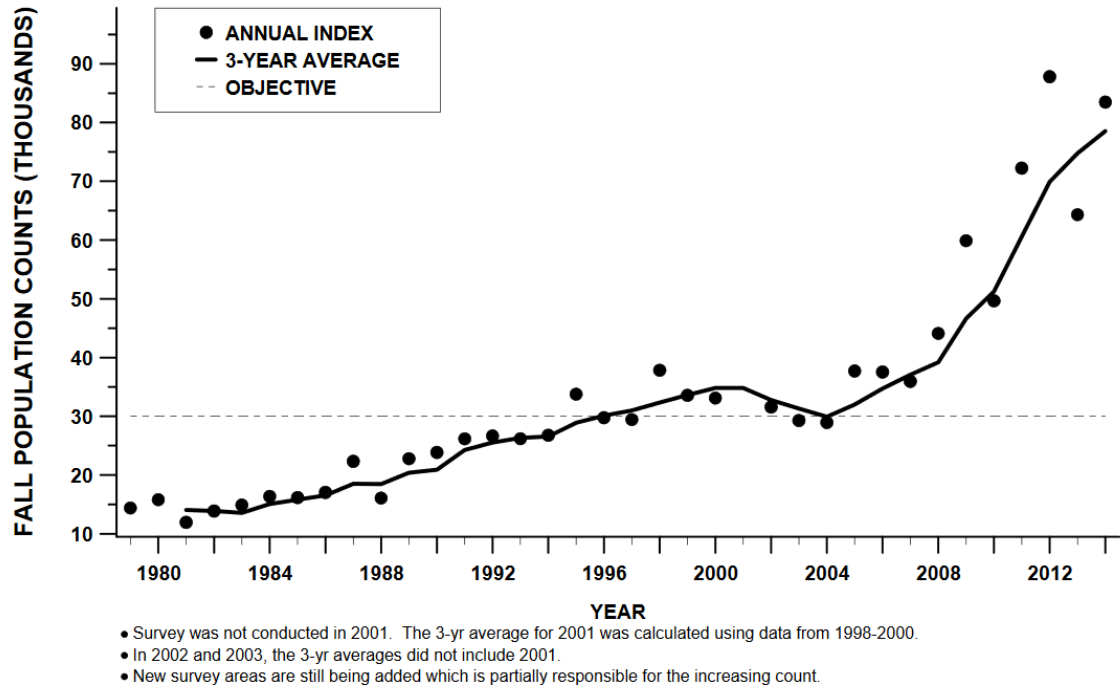
Figure 1.3 Population trend for Eastern Population Sandhill Cranes (*Antigone canadensis tabida*) estimated from annual USFWS fall counts (adapted from Kruse & Dubovsky 2015).

The Canadian portion of the effort aimed to achieve the following goals:

1. Collect a minimum provincial population estimate for the EP in Ontario during autumn migration.

2. Estimate EP autumn recruitment (as measured by juvenile:adult ratios).

3. Establish a preliminary understanding of EP crane autumn migratory chronology in Ontario.

While my study does not explicitly address these specific goals, it is noteworthy that they were addressed by the separate research undertaking described above. A technical report summarizing the applied findings of the Canadian portion of the project was produced and provided to CWS and other concerned parties (Hanna *et al*. 2014). Furthermore, two publications describing the distribution and migration chronology (Fronczak *et al*., In press) and annual survival rates (Fronczak *et al*. 2015) of EP cranes have resulted from this project. Finally, I also published a methods article describing my evaluation of a vacuum technique designed to estimate abundance of waste barley (Hanna *et al*. 2015). Collectively, these publications (as well as those planned for the chapters of this study) have made/will make important contributions to the management of EP cranes specifically and avian populations in general.

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2 Numerical response and foraging scale of Greater Sandhill Cranes (*Antigone canadensis tabida*) feeding in harvested agricultural grain fields during autumn staging

2.1 Introduction

Food resources made available from modern agricultural practices are utilized by many species of wildlife (Amin *et al.* 2015, Jankowiak *et al.* 2015, Li *et al.* 2015, Chudzińska *et al.* 2016). For migratory granivorous birds specifically, these food resources most often come in the form of waste grain (i.e., grain incidentally spilled or missed by standard agricultural crop harvesting practices; grain herein). Grain food resources are particularly important before and during migration because they are relatively abundant, accessible, energy-dense, digestible, and available during a period of increased energetic demand (Littlefield 1986, Kaminski *et al*. 2003, Galle *et al*. 2009, Anteau *et al*. 2011). Several studies have reported effects of waste grain abundance on avian carrying capacities (Krapu *et al*. 2004, Pearse *et al*. 2010, Wiseman *et al*. 2010, also see Drahota & Reichart 2015), demonstrating the relative importance of these resources in sustaining some populations. Moreover, habitat (including grain food resources) can have cross-seasonal effects on individual reproduction in some avian groups, including waterfowl (Davis *et al*. 2014, Sedinger & Alisauskas 2014).

How migratory birds respond to changing grain food resources varies by migratory season, as autumn and spring migration follow and precede disparate life history stages (i.e., raising and fledging young prior to autumn departure and initiating nesting upon arrival in spring; Stafford *et al*. 2014). In spring migration, migratory birds employ various strategies to acquire energetic reserves necessary for reproduction (e.g., capital

breeders vs. income breeders; Jaatinen *et al*. 2016). In contrast, during late summer and early autumn migration, birds must balance the energetic demand of moulting and migratory flight as they travel to overwintering sites (Benson & Winker 2015). These seasonal differences in selective pressure often result in greater migratory speeds during spring than autumn (Kölzsch *et al.* 2016). Migratory granivorous birds modulate behaviour in accordance with grain availability and abundance as well as with energetic requirements at staging areas to optimize net energy intake and presumably maximize fitness following migration (*sensu* Pyke *et al.* 1977, Pearse *et al*. 2011, Beatty *et al.* 2014).

Such exploitative foraging behaviour is governed by a form of optimization and appears broadly in modern studies of behavioural ecology (e.g., Fujioka *et al.* 2016, Mahjoub *et al.* 2016, Tyson *et al.* 2016). Recently, competing explanations have been advanced by other scientific fields (e.g., Lévy walks in the physical sciences; Reynolds 2015, but see Humphries 2015). Nevertheless, studies of optimal relationships in foraging ecology persist (optimal foraging theory; Werner & Hall 1974). These studies typically describe the proportion of time animals spend engaged in various behaviours and relate those activities back to some form of profit gained via foraging (typically energetic income), often devising energetic budgets (Tacha *et al.* 1987, Mori & Boyd 2004, Willisch & Ingold 2007).

However, the pressure to optimize foraging behaviour is likely also present at larger, varying spatial scales, contingent on species and ecological context (marginal value theorem, MVT; *sensu* Krebs 1974 and Charnov 1976). Whereas MVT has typically been used to explain how animals decide how long to stay in patches within a given habitat

unit (e.g., field), the theory may also be useful in explaining how animals decide between the habitat units that contain food patches. For example, Ivey *et al.* (2015) reported differing foraging scales between two sympatric subspecies, Greater and Lesser Sandhill Cranes (*Antigone canadensis tabida* and *A. c. canadensis*, respectively), during winter as inferred from tracking data. In that study, *A. c. tabida* had a shorter average foraging flight distance (FFD) from roost wetlands to feeding sites than *A. c. canadensis*. Some difference in the pressure to optimize foraging behaviour likely exists between these sympatric subspecies. Therefore, establishing the seasonal foraging scale for a species at a particular time/location, in light of factors affecting energy acquisition and expenditure, would provide useful information to wildlife researchers and conservation planners (Callicutt *et al*. 2011, Krapu *et al.* 2011).

In the case of migratory cranes in general (family *Gruidae*), there exists an important additional distinction relating to variation in foraging behaviour. Juvenile (hatched during the current calendar year or "hatch year", HY herein) cranes continue to grow and develop throughout autumn migration and are smaller than adult conspecifics (hatched prior to the current calendar year or "after hatch year", AHY herein; Inoue *et al.* 2013). Therefore, HY cranes face distinct behavioural (e.g., lack of experience foraging in agricultural fields) and physiological challenges (e.g., continued growth of long bones and muscle mass; Krapu & Johnson 1990, Curro *et al.* 1996, Nowald 2001) relative to AHY cranes during autumn. Furthermore, in Sandhill Cranes (*Antigone canadensis*), there is an AHY non-breeding sub-demographic (i.e., adult appearance but typically do not reproduce) that persists from one to approximately five years of age, though estimates vary between individuals and migratory populations (Tacha *et al.* 1989, Nesbitt 1992,

Drewien *et al.* 1995). Unfortunately, no reliable method for distinguishing parental from non-parental AHY cranes in the field has been described to date (beyond direct observation of adults with young or intensive marking programs). Thus, it remains challenging to quantify the parental status of AHY cranes in autumn.

Even with knowledge of these demographic-specific differences in ecology and physiology, researchers are often forced to pool observations of all crane demographic groups due to logistical constraints associated with collecting data in the field (Nilsson *et al.* 2016). Unfortunately, such pooling prevents the analysis of behavioural differences amongst age classes and demographics (i.e., AHY vs. HY and parental vs. non-parental AHY). Therefore, collecting age-specific data that describe foraging behaviour and at least aggregating observations by age class (HY and AHY) should allow for meaningful inference towards age-/demographic-specific behaviour during autumn staging when disparate challenges exist between these groups. Specifically, such data would at least allow researchers to use HY numbers as an index of family group behaviour and in comparison to AHY behaviour (represented by a composite sample of parental and non-parental AHY cranes).

In my study, I sought to determine the age-specific effects of spatial and temporal variation in grain density and distribution during autumn staging on the foraging ecology of Eastern Population (EP) Greater Sandhill Cranes (*Antigone canadensis tabida*; cranes herein). I used road-based observations of field-feeding cranes coupled with Global Positioning System (GPS) tracking data and estimates of food density and distribution at multiple spatial scales to analyze the relationship between numerical response (i.e., aggregational behaviour of field-feeding cranes) and, not only food density and

distribution within fields where I observed cranes, but also food resources in neighbouring fields (i.e., foraging scale). I estimated mean FFD from GPS-marked cranes to determine the spatial scales to include in models. I also included spatial data in my analysis to control for larger landscape scale effects beyond food density and distribution. Most importantly, I sought to test the hypothesis that the numerical response of cranes is primarily driven by changes in grain density but that the relationship varies in nature between family and non-family groups due to differences in behaviour and physiology between AHY and HY cranes. Information of this nature provides insight towards how AHY and HY cranes navigate the nutritional landscape, and towards the foraging scale relevant to these birds at this study area during autumn staging.

2.2   Methods

2.2.1   Study Area

All field components of my study were conducted at Manitoulin Island (Manitoulin herein), Ontario, Canada (UTM Zone 17 N, 0394968 E, 5065491 N; see Figure 1.2 in Chapter 1). Manitoulin is the largest freshwater island in the world at 2,766 km^2 (Chapman & Putnam 1973, Kraus *et al*. 2009) and is located at the northern end of Lake Huron. The landscape varies from coastal alvar and wetland habitats (i.e., swamps, fens, and bogs) to upland deciduous forest and cleared agricultural fields.

Manitoulin is an important patch of habitat for migrating EP cranes, especially during autumn. During summer, roughly 200-300 cranes inhabit Manitoulin (unpub. data). In contrast, during autumn staging, >6,000 cranes are present on Manitoulin (Hanna *et al*.

2014). Autumn staging typically starts in late August and extends until late

September/early October when cranes begin to depart (Hanna *et al*. 2014). Because of

the difference in numbers between summer and autumn staging, most cranes present

during autumn staging likely travel from locations further north (no evidence of northerly

migration during autumn to date). The agricultural land stretching along the North Shore

of Lake Huron is relatively isolated as the landscape to the north is primarily mixed-wood

forest and extends to the coniferous boreal forest several hundred kilometres north.

Therefore, Manitoulin may provide the first agricultural grain for many HY and AHY

cranes during autumn migration. Thus, waste grain likely represents a novel yet

important nutritional resource for HY cranes arriving on Manitoulin in late summer and

early autumn.

My study area included the agricultural area, and associated wetlands, located in the

south central portion of Manitoulin. Generally, I collected data in the area east of Mud

Lake, south of Lakes Kagawong and Mindemoya, and west of Mindemoya, extending

south to the shore of Lake Huron.

2.2.2   *Grain Sampling*

At the start of each field season (early August), I assessed and classified all fields in

my study area based on crop type (i.e., grain vs. non-grain). Grain fields were planted in

either pure wheat (*Triticum* sp. Linnaeus), barley (*Hordeum vulgare* Linnaeus), oats

(*Avena sativa* Linnaeus), or a mixture of grain crops. A 50-50 mix of barley and oats was

the most common mixed crop at my study site (personal obs.). In each of the 2011 and

2012 seasons, I selected a random subsample of focal fields (n = 20 of 37 grain fields and

23 of 34 grain fields, respectively; Figure 2.1). Four of the 20 selected focal fields in

2011 were inaccessible, resulting in a reduced sample size of 16 focal fields in that year.

In 2012, I randomly selected 11 of the 23 focal fields as "experimental" (see Section

3.3.4 in Chapter 3 for experimental grain sampling methods) and retained the other 12 as

"observational" focal fields. One of the observational focal fields in 2012 was

inaccessible, and another field initially selected for the experiment was deemed not viable

due to landowner concerns so was added to the observational set of fields, resulting in 12

and 11 observational and experimental fields, respectively. In total, I collected data from

28 unique observational focal fields over two autumn staging periods (Figure 2.2).
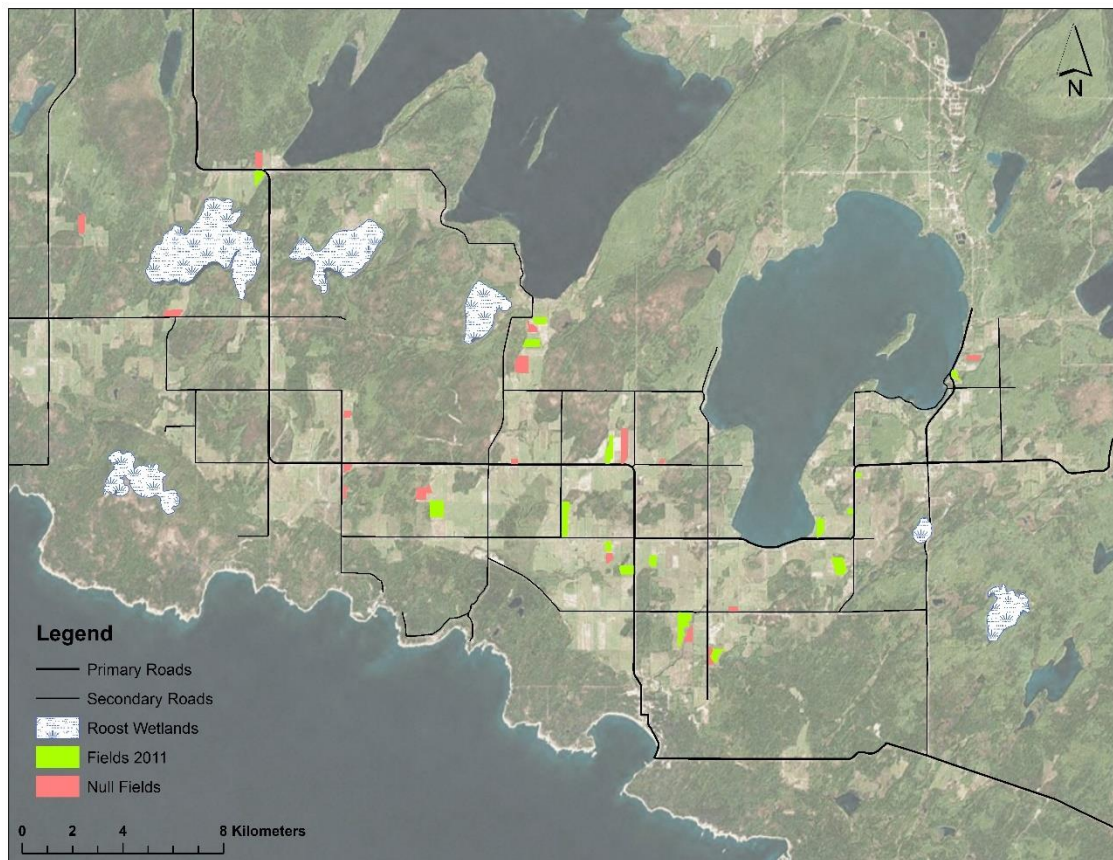
Figure 2.1 Focal (Fields 2011; green) and null grain fields (Null Fields; coral) at Manitoulin Island, Ontario, Canada used to study agricultural waste grain density and distribution effects on Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) behavioural ecology during autumn staging in 2011 and 2012.
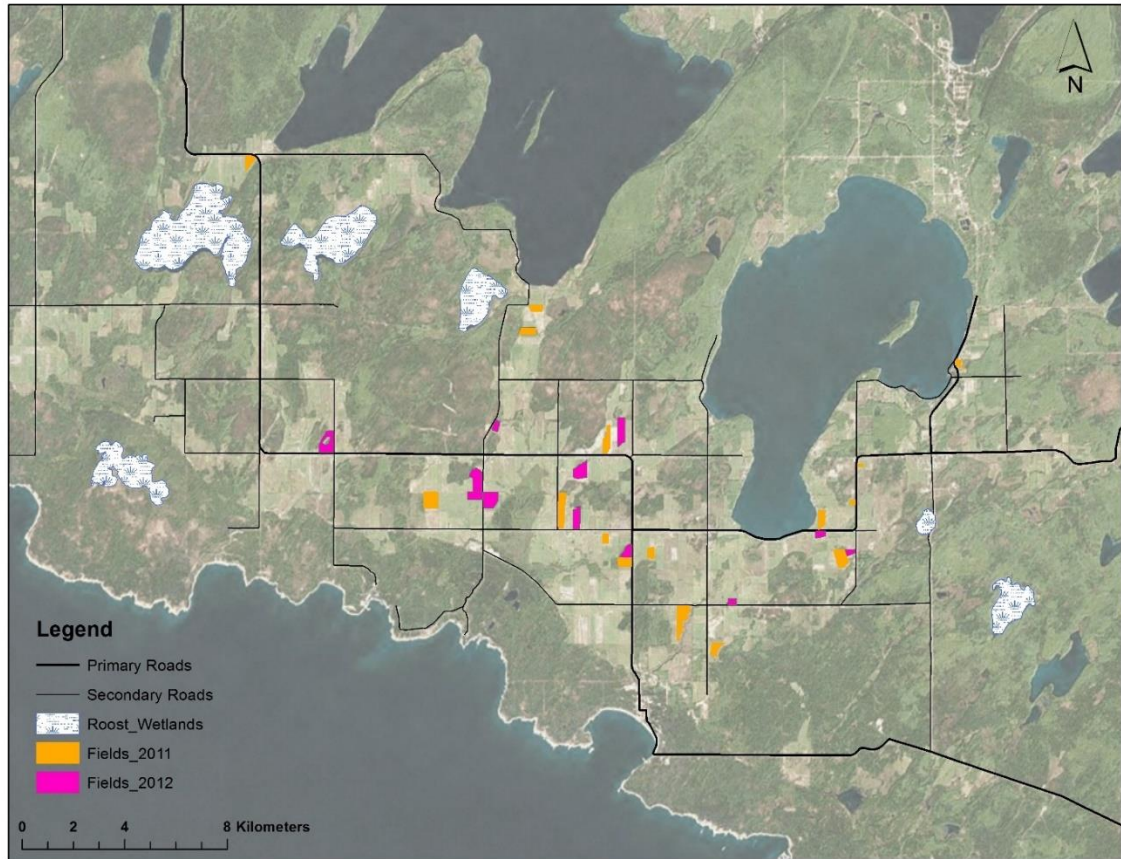
Figure 2.2 "Observational" focal grain fields at Manitoulin Island, Ontario, Canada used to study agricultural waste grain density and distribution effects on Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) behavioural ecology during autumn staging in 2011 and 2012.

I established sampling points ($n = 20$) in each harvested focal field as soon after harvesting as possible in August 2011 and 2012 using a systematic approach to estimate waste grain density and distribution. Before the 2011 sampling period, I estimated the necessary number of sampling points per field using pilot data collected from non-focal ("null") fields. I randomly selected three non-focal fields planted in barley, and sampled grain density therein by collecting 50 samples per field (see Page 39 below for grain sample collection methodology). I weighed the resulting samples to estimate density and distribution at and between each sampling point within fields. I assumed that grain density and distribution in pilot fields were representative of fields in my study area.

I ran simulations with the resulting data to determine the sample size at which the coefficient of variation (CV; sample standard deviation divided by the sample mean) decreased by 1% or less per addition of a sample. I automated the process so that 100 random subsets of a given sample size were analyzed during each run. I calculated a mean CV from the simulated subsets for each sample size in each field. I used this simulation process to control for disproportionate effects on CV estimation that could have been introduced by anomalously large or small samples being included in a given sample size subset. I also plotted the simulated data to visually inspect for an asymptote in the relationship between CV and sample size (Figure 2.3). I determined that the 1% stability threshold was reached at $n = 13$, 16, and 11 in my pilot data so I increased the sample size to $n = 20$ to ensure accurate representation of natural variation in grain density. I assumed that most of the variation present in data collected with this level of sampling effort would be a reasonable approximation of actual variation in grain density instead of an artifact of variation resulting from my sampling design.
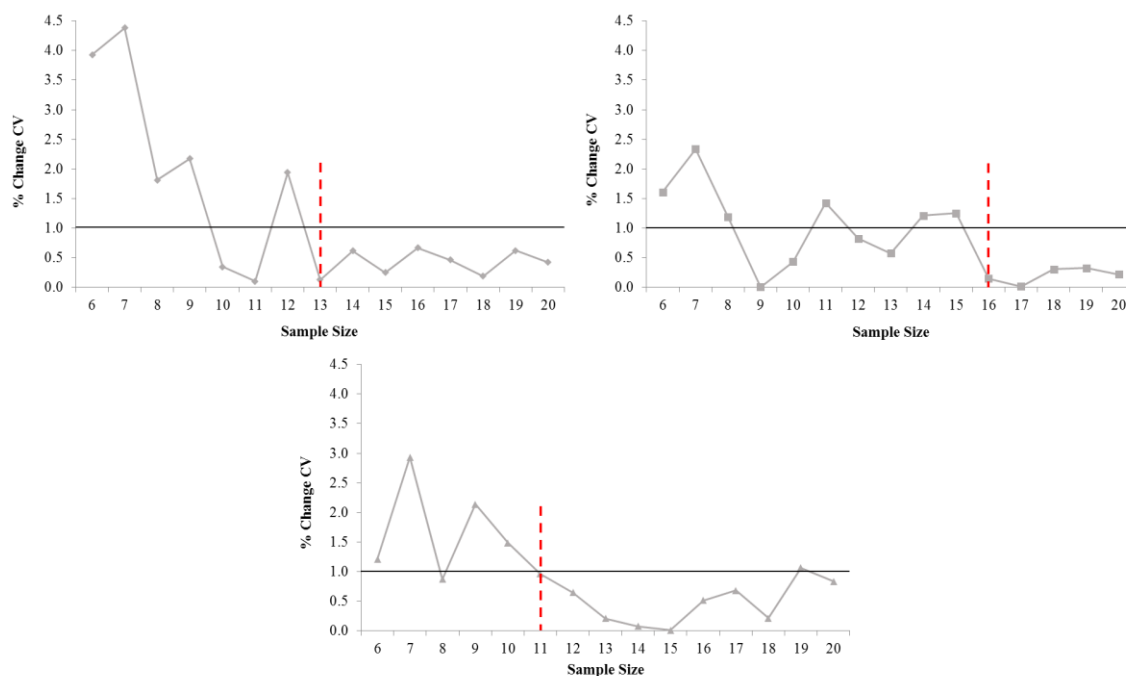
Figure 2.3 Performance curves from coefficient of variation (CV) simulations using waste agricultural grain samples. Data points represent mean values from 100 simulations per sample size. Horizontal solid black line indicates 1% threshold. Vertical dashed red line indicates sample size where % Change CV <1. Data were collected in pilot harvested barley fields at Manitoulin Island, Ontario, Canada August 2011. Plots depict Fields 1, 2, and 3 (clockwise from top left).

I distributed equidistant sampling points parallel to the longest axis of each field in four or five rows, depending on field shape and dimensions (Figure 2.4). I georeferenced each sampling point (UTM coordinate system) with handheld Garmin GPS units (Garmin International, Inc., Olathe, KS, USA; accuracy = <5 m) for relocation in subsequent grain sampling rotations. I made improvised sampling frames of known area (area = 0.096 m^2) by removing the bottom of generic, plastic grain buckets (radius = 17.5 cm). These improvised sampling frames worked well in this application because they were 1) structurally robust (little variation in sampling area between sampling points), 2) lightweight, and 3) inexpensive to produce (Figure 2.5). I placed the sampling frames on the field substrate and handpicked all grain found inside.
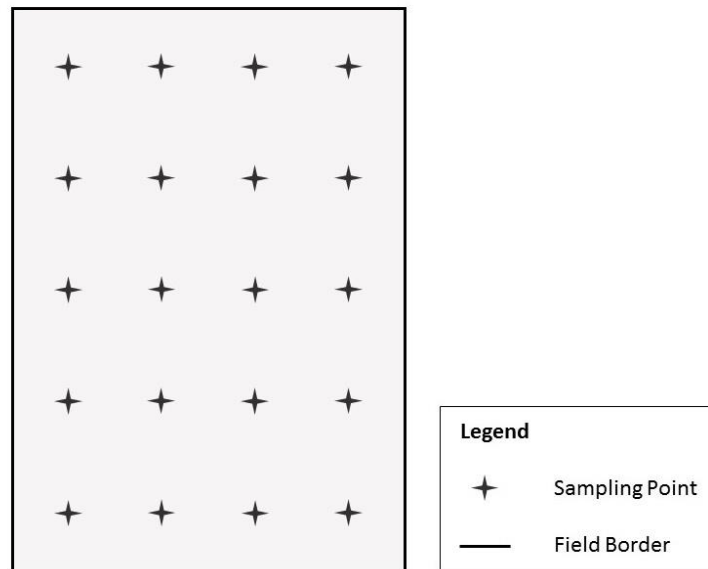
Figure 2.4 Depiction of typical systematic sampling point distribution used to collect waste grain samples in harvested agricultural fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012 as part of a study of Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) foraging ecology. Sampling points were distributed systematically due to a lack of knowledge of variation in waste grain distribution within and amongst focal fields at my study area and to ensure samples were collected at a scale that was ecologically relevant to cranes.

Figure 2.5 Improvised plastic sampling frame, GPS unit, resealable grain sample bags, and sample point data sheet in use during field work. Sampling frames were built by removing the bottom of generic, plastic grain buckets and were used for collecting waste agricultural grain from known area units in harvested agricultural fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

I visited harvested (cut herein) fields at an approximately 10-day sampling rotation. This sampling rotation resulted in a maximum of five and four visits to each field in 2011 and 2012, respectively. Certain fields were visited less than the maximum because they were not harvested when sampling commenced (e.g., 2011-O19 was not cut until 11 October 2011). At subsequent sampling visits, I moved all sampling points five metres in the same random cardinal direction to prevent anomalous results from sampling previously sampled locations (Figure 2.6). In 2011, I tested a gas-powered vacuum sampling device designed for sampling moist-soil seeds as per Penny *et al*. (2006). The vacuum sampling device did not perform as well as hand-picking barley grain (Hanna *et al*. 2015) so it was not used for this study. I observed and recorded dates that focal fields were cut each year. For fields cut before observation, I consulted landowners for approximate harvest dates. If landowner information was not available, I estimated approximate harvest date using harvest dates from nearby fields. I converted the cut date to Julian date and calculated the number of days since cut (DSC) for each sampling rotation for each field.

I stored grain samples in labelled resealable plastic bags in the field and transported the bags back to the field office for freezing. I stored all samples frozen at -10° C until they were returned to the lab for analysis (see Section 2.3.3 below).
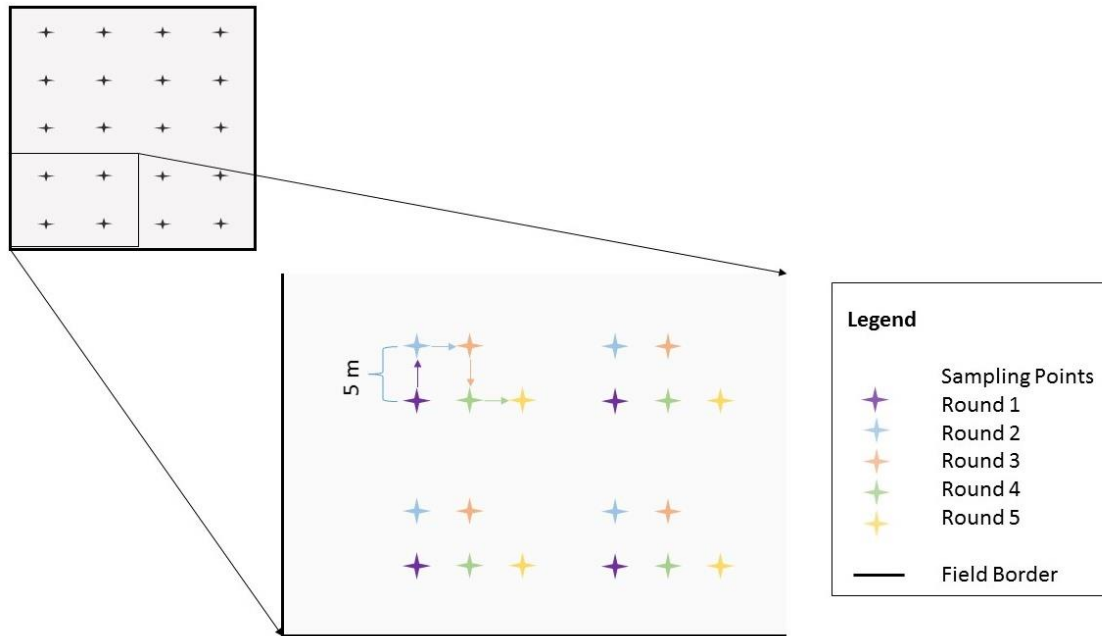
Figure 2.6 Depiction of typical sampling point rotation used to collect waste grain samples in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012 as part of a study of Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) foraging ecology. Sampling points were relocated between visits to avoid resampling previously sampled locations.

2.2.3 Laboratory Procedures

In the lab, I thawed grain samples and separated individual grains from chaff (i.e., husks and stems). Following sorting, I measured and recorded initial mass for each sample (i.e., wet mass) to the nearest 0.001 gram using an electronic mass balance (AMF2002, Fisher Scientific, Waltham, MA, USA). I placed grain samples into individual aluminum trays per year, sampling rotation, and sampling point. I placed all trays from each visit ($n = 20$ per visit) on individual aluminum baking sheets and placed them in drying ovens (Hobart Food Equipment Group Canada, Toronto, ON, Canada) set to 65º C. I removed samples every 12 hours and recorded mass. When a change of less than 1% from the most recent mass was detected (typically 48 hours), I considered samples to be dry. I recorded dry mass for each aluminum tray for subsequent use in grain density and distribution estimation (see Section 2.3.6.2 below). Because ambient moisture conditions varied between sampling point, sampling rotation, field, and year, I did not attempt to use a predictive wet-to-dry mass equation (e.g., Yang *et al*. 2015); therefore, I dried and weighed all samples collected in 2011 and 2012 ($n = 121$ sampling visits or 2,420 individual samples). I estimated grain density by calculating the average mass of grain per field in each sampling rotation using the aggregate of all 20 sampling frames divided by the total area sampled. I also calculated the mean CV per field per sampling rotation in the same manner. These calculations resulted in an estimated mean density (kg/ha) and mean CV for each field and sampling rotation ($n = 121$ total).

2.2.4   Field Use Observations

I established road-based transects (55.7 km and 36.8 km in 2011 and 2012,

respectively) to quantify numerical response to grain density and distribution in cranes

(Figures 2.7 and 2.8). I used the number of cranes occupying a field during each survey

as an estimate of numerical response (*sensu* Hagy & Kaminski 2012). I designed

transects to allow for use of unobstructed sightlines from relatively close vantage points.

I paid special attention to ensure viewing points did not cause disturbance to cranes while

I made and recorded observations because of the potential to bias data collected in

subsequent focal fields along the transect (e.g., double-counting cranes that were scared

to other fields by field observation activities).

I generated a survey schedule with randomized start points (east or west end) and start

times (morning or afternoon/evening) for use during August - October 2011 and 2012. I

ran morning (AM) transects between one hour after sunrise and 1100 hr to ensure cranes

had left roost wetland sites and settled at feeding locations and afternoon/evening (PM)

transects between 1300 hr and one hour before sunset to ensure cranes had not departed

for roost wetlands prior to being counted at feeding locations.

I made observations from vehicles on road beds using spotting scopes (Spacemaster

15-45× – 60 mm, Bushnell Outdoor Products, Overland Park, KS, USA) and binoculars

(Viper 10× 42 mm, Vortex Optics, Middleton, WI, USA). I counted all cranes in each

focal field and assigned each to either the AHY or HY age class according to head

plumage characteristics (Nesbitt & Schwikert 1998; Figure 2.11). I first attempted to

distinguish between parental and non-parental AHY cranes in the field in 2011 to

appropriately quantify HY constraints on family group field use. However, these efforts

were largely unsuccessful because of the number of cranes in some fields (e.g., >500), the

often relatively broad spatial distribution of cranes in feeding fields, and the species'

general propensity to travel relatively long distances in fields while foraging. Therefore,

I instead counted the number of HY cranes in each field and used that number as an index

of family group behaviour (i.e., HY cranes are distinguishable from AHY cranes and

their abundance is representative of family group behaviour). That is, if the disparate

behavioural and physiological challenges faced by HY cranes affected crane behaviour, I

expected to detect a difference in numerical response by comparing a composite AHY

(i.e., parental and non-parental) and HY (family group) sample. Thus, herein AHY and

HY notations are used to represent composite adult and family group behaviour,

respectively. Consequently, I summarized observations by age category in each focal

field in each year.
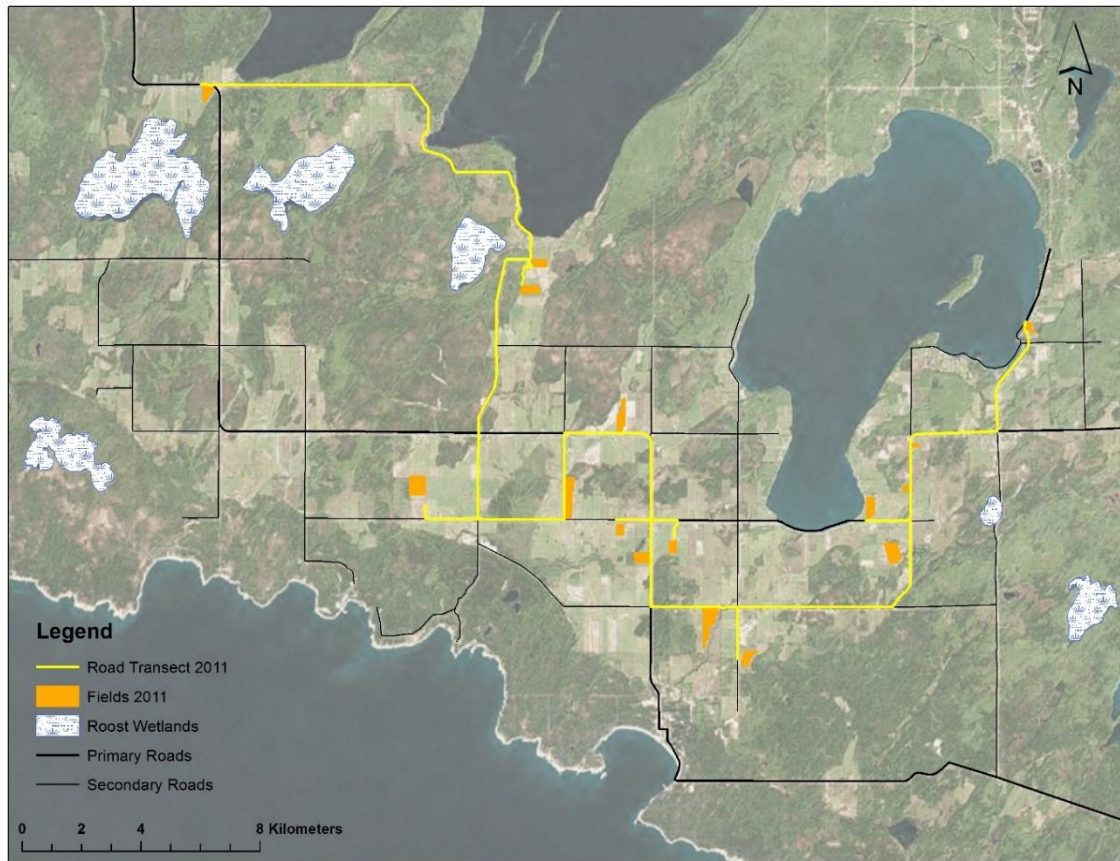
Figure 2.7 Road transect used to estimate use of harvested agricultural grain fields by adult

(AHY) and juvenile (HY; index of family groups) Eastern Population Greater Sandhill Cranes

(*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011.
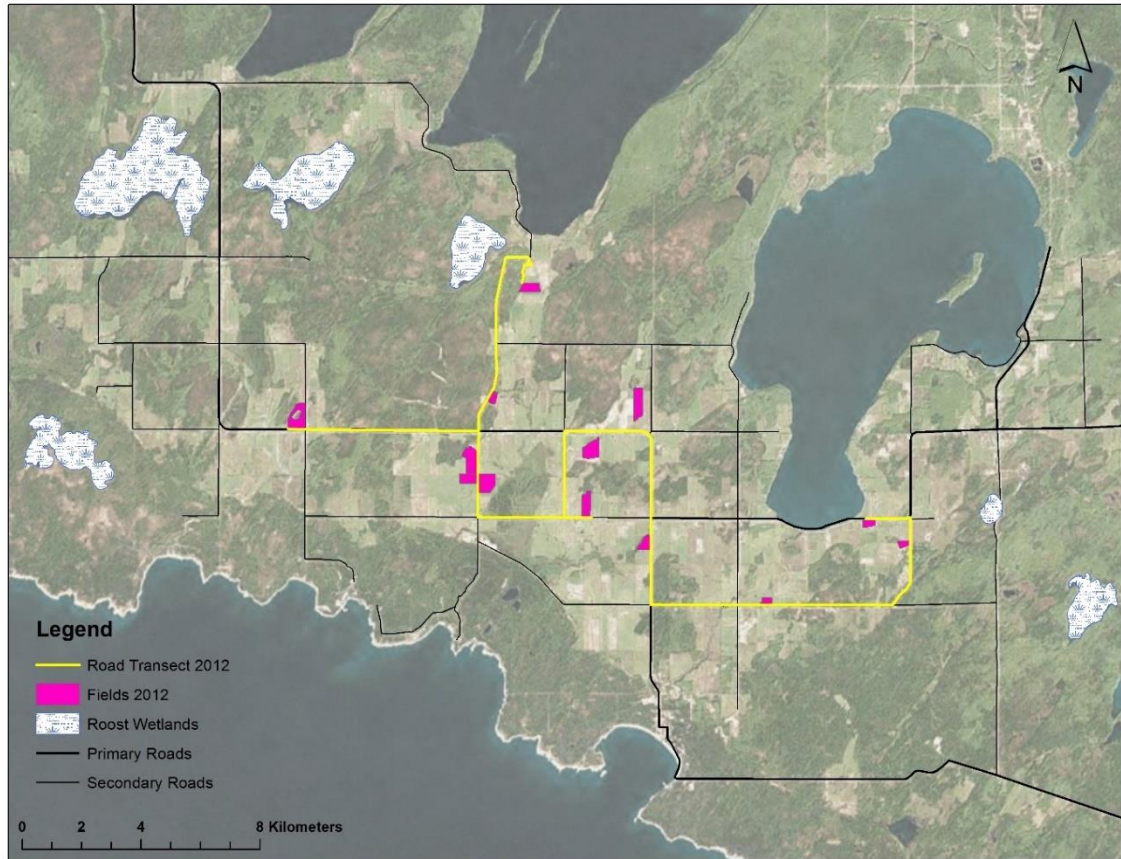
Figure 2.8 Road transect used to estimate use of harvested agricultural grain fields by adult

(AHY) and juvenile (HY; index of family groups) Eastern Population Greater Sandhill Cranes

(*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2012.

2.2.5   Crane Capture & GPS Deployment

During July and August 2010, I captured cranes to deploy GPS transmitters ($n = 9$), primarily as part of a larger study of EP migratory chronology (Hanna *et al*. 2014, Fronczak *et al*. 2015, Fronczak *et al*., In press). However, the resulting data were also used to inform my data collection methodology, calculate FFDs, and validate the foraging ecology models developed in this study (see Section 2.3.6.3 below).

In June 2010, I used road-based observations to identify potential trap sites as areas with greater concentrations of cranes. I established trap sites at locations where I was granted landowner permission and where vehicle access (necessary for transporting trapping and banding equipment and supplies) was possible. I identified ideal locations for rocket net placement as those locations with 1) minimal slope, 2) low vegetative cover, 3) nearby cover for concealment, and 4) no livestock present. Sloped terrain can increase or decrease the relative trajectory of nets thereby creating dangerous conditions that could cause harm to cranes and potentially reduce capture efficiency. Low vegetative cover allows nets to be deployed with minimal physical impediment, improving capture efficiency; however, camouflaging nets where vegetation is sparse can be more difficult. Ensuring nets are completely camouflaged with native site substrate is critical as cranes appear to be sensitive to and avoid visually obtrusive objects (personal obs.). Nearby cover is necessary for researchers to use for hiding while watching baited sites in wait for cranes. Typically cover was located within 100 - 200 m of baited sites to allow for accurate determination of crane locations relative to the net with spotting scopes and binoculars.

Livestock are attracted to grain piles intended to bait cranes at trap sites. Domestic cattle (*Bos taurus*) can trample nets, consume bait, and generally disrupt trapping activities. Thus, while most trap sites were in grazed pasture fields, they were only placed at sites without cattle.

Once appropriate baiting and capture sites were identified, I piled bait (barley and whole kernel corn, *Zea mays* Linnaeus) to attract cranes to the sites. Typically, cranes took several days to locate bait piles, though some sites were discovered more quickly than others. I allowed cranes at least three days of consistent, undisrupted feeding at bait sites prior to attempting capture.

Where cranes became accustomed to feeding at bait piles, I accessed trapping sites at night so as not to disturb the cranes using the area. I used a 35 × 50 ft. net and made certain the net was carefully folded back onto itself to prevent tangling during deployment (Figure 2.9). I ran a length of electrical wire from the blind to the net location to serve as a connection between the rockets and the power (trigger). I used a MotoMaster Nautilus marine grade battery pack with an 800-cold cranking Amp rating (Canadian Tire Corporation, Ltd., Toronto, ON, Canada) as a manual trigger for the rockets. I placed the trigger in the blind in the field so that I could simultaneously watch the set and deploy the net. I tested wiring for continuity using a Mastercraft digital five-function multimeter (Canadian Tire Corporation, Ltd., Toronto, ON, Canada). I setup the electrical trigger system (wiring) as a series circuit. I used a series circuit to prevent deployment of the net where less than all three rockets would fire at the same time. If there was a short in the circuit, none of the rockets would fire. In a parallel circuit, individual rockets could fire even if others did not.

Once the circuit was established and tested, I attached three rockets to the front line of the net and 10 lb. metal drag plates to the back line of the net with metal chains. The metal drag plates ensured that the rear end of the net stayed on the ground to envelope any cranes in the throw with the net. I placed the rockets on metal guides dug into the ground to control angle of launch. I fine-tuned rocket guide angle using a Rieker 2058 mechanical inclinometer (Rieker Inc., Aston, PA, USA). I placed rocket guides in holes dug below the soil surface to minimize the chance of visual detection by cranes.

Once I placed the rockets (without propellant) and attached them to the net, I covered the entire setup with vegetation from the trap site. I used broken-off branches from nearby trees and shrubs to mark the borders of the approximate throw of the net (Figure 2.10). Marking the borders of the throw was critical to allow for accurate determination of crane locations relative to the net from a distance using spotting scopes and binoculars. Deployment when cranes are too far from the net or laterally outside the throw reduces capture efficiency. Deployment when cranes are too close, standing on, or standing with extended necks near the net can result in injuries or mortalities.

As a final step, I filled rockets with propellant and squib charges (miniature explosive device used to ignite propellant) to minimize safety concerns related to accidental deployment while making the set. I ensured the electrical trigger wire was not attached to the battery pack and, as an additional precaution, that the power was off before wiring the propellant into the circuit.

Figure 2.9 Folded rocket net during setup (top) and extended rocket net after deployment

(bottom). Rocket net measures 35 × 50 ft. and was used to capture Eastern Population Greater

Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in July and
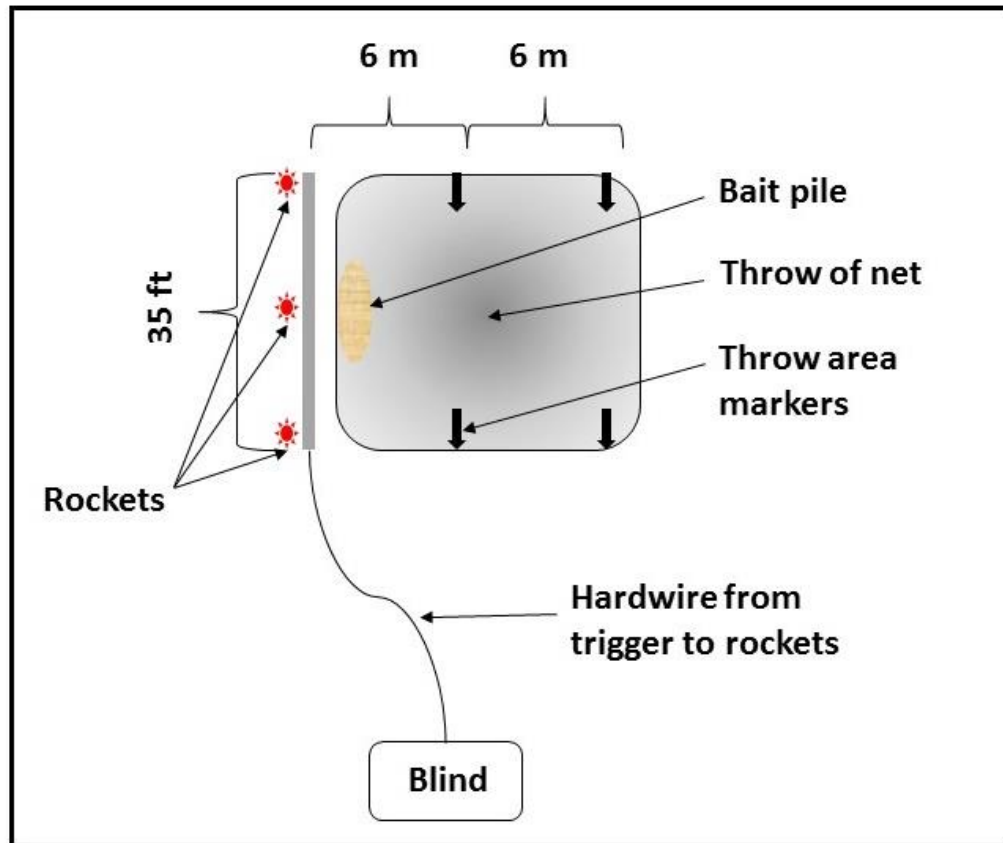
August 2010.

Figure 2.10 Depiction of rocket net setup used for capturing Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in July and August 2010. Nets were folded back in a narrow row and covered with vegetation from the surrounding area for camouflage.

Accompanied by field technicians, I entered blinds before sunrise and waited (repeated over several days in many cases) for cranes to feed on the bait. We watched cranes with spotting scopes and binoculars using the branches along the throw of the net to determine ideal timing for deployment.

Following deployment, we attended to the captured birds as quickly as possible to minimize the potential for cranes to inflict self-injuries. We immediately used the net to physically immobilize captured cranes (Figure 2.11). We quickly counted the number of cranes captured and determined the number to retain for processing by keeping a maximum of two cranes per technician present to assist with handling. We made note of age and immediately released any surplus individuals following the aforementioned equation starting with those cranes that appeared particularly stressed from capture and handling. We loosely secured each crane's beak in the closed position using a strip of black electrical tape placed anterior to the nares. We placed those individuals to be retained for measurement and banding in canvas bags to reduce visual stimuli and for physical restraint.

We collected the following standard morphometric measurements from all cranes prior to banding: 1) weight, 2) post-nares culmen length, 3) wing chord, and 4) tarsus (tarsometatarsus) length (Figure 2.11). We classified each crane as either AHY or HY according to head plumage characteristics (Nesbitt & Schwikert 1998; Figure 2.11). If we observed socialization prior to capture, coupled with physical stature, we estimated and assigned sex for AHY cranes whereas we classified all HY cranes as unknown sex.

Figure 2.11 Removing a captured Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) from a rocket net (top left), measuring post-nares culmen length on captured crane (top right), and distinctive head plumage (papulose red skin) of an AHY crane (bottom).

Although cranes are socially monogamous and share parental care, females lay and incubate eggs and are philopatric to breeding sites (Walkinshaw 1949, Fronczak *et al*. 2015) and their behavioural data are more useful to managers. Thus, I attempted to place GPS platform transmitter terminal (PTT) tracking units only on AHY females. Furthermore, where the social status of captured cranes was not known, I only deployed one GPS unit per capture event to minimize the potential for collecting redundant and non-independent data (e.g., by marking both members of a mated pair).

GPS transmitters were manufactured by North Star Science and Technology, LLC (King George, VA, USA) and programmed and powered by GeoTrak technology (Apex, NC, USA). Transmitters were solar-powered by three separate solar panels. Because I required transmitters for deployment in a vertical orientation and underneath the body on the leg (proximal to the intertarsal joint) and solar-powered units require solar radiation, I had the transmitters customized for crane application by adding two additional solar panels to the sides of the unit and increasing the length of the whip antenna.

I had customized three-inch black polyvinyl chloride (PVC) bands manufactured for transmitter mounting. Unique alphanumeric codes (0K through 9K) were engraved in white on the exterior of the PVC bands (Haggie Engraving, Crumpton, MD, USA), opposite to the side where transmitters were mounted (Figure 2.12). White engraving on a black background was used to increase readability in the field, allowing for encounter data without recapture. I lined the inside of the PVC bands with neoprene to improve comfort and prevent chaffing. I affixed each transmitter using a 3/16" hand rivet tool (Fastenal, Winona, MN, USA) by inserting and securing rivets through pre-drilled holes at all four corners of the seam. I lined the seam with Plumber's Amazing GOOP

(Eclectic Products, Eugene, OR, USA) before connecting the two halves of the PVC band to increase the security of the connection.

Finally, I reinforced the connection between the whip antenna and the transmitter by applying a thick coat of steel reinforced Cold-Weld epoxy (J-B Weld, Sulphur Springs, TX, USA). I also banded all captured cranes with standard Size 9 United States Fish and Wildlife Service (USFWS) aluminum lock-on bands. Where an individual received a GPS transmitter band, I placed the aluminum band above the tarsometatarsus joint on the opposite leg.

Transmitters weighed approximately 85 grams which represented 1.6 - 2.5% of live body weight amongst the individuals I captured. Thus, transmitter weight was within the less than 5% of body weight limit on markers for flying birds (Fair *et al*. 2010). Transmitters were programmed to attempt to acquire GPS locations every six hours and last one to three years. Tracking data were relayed via the Argos Satellite System every 60-84 hours. I accessed, downloaded, and archived tracking data through the CLS website at least once every ten days. I used an in-house software application produced by North Star Science and Technology, LLC to parse transmitted data into interpretable formats. All capture and banding activities were sanctioned under Western University Animal Use Protocol #2010-213 (Appendix I) and Canadian Wildlife Service Scientific Permit to Capture and Band Migratory Birds #10787 D (with rocket net authorization; Appendix II).

Figure 2.12 Leg band-mounted GPS PTT deployed on an Eastern Population Greater Sandhill

Crane (*Antigone canadensis tabida*) captured using a rocket net at Manitoulin Island, Ontario,

Canada in July 2010.

2.2.6   Data Handling & Analysis

2.2.6.1   Spatial Analysis

I digitized spatial features of interest using ArcGIS 10.4 (V10.4.0.5524, ESRI 2015). I calculated area (m^2; "Area") and perimeter (m; "Perimeter") for all focal fields. I digitized satellite imagery (Landsat 2008 imagery) of the six primary roost wetlands in my study area and calculated the straight-line distance from each field to the nearest roost wetland (m; "Prox_Roost") using Near Analysis from the Geoprocessing toolbox.

I established two spatial buffers around each focal field to represent potential foraging scales of cranes (≤1 km and ≤5 km) based on estimated FFD at my study site and previously described commuting flight distances from other studies (Ivey *et al*. 2015). Within years, I determined which fields were within each of the spatial buffers (polygon edge to polygon edge) using Buffer analysis from the Geoprocessing toolbox (Figure 2.13). If fields were included in the ≤1 km category, I also included them in the ≤5 km category. I included the focal field grain density (kg/ha) in calculations for both foraging scales. I estimated total grain density at each spatial scale by summing density values amongst all fields within the respective buffers to produce a unique local grain density value for each field ("X1_km_Dens" and "X5_km_Dens"). I also estimated relative grain density for each field at both spatial scales ("X1_km_Rel_Dens" and "X5_km_Rel_Dens") by dividing the estimated within-field density by the total grain density for that spatial scale (proportional variable). Relative grain density at both spatial scales was conceptualized to represent the relative attractiveness of a field at a given spatial scale. Grain density values (except relative values) were estimated as described in Section 2.2.6.2.
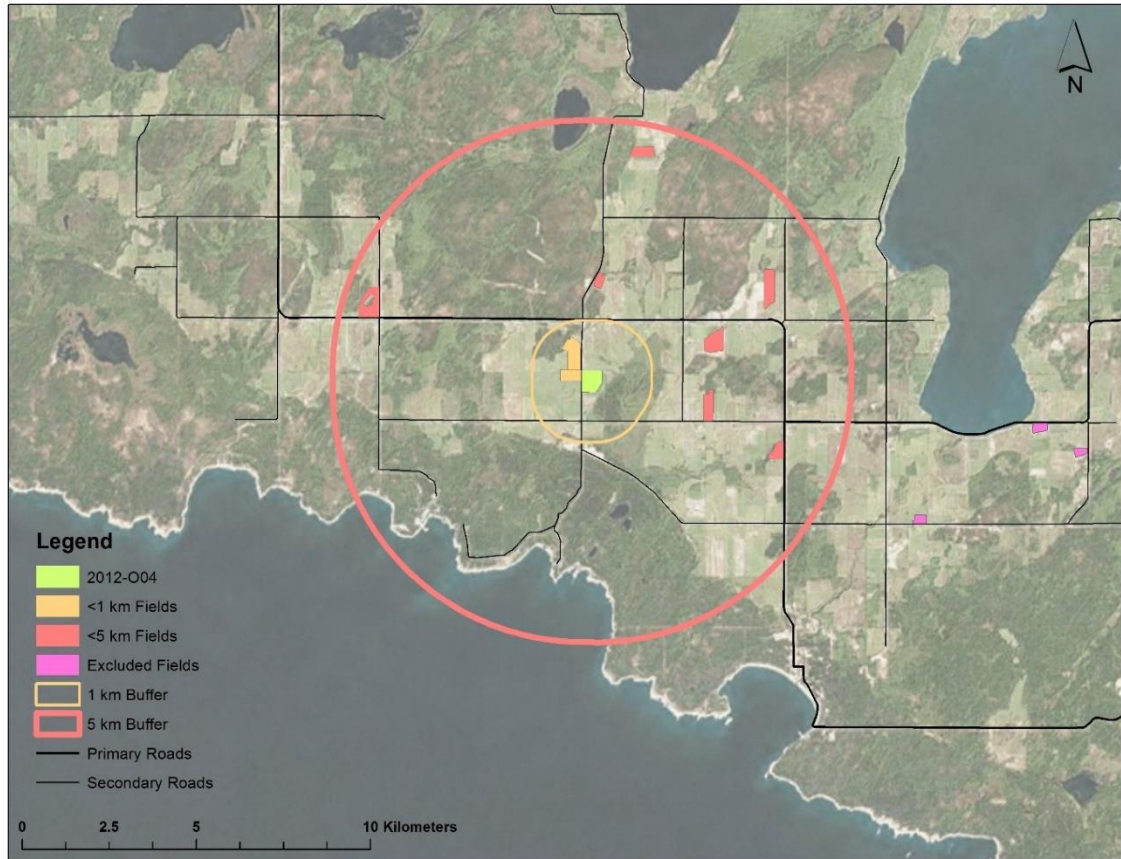
Figure 2.13 Subsets of fields at two spatial scales used to analyze foraging scale effects on field use in adult (AHY) and juvenile (HY; index of family groups) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

2.2.6.2   Estimating Grain Density & Variation

Because most of my behavioural observations were collected on days in which I did

not collect grain density samples, I needed to estimate field-specific daily values. I

estimated field-specific daily values for grain density and distribution (CV) using linear

mixed-effects (LME) models with maximum likelihood estimation in the *lme4* package

(function: *lme*; Bates *et al*. 2015) in R Studio (V3.3.0, R Core Team 2016). I compared

four models (Table 2.1) to estimate daily grain density values, each with log-transformed

grain density ("Log_Density") as the continuous response variable and year-specific field

identifier as a random effect ("1|fField"). These models differed in the use of Julian date

("Julian") versus days since cut ("DSC") as predictors and in whether they included a

random intercept or random intercept plus slope (Table 2.1). Following an information-

theoretic approach (Burnham & Anderson 2002), I compared AIC values to select the

most parsimonious predictive model, which I used to predict daily grain density values

for each field in each year. I used first-order AIC because my sample size was

sufficiently large compared to the number of parameters in my models.

I repeated the same modelling process using my CV data (Table 2.2). I estimated

daily values for both grain density and CV with the top model (i.e., lowest AIC value)

from each candidate set (function: *predict*) for use as predictor variables in subsequent

modelling.

Table 2.1 Candidate linear mixed-effects models using days since cut (DSC) and Julian date (Julian) as predictors with random intercept and random slope and intercept terms. The most parsimonious model (lowest AIC value) was used to predict daily grain density (continuous response) values for subsequent modelling of numerical response data. Model names (Model) and structures (Structure) are shown.

Model	Structure
lmeDSCRI	Log_Density ~ DSC, random: fField_ID
lmeJDRI	Log_Density ~ Julian, random: fField_ID
lmeDSCRIS	Log_Density ~ DSC, random: DSC | fField_ID
lmeJDRIS	Log_Density ~ Julian, random: Julian | fField_ID

Table 2.2 Candidate linear mixed-effects models using days since cut (DSC) and Julian date (Julian) as predictors with random intercept and random slope and intercept terms. The most parsimonious model (lowest AIC value) was used to predict daily grain distribution (coefficient of variation; CV; continuous response) values for subsequent modelling of numerical response data. Model names (Model) and structures (Structure) are shown.

Model	Structure
CVlmeDSCRI	CV ~ DSC, random: fField_ID
CVlmeJDRI	CV ~ Julian, random: fField_ID
CVlmeDSCRIS	CV ~ DSC, random: DSC | fField_ID
CVlmeJDRIS	CV ~ Julian, random: Julian | fField_ID

2.2.6.3   Foraging Flight Distance

I used GPS tracking data collected from marked cranes in 2011 and 2012 (n = 8 and 5 cranes, respectively) to estimate mean FFD at my study site. I only included GPS locations ("fixes") that were collected during September and October, to temporally align with my grain sampling and behavioural observations. I also only included fixes that were acquired via GPS technology because GPS fixes are more accurate than those estimated via Doppler technology (~ 20 m and ~ 250 m maximum accuracy, respectively). If a feeding GPS fix was not acquired in the morning on a given day, I did not use afternoon feeding location fixes because they likely did not represent the true roost-to-field FFD (i.e., where cranes travel from roost to feeding sites in the morning) I was attempting to quantify.

To isolate fixes before and after roost-to-field foraging flights, I built a template using a hierarchical series of logical tests in Microsoft Excel (2016) to identify changes in latitude and longitude greater than 0.001 degrees between consecutive fixes when arranged by 1) PTT ID and 2) date of acquisition. I visually inspected candidate foraging flight fixes before calculating distances. I used the following equation to calculate distance between roost and field fixes (km) for pairs of fixes that I determined were true roost-to-field foraging flights:

$$
\begin{aligned}
\boldsymbol{Distance} = (6371 * ACOS(COS(RADIANS(90 - Lat1)) \\
* COS(RADIANS(90 - Lat2)) + SIN(RADIANS(90 - Lat1)) \\
* SIN(RADIANS(90 - Lat2)) * COS(RADIANS(Long1 - Long2)))
\end{aligned}
$$

where ACOS is a function that calculates the arccosine, COS is a function that calculates the cosine, RADIANS is a function that converts degrees to radians, SIN is a function that calculates the sine, Lat1 and Lat2 are the roost and field fix latitudes, respectively, and Long1 and Long2 are the roost and field fix longitudes, respectively.

2.2.6.4 Numerical Response Analysis

Using grain density and CV values estimated from the modelling procedures described above as continuous predictors, and numerical response as a count response variable, I built negative binomial generalized linear mixed-effects models (GLMM) in the *lme4* package (function: *glmer.nb*; Bates *et al*. 2015) in R Studio (V3.3.0, R Core Team 2016) to analyze the age-specific numerical response and foraging scale of cranes as they relate to grain density and distribution (see Table 2.3 for a description of predictor variables). I first attempted to run Poisson GLMMs but found that negative binomial GLMMs were a better fit to my actual data. I used a GLMM approach with maximum likelihood (Laplace approximation) to fit models. I followed identical modelling procedures to analyze adult (AHY) and juvenile (HY) observational data separately, using each as a count response variable representing age-specific crane abundance. I inspected data for outliers using scatterplots and boxplots prior to building models. I used log transformations to improve predictor variable distributions where outliers were suspected (see Section 2.3.3 for treatment of outliers). I compared a candidate set of ten models each for each of the AHY and HY response variables (Table 2.4) and compared AIC values to select the most parsimonious models. I used first-order AIC because my sample size was sufficiently large compared to the number of parameters in my models. I

calculated Akaike differences (ΔAIC) and normalized their values to sum to 1.0 to assess

the relative support for each of my candidate models. I selected the model with the

lowest AIC value as the best from the candidate set.

Because overparameterization in GLMMs can cause convergence issues during

parameter estimation, I attempted to develop models with a minimal number of predictor

variables (other than the fully saturated model) and, where necessary, increased the

number of iterations to 100,000 (default = 10,000 in *glmer.nb*). If convergence warnings

were returned and increasing iterations did not resolve the issue, I calculated and

compared gradient and Hessian equivalent values for models that initially produced

convergence warnings. As suggested by designers of the *lme4* package (Bates *et al*.

2015), if the calculated value was <0.001, I retained the model, whereas I did not proceed

with interpreting results from models exceeding the <0.001 tolerance threshold.

I also analyzed the numerical response data using two different approaches to

compare with the results from the approach outlined above. First, I combined AHY and

HY observations into one numerical response variable and reran the models as specified

above. Second, I analyzed AHY and HY observations concurrently by including a

categorical "Age" variable (with two levels), also using the models as specified above.

Neither of these alternate approaches generated results that were substantially different

from those produced by my initial approach described above (i.e., identical model

structures and comparable effect sizes), so I present and interpret results only from the

initial approach following.

Table 2.3 Predictor variables used to analyze numerical response and foraging scale effects on field use in adult (AHY) and juvenile (HY; index of family groups) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) feeding in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

Variable Name	Description	Specific Use
Field_ID	Field name and observation year	Year/field combination unique identifier with 28 levels (random effect)
Stratum	Timing of survey	Fixed categorical predictor with two levels (AM or PM)
Area	Area of field (m^2)	Fixed continuous predictor; metric of field size effects
Perimeter	Perimeter of field (m)	Fixed continuous predictor; metric of field size effects
Prox_Roost	Edge-to-edge distance from field to nearest roost (m)	Fixed continuous predictor; metric of field location effects
Density	Daily within-field grain density (kg/ha)	Fixed continuous predictor; metric of numerical response
CV	Daily coefficient of variation from grain density estimates	Fixed continuous predictor; metric of numerical response
X1_km_Dens	Sum of grain density at 1-km spatial scale (kg/ha)	Fixed continuous predictor; metric of foraging scale
X5_km_Dens	Sum of grain density at 5-km spatial scale (kg/ha)	Fixed continuous predictor; metric of foraging scale
X1_km_Rel_Dens	Within-field density divided by sum at 1-km spatial scale (kg/ha)	Fixed continuous predictor; metric of foraging scale
X5_km_Rel_Dens	Within-field density divided by sum at 5-km spatial scale (kg/ha)	Fixed continuous predictor; metric of foraging scale

I developed an *a priori* candidate set of models (Table 2.4) based on existing knowledge of the species' foraging behaviour during autumn staging at my study site. I built this candidate set using the following approach.

I included the field area (Area) and proximity to roost (Prox_Roost) terms in all candidate models because I wanted to evaluate the relative importance of these variables in determining numerical response and had no reason to believe they would not improve explanatory power. I included field area to control for the fact that A) larger fields are likely to attract greater numbers of cranes, B) it is reasonable to expect a positive linear relationship between field area and total amount of food available (not food density), and C) cranes may prefer larger fields to minimize perceived predation risk (*sensu* Chudzińska *et al*. 2015). I included survey stratum (fStratum) as a fixed categorical variable in all models to control for temporal differences in behaviour between morning and evening surveys. I also included field identifier (fField_ID) as a random variable in all models to preserve field-level effects.

I created Modnull and Modfull for comparison as per standard information-theoretic model selection procedure (Burnham & Anderson 2002) while observing the limitations of GLMM analysis. I included all additive (random and fixed) effects in Modfull. I built Mod1 to account for the singular effects of grain density (Log_Density) on numerical response at the within-field scale. If within field giving-up densities (GUD) were important in determining crane field use (numerical response), I expected within-field grain density to contribute substantially to the best model, and for the associated within-field grain density parameter estimate to serve as an estimate of the GUD effect on numerical response. I added grain distribution (CV) to Mod2 to allow for effects of both

grain density and distribution on numerical response at the within-field scale. In Mod3, I

included total grain density and relative within-field grain density at the 1-km scale

(X1_km_Dens and X1_km_Rel_Dens, respectively) to represent a 1-km foraging scale in

isolation of within-field grain density and distribution. In Mod4, I included total grain

density and relative within-field grain density at the 5-km scale (X5_km_Dens and

X5_km_Rel_Dens, respectively) to represent a 5-km foraging scale in isolation of within-

field grain density and distribution. In Mod5, I again considered the 1-km foraging scale

but also included within-field grain density and distribution. In Mod6, I considered the 5-

km foraging scale but also included within-field grain density. Finally, in Mod7 and

Mod8, I removed the within-field grain distribution effect as included in Mod5 and

included an interaction term between total grain density and relative within-field grain

density at the 1- and-5-km scale, respectively.

In aggregate, I developed these models to investigate the numerical response and

foraging scale of cranes during autumn staging at my study site.

Table 2.4 Candidate negative binomial generalized linear mixed-effects models used to analyze foraging scale and numerical response of Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) feeding in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Either adult (AHY) or juvenile (HY; index of family groups) was substituted for "Mod" in the respective modelling procedure. Variables written with an "L" (e.g., LArea) were log transformed. Variables written with an "f" (e.g., fStratum) were treated as factors. All models listed below also included field ID as a random effect.

Model	K	Structure
Modnull	1	1
Mod1	5	LArea + LProx_Roost + fStratum + Log_Density
Mod2	6	LArea + LProx_Roost + fStratum + Log_Density + LCV
Mod3	6	LArea + LProx_Roost + fStratum + X1_km_Dens + LX1_km_Rel_Dens
Mod4	6	LArea + LProx_Roost + fStratum + X5_km_Dens + LX5_km_Rel_Dens
Mod5	8	LArea + LProx_Roost + fStratum + Log_Density + LCV + X1_km_Dens + LX1_km_Rel_Dens
Mod6	7	LArea + LProx_Roost + fStratum + Log_Density + X5_km_Dens + LX5_km_Rel_Dens
Mod7	8	LArea + LProx_Roost + fStratum + Log_Density + X1_km_Dens*LX5_km_Rel_Dens
Mod8	8	LArea + LProx_Roost + fStratum + Log_Density + X5_km_Dens*LX1_km_Rel_Dens
Modfull	10	LArea + LProx_Roost + fStratum + Log_Density + LCV + X1_km_Dens + LX1_km_Rel_Dens + X5_km_Dens + LX5_km_Rel_Dens

I selected the model with the lowest AIC value for subsequent analysis and validation. I used a backwards single term deletion procedure (function: *drop1*) to determine if removing a predictor variable from the top model would improve model performance (i.e., reduce the AIC value). If model performance was improved by removing a predictor variable per single term deletions, I continued removing predictor variables and refitting the model until the AIC value could not be improved. Where I built an improved reduced model using the single term deletion procedure, I selected the model for further analysis and interpretation. I plotted standardized (Pearson) residuals against all fixed, continuous predictor variables (i.e., not included, dropped, and retained) to evaluate the performance of the retained model. If I did not find patterns in my residual plots, I proceeded with the model validation procedure described below. I also estimated and report variance for random effects as an additional model evaluation statistic.

To isolate the individual contribution of each retained fixed, continuous predictor variable, I simulated new datasets ($n = 100$) for each predictor variable and predicted new values for the response variable using my final GLMM. I set data points for the focal variable in each simulated dataset to equidistant values starting at the minimum value from my observations and extending to the maximum. I set data points for non-focal variables to the respective mean value from my observations. I excluded the random effect (Field_ID) from the prediction (function: *predict*; re.form=~0) and used two separate simulated datasets for each response variable to compare to my observations at each level of Stratum (i.e., AM and PM). I plotted predicted values against observed

values for both AHY and HY observations to graphically convey estimated predictor-specific effects.

The approach to model selection and reduction that I used is one of many distinct options for this type of analysis. An alternate approach to model selection would have involved comparing amongst a complete set of candidate models (i.e., all possible variable combinations). However, because I had relatively good knowledge of the system before analyzing my data, I could develop a set of hypotheses that translated into models and compare the performance thereof. It is noteworthy though that changing my data analysis approach may have led to different results.

2.2.6.5   Model Validation with GPS Data

I used numerical response data calculated via GPS tracking technology to validate my observational numerical response data with known individual crane field use. I only included fixes that were acquired via GPS technology as they are more accurate than locations estimated via Doppler technology (~ 20 m and ~ 250 m maximum accuracy, respectively). I omitted fixes from the same crane in the same field on the same day to avoid within bird/field/day combination pseudoreplication. I treated each GPS fix as an observation in a given field on a given day and calculated daily values (numerical response) for that observation following the approach described above for observational counts of cranes in fields. This procedure yielded observations with values for the same predictor variables used to model numerical response as described above.

I constructed kernel density plots for the predictor variables included in my final reduced models using both my GPS field use dataset and my observational dataset to qualify the accuracy of the data I used in the modelling procedures described above. I considered the GPS field use dataset independent and thus expected to find similar relationships between my response and predictor variables in both datasets if they were relatively accurate representations of crane foraging behaviour (i.e., unbiased estimates of crane numerical response).

2.3 Results

2.3.1 Grain Density & Variation Estimation

Grain density varied between fields, and generally decreased between subsequent visits to fields in the same year. In comparison, grain variation generally increased between subsequent visits to fields in the same year (Table 2.5).

Among the four LME models predicting grain density (Table 2.1), the model including the random intercept and slope, and DSC rather than Julian date, received most of the support (i.e., ^{W}AIC: ~1.0; Table 2.6). Thus, I used this model in estimating daily grain density values (Figure 2.14). According to this top model, grain density (log kg/ha) decreased by 0.05 ± 0.004 (mean $\pm$ SE) with each day since cut (Table 2.7).

Table 2.5 Grain density (kg/ha) and variation (CV) estimates from harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

Statistic	Density (kg/ha)	Variation (CV)
n	121	121
Mean	98.8	0.02
SD	147.6	0.03
Max	620.7	0.31
Min	0.1	0.01

SD = sample standard deviation.

Table 2.6 Candidate linear mixed-effects models using days since cut (DSC) and Julian date (Julian) as predictors with random intercept and random slope and intercept terms. Model names (Model) and structures (Structure), number of parameters (K), and Akaike's Information Criterion scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown. The most parsimonious model (lowest AIC value) was used to predict daily grain density (continuous response) values for subsequent modelling of numerical response.

Model	Structure†	K	AIC	ΔAIC	^{W}AIC
lmeDSCRIS	GD = 2, RIS	2	176.1	0.0	0.99
lmeJDRIS	GD = 2, RIS	2	185.1	9.0	0.01
lmeDSCRI	GD = 1, RI	2	201.8	25.7	0.00
lmeJDRI	GD = 2, RIS	2	217.4	41.3	0.00

† GD = grain density, **1** = days since cut, **2** = Julian date, **RI** = random intercept, **RIS** = random intercept and slope.

Table 2.7 Top linear mixed-effects model using days since cut (DSC) as a predictor of grain density (kg/ha) with random intercept and slope terms. Parameter estimates ± standar errors (SE) are given.

Model	df	K	AIC	Intercept	DSC
DSCRIS	92	2	176.1	3.01 ± 0.143	-0.05 ± 0.005

I also attempted to run four grain CV LME models using data ($n = 121$ grain CV estimates) from 28 groups (fields). For both the DSC and Julian predictors, I could not successfully retrieve modelling results from the random intercept and slope models for CV data due to a lack of convergence. Therefore, I selected the most parsimonious model from the two random intercept only models for use in predicting daily grain CV values. Although the DSC predictor model only performed marginally better than the Julian predictor model (^{W}AIC = 0.55 for DSC and 0.45 for Julian; Table 2.8), I opted to use it to estimate daily grain CV values (Figure 2.14) for use in subsequent modelling. According to the DSC model, grain distribution (CV) increased by 0.0004 ± 0.0002 (mean $\pm$ SE) with each day since cut (Table 2.9).

Table 2.8 Candidate linear mixed-effects models using days since cut (DSC) and Julian date
(Julian) as predictors with random intercept and random slope and intercept terms. Model names
(Model) and structures (Structure), number of parameters (K), and Akaike's Information Criterion
scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown. The most parsimonious model
(lowest AIC value) was used to predict daily grain distribution (coefficient of variation;
continuous response) values for subsequent modelling of numerical response.

Model	Structure†	K	AIC	ΔAIC	^{W}AIC
CVlmeDSCRI	CV = 1, RI	2	-475.3	0.0	0.55
CVlmeJDRI	CV = 2, RI	2	-474.9	0.4	0.45
CVlmeDSCRIS	CV = 1, RIS	2	Did not converge	--	--
CVlmeJDRIS	CV = 2, RIS	2	Did not converge	--	--

† **CV** = coefficient of variation, **1** = days since cut, **2** = Julian date, **RI** = random intercept, **RIS** = random
intercept and slope.

Table 2.9 Top linear mixed-effects model using days since cut (DSC) as a predictor of grain variation (CV) with random intercept and slope terms. Parameter estimates ± standar errors (SE) are given.

Model	df	K	AIC	Intercept	DSC
DSCRIS	92	2	-475.3	-2.07 ± 0.043	0.01 ± 0.001
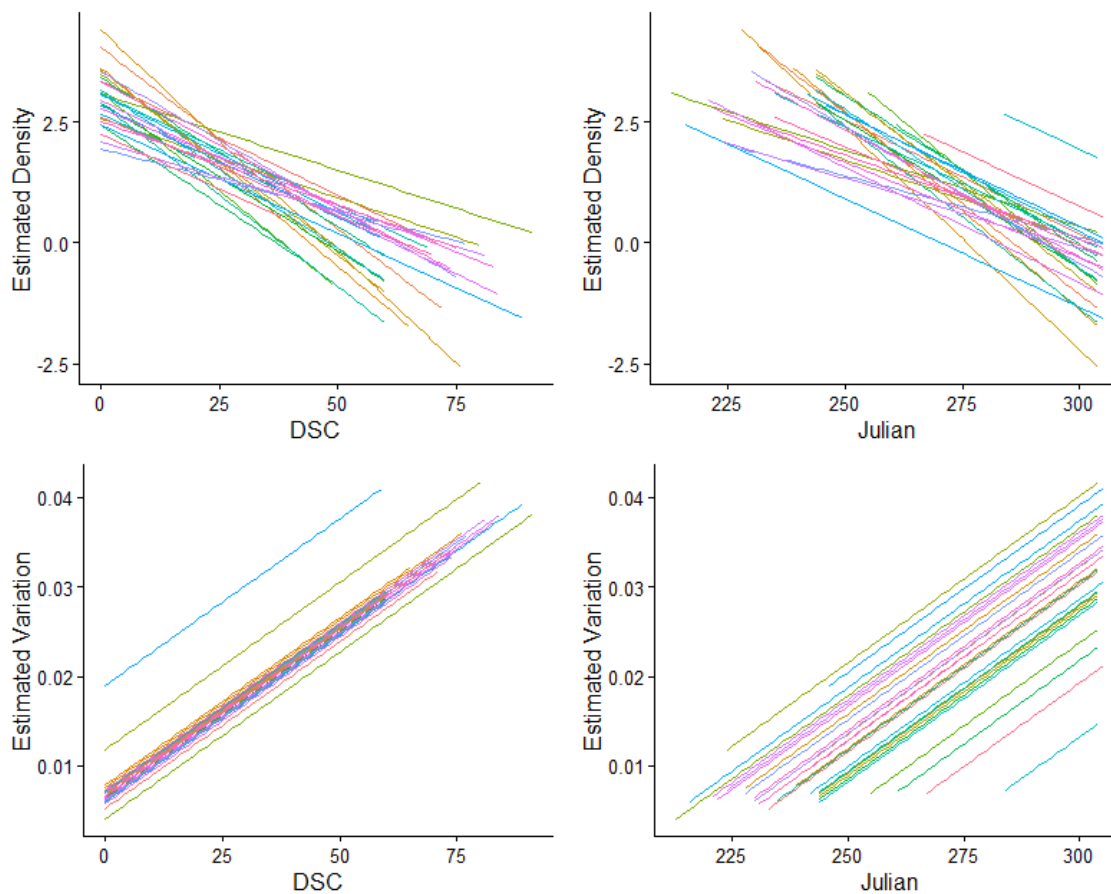
Figure 2.14 Estimated grain density and distribution values calculated with linear mixed-effects models including random slope and intercept (upper; density) and random intercept (lower; distribution) terms plotted against days since cut (DSC) and Julian date (Julian). DSC was defined as a number starting at 0 on the day a field was cut that increased by one for each day since cutting (e.g., DSC = 6 for the seventh day after being cut). Estimated density was calculated in kg/ha but is displayed log transformed (log kg/ha). Estimated variation was calculated as the coefficient of variation amongst grain density samples. Line colours show field/year combinations ($n = 28$). Data were collected in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

2.3.2 Foraging Flight Distance

Because I deployed transmitters in summer 2010 ($n = 9$), some units were offline prior to autumn 2011 and 2012, reducing my sample of marked cranes ($n = 8$ and 5, respectively). In total, I analyzed 2,690 GPS fixes collected in September and October 2011 ($n = 1,667$) and 2012 ($n = 1,023$). I omitted 1,407 fixes in 2011 and 887 fixes in 2012 that were not paired roost-to-field fixes (i.e., where cranes travel from roost to feeding sites in the morning), reducing my FFD sample size to 398 (2011: $n = 261$, 2012: $n = 137$).

I estimated mean FFD (±SE) at 6.36 ± 0.153 km for September and October of 2011 and 2012 combined (Table 2.10). Mean FFD remained relatively constant during autumn staging (Figure 2.15). I did not find a significant difference ($\alpha = 0.05$) in mean FFD between years ($t_{396} = 1.66$, $p > 0.09$) or months within year (2011: $t_{222} = 1.35$, $p > 0.1$; 2012: $t_{132} = 1.08$, $p > 0.1$) using two-tailed two-sampled Student's t-tests assuming equal variance between samples.

Table 2.10 Mean foraging flight distances (FFD) from GPS-marked adult (AHY) Eastern

Population Greater Sandhill Cranes (*Antigone canadensis tabida*) staging at Manitoulin Island,

Ontario, Canada in September-October 2011 (*n* = 5) and 2012 (*n* = 8).

Year	Month	# of Cranes	# of Fixes	Mean FFD ± SE (km)
2011 + 2012	September + October	8/5	398	6.36 ± 0.153
2011	September + October	8	261	6.55 ± 0.191
2012	September + October	5	137	6.01 ± 0.252
2011	September	8	222	6.65 ± 0.208
2011	October	5	39	5.93 ± 0.470
2012	September	5	132	6.06 ± 0.259
2012	October	1	5	4.61 ± 0.679
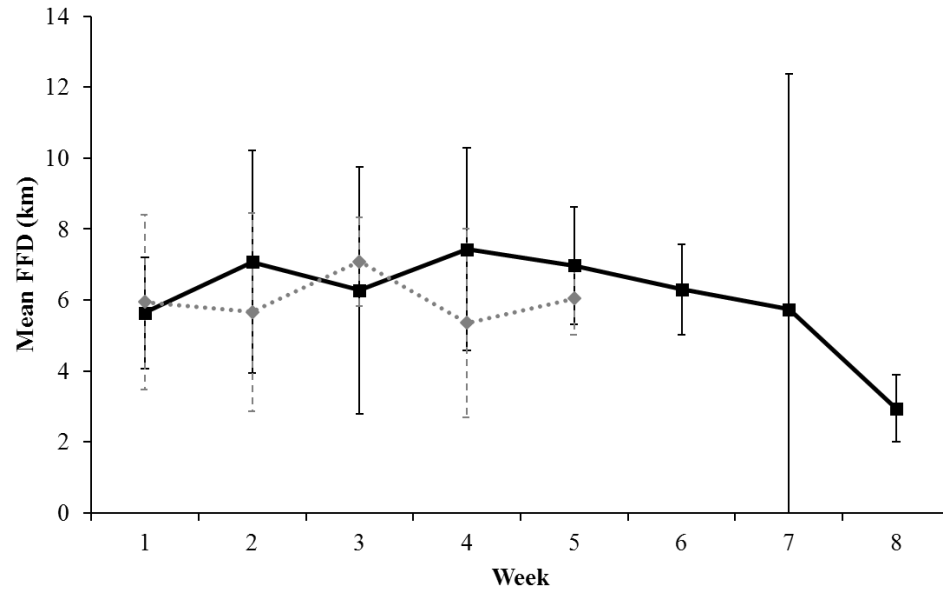
Figure 2.15 Mean (km ± SE) weekly foraging flight distances (FFD) from GPS-marked adult

(AHY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) staging at

Manitoulin Island, Ontario, Canada in September and October 2011 (n = 5) and 2012 (n = 8).

Solid, black line = 2011 and dashed, grey line = 2012. Week 1 starts on 1 September in both

years.

2.3.3   Numerical Response Analysis

I attempted to distribute sampling effort evenly amongst fields within years; however, the number of observation events per field per year was ultimately determined by a combination of logistical constraints and where cranes were located during surveys (i.e., zero data were not included in this analysis). My AHY observations resulted in 59 and 188 observation events in 2011 and 2012, respectively. Similarly, my HY observations resulted in 59 and 172 observation events in 2011 and 2012, respectively. I omitted 16 AHY and HY observation events each from 2012 because they were collected in a field where I was not able to gain access to collect grain samples. Thus, my 2012 AHY and HY sample sizes were reduced to 172 and 156, respectively ($n = 231$ AHY and 215 HY observation events total both years combined; Figure 2.16 and 2.17).

Numerical response varied from single family groups (i.e., two AHY and one HY) to mixed flocks of several hundred cranes at a time (Table 2.11).
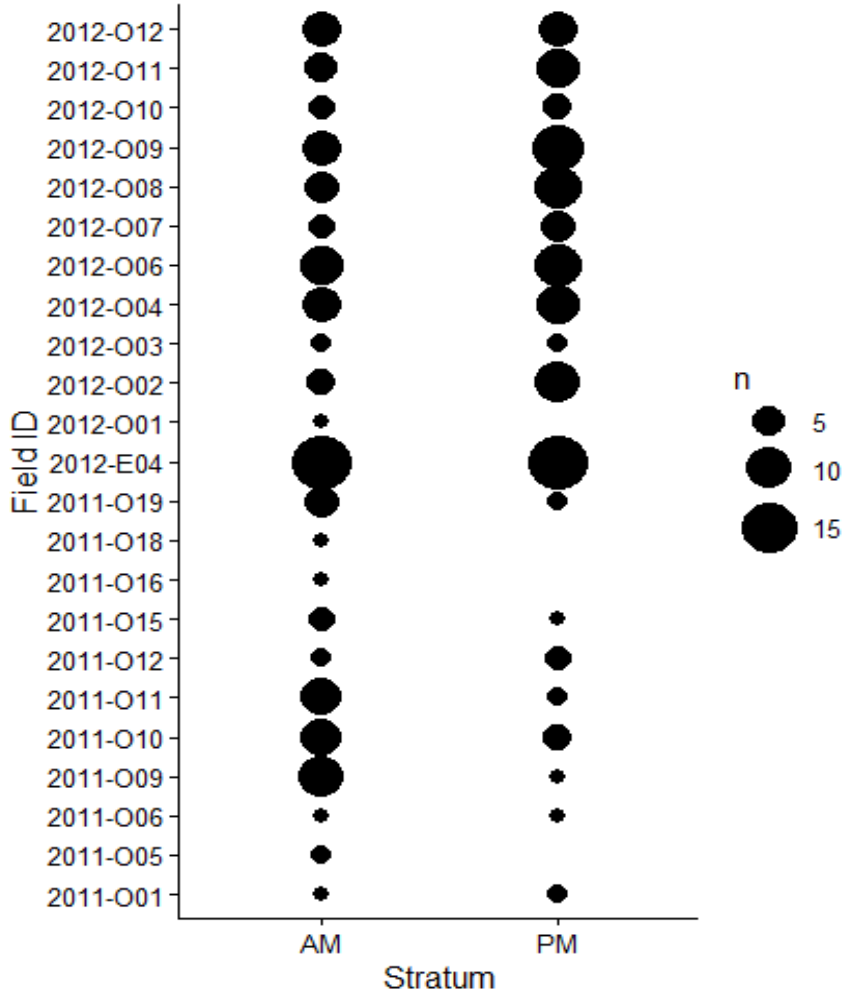
Figure 2.16 Distribution of sampling events (*n* = 231) by field (year-specific label) and survey

stratum (AM or PM) used to collect numerical response data for adult (AHY) Eastern Population

Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at

Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
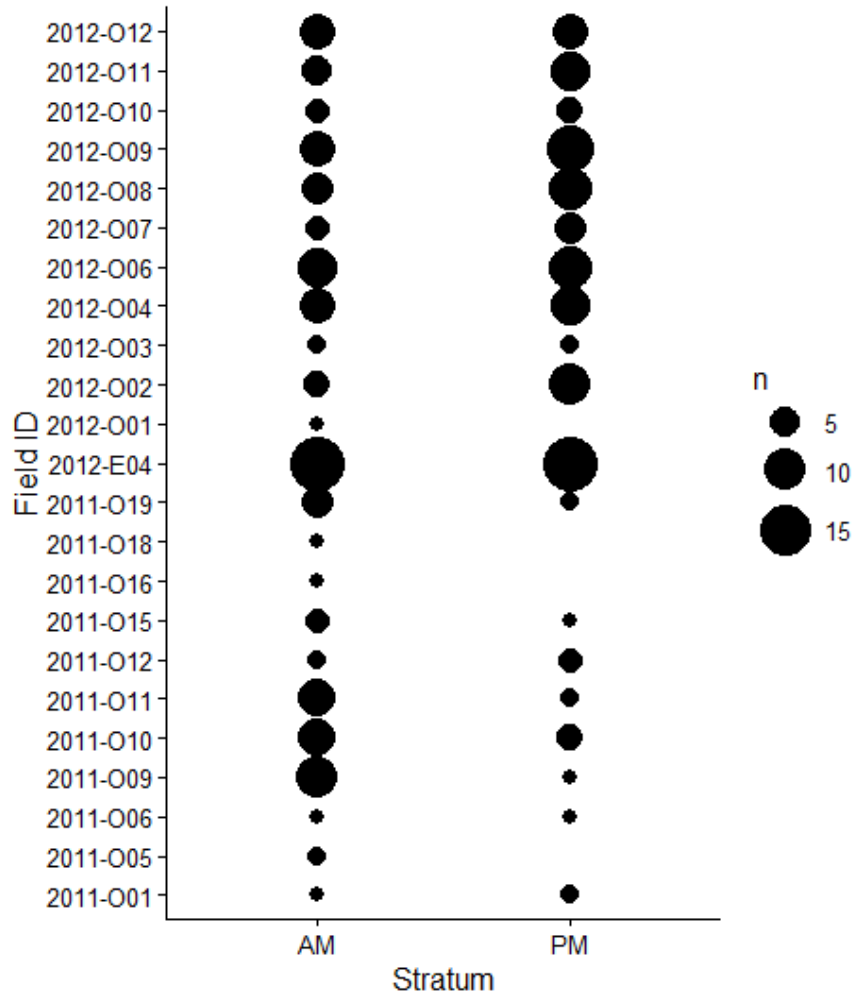
Figure 2.17 Distribution of sampling events (*n* = 215) by field (year-specific label) and survey

stratum (AM or PM) used to collect numerical response data for juvenile (HY; index of family

groups) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested

agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

Table 2.11 Summary statistics describing numerical response of Eastern Population Greater

Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at

Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

Year	Age	*n*	Mean	SD	Max	Min
	AHY	59	81.8	104.52	407	2
2011	HY	59	16.8	22.01	90	2
	Combined	118	49.3	81.98	407	2
	AHY	188	82.5	147.62	895	1
2012	HY	170	9.8	13.46	78	1
	Combined	358	48.0	113.24	895	1
2011+2012	Combined	476	48.3	106.27	895	1

The top model in fitting my AHY numerical response data (AHY4) included the following terms (no interactive effects): field area, proximity to roost wetland, survey stratum, total grain density at the 5-km scale, and relative grain density at the 5-km scale. Model AHY4 received 63% of the available support according to AIC weight calculations (Table 2.12). The second-best model (AHY6) received 24% of the available support and only included one additional additive term compared to AHY4, within-field grain density. Backwards single term deletion for model AHY4 suggested removing the proximity to roost wetland term to improve model performance (i.e., decrease the AIC score). The reduced top model (AHY4.1) improved the AIC score by 1.9 units (AIC = 2387.6 and 2385.7, respectively). Parameter estimates ($\pm$SE) and plots of predicted values from the reduced top model suggested positive additive effects from field area (2.878 $\pm$ 1.2), PM survey stratum (0.282 $\pm$ 0.2), total grain density at the 5-km scale (0.041 $\pm$ 0.03), and relative grain density at the 5-km scale in terms of AHY crane abundance (6.600 $\pm$ 1.1; Table 2.13, Figure 2.18).

Because I identified a potential disproportionate effect on model fit being caused by the area of Field 2012-O11 (area = 3,667 m^2, mean area $\pm$ SD for all fields = 95,316.4 $\pm$ 53,611.4 m^2), I reran my AHY analyses with Field 2012-O11 removed. While parameter estimates changed, the final model structures (following model comparison via AIC and backwards single term deletion procedure) remained consistent following both analyses (Table 2.14).

Table 2.12 Candidate negative binomial generalized linear mixed-effects models used to analyze adult (AHY) Eastern Population Greater Sandhill

Crane (*Antigone canadensis tabida*) numerical response to grain density and distribution at Manitoulin Island, Ontario, Canada in autumn 2011

and 2012. Model names (Model) and structures (Structure), number of parameters (K), degrees of freedom (df), and Akaike's Information

Criterion scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown.

Model	Structure†	K	df	AIC	ΔAIC	^{W}AIC
AHY4	NR = 1+2+3+8+9	6	8	2387.6	0.0	0.63
AHY6	NR = 1+2+3+4+8+9	7	9	2389.5	1.9	0.24
AHY7	NR = 1+2+3+4+(6*9)	8	10	2392.0	4.4	0.07
AHYfull	NR = 1+2+3+4+5+6+7+8+9	10	12	2393.0	5.4	0.04
AHY8	NR = 1+2+3+4+(8*7)	8	10	2394.8	7.3	0.02
AHY3	NR = 1+2+3+6+7	6	8	2397.8	10.2	0.00
AHY1	NR = 1+2+3+4	5	7	2398.1	10.6	0.00
AHY2	NR = 1+2+3+4+5	6	8	2399.7	12.2	0.00
AHY5	NR = 1+2+3+4+5+6+7	8	10	2400.9	13.4	0.00
AHYnull	NR = null	1	3	2403.8	16.3	0.00

† **NR** = numerical response (number of cranes), **1** = field area, **2** = proximity to roost, **3** = survey stratum, **4** = grain density, **5** = grain variation (CV), **6** = 1-km
grain density, **7** = 1-km relative grain density, **8** = 5-km grain density, **9** = 5-km relative grain density.

Table 2.13 Top (AHY4) and reduced (AHY4.1) negative binomial generalized linear mixed-effects models used to analyze adult (AHY) Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) numerical response to grain density and distribution at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Model names (Model), number of parameters (K), degrees of freedom (df), Akaike's Information Criterion score (AIC), theta (Θ), random effect variance (Random Var; Field_ID), and coefficient estimates ± standard errors are given. Reduced model was obtained via backwards single term deletion.

Model	K	df	AIC	Θ	Random Var	Intercept	Area	Prox_Roost	Stratum	X5_km_Dens	X5_km_Rel_Dens
AHY4	6	8	2387.6	0.643	0.097	0.989±2.2	2.669±1.3	1.077±2.9	0.279±0.2	0.040±0.03	6.672±1.1
AHY4.1	5	7	2385.7	0.642	0.092	1.629±1.3	2.878±1.2	---	0.282±0.2	0.041±0.03	6.600±1.1
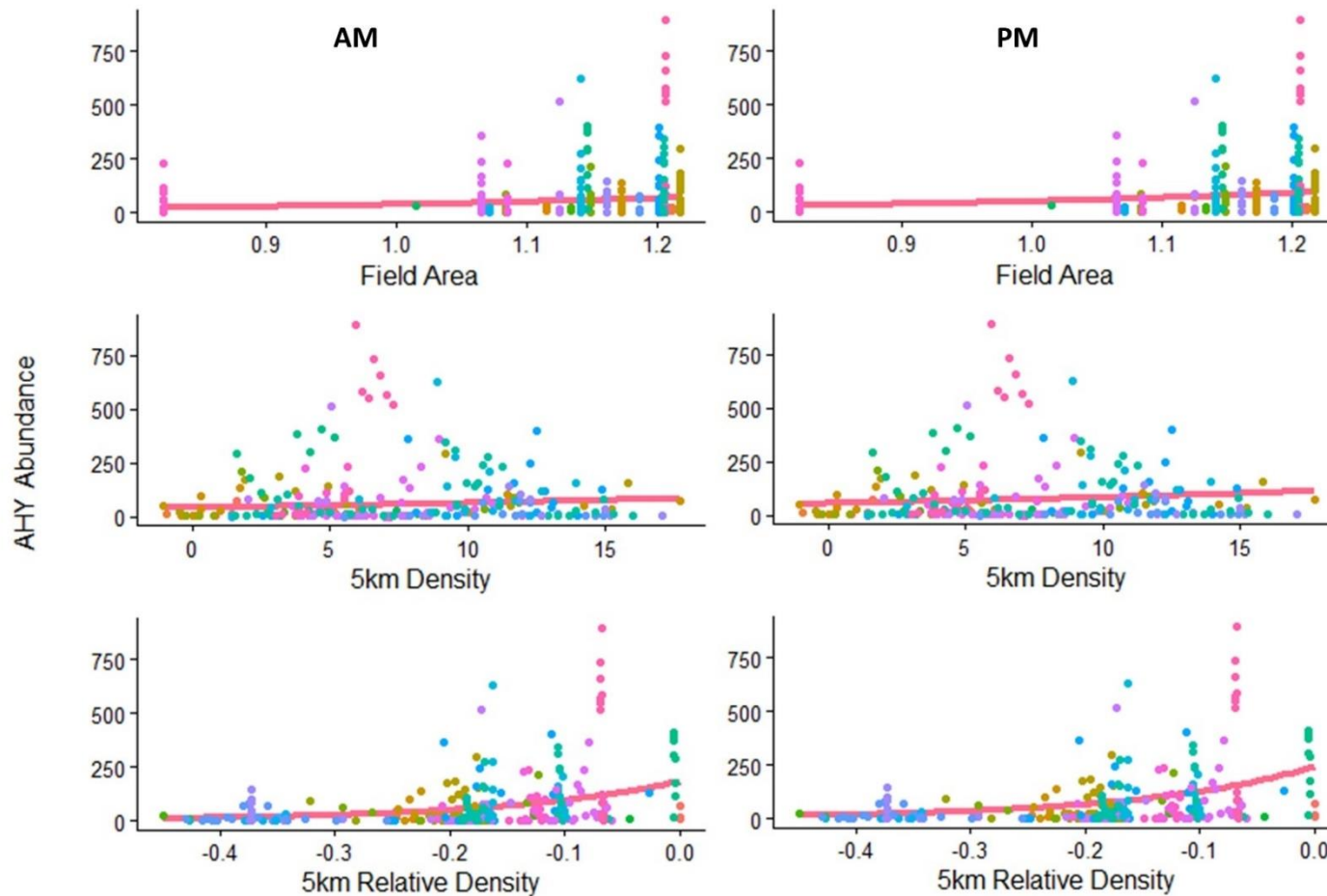
Figure 2.18 Predicted lines for retained predictor variables (backwards single term deletions) from negative binomial generalized linear mixed-effects modelling plotted against counts of adult (AHY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other predictor variables were set to mean values to isolate predictor-specific effects. Dot colours show field/year combinations. Data were collected from cranes using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

Table 2.14 Change in model output from negative binomial generalized linear mixed-effects models used to analyze adult (AHY) Eastern

Population Greater Sandhill Crane (*Antigone canadensis tabida*) numerical response to grain density and distribution at Manitoulin Island,

Ontario, Canada in autumn 2011 and 2012. Model AHY4.1 included a potentially anomalous set of observations (Field 2012-O11) whereas

Model AHY4.1 (2) did not. Model names (Model), theta (Θ), random effect variance (Random Var; Field_ID), and coefficient estimates $\pm$

standard errors are given. Absolute and proportional change in estimates are also included.

Model	Θ	Random Var	Intercept	Area	Stratum	X5_km_Dens	X5_km_Rel_Dens
AHY4.1	0.642	0.092	1.629±1.3	2.878±1.2	0.282±0.2	0.041±0.03	6.600±1.1
AHY4.1 (2)	0.653	0.071	-3.850±2.6	7.596±2.2	0.379±0.2	0.037±0.03	6.546±1.0
Absolute Change	0.011	0.021	5.479	4.718	0.097	0.004	0.054
Proportional Change	1.7%	22.8%	336.3%	163.9%	34.4%	9.8%	0.8%

The top model in fitting my HY numerical response data (HY4) included the following terms (no interactive effects): field area, proximity to roost wetland, survey stratum, total grain density at the 5-km scale, and relative grain density at the 5-km scale. Model HY4 received 59% of the available support according to AIC weight calculations (Table 2.15). The second-best model (HY6) received 22% of the available support and included one additional term (within-field grain density) compared to HY4. Backwards single term deletion for model HY4 suggested removing the proximity to roost wetland and total grain density at the 5-km scale terms (in that order) to improve model performance. The reduced top model (HY4.2) improved the AIC score by 3.6 units (AIC = 1472.3 and 1468.7, respectively). Parameter estimates ($\pm$SE) and plots of predicted values from the reduced top model showed positive additive effects from field area (3.321 $\pm$ 1.1), PM survey stratum (0.243 $\pm$ 0.1), and relative grain density at the 5-km scale (4.242 $\pm$ 0.9) in terms of HY crane abundance (Table 2.16, Figure 2.19).

Once more, because I identified a potential disproportionate effect on model fit being caused by the area of Field 2012-O11 (area = 3,667 m^2, mean area $\pm$ SD for all fields = 95,316.4 $\pm$ 53,611.4 m^2), I reran my HY analyses with Field 2012-O11 removed. While parameter estimates changed, the final model structures (following model comparison via AIC and backwards single term deletion procedure) remained consistent following both analyses (Table 2.17).

Table 2.15 Candidate negative binomial generalized linear mixed-effects models used to analyze juvenile (HY; index of family groups) Eastern

Population Greater Sandhill Crane (*Antigone canadensis tabida*) numerical response to grain density and distribution at Manitoulin Island,

Ontario, Canada in autumn 2011 and 2012. Model names (Model) and structures (Structure), number of parameters (K), degrees of freedom (df),

and Akaike's Information Criterion scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown.

Model	Structure†	K	df	AIC	ΔAIC	^{W}AIC
HY4	NR = 1+2+3+8+9	6	8	1472.3	0.0	0.59
HY6	NR = 1+2+3+4+8+9	7	9	1474.3	2.0	0.22
HY7	NR = 1+2+3+4+(6*9)	8	10	1475.7	3.3	0.11
HY8	NR = 1+2+3+4+(8*7)	8	10	1477.3	4.9	0.05
HYfull	NR = 1+2+3+4+5+6+7+8+9	10	12	1480.0	7.6	0.01
HY1	NR = 1+2+3+4+5	5	7	1480.3	8.0	0.01
HY2	NR = 1+2+3+4	6	8	1481.8	9.5	0.01
HY3	NR = 1+2+3+6+7	6	8	1482.4	10.1	0.00
HYnull	NR = null	1	3	1484.3	12.0	0.00
HY5	NR = 1+2+3+4+5+6+7	8	10	1484.6	12.2	0.00

† **NR** = numerical response (number of cranes), **1** = field area, **2** = proximity to roost, **3** = survey stratum, **4** = grain density, **5** = grain variation (CV), **6** = 1-km grain density, **7** = 1-km relative grain density, **8** = 5-km grain density, **9** = 5-km relative grain density.

Table 2.16 Top (HY4) and reduced (HY4.1 and HY4.2) negative binomial generalized linear mixed-effects models used to analyze juvenile (HY; index of family groups) Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) numerical response to grain density and distribution at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Model names (Model), number of parameters (K), degrees of freedom (df), Akaike's Information Criterion score (AIC), theta (Θ), random effect variance (Random Var; Field_ID), and coefficient estimates ± standard errors are given. Reduced models were obtained via backwards single term deletion.

Model	K	df	AIC	Θ	Random Var	Intercept	Area	Prox_Roost	Stratum	X5_km_Dens	X5_km_Rel_Dens
HY4	6	8	1472.3	1.258	0.094	-1.145±1.9	3.149±1.2	0.543±2.4	0.241±0.1	0.010±0.02	4.348±0.9
HY4.1	5	7	1470.4	1.256	0.093	-0.821±1.2	3.251±1.1	---	0.241±0.1	0.011±0.02	4.299±0.9
HY4.2	4	6	1468.7	1.250	0.085	-0.833±1.2	3.321±1.1	---	0.243±0.1	---	4.242±0.9
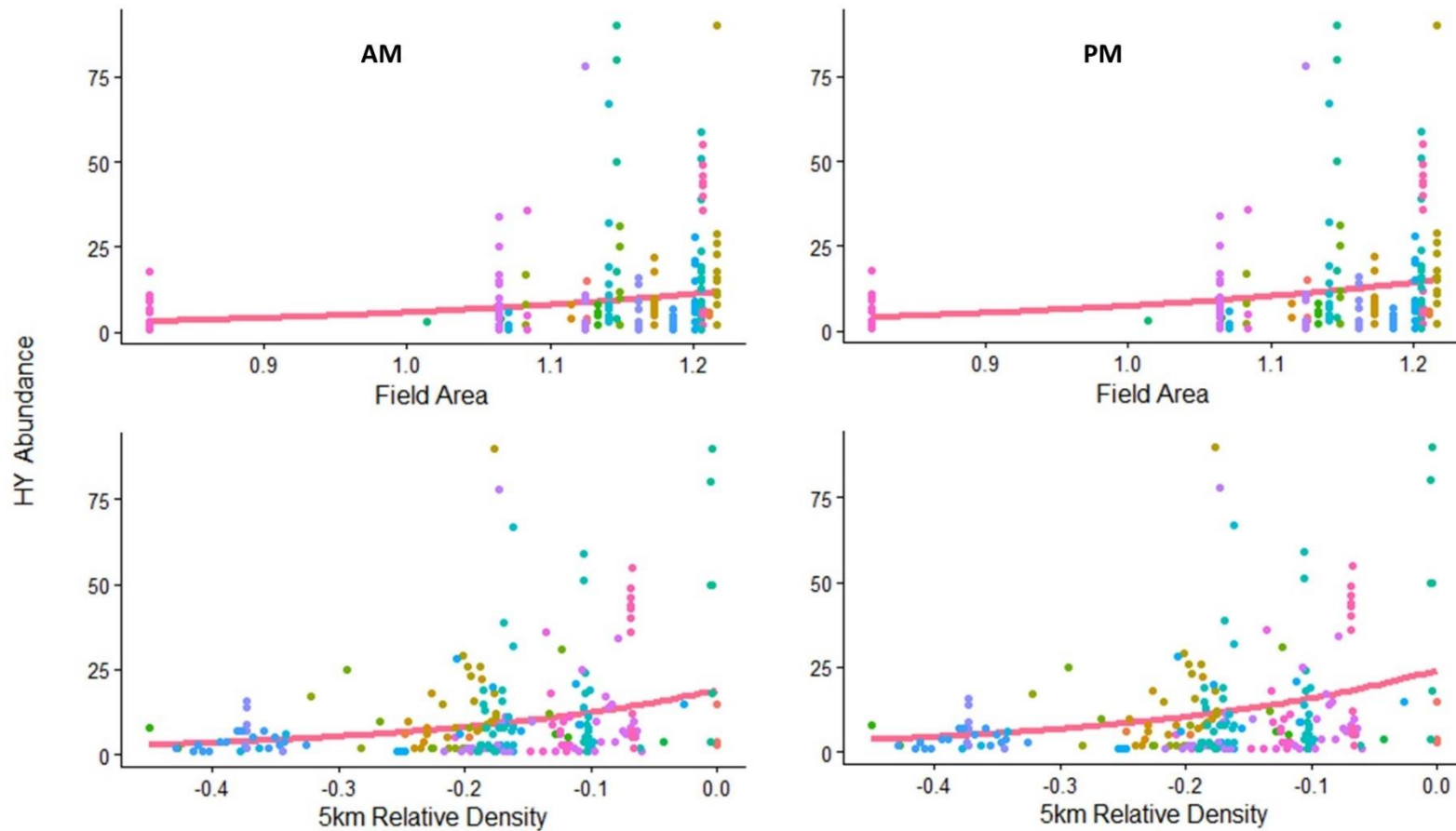
Figure 2.19 Predicted lines for retained predictor variables (backwards single term deletions) from negative binomial generalized linear mixed-effects modelling plotted against counts of juvenile (HY; index of family groups) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other predictor variables were set to mean values to isolate predictor-specific effects. Dot colours show field/year combinations. Data were collected from cranes using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

Table 2.17 Change in model output from negative binomial generalized linear mixed-effects models used to analyze juvenile (HY; index of family groups) Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) numerical response to grain density and distribution at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Model HY4.2 included a potentially anomalous set of observations (Field 2012-O11) whereas Model HY4.2 (2) did not. Model names (Model), theta (Θ), random effect variance (Random Var; Field_ID), and coefficient estimates ± standard errors are given. Absolute and proportional change in estimates are also included.

Model	Θ	Random Var	Intercept	Area	Stratum	X5_km_Rel_Dens
HY4.2	1.250	0.085	-0.833±1.2	3.321±1.1	0.243±0.1	4.242±0.9
HY4.2 (2)	1.243	0.091	-3.466±2.4	5.566±2.1	0.276±0.1	4.182±0.9
Absolute Change	0.007	0.006	2.633	2.245	0.033	0.060
Proportional Change	0.6%	7.1%	316.1%	67.6%	13.6%	1.4%

2.3.4   Model Validation with GPS Data

My GPS tracking data yielded 307 GPS fixes in focal fields in 2011 and 2012 combined ($n = 261$ and 46, respectively; Figure 2.20). I omitted fixes in 2011 ($n = 57$) and 2012 ($n = 8$) that were collected by the same transmitter in the same field on the same day reducing my sample size ($n = 204$ and 38, respectively). I omitted three fixes from 2012 because they were in a field (i.e., 2012-O05) for which I could not gain access to collect grain samples. Thus, my 2012 GPS tracking sample size was reduced further ($n = 35$, 239 both years combined; Figure 2.21).

Comparison of kernel density plots generated for predictor variables retained in my reduced top models based on field observation data and GPS tracking data demonstrated relatively consistent agreement with both the AHY (Figure 2.22) and HY (Figure 2.23) numerical response datasets. GPS-marked cranes appeared to respond less to decreased relative grain density at the 5-km scale.
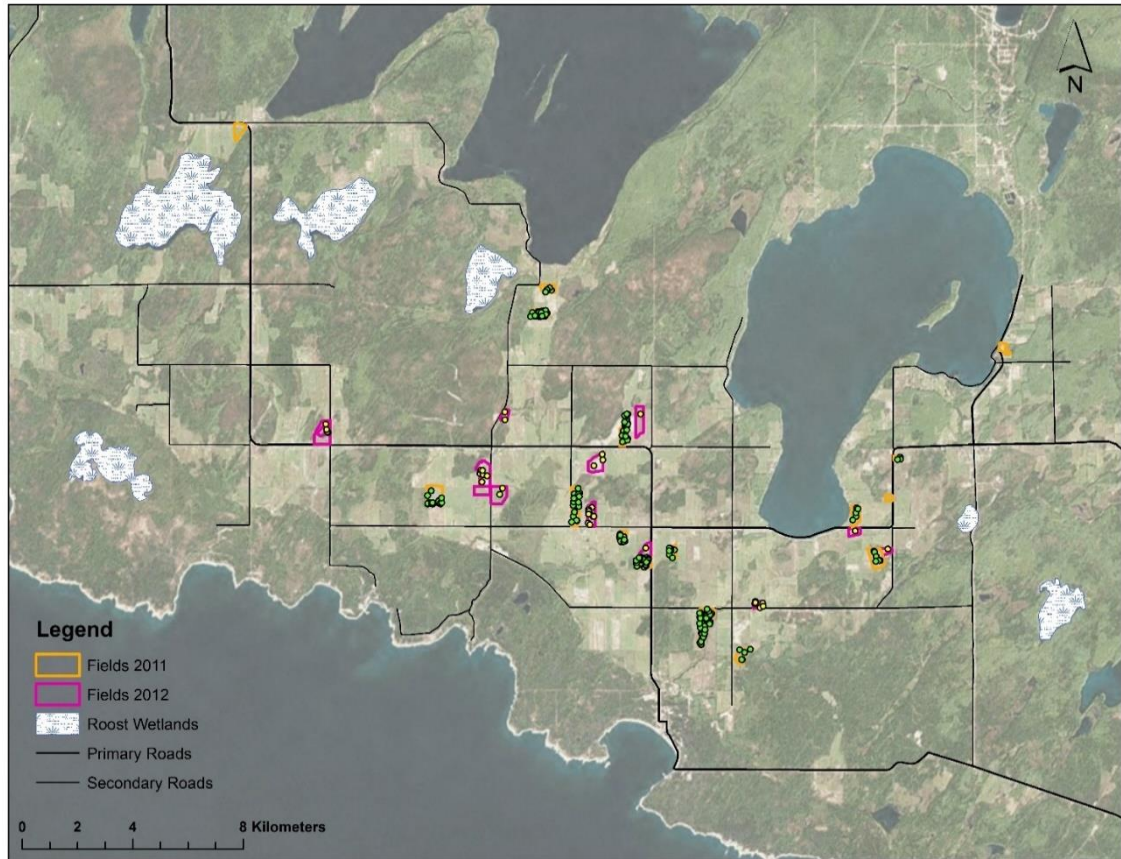
Figure 2.20 GPS fixes (*n* = 239) collected from marked adult (AHY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using focal harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012 where grain density and distribution data were concurrently collected. Green dots = 2011 fixes; yellow dots = 2012 fixes.
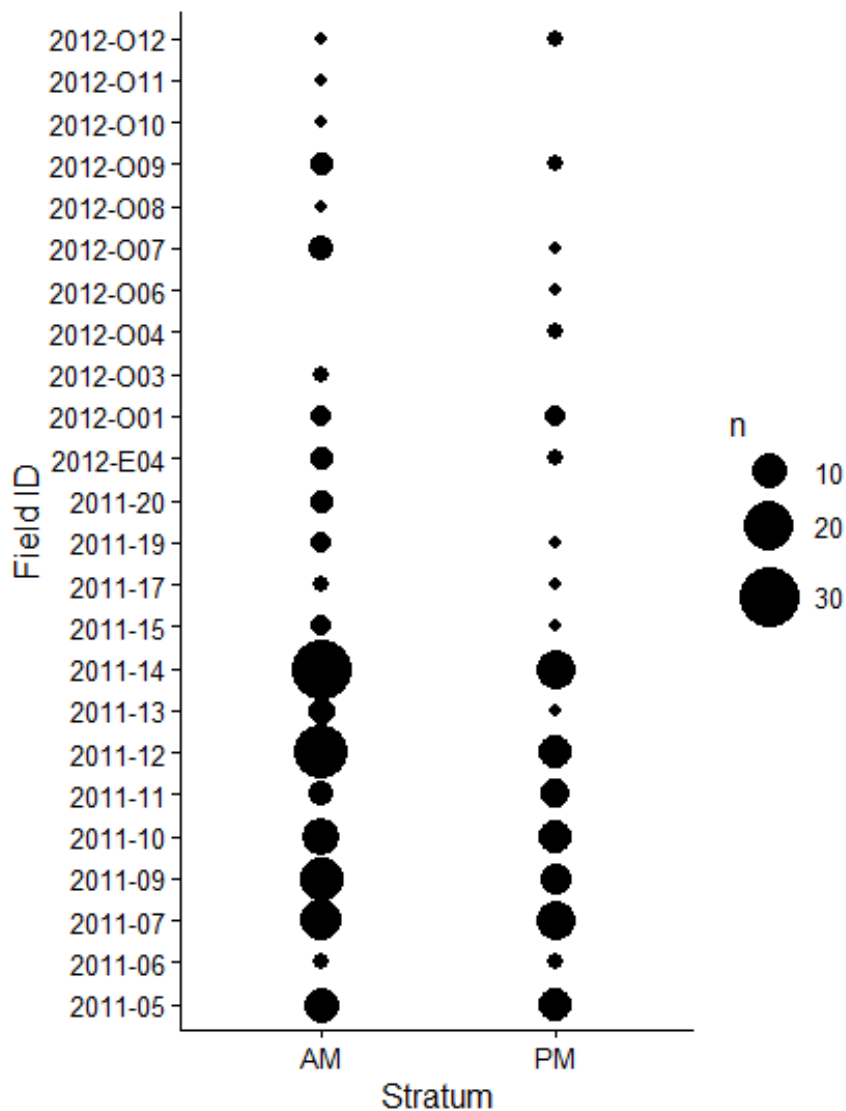
Figure 2.21 Distribution of GPS fixes (*n* = 239) by focal field (year-specific label) and survey stratum (AM or PM) used to validate numerical response models for adult (AHY) and juvenile (HY; index of family groups) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
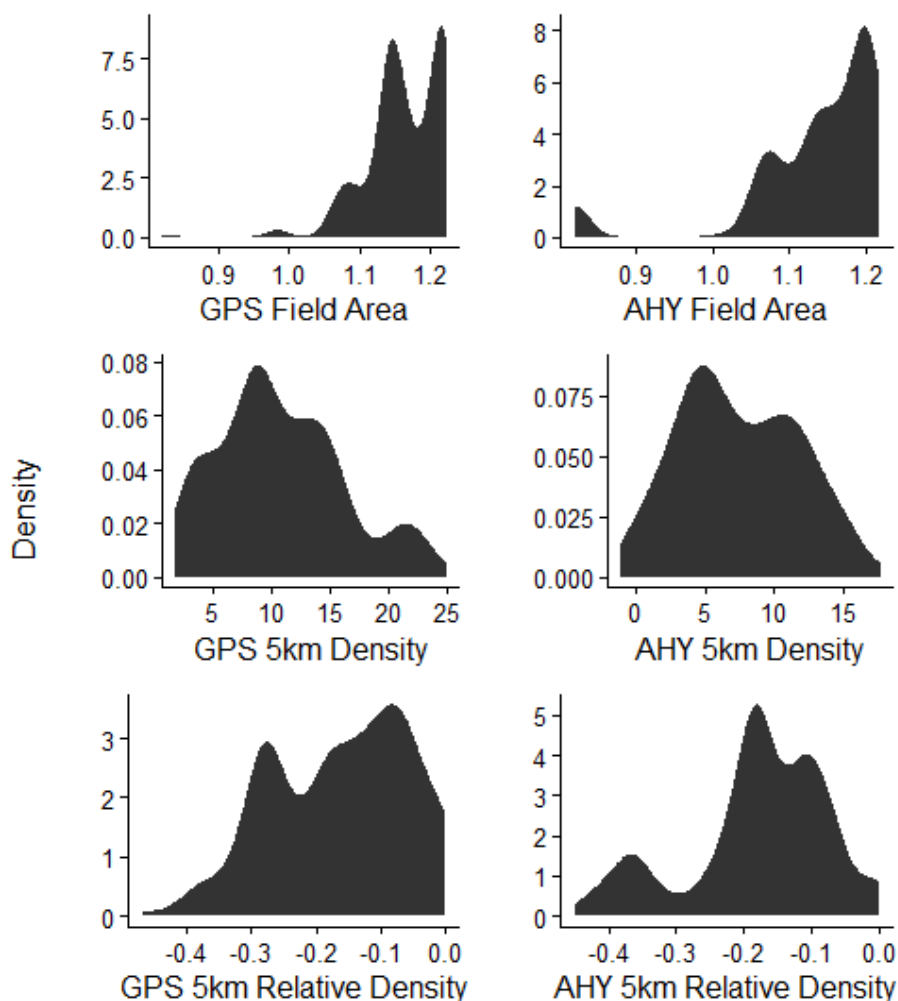
Figure 2.22 Comparison of kernel density plots generated for predictor variables retained in reduced top negative binomial generalized linear mixed-effects models based on field observations (observational AHY sample; right column) and GPS tracking data from adult cranes (left column). Data were collected from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
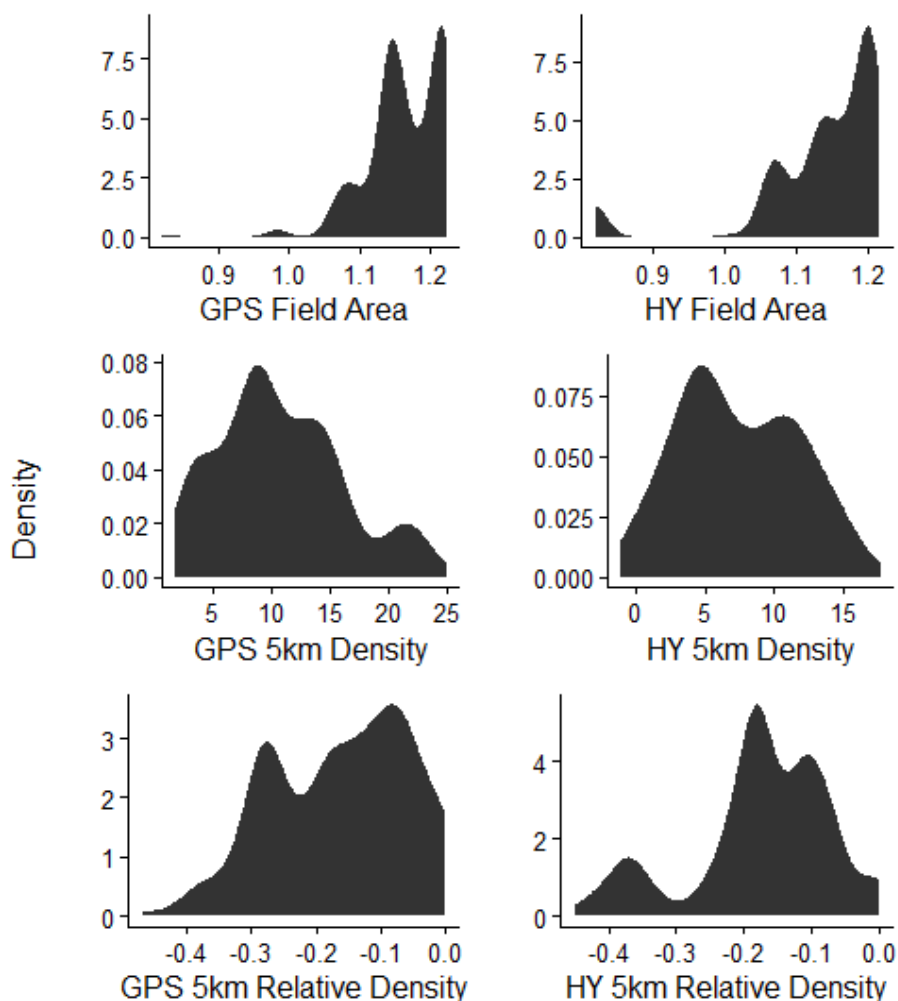
Figure 2.23 Comparison of kernel density plots generated for predictor variables retained in reduced top negative binomial generalized linear mixed-effects models based on field observations of juvenile cranes (HY; index of family groups; right column) and GPS tracking data from adult cranes (left column). Data were collected from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

2.4 Discussion

2.4.1 General Findings

In general, my analysis provided partial support for my predictions relating to age-specific behaviour and grain density. I did not find important age-specific differences in numerical response. Though effect sizes varied between my adult (AHY) and juvenile (HY; index of family groups) analyses, model structures were similar. This similarity suggests the behavioural and/or physiological challenges faced by HY cranes may not be sufficiently important to affect family group behaviour and/or that my index of family groups may not work in application, perhaps due to the flocking behaviour of cranes.

While grain density was an important determinant of crane numerical response in harvested agricultural grain fields, the spatial scale at which cranes appeared to respond to their nutritional landscape somewhat unexpectedly extended beyond the within-field scale. More specifically, retention of the predictor term describing relative grain density at the 5-km scale in my top models for both the AHY and HY analyses suggests that cranes likely perceive their nutritional landscape at or greater than a 5-km scale. However, it is important to note that I only considered three potential spatial scales in my analyses (within-field, 1-km, and 5-km) and picked the best predictor therefrom. Nevertheless, my analyses did not suggest dropping the relative grain density at the 5-km scale term and showed that an increase of one unit in log relative grain density at the 5-km scale resulted in an increase ($\pm$SE) of 6.6 ± 1.1 and 4.2 ± 0.9 AHY and HY cranes, respectively. This finding suggests that cranes can collect and process information relating to food resources at a relatively broad spatial scale and employ that information

to target the most profitable feeding locations amongst the suite available within a spatial range.

Autumn migration is a period of increased energetic demand in migratory birds (Stafford *et al*. 2006, Sherfy *et al*. 2011). During periods of increased nutritional demand, agricultural grain can provide a relatively abundant, accessible, energy-dense food source (Reinecke & Krapu 1986). Optimal foraging theory (Pyke *et al*. 1977) and the principles of the marginal value theorem (Krebs 1974, Charnov 1976) explain the selective pressure driving organisms to exploit the nutritional landscape such that energetic intake is optimized, thus, maximizing fitness. Therefore, cranes at this northern staging site likely used the relative grain density of fields within a 5-km radius to optimize foraging behaviour, and thus maximize fitness. This finding indicates that the foraging scale of the species in this study system is at least 5 km in radius.

There is an established need to consider the scale at which decisions are made and how resources are distributed on the landscape in developing foraging behaviour models (Ritchie 1998). Identification of that need has led to application in research endeavours using a synthetic approach that integrates both of these key factors (e.g., Ferreira *et al*. 2012, Nash *et al*. 2014, McCarthy *et al*. 2016). Building from these endeavours, by developing predictor variables that included relative grain density (resource distribution) at various spatial scales and modelling their relationship with numerical response in a nearly closed setting, my analyses provide empirical evidence describing crane foraging behaviour during autumn.

2.4.2   Numerical Response

2.4.2.1   Relative Grain Density within a 5-km Radius

The relative importance of the 5-km foraging scale in crane numerical response

supported by my analyses seems ecologically reasonable given that the value roughly

coincides with estimates of mean FFDs (mean ± SD) in samples of wintering geese and

dabbling ducks (7.8 ± 7.2 and 5.1 ± 4.4 km, respectively; Johnson *et al*. 2014), GPS-

tracked cranes in my study (6.4 ± 0.15 km), wintering Central Valley Population Greater

Sandhill Cranes in California, USA (4.5 ± 0.01 km; Ivey *et al*. 2015), and other crane

subspecies during spring migration along the Platte River in Nebraska, USA (assumed to

be a combination of Greater, Canadian, and Lesser subspecies) belonging to the Mid-

Continent Population (6.8 ± 3.8 km; Sparling & Krapu 1994). Moreover, Ivey *et al*.

(2015) reported that 95% of "commuting flights" for Greater Sandhill Cranes were <5 km

in length. Thus, the scale at which cranes appeared to interpret the nutritional landscape

in my analyses may be a result of the energetic cost of FFDs beyond the 5-8 km range

(Pearse *et al*. 2010). That is, there is likely an energetic advantage to search as far as

possible from roost wetlands but not to exceed the upper limit of the 5-8 km range

threshold. Pearse *et al*. (2010) estimated the daily cost of flight for cranes as a function

of cost per unit time (using eq. 7.35 from Norberg 1996), assuming a mean flight speed of

43 km/hr (as per the median value reported by Gerber *et al*. 2014). The cost of flight

represented 6% of the energy consumption for cranes at their study site during spring

migration. Thus, an analogous mechanism to that which limits foraging/commuting

flight distance as described above may also regulate foraging scale. This regulatory

function may be especially important during spring and autumn migration when energetic

reserves become more critical to survival for migratory birds (Krapu *et al*. 2004). Regulation of foraging scale via such a mechanism would effectively dictate the maximum range at which cranes can afford to consider patches for foraging (fields in my study), hence the relative importance of the 5-km grain density predictors in my analyses.

Disturbance effects on field use may provide a secondary explanation for the relative importance of grain density at the 5-km spatial scale. On several occasions, I observed cranes that were feeding in harvested grain fields being disturbed or harassed by farmers, hunters, and bird watchers. Such disturbance often caused cranes to abandon what were presumably top choice feeding sites and settle at potentially less desirable locations. If the relative grain density at the 5-km scale was used to select the optimal field, total grain density at the 5-km spatial scale may have been used to select a community of potential feeding sites when facing relatively frequent and potentially energetically costly disturbance (Madsen 1994, Klaassen *et al*. 2006). Thus, limiting knowledge of the nutritional landscape to the 1-km or within-field scale would not only reduce available food resources but also the number of fields available following disturbance. Therefore, future research investigating feeding field use in cranes and other similar species would likely benefit from including metrics of disturbance, including predictability of disturbance (Chudzińska *et al*. 2013).

2.4.2.2   Within-field Relative and Total Grain Density

Interestingly, neither the total nor relative grain density at the 1-km scale predictors were included in the top AHY or HY models. However, given the relative importance of grain density at the 5-km scale, the 1-km scale grain density predictors may not have

been considered important in my analyses because fields within the 1-km buffer were also included in the 5-km buffer, in aggregate with additional fields captured at the larger spatial scale. Using the estimates of daily flight distances for cranes cited above, the 1-km scale may have simply been too fine to be ecological relevant given reported estimates of crane flight and foraging behaviour.

While I expected to find an important relative grain density effect at one of the two larger spatial scales (1- and 5-km), I also expected that grain density and/or distribution at the within-field scale would influence numerical response. Grain density and distribution at the within-field scale were hypothesized to be primary determinants of numerical response in cranes, as in field-feeding waterfowl (i.e., analogous to a giving-up density, GUD; Price & Correll 2001, Hagy & Kaminski 2012, Bedoya-Perez *et al*. 2013, Carthey & Banks 2015).

The GUD for field-feeding waterfowl has been estimated at approximately 50 kg/ha (Foster *et al*. 2010) and has received wide use and study in the field of waterfowl biology and management (Hagy & Kaminski 2012). However, several key studies provide a basis to explain the lack of a similar GUD effect on field-feeding crane behaviour as reported in my study. Bedoya-Perez *et al*. (2013) described seven key conditions that must be met in GUD studies. Amongst those conditions are effects of group foraging, patch predictability, and behavioural traits of the forager.

Group foraging can affect GUD (Carthey & Banks 2015), resulting in a trade-off between perceived risk and realized GUD (i.e., safety in numbers; Tsurim *et al.* 2008, Eparza-Carlos *et al.* 2016). Patch predictability and variability can also affect GUD (Berger-Tal *et al*. 2014). Specifically, animals can use information concerning the

richness of a patch relative to other nearby patches to adapt foraging behaviour. In this way, it is appropriate that cranes apparently responded primarily to relative grain density at the 5-km scale and not within-field densities as reported in studies of field-feeding waterfowl (i.e., traditional GUD; Hagy & Kaminski 2012).

No studies to date have reported similar spatial scale effects on waterfowl field use behaviour, but this may be because relative and total grain density effects at the 5-8 km range have not been analyzed as presented here (see Johnson *et al.* 2014 for a review of waterfowl FFDs). Finally, the effects of changes in grain density and distribution on crane foraging behaviour may not be apparent at the within-field scale because they are in fact more important factors in determining how instead of where cranes feed in harvested grain fields (see Chapter 3).

2.4.2.3   Field Area

I included field area as a predictor in all candidate models (except for the null) to account for the expected linear relationship between field size and the number of cranes a field can hold and because I also included terms describing grain density and not abundance in my analyses. However, cranes only moderately modulated field use behaviour in relation to field size. The field area effect size was relatively moderate in both AHY and HY models ($\pm$SE; 2.9 $\pm$ 1.2 and 3.3 $\pm$ 1.1 cranes, respectively). I consider this finding appropriate, in part, because larger fields generally hold more cranes. However, larger fields may also present safer feeding sites for cranes because maximum distance to edge generally increases with field area (pending shape/dimensions). In spring migrating Pink-footed Geese (*Anser brachyrhynchus*), selection of larger fields has

been attributed to an inverse relationship between field area and perceived predation risk in a study of field-feeding behaviour (Chudzińska *et al*. 2015). Similarly, cranes may use larger fields to reduce predation risk. This consideration may be especially important in the case of family group field-feeding behaviour as HY cranes are generally smaller and likely more susceptible to predation. Thus, the greater effect size of field area on field use in the HY model may be a result of age- or demographic-specific predation risk.

2.4.2.4 Proximity to Roost

I included proximity to roost as a predictor in all candidate models (except for the null) to analyze effects related to the distance cranes travel from roost wetlands to feeding sites. I expected a proximity to roost effect because a negative correlation to proportion of individuals feeding was reported in field-feeding Pink-footed Geese during spring migration in Norway (Chudzińska *et al*. 2013). However, proximity to roost was not included in either the top AHY or HY model. Proximity to roost may not have affected field use in my study because the maximum flight distance between suitable roost wetlands and feeding sites was too short. Maximum flight distance may have been less than the threshold where selection favours use of proximity to roost sites in deciding where to feed (Pearse *et al*. 2010, Ivey *et al*. 2015).

2.4.2.5 Survey Stratum

Non-parental (AHY) and family group (HY) field use was greater in afternoon compared to morning; however, survey stratum had a relatively minor effect (±SE) on

AHY and HY field use (0.3 ± 0.2 and 0.2 ± 0.1 cranes, respectively; PM compared to AM). My observations also suggested lesser grain field use in the morning because cranes would often gather in non-grain fields (e.g., pastures) before flying to feeding fields, especially earlier in the staging period. Chudzińska *et al*. (2013) reported that peak feeding behaviour in Pink-footed Geese occurred at mid-day during migration in Norway; however, flocks were also largest and closest to the roost in early afternoon. I primarily included survey stratum to control for diel variation in field use. However, modelling the interaction between survey stratum or an equivalent time of day metric and proximity to roost may be warranted in future studies of numerical response in cranes and similar field-feeding species. Including this interactive effect may allow for better understanding of changes in field use through the day.

2.4.2.6   Age-/Demographic-specific Effects

Age-specific effects on avian ecology associated with variation in habitat characteristics are widely reported in the literature, ranging from effects of ice characteristics on survival during migration in Adélie penguins (*Pygoscelis adeliae*; Emmerson & Southwell 2011) to breeding incidence, and nest and brood survival in Mallards (*Anas platyrhynchos*; Dugger *et al*. 2016) to drought and climate change effects on juvenile recruitment of cranes to the Rocky Mountain Population of western North America (Gerber *et al*. 2015). The likely causes of these differences range in scope but are usually tied to differences between juvenile and adult behaviour and/or physiology. In my analysis, I expected to find different sets of predictors for the top AHY and HY models. I made these predictions mainly due to predicted effects on family group

behaviour from the behavioural inexperience and different nutritional requirements of HY cranes. My results did not provide support for this prediction. Though there was a structural difference in the respective models (i.e., total grain density at the 5-km scale was dropped from the HY model), the respective top models were otherwise similar. Thus, it appears that the disparate nutritional, physiological, and possible stamina challenges faced by HY cranes were not sufficiently important to affect family group field use in autumn staging cranes, or perhaps that my index of family group behaviour was not effective.

2.4.3   Management Implications

Describing the foraging ecology of a little-known species or system advances understanding of foraging ecology in general but also advances understanding necessary for future management decisions. For example, managing land-use at key staging areas requires an understanding of the spatial scale at which cranes perceive their environment – from foraging sites to roost wetlands (i.e., foraging scale). The most important spatial scale for food effects on behaviour was at least 5 km in my study. There exists potential for changes in agricultural commodity demand and prices that could result in drastic landscape-level shifts in terms of the types and proportions of crops being produced, including proximity to suitable roost wetlands. For example, small grain is often more common at northern staging sites whereas corn is more prevalent at staging sites further south. Given the apparent relative importance of agricultural grains as food, changes in availability, distribution, and/or timing of harvest could result in the reallocation of critical energetic reserves or substantial shifts in staging sites located along established

migratory pathways (Pearse *et al*. 2010, Krapu *et al*. 2014). Furthermore, cranes may need more than a select set of isolated fields to forage successfully. If feeding sites become too isolated or sparse, and/or if disturbance increases, cranes may not be able to continue use of traditional staging sites. Thus, the 5-km foraging scale for EP cranes reported here, and values from studies of other migratory populations in North America (Ivey *et al*. 2015), provide a minimum estimate of the spatial scale that conservation planners and managers should consider to create and conserve sufficient and accessible crane staging habitat.

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3 Age-specific foraging efficiency of Greater Sandhill Cranes (*Antigone canadensis tabida*) in harvested agricultural grain fields during autumn staging

3.1 Introduction

Many species exploit the vast amount of food resources made available from modern agricultural practices (Amin *et al.* 2015, Jankowiak *et al.* 2015, Li *et al.* 2015, Chudzińska *et al.* 2016). Many granivorous birds now rely on waste grain (i.e., grain incidentally spilled or missed by standard agricultural crop harvesting practices; grain herein), particularly before and during migration. This importance can be attributed to grain's relative abundance, accessibility, energetic density, and digestibility during a period of increased energetic demand (Reinecke & Krapu 1986, Stafford *et al.* 2006, Galle *et al.* 2009, Anteau *et al.* 2011). Grain abundance can affect carrying capacities in avian populations (Krapu *et al.* 2004, Pearse *et al.* 2010, Wiseman *et al.* 2010; also, see Drahota & Reichart 2015). Moreover, habitat (including grain food resources) can have cross-seasonal effects on individual reproduction and survival (Davis *et al.* 2014, Sedinger & Alisauskas 2014). Use of agricultural grain by migratory birds generally varies by season (i.e., spring vs. autumn migration), as the two seasons follow and precede disparate life history stages (i.e., breeding and overwintering; Stafford *et al.* 2014). Thus, granivorous birds modulate behaviour following nutritional needs and grain availability at staging areas during migration (Pearse *et al.* 2011, O'Neal *et al.* 2012, Beatty *et al.* 2014).

Given increased nutritional requirements during migration, there likely exists substantial selective pressure to exploit grain via energetically-positive foraging behaviours (*sensu* Pyke *et al.* 1977). The concept of foraging behaviour optimization is prevalent in modern studies of behavioural ecology (e.g., Fujioka *et al.* 2016, Mahjoub *et al.* 2016, Tyson *et al.* 2016, etc.), though competing explanations exist (e.g., Lévy walks in the physical sciences; Reynolds 2015; but see Humphries 2015). Nevertheless, studies of optimal relationships in foraging ecology persist (i.e., optimal foraging theory; Werner & Hall 1974).

Studies of optimal foraging often describe the relative amount of time animals engage in various behaviours and use those values to estimate some metric of the energetic profit gained via foraging (Tacha *et al.* 1987, Mori & Boyd 2004, Willisch & Ingold 2007). This energetic profit is typically assumed to directly or indirectly affect fitness. Some studies have even modelled the mortality risk per unit of food consumed to test hypotheses of optimal foraging (Yearsley *et al.* 2002). Other studies describe this relationship at larger, varying spatial scales and, in some cases, have shown that large-scale avian migratory behaviour is determined by the pressure to optimize foraging behaviour (e.g., reduced stopover duration, O'Neal *et al.* 2012; timing of migratory departure, Duriez *et al.* 2009). Clearly, the use of optimal foraging has broad application to the study of behavioural ecology, from foraging behaviour (Werner & Hall 1974) to feeding (Chapter 2) and roost site use (Chapter 4).

Amongst migratory cranes inhabiting temperate regions (family *Gruidae*), juveniles (hatched during the current calendar year or "hatch year", HY herein) continue to grow and develop during autumn migration so they remain smaller than adult conspecifics

(hatched prior to the current calendar year or "after hatch year", AHY herein; Inoue *et al.* 2013). Thus, relative to AHY conspecifics, HY cranes have different behavioural experience (e.g., lack of experience foraging in agricultural fields) and physiological requirements (e.g., continued growth of muscle and long bones; Krapu & Johnson 1990, Curro *et al.* 1996, Nowald 2001) at autumn staging sites. Similarly, in other taxa, physiological challenges related to size affect foraging behaviour, for example, in a species of endothermic fish (bigeye tuna, *Thunnus obesus*; Thygesen *et al.* 2016). As well, premigratory Ruby-throated Hummingbirds (*Archilochus colubris*) optimize fat gain by modulating feeding behaviour prior to migratory departure using age-specific strategies (Hou & Welch 2016). Age-specific optimal diets and foraging tactics may be related to individual reproductive value, with a stronger impetus for younger individuals (greater reproductive value) to forage optimally (Engen & Stenseth 1989).

In North American populations of Sandhill Crane (*Antigone canadensis*) that breed north of agricultural areas, HY and AHY age classes have different behavioural experience foraging in harvested agricultural grain fields in particular during autumn migration. These differences are particularly prominent during autumn at more northerly staging sites along the forested-cleared land interface. Cleared agricultural land is novel to juvenile cranes travelling south for the first time from natal areas with few, if any, agricultural grain fields. The North Shore of Lake Huron presents such a patch of habitat for the Eastern Population (EP) that breeds north of the Great Lakes region in northern Ontario, Canada (Hanna *et al.* 2014, Fronczak *et al.* 2015, In press).

Sandhill Crane populations include a sub-demographic of non-breeding AHY cranes that look like adults but typically do not reproduce. This sub-demographic persists from

one to approximately five years of age, though estimates vary between populations (Tacha *et al.* 1989, Nesbitt 1992, Drewien *et al.* 1995). Beyond direct observation of adults with or without young, or intensive marking programs, no reliable field method for distinguishing parental from non-parental AHY cranes has been described. However, the implicit parental responsibility of the former, coupled with an inability to distinguish them from non-parental conspecifics, increases the complexity of studying the age-specific foraging ecology of this species during autumn migration.

Even with knowledge of these demographic differences in ecology and physiology, researchers are often forced to pool observations of all crane demographic groups due to logistical constraints associated with collecting data in the field (Nilsson *et al.* 2016). Unfortunately, pooling data in this manner prevents the analysis of age-specific effects. Therefore, collecting age-specific data that describe foraging behaviour aggregated by age class (i.e., AHY and HY) would allow for analysis of age-specific behaviour during autumn migration when disparate challenges exist between these groups.

Here, my objective was to study the age-specific relationship between grain density and variation and foraging efficiency in EP Greater Sandhill Cranes (*A. c. tabida*; cranes herein). I used estimates of grain density and spatial distribution (variation herein) to analyze observational and experimental behavioural data describing the age-specific foraging efficiency of cranes during autumn staging. I predicted that HY cranes feed less efficiently (i.e., increased search time for food) relative to AHY conspecifics. I also expected to find a negative relationship between grain variation and foraging efficiency in both age classes because finding heterogeneously-distributed food is generally more difficult (Foo *et al*. 2016). Finally, I predicted that foraging efficiency would increase

through the autumn staging period, even as grain density decreases and variation

increases, because HY cranes continue to learn to forage on grain and grow long bones

and muscle while the pressure to prepare for migration increases. Concurrent study of

age-specific foraging behaviour and food availability (*sensu* Callicutt *et al*. 2011) will

offer an advanced understanding of how EP crane behaviour is affected by spatial and

temporal variation in grain during autumn staging while generally improving

understanding of foraging behaviour optimization.

3.2   Methods

3.2.1   Study Area

   All field components of my study were conducted at Manitoulin Island (Manitoulin

herein), Ontario, Canada (UTM Zone 17 N, 0394968 E, 5065491 N; see Figure 1.2 in

Chapter 1). Manitoulin is the largest freshwater island in the world at 2,766 km^2

(Chapman & Putnam 1973, Kraus *et al*. 2009) and is located at the northern end of Lake

Huron. The landscape varies from coastal alvar and wetland habitats (i.e., swamps, fens,

and bogs) to upland deciduous forest and cleared agricultural fields. Please refer to

Section 2.2.1 in Chapter 2 for a description of the ecological context of Manitoulin as it

relates to cranes in my study.

3.2.2   Observational Field Grain Sampling

   At the start of each field season (early August), I assessed and classified all fields in

my study area per crop type (i.e., grain vs. non-grain) and sampled grain in a focal subset

of fields. For a comprehensive description of grain field sampling methods, please refer to Section 2.2.2 in Chapter 2.

3.2.3 Laboratory Procedures

I thawed and weighed grain samples in the lab after the completion of each field season to quantify spatial and temporal variation in density and variation. For a comprehensive description of grain laboratory procedures, please refer to Section 2.2.3 in Chapter 2.

3.2.4 Experimental Field Grain Sampling

Because I did not receive permission from landowners to carry out experimental procedures in two of the eleven experimental fields selected for study (2012-E04 and 2012-E011; Figure 3.1), I established four experimental plots ($n = 4$) in a reduced sample of experimental fields for this portion of my study ($n = 9$).

In each of those fields where I received permission to carry out experimental procedures, I established four square 30 by 30 m (900 m^2) experimental plots (plots herein). I could not randomize the location of plots within fields because of logistical constraints associated with viewing cranes from road-based observation points (see Section 3.3.5 below for further detail). Therefore, I placed plots strategically so that they did not align as viewed from observation points to make distinguishing which plot cranes were in during observations easier. I attempted to maximize the distance between roads and plots to minimize potential for disturbance from vehicular traffic (including vehicles

part of my study). I maintained at least 10 m between plots. I used standard ~1 m

bamboo gardening stakes to mark the four corners of each experimental plot. I also

marked the top of each bamboo stake with coloured flagging tape to increase visibility

from observation points. I made field maps indicating the treatment of each plot within

each field for use when making and recording behavioural observations. I randomly

selected the ordering of plots in each field to minimize the potential for carry-over effects

from grain treatments in neighbouring plots.
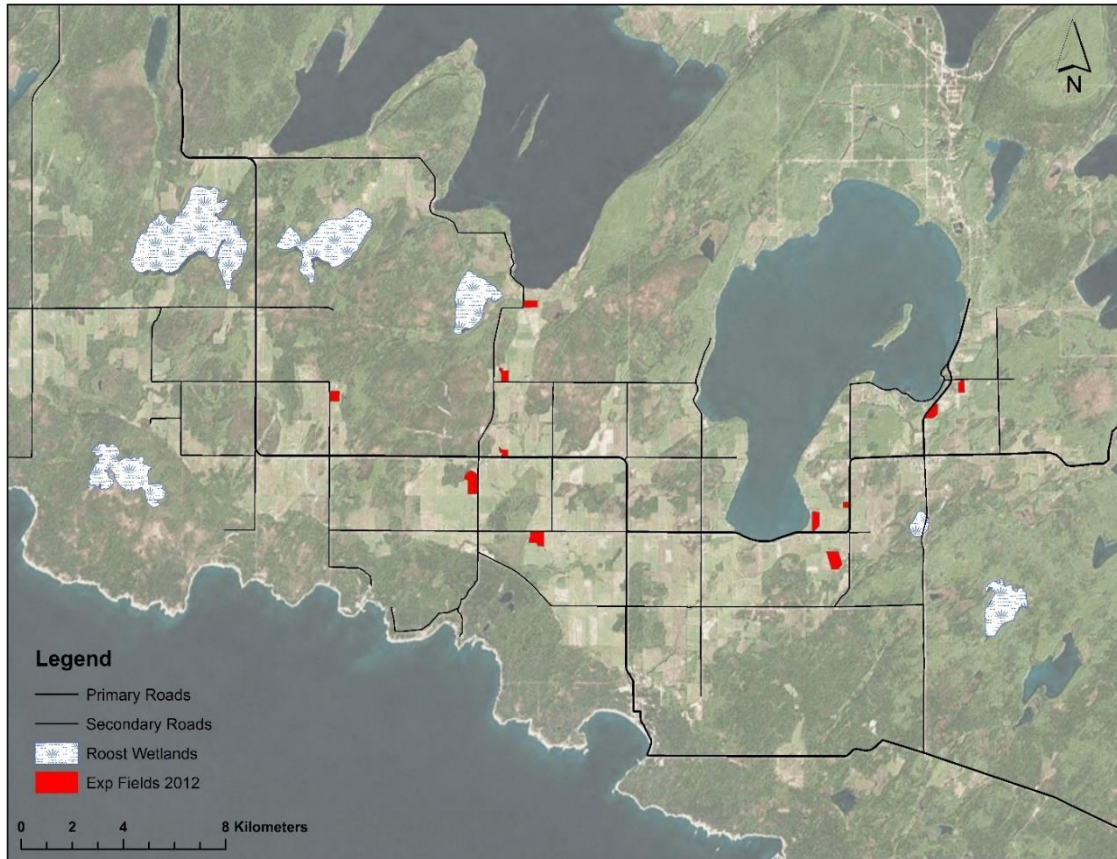
Figure 3.1 Location of experimental focal grain fields used to study agricultural waste grain

density and variation effects on foraging behaviour of Eastern Population Greater Sandhill Cranes

(*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2012.

I classified my four experimental treatments as high, medium, low, and control grain density. I established the target density for each treatment using the maximum grain density and standard deviation (SD) in grain density amongst fields estimated from observational fields in 2011 (maximum = 528.8 kg/ha, SD = 157.6 kg/ha) collected following the sampling protocol described above. The high (686.4 kg/ha) and low (371.2 kg/ha) treatments represented maximum density plus and minus one SD, respectively. The medium treatment represented the maximum grain density. The control treatment was the base density in each experimental field and thus varied between fields.

Before adding barley (*Hordeum vulgare* Linnaeus) to the plots to manipulate grain density, I estimated the base density in each field using the same grain sampling protocol described above (i.e., $n = 20$ systematically placed sampling points per field). Using my base grain density estimate for each field and adjusting for wet mass using a conversion factor, I calculated from the 2011 data (Chapter 2), I calculated the total mass of dried grain to be added to each plot to achieve the experimental density thresholds described above (Table 3.1). I modified standard manual rotary broadcast fertilizer devices (Figure 3.2) to allow for near homogeneous distribution of barley in experimental plots. I estimated rate of distribution for each fertilizer device before use in the field by measuring the distance required to spread a known mass of barley. Using my estimates of rate of distribution, I determined how many equidistant passes would be required to distribute the mass of barley necessary in a given plot to achieve near-homogeneous coverage (i.e., to avoid creating patchy distributions). I distributed predetermined masses of barley in plots on 18 and 19 September 2012.

Table 3.1 Calculations used for creating experimental treatments in fields as part of a study of foraging behaviour in Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2012. Base density (kg/ha), required mass of grain to achieve experimental grain density thresholds (kg), and number of passes required to evenly distribute grain in high (H), medium (H), and low (L) experimental plots are shown.

Field	Base Density (kg/ha)	Grain Added H/M/L (kg)	Passes Required H/M/L
2012-E01	127.9	56.5/40.6/24.6	88/63/39
2012-E02	183.2	50.9/35.0/19.0	80/55/30
2012-E03	23.9	67.0/51.1/35.1	105/80/55
2012-E05	13.1	68.1/52.2/36.2	106/82/57
2012-E06	118.3	57.5/41.5/25.6	90/65/40
2012-E07	119.5	57.4/41.4/25.5	90/65/40
2012-E08	96.6	59.7/43.7/27.8	93/68/43
2012-E09	32.3	66.2/50.2/34.3	103/79/54
2012-E10	8.3	68.6/52.7/36.7	107/82/57

Figure 3.2 Modified standard rotary broadcast fertilizer devices used to distribute barley grain (*Hordeum vulgare* Linnaeus) in 900 m^2 experimental plots.

Following experimental manipulation of grain density in plots, I collected grain samples using the sampling protocol as described above for observational fields. My experimental grain sampling protocol varied in that I collected fewer samples per plot per visit ($n = 15$) than for observational fields per visit ($n = 20$) and that I returned to each plot on an approximately eight- instead of ten-day sampling rotation resulting in a total of two grain sampling events after experimental treatment for each plot.

3.2.5   Behavioural Observations

I checked all observational and experimental focal fields once per day between sunrise and sunset to visually search for cranes and to make and record behavioural observations from vehicles situated at strategic viewing locations. I randomized the order in which fields were visited to prevent bias from repeatedly visiting fields/plots in the same order each day. Where I found cranes anywhere in observational focal fields or within plots in experimental fields, I used a continuous, focal animal sampling protocol to instantaneously classify behaviour to the nearest second according to a crane-specific ethogram (adapted from Tacha *et al*. 1987; Table 3.2). I selected focal cranes for behavioural observation using stratified sampling. I estimated the center of the flock and pointed my spotting scope at that point. I then identified the center of the field of view and searched outwards through the flock either up, left, right, or down (randomized). I selected the first crane encountered searching in the predetermined direction. I first determined the age of each focal crane as either AHY or HY according to head plumage characteristics (Nesbitt & Schwikert 1998). I observed each focal crane for 600 seconds using a spotting scope and digital watch to record the time of each change in behaviour. I

sampled a maximum of three AHY and three HY cranes from each field/plot per visit to

minimize the probability of repeatedly sampling the same individual and to distribute

samples somewhat evenly between observational focal fields/plots in experimental fields.

I aggregated the duration of time spent in each behaviour for individual cranes and

calculated the proportion for each behavioural category.

Table 3.2 Ethogram used to instantaneously classify Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) behaviour in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Adapted from Tacha *et al*. (1987).

Behaviour	Description
Aerial	Feet not in contact with substrate, outside of courtship/socializing (see Alert/Social).
Alert/Social	Vigilant behaviour (e.g., scanning for predators; vocalizing; courtship and distress calls included.
Comfort	Preening feathers with bill or foot, or stretching a limb.
Feeding	Actively probing substrate or standing vegetation, gathering and consuming food items.
Locomotion	Walking or running with head up (not to be confused with Searching).
Out of Sight	Either completely or partially out of view preventing accurate classification of behaviour.
Resting	Sleeping with neck folded down or under wing, or otherwise resting on feet or laying down.
Searching	Typically walking (but can be standing) between bouts of feeding with attention focused on immediate substrate.

3.2.6   Data Handling & Analysis

3.2.6.1   Spatial Analysis

I digitized spatial features of interest related to focal observational fields using

ArcGIS 10.4 (V10.4.0.5524, ESRI 2015). I digitized satellite imagery (Landsat 2008

imagery) of the six primary roost wetlands in my study area and calculated the straight-

line distance, in metres, from the nearest border of each field to the nearest border of the

nearest roost wetland using Near Analysis from the Geoprocessing toolbox. I calculated

area, in square-metres, for all focal observational fields. I estimated total grain (kg;

"T_Grain") for each field by multiplying the estimated grain density (converted to kg/m^2)

by the calculated field area to develop a metric of both field size and total food available.

I estimated grain density values as described in Section 3.2.6.2.

3.2.6.2   Estimating Grain Density & Variation

Because most of my foraging behaviour data were collected on days that I did not

collect grain samples, I needed to estimate field- and plot-specific daily values. I

estimated field-specific daily values for grain density and variation (CV) using linear

mixed-effects (LME) models with maximum likelihood estimation in the *lme4* package

(function: *lme*; Bates *et al*. 2015) in R Studio (V3.3.0, R Core Team 2016). For a

comprehensive description of modelling grain density and variation, please refer to

Section 2.2.6.2 in Chapter 2.

I also estimated plot-specific daily values for grain density and variation (CV) using

LME models with maximum likelihood estimation in the *lme4* package (function: *lme*;

Bates *et al*. 2015) in R Studio (V3.3.0, R Core Team 2016). I ran six models with log-

transformed grain density ("LDensity") as the continuous response variable and field identifier as a random effect ("1|fField") to estimate daily grain density values. I included an additive treatment effect (control, low, medium, or high as defined in Section 3.2.4/Table 3.1 above; "fTreat") as well as an interactive effect with days since treatment ("DST"). To determine which model best fit my data, I ran six models alternating between random intercept and random intercept and slope models with interactive and additive effects to model the rate of change in grain density (slope) as it related to initial value after treatment (intercept) within plots (Table 3.3). I compared AIC values to select the most parsimonious predictive model from my candidate set. I identified and retained the most parsimonious model to predict daily grain density values for each plot. I repeated the same modelling process using my plot-specific CV data (Table 3.4). I estimated daily values for both grain density and CV with the top model (i.e., lowest AIC value) from each candidate set (function: *predict*) for use as predictor variables in subsequent modelling.

Table 3.3 Candidate linear mixed-effects models using days since treatment ("DST") as a continuous predictor and treatment level ("fTreat") with random intercept and random slope and intercept terms used to predict log-transformed grain density (log kg/ha; "LDensity") in experimental plots. The most parsimonious model (lowest AIC value) was used to predict daily grain density (continuous response) values for subsequent modelling of foraging behaviour data. Model names (Model) and structures (Structure) are shown.

Model	Structure
explmD1	LDensity ~ DST, random: fField_ID
explmD2	LDensity ~ DST + fTreat, random: fField_ID
explmD3	LDensity ~ DST*fTreat, random: fField_ID
explmD4	LDensity ~ DST, random: DST | fField_ID
explmD5	LDensity ~ DST + fTreat, random: DST | fField_ID
explmD6	LDensity ~ DST*fTreat, random: DST | fField_ID

Table 3.4 Candidate linear mixed-effects models using days since treatment (DST) as a continuous predictor and treatment level (fTreat) with random intercept and random slope and intercept terms. The most parsimonious model (lowest AIC value) was used to predict daily variation (coefficient of variation; CV; continuous response) values for subsequent modelling of foraging behaviour data. Model names (Model) and structures (Structure) are shown.

Model	Structure
explmCV1	CV ~ DST, random: fField_ID
explmCV2	CV ~ DST + fTreat, random: fField_ID
explmCV3	CV ~ DST*fTreat, random: fField_ID
explmCV4	CV ~ DST, random: DST | fField_ID
explmCV5	CV ~ DST + fTreat, random: DST | fField_ID
explmCV6	CV ~ DST*fTreat, random: DST | fField_ID

3.2.6.3   Observational Foraging Behaviour

To develop a metric to represent foraging efficiency, I calculated a searching-to-feeding ratio (SF) by dividing time spent searching by time spent feeding. As such, SF values greater than one indicate more time searching than feeding, and values less than one indicate more time feeding than searching (i.e., greater foraging efficiency). Before SF calculation, I added 30 seconds to both searching and feeding times for each observation to improve zero-truncation/inflation. I excluded observations where cranes spent no time feeding. Because I was not able to measure actual consumption rates, I used time spent feeding as a proxy as in other studies of ground-foraging birds (Morgan & Fernández-Juricic 2007; but see Powolny *et al*. 2012).

Using grain density and CV values estimated from the modelling procedures described above as continuous predictors, I built LME models using maximum likelihood estimation in the *nlme* package (function: *lmer*; Pinheiro *et al*. 2016) in R Studio (V3.3.0, R Core Team 2016) to analyze the age-specific response of crane foraging efficiency as it relates to grain density and variation. Predictor variables are explained in Table 3.5. I inspected data for outliers using scatterplots and boxplots prior to building models. I used log transformations to improve predictor variable distributions where outliers were suspected (see Section 3.3.3 for treatment of outliers). I ran a candidate set of eight observational models (Table 3.6) and compared AIC values to select the most parsimonious model. I calculated Akaike differences (ΔAIC) and normalized their values to sum to 1.0 to assess the relative support for each of my candidate models (^{W}AIC). I selected the model with the lowest AIC value as the best from the candidate set.

Table 3.5 Predictor variables used to analyze observational foraging behaviour of adult (AHY) and juvenile (HY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) feeding in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

Variable Name	Description	Specific Use
Month	Month behavioural observation was recorded	Categorical predictor with three levels (August, September, or October)
Age	Focal crane age class	Categorical predictor with two levels (juvenile, HY, or adult, AHY
Field_ID	Field label	Identifier with 39 levels used to control for random (field) effects
Prox_Roost	Straight line distance from field edge to nearest roost wetland edge (m)	Continuous predictor; metric of field location effects
Density	Daily grain density (kg/ha)	Continuous predictor; metric of foraging efficiency
CV	Daily coefficient of variation from grain estimates	Continuous predictor; metric of foraging efficiency
Total Grain	Estimated total mass of grain available in each field (kg)	Continuous predictor; metric of foraging efficiency

I developed an *a priori* candidate set of models (Table 3.6) based on existing knowledge of the species' foraging behaviour during autumn staging at my study site. I built this candidate set using the following approach.

I included the observation month (Month), proximity to roost (Prox_Roost), and crane age (Age) terms in all candidate models because I wanted to evaluate the relative importance of these variables in determining foraging behaviour. I included observation month to control for seasonal changes in foraging ecology as foraging behaviour is known to change in relation to departure date in migratory birds (Prop *et al*. 2003, Smith & McWilliams 2014, Cohen *et al*. 2014). I converted the proximity to roost variable from metres to kilometres to mitigate issues with substantial differences in variable scales when running mixed-models. I included crane age in all models to account for age-specific differences in foraging behaviour. Lastly, I included field identifier (fField_ID) as a random variable in all models to preserve field-level effects.

I created Modnull and Modfull for comparison as per standard information-theoretic model selection procedure (Burnham & Anderson 2002). I included all additive (random and fixed) effects in Modfull. I built Mod1 to account for the singular effects of grain density (Density) on foraging behaviour. I replaced grain density with grain variation (CV) in Mod2 to account for the singular effects of grain variation on foraging behaviour. In Mod3, I included both grain density and variation to account for concurrent additive effects on foraging behaviour. In Mod4, I included grain density and total grain mass (T_Grain) to model concurrent additive effects of food density and total amount of food on foraging behaviour. In Mod5, I included grain variation and total grain mass to model concurrent additive effects of grain variation and total amount of food on foraging

behaviour. Finally, in Mod6, I considered the singular effect of total grain mass on foraging behaviour.

In aggregate, I developed these models to investigate the age-specific relationship between crane foraging behaviour and food density and variation during autumn staging at my study site. I predicted that grain density and variation are important variables in determining foraging behaviour and that their effects are age-specific. That is, I expected to find a stronger effect from food density and variation for HY cranes as compared to AHY conspecifics in my top model.

Table 3.6 Candidate set of linear mixed-effects models used to analyze observational foraging behaviour of Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) feeding in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Variables written with an "L" (e.g., LDensity) were log transformed. Variables written with an "f" (e.g., fMonth) were treated as factors. All models listed below also included field ID as a random effect.

Model	K	Structure
Modnull	1	1
Mod1	5	fMonth + Prox_Roost + fAge + LDensity
Mod2	5	fMonth + Prox_Roost + fAge + LCV
Mod3	6	fMonth + Prox_Roost + fAge + LDensity + LCV
Mod4	6	fMonth + Prox_Roost + fAge + LDensity + LT_Grain
Mod5	6	fMonth + Prox_Roost + fAge + LCV + LT_Grain
Mod6	5	fMonth + Prox_Roost + fAge + LT_Grain
Modfull	7	fMonth + Prox_Roost + fAge + LDensity + LCV + LT_Grain

I selected the model with the lowest AIC value for subsequent analysis and validation. I used a backwards single term deletion procedure (function: *drop1*) to determine if removing a particular predictor variable from the top model would improve model performance (i.e., reduce the AIC value). If model performance was improved by removing a predictor variable according to single term deletions, I continued removing predictor variables and refitting the model until the AIC value could not be improved. Where I built an improved reduced model using the single term deletion procedure, I selected the model for further analysis and interpretation. I plotted standardized (Pearson) residuals against all fixed, continuous predictor variables (i.e., not included, dropped, and retained) to evaluate the performance of the retained model. If I did not find patterns in my residual plots, I proceeded with the model validation procedure described below. I also estimated and report variance for random effects as an additional model evaluation statistic.

To isolate the individual contribution of each retained fixed, continuous predictor variable, I simulated new datasets ($n = 100$) for each predictor variable and predicted new values for the response variable using my final LME model. I set data points for the focal variable in each simulated dataset to equidistant values starting at the minimum value from my observations and extending to the maximum. I set data points for non-focal variables to the respective mean value from my observations. I excluded the random effect (Field_ID) from the prediction (function: *predict*; re.form=~0). I used separate simulated datasets for each combination of levels from retained categorical predictors ($n = 18$ unique simulated datasets). I plotted predicted values against observed values to graphically convey estimated predictor-specific effects.

3.2.6.4 Experimental Foraging Behaviour

I calculated SF values for experimental foraging behaviour data in the same manner as described above. I also used grain density and CV values estimated from the modelling procedures described above as continuous predictors in building LME models using maximum likelihood estimation in the *nlme* package (function: *lmer*; Pinheiro *et al*. 2016) in R Studio (V3.3.0, R Core Team 2016) to analyze the age-specific response of crane foraging efficiency as it relates to grain density and variation in an experimental context (see Table 3.7 for a description of predictor variables). I inspected, handled, and treated experimental data identically to observational data (see Section 3.3.4 for treatment of outliers). I ran a candidate set of six experimental models (Table 3.8) and used an information-theoretic approach to identify the best model for my experimental dataset.

Table 3.7 Predictor variables used to analyze experimental foraging behaviour of adult (AHY) and juvenile (HY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) feeding in experimental plots in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2012.

Variable Name	Description	Specific Use
Treatment	Experimental treatment	Categorical predictor with four levels (High, Medium, Low, and Control)
Age	Focal crane age	Categorical predictor with two levels: juvenile (HY) or adult (AHY)
Field_ID	Field label	Unique identifier with 9 levels used to control for random (field) effects
Density	Daily grain density (kg/ha)	Continuous predictor; metric of foraging efficiency
CV	Daily coefficient of variation from grain estimates	Continuous predictor; metric of foraging efficiency

Similar to my observational analysis, I developed an *a priori* candidate set of models for my experimental analysis (Table 3.8) based on existing knowledge of the species' foraging behaviour in grain fields during autumn staging at my study site. I built the candidate set of models shown in Table 3.8 using the following approach.

I included experimental treatment (Treatment) and crane age (Age) terms in all candidate models because I wanted to evaluate the relative importance of these variables in determining foraging behaviour. I included crane age in all models to account for age-specific differences in foraging behaviour and field identifier (fField_ID) as a random effect.

As described above for my observational behaviour analysis, I created Modnull and Modfull to serve as benchmarks (Burnham & Anderson 2002) and used an identical approach to develop five candidate models (Mod1-Mod5) to experimentally investigate the age-specific relationship between crane foraging behaviour and grain density and variation during autumn staging.

Table 3.8 Candidate set of linear mixed-effects models used to analyze experimental foraging behaviour of Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) feeding in harvesed agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2012. Variables written with an "L" (e.g., LDensity) were log transformed. Variables written with an "f" (e.g., fMonth) were treated as factors. All models listed below also included field ID as a random effect.

Model	K	Structure
Modnull	1	1
Mod1	4	fTreat + fAge + LDensity
Mod2	4	fTreat + fAge + LCV
Mod3	4	fTreat + fAge*LDensity
Mod4	4	fTreat + fAge*LCV
Modfull	5	fTreat + fAge*LDensity*LCV

In interpreting the results of my experimental data analysis, I followed the same model reduction and inspection procedures as described above for my observational data analysis. I also simulated datasets as appropriate to isolate the individual contribution of each retained fixed, continuous predictor variable in my experimental data analysis using my final experimental LME model. I plotted predicted values against observed values to graphically convey estimated predictor-specific effects.

3.3   Results

3.3.1   *Observational Grain Density & Variation Estimation*

I selected the random intercept and slope DSC predictor model for use in estimating daily grain density values. For a comprehensive summary of observational grain density results, please refer to Section 2.4.1 in Chapter 2.

I also attempted to run four grain CV LME models using data ($n = 121$ grain CV estimates) from 28 groups (fields). For both the DSC and Julian predictors, I could not successfully retrieve modelling results from the random intercept and slope models for CV data due to a lack of convergence in parameter estimation. I opted to use the DSC predictor model to estimate daily grain CV values for use in subsequent modelling. For a comprehensive summary of observational grain variation results, please refer to Section 2.4.1 in Chapter 2.

3.3.2   Experimental Grain Density & Variation Estimation

I ran six LME models using experimental data ($n = 72$ grain density estimates) from 36 unique treatment by field group combinations. I used a log transformation to improve the distribution of grain density prior to running models. Neither of my random intercept and random slope models that included DST and Treatment converged, so I did not include them in further analyses. Both random intercept only models that included additive or interactive effects from DST and Treatment received most of the support in the analysis (i.e., ^{W}AIC: ~1.0). In comparing the two top models, the additive DST and Treatment model received most of the support comparing AIC weights (^{W}AIC = 0.94 for additive and 0.06 for interactive; Table 3.9). Thus, I selected the additive DST and Treatment model for use in estimating daily grain density values (Figure 3.4). According to the top predictor model, an increase of one unit in DST resulted in a change ($\pm$ SE) of -0.07 $\pm$ 0.01 in grain density (log kg/ha). In terms of the size of the treatment effects (coefficient $\pm$ SE) compared to the Control level, the Medium treatment (0.79 $\pm$ 0.12) had the greatest effect, followed by the High (0.65 $\pm$ 0.12) and then Low treatments (0.60 $\pm$ 0.12).

Table 3.9 Candidate linear mixed-effects models using days since treatment (DST) with random intercept and random slope and intercept terms. Model names (Model) and structures (Structure), number of parameters (K), and Akaike's Information Criterion scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown. The most parsimonious model (lowest AIC value) was used to predict daily grain density (continuous response) values for subsequent modelling of experimental foraging behaviour data.

Model	Structure†	K	AIC	ΔAIC	^{W}AIC
explmD2	GD = 1+2, RI	3	86.2	0.0	0.94
explmD3	GD = 1*2, RI	3	91.8	5.6	0.06
explmD1	GD = 1, RI	2	120.5	34.3	0.00
explmD4	GD = 1, RIS	2	124.5	38.3	0.00
explmD5	GD = 1+2, RIS	3	Did not converge	--	--
explmD6	GD = 1*2, RIS	3	Did not converge	--	--

† **GD** = grain density, **1** = days since treatment, **2** = treatment (H, M, L, or C), **RI** = random intercept, **RIS** = random intercept and slope.

I ran six LME models using experimental data ($n = 72$ grain variation estimates) from 36 unique treatment by field group combinations. Both of my random intercept and random slope models that included DST and Treatment did not converge once more so I did not include them in further analyses. Both random intercept only models that included additive or interactive effects from DST and Treatment received most of the support in the analysis (i.e., ^{W}AIC: ~1.0). In comparing the two top models, the additive DST and Treatment model received most of the support comparing AIC weights (^{W}AIC = 0.91 for additive and 0.09 for interactive; Table 3.10). Thus, I selected the additive DST and Treatment model for use in estimating daily grain variation values (Figure 3.4). According to the top predictor model, an increase of one unit in DST resulted in a change ($\pm$SE) of 0.0004 ± 0.0001 in grain density (log kg/ha). In terms of the size of the treatment effects (coefficient $\pm$ SE) compared to the Control level, the High treatment (-0.007 ± 0.001) had the greatest effect, followed by Medium (-0.006 ± 0.001) and Low treatments (-0.006 ± 0.001).

Table 3.10 Candidate linear mixed-effects models using days since treatment (DST) with random intercept and random slope and intercept terms. Model names (Model) and structures (Structure), number of parameters (K), and Akaike's Information Criterion scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown. The most parsimonious model (lowest AIC value) was used to predict daily grain variation (continuous response) values for subsequent modelling of experimental foraging behaviour data.

Model	Structure†	K	AIC	ΔAIC	^{W}AIC
explmCV2	CV = 1+2, RI	3	-591.6	0.00	0.91
explmCV3	CV = 1*2, RI	3	-587.0	4.6	0.09
explmCV1	CV = 1, RI	2	-561.6	30.0	0.00
explmCV4	CV = 1, RIS	2	-557.6	34.0	0.00
explmCV5	CV = 1+2, RIS	3	Did not converge	--	--
explmCV6	CV = 1*2, RIS	3	Did not converge	--	--

† **CV** = coefficient of variation, **1** = days since treatment, **2** = treatment (H, M, L, or C), **RI** = random intercept, **RIS** = random intercept and slope.
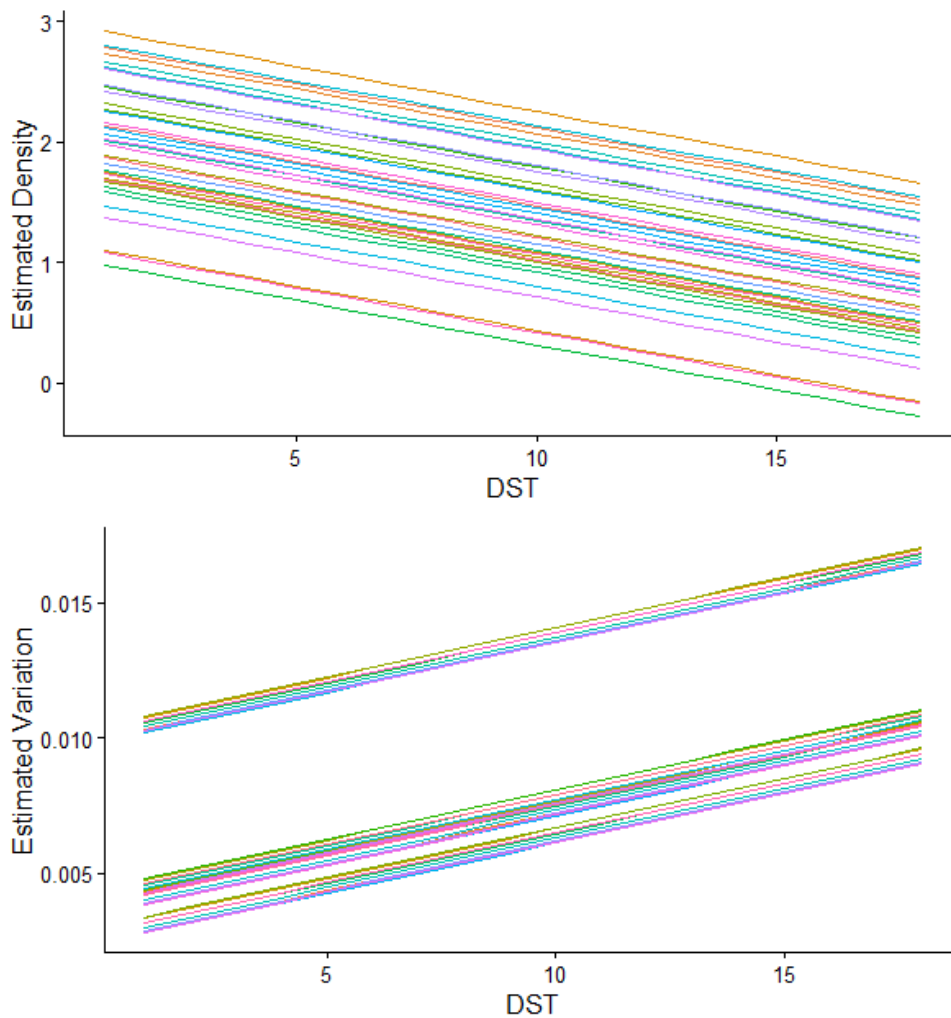
Figure 3.4 Estimated grain density (log kg/ha) and variation (CV) values calculated with linear

mixed-effects models including random intercept terms plotted against days since treatment

(DST). DST refers to the number of days since a plot was experimentally treated (i.e., with grain

supplementation). Grain density was calculated in kg/ha but is displayed log transformed (log

kg/ha). Grain variation was calculated as the coefficient of variation amongst grain density

samples. Line colours indicate field/treatment combinations ($n = 36$; four treatments in nine

fields). Data were collected in experimental plots in harvested agricultural grain fields at

Manitoulin Island, Ontario, Canada in autumn 2012.

3.3.3   Observational Behaviour

I attempted to collect approximately equal samples between age classes. Over the

course of two years, I recorded a total of 825 observations of AHY ($n = 117$ and 306 in

2011 and 2012, respectively) and HY cranes ($n = 127$ and 275 in 2011 and 2012,

respectively). In aggregate, I observed cranes in observational focal fields for 40.7 and

96.8 hours in 2011 and 2012, respectively. I omitted 14 observations each of the AHY

and HY datasets because I was not able to gain access for grain sampling. I also omitted

another 16 AHY observations ($n = 4$ in 2011 and 12 in 2012) and 4 HY observations (all

in 2012) where cranes did not spend any time feeding during observation. Finally, I

omitted two AHY observations from 2012 and one HY observation from 2011 that I

considered outliers by comparing those SF values (26.3 and 54.0, and 12.4, respectively)

to the mean SF ($\pm$ SD) 1.24 ± 0.6 from my dataset. This resulted in a total of 774

observations ($n = 391$ AHY and 383 HY observations; Figure 3.5).

HY cranes tended to spend greater proportions of time feeding compared to AHY

cranes, though differences were greater in 2011 than in 2012 (Figure 3.6). Foraging

efficiency increased from September to October for both HY and AHY cranes in 2011

but not in 2012 (Figure 3.7). Foraging efficiency appeared to increase for both age

classes approaching migratory departure in 2011 but not in 2012 (Figure 3.8).
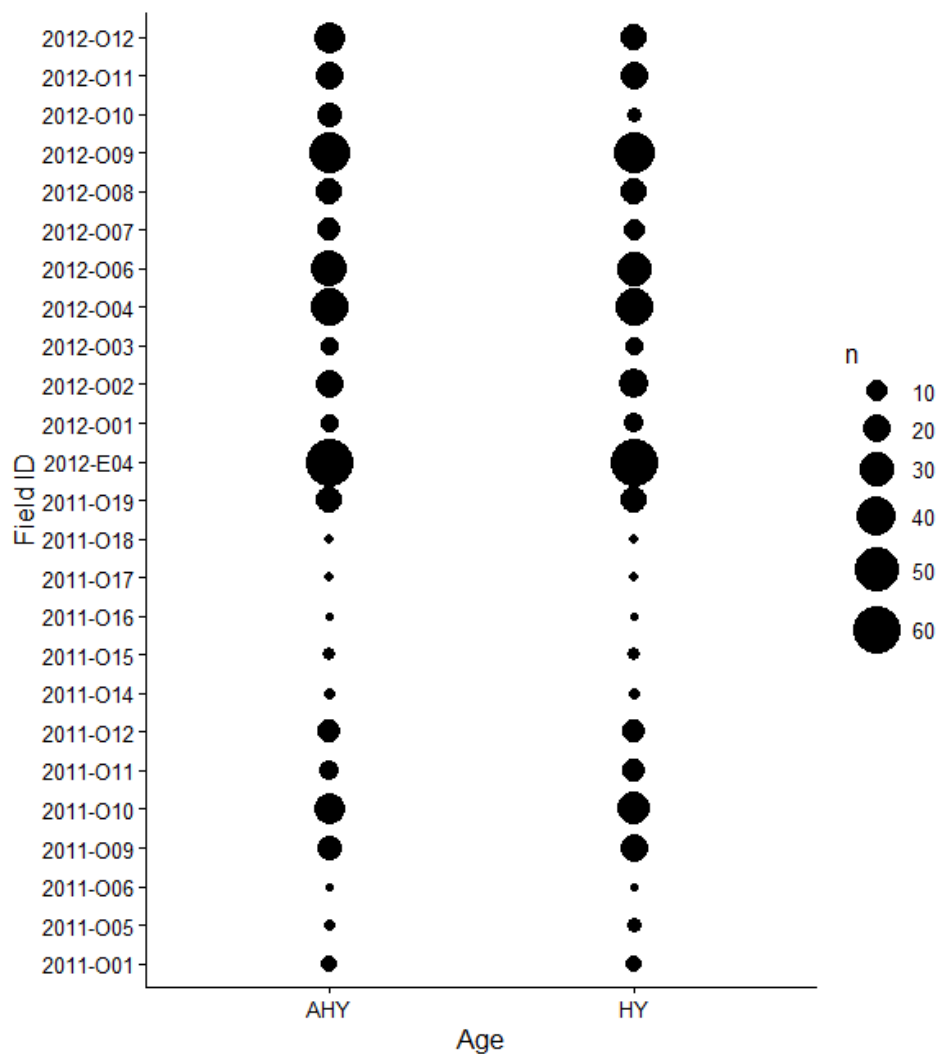
Figure 3.5 Distribution of observation events (*n* = 774) by field (year-specific label) and age (adult = AHY or juvenile = HY) used to collect foraging behaviour data from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
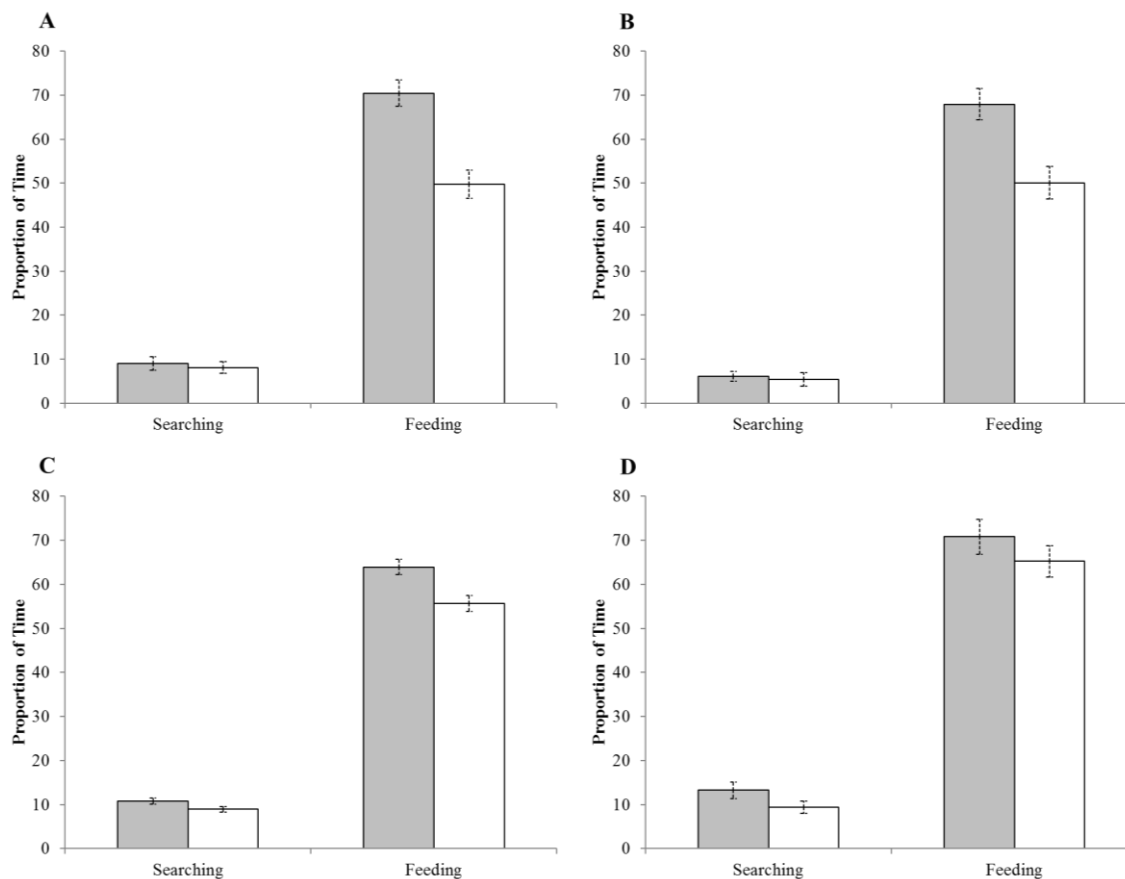
Figure 3.6 Mean (% ± SE) age-specific proportional searching and feeding time by month/year combination; **A**) September 2011, **B**) October 2011, **C**) September 2012, and **D**) October 2012. Shaded bars represent juvenile (HY) cranes and open bars represent adult (AHY) cranes. Data were collected from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
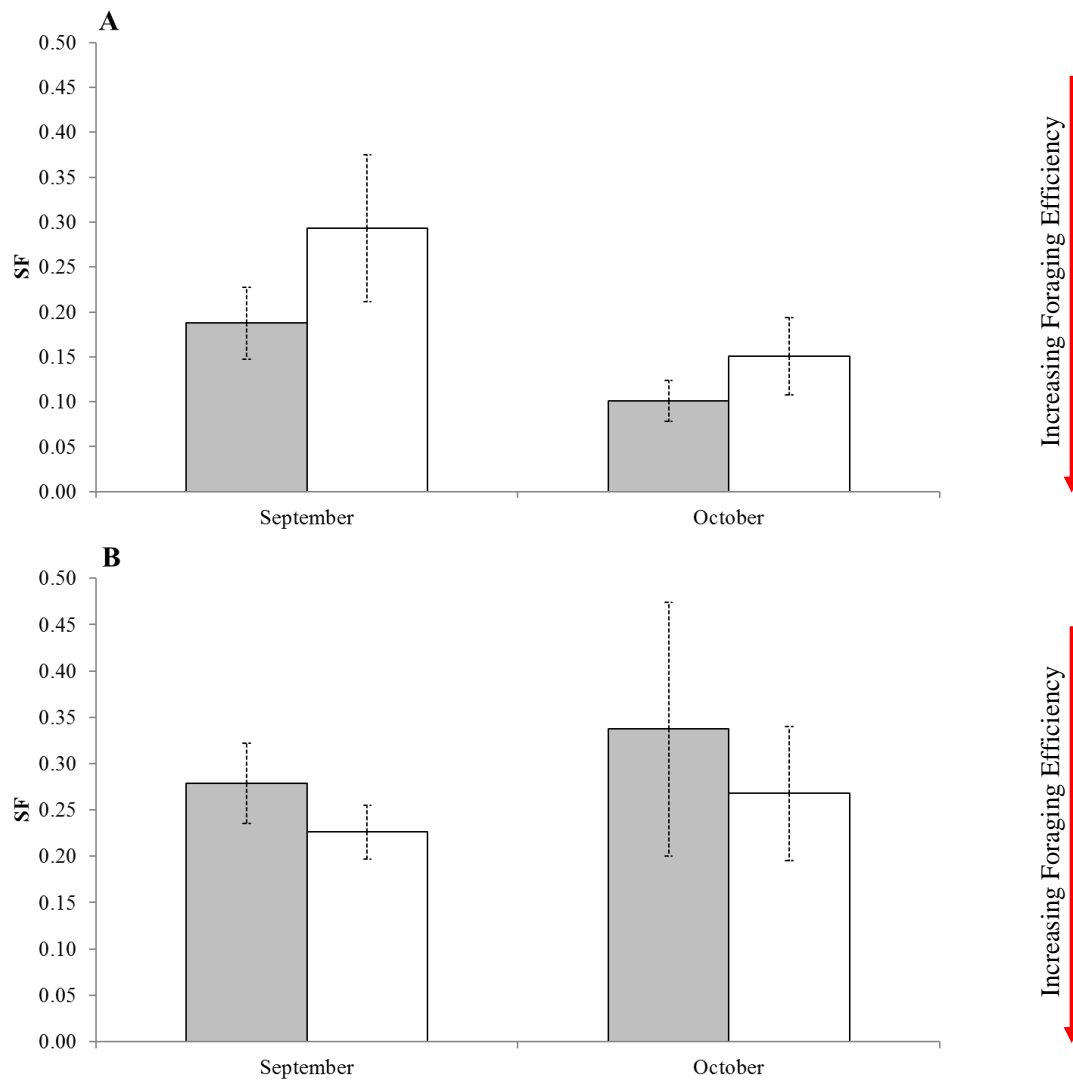
Figure 3.7 Mean (±SE) age-specific foraging efficiency (searching:feeding ratio; SF) by month/year combination; **A**) 2011 and **B**) 2012. Lesser SF values indicate greater foraging efficiency. Shaded bars represent juvenile (HY) cranes and open bars represent adult (AHY) cranes. Data were collected from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
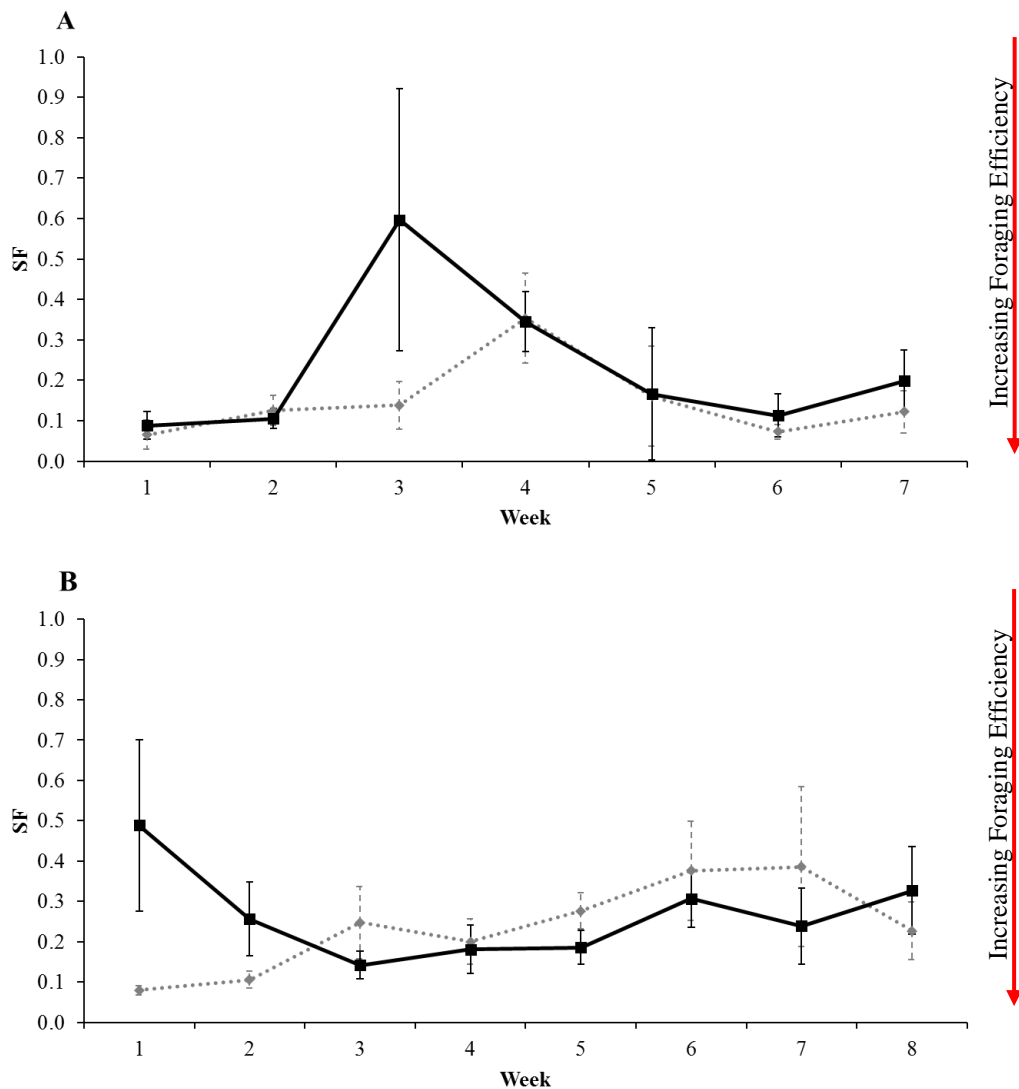
Figure 3.8 Mean (±SE) age-specific foraging efficiency (searching:feeding ratio; SF) by week (Week 1 = 5 September and 20 August for 2011 and 2012, respectively) and year; **A**) 2011 and **B**) 2012. Lesser SF values indicate greater foraging efficiency. Dashed, grey line = juvenile (HY) cranes and solid, black line = adult (AHY) cranes. Data were collected from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

I used a log transformation to improve the distribution of the SF response variable before initiating the modelling procedure. I also log-transformed grain density, grain variation, and total grain.

The top model in fitting my behavioural observation dataset (Mod5) included the following additive effects: observation month, distance to roost wetland, crane age, log-transformed grain variation (CV), and log-transformed total grain. Mod5 received 32% of the available support per AIC weight calculations (Table 3.11). The second-best model (Mod6) received 17% of the available support and differed from Mod5 only in lacking the log-transformed CV term. Backwards single term deletions did not suggest removing any of the original terms in Mod5 to improve model performance (Table 3.12). Cranes foraged with greater efficiency in September and October as compared to August and HY cranes foraged with greater efficiency as compared to AHY conspecifics (parameter estimates in Table 3.13; plots of predicted values from my final top model in Figures 3.9-3.14). In addition, foraging efficiency decreased with distance to roost wetlands and greater grain variation and increased with increasing total grain.

Table 3.11 Candidate linear mixed-effects models used to analyze Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) foraging behaviour related to grain density and variation at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Model names (Model) and structures (Structure), number of parameters (K), degrees of freedom (df), and Akaike's Information Criterion scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown.

Model	Structure†	K	df	AIC	ΔAIC	^{W}AIC
Mod5	FE = 1+2+3+5+6	6	9	-1669.3	0.0	0.32
Mod6	FE = 1+2+3+6	7	8	-1668.1	1.2	0.17
Mod2	FE = 1+2+3+5	8	8	-1667.5	1.9	0.13
Modfull	FE = 1+2+3+4+5+6	10	10	-1667.4	2.0	0.12
Mod3	FE = 1+2+3+4+5	8	9	-1667.3	2.0	0.11
Mod4	FE = 1+2+3+4+6	6	9	-1666.6	2.7	0.08
Mod1	FE = 1+2+3+4	5	8	-1666.4	3.0	0.07
Modnull	FE = null	1	3	-1642.6	26.7	0.00

† FE = foraging efficiency (searching:feeding ratio), **1** = month, **2** = proximity to roost, **3** = age class, **4** = grain density, **5** = grain variation (CV), **6** = total grain.

Table 3.12 Results from backwards single term deletion procedure for top linear mixed-effects model used to analyze Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) foraging behaviour with grain density and variation at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Name of predictor variable being removed (Removed Predictor), change in degrees of freedom (df), Akaike's Information Criterion scores (AIC), and potential change in AIC (ΔAIC) are shown.

Predictor Removed	df	AIC	ΔAIC
None	--	-1669.3	--
Month	2	-1665.4	+3.9
T_Grain	1	-1667.5	+1.8
CV	1	-1668.1	+1.2
Age	1	-1668.6	+0.7
Prox_Roost	1	-1669.2	+0.1

Table 3.13 Top linear mixed-effects model used to analyze Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) foraging behaviour with grain density and variation at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Model names (Mod), number of parameters (K), degrees of freedom (df), Akaike's Information Criterion score (AIC), random effect variance (RV; Field_ID), and coefficient estimates (±SE) are given. Mo9 and Mo10 represent changes in the response variable from August to the September and October month categories, respectively. AgeHY represents changes in the response variable from the adult (AHY) to juvenile (HY) age categories.

Mod	K	df	AIC	RV	Intercept	Mo9	Mo10	Prox_Roost	AgeHY	CV	T_Grain
Mod5	6	9	-1669.4	0.0002	0.03±0.07	-0.02±0.01	-0.04±0.01	0.004±0.003	-0.01±0.006	0.36±0.19	-0.07±0.04
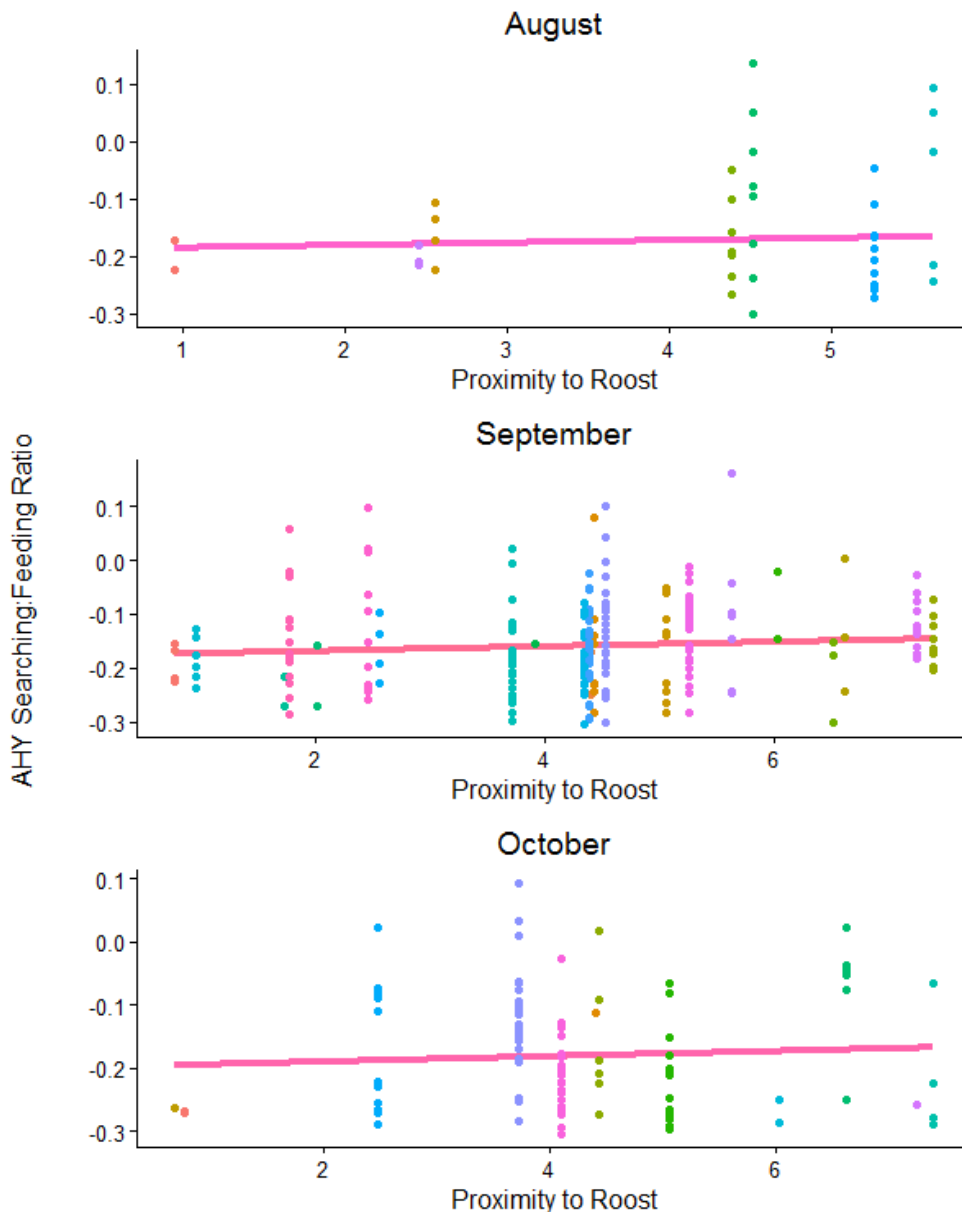
Figure 3.9 Predicted lines for retained predictor variables (Proximity to Roost; km) from linear mixed-effects modelling plotted against log-transformed foraging efficiency of adult (AHY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other continuous predictor variables were set to mean values at all levels of categorical predictors to isolate predictor-specific effects. Dot colours show field/year combinations. Data were collected from cranes in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
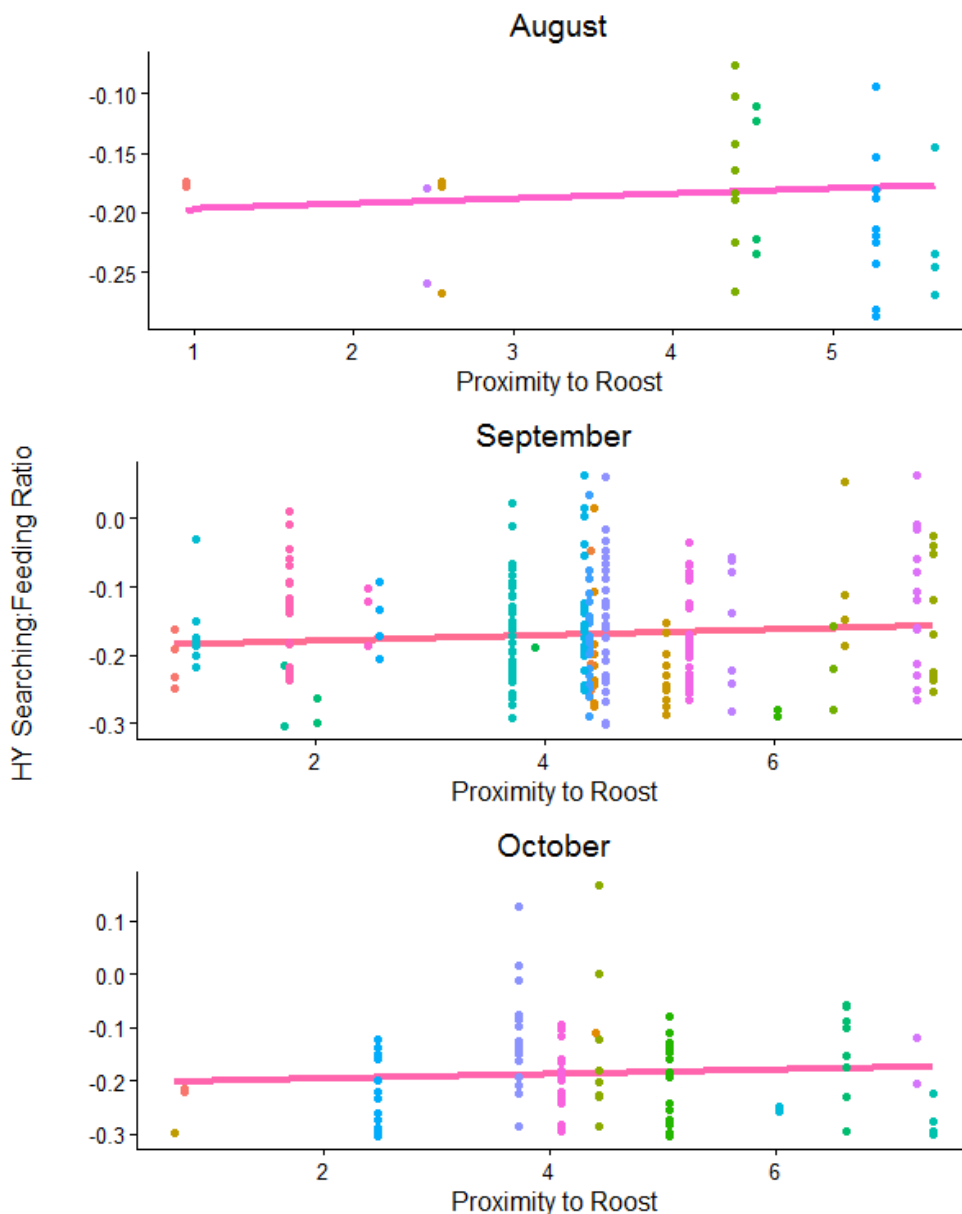
Figure 3.10 Predicted lines for retained predictor variables (Proximity to Roost; km) from linear mixed-effects modelling plotted against log-transformed foraging efficiency of juvenile (HY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other continuous predictor variables were set to mean values at all levels of categorical predictors to isolate predictor-specific effects. Dot colours show field/year combinations. Data were collected from cranes in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
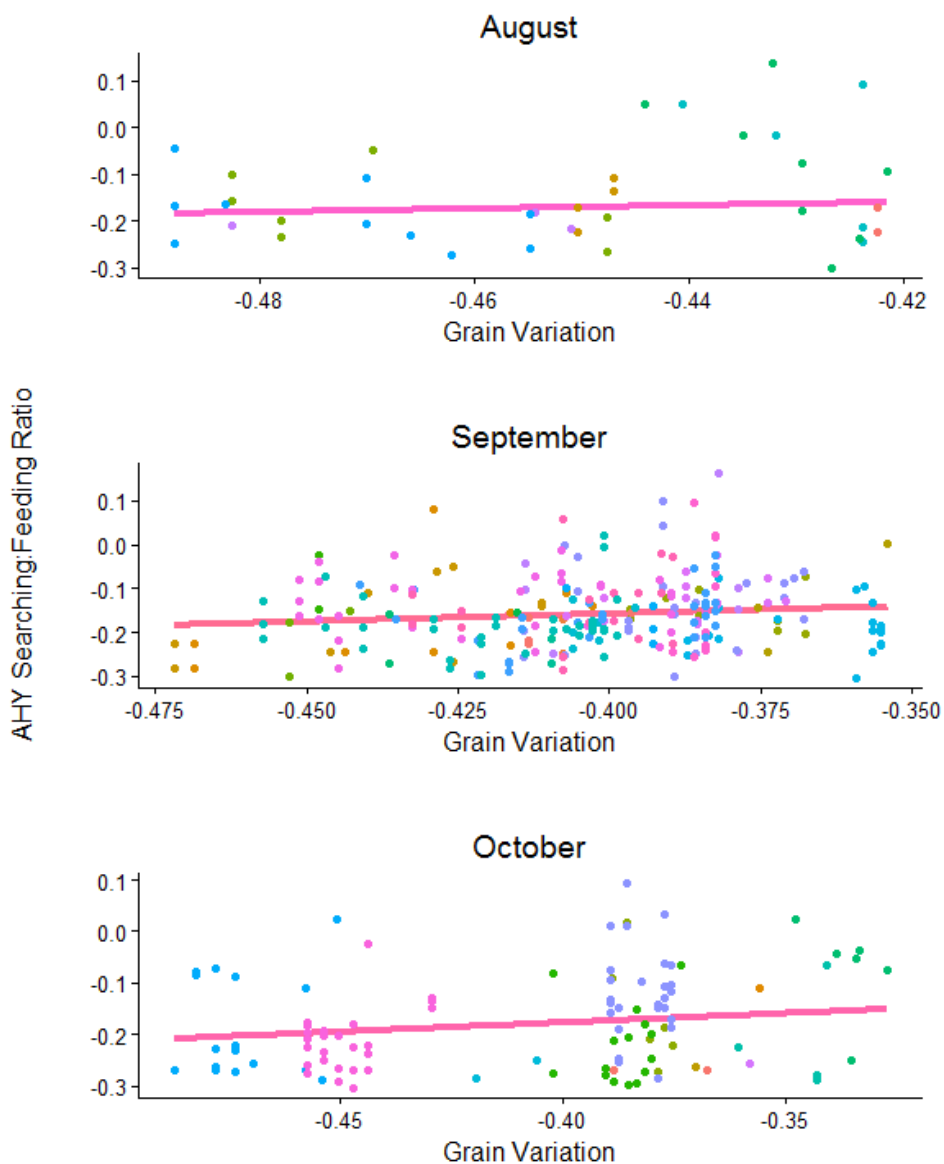
Figure 3.11 Predicted lines for retained predictor variables (Grain Variation; coefficient of variation) from linear mixed-effects modelling plotted against log-transformed foraging efficiency of adult (AHY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other continuous predictor variables were set to mean values at all levels of categorical predictors to isolate predictor-specific effects. Dot colours show field/year combinations. Data were collected from cranes in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
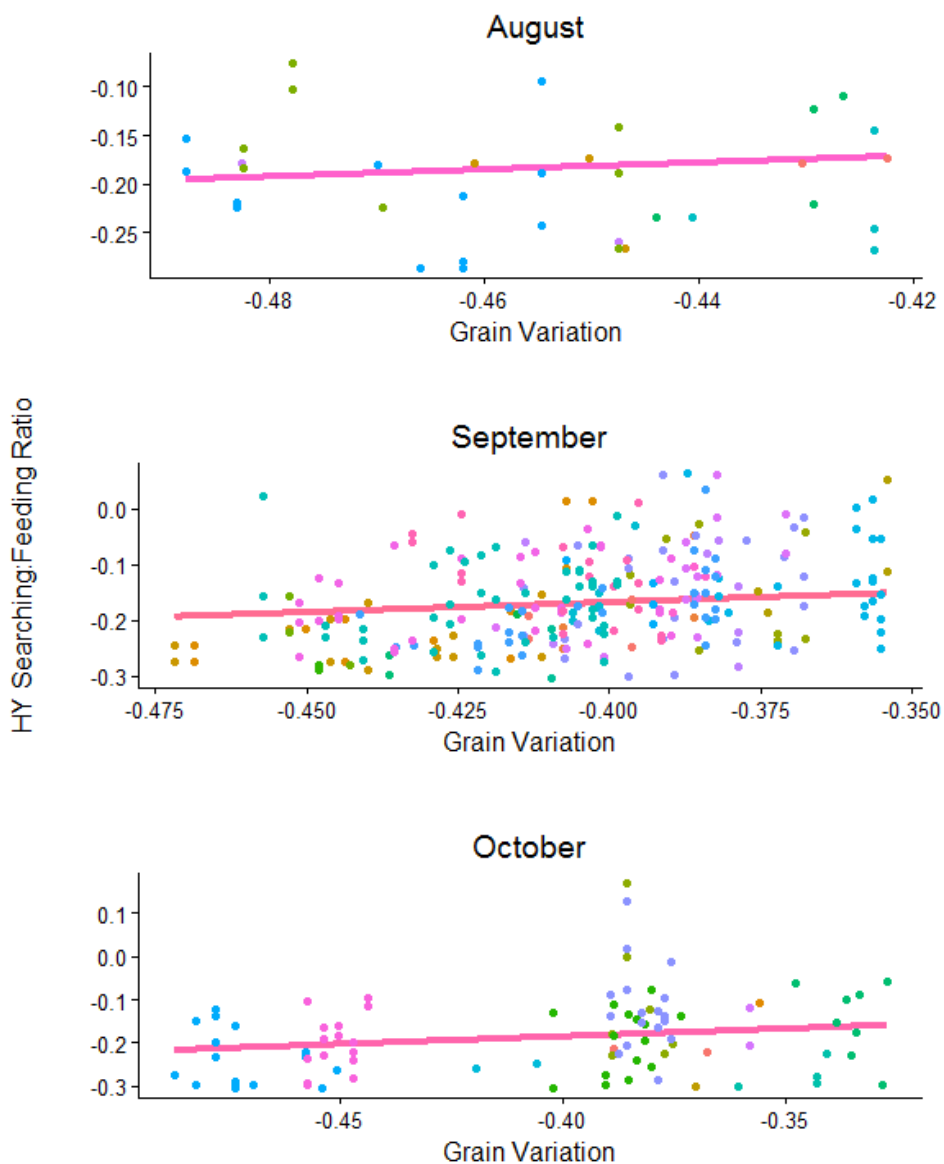
Figure 3.12 Predicted lines for retained predictor variables (Grain Variation; coefficient of variation) from linear mixed-effects modelling plotted against log-transformed foraging efficiency of juvenile (HY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other continuous predictor variables were set to mean values at all levels of categorical predictors to isolate predictor-specific effects. Dot colours show field/year combinations. Data were collected from cranes in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
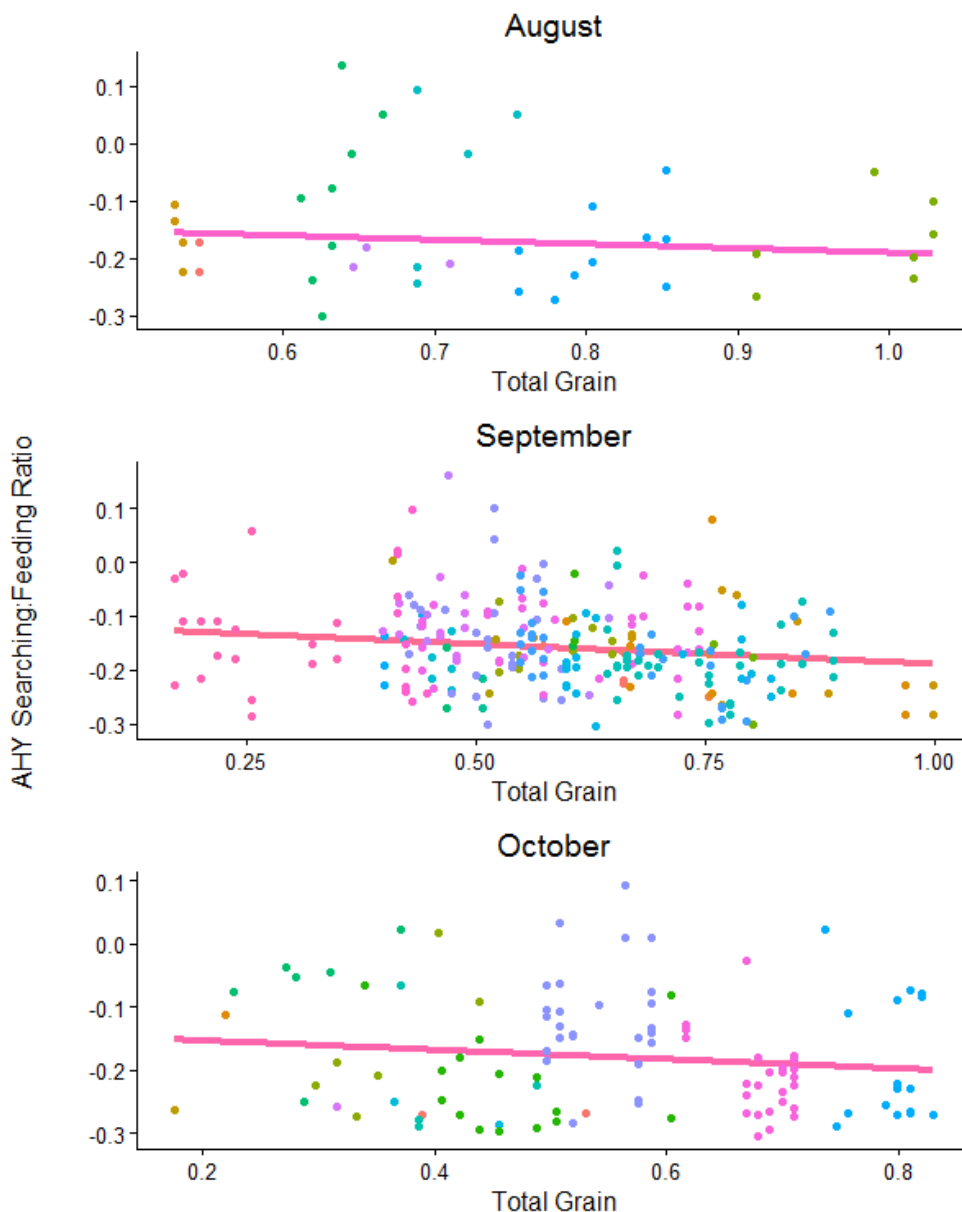
Figure 3.13 Predicted lines for retained predictor variables (Total Grain; kg) from linear mixed-effects modelling plotted against log-transformed foraging efficiency of adult (AHY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other continuous predictor variables were set to mean values at all levels of categorical predictors to isolate predictor-specific effects. Dot colours show field/year combinations. Data were collected from cranes in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
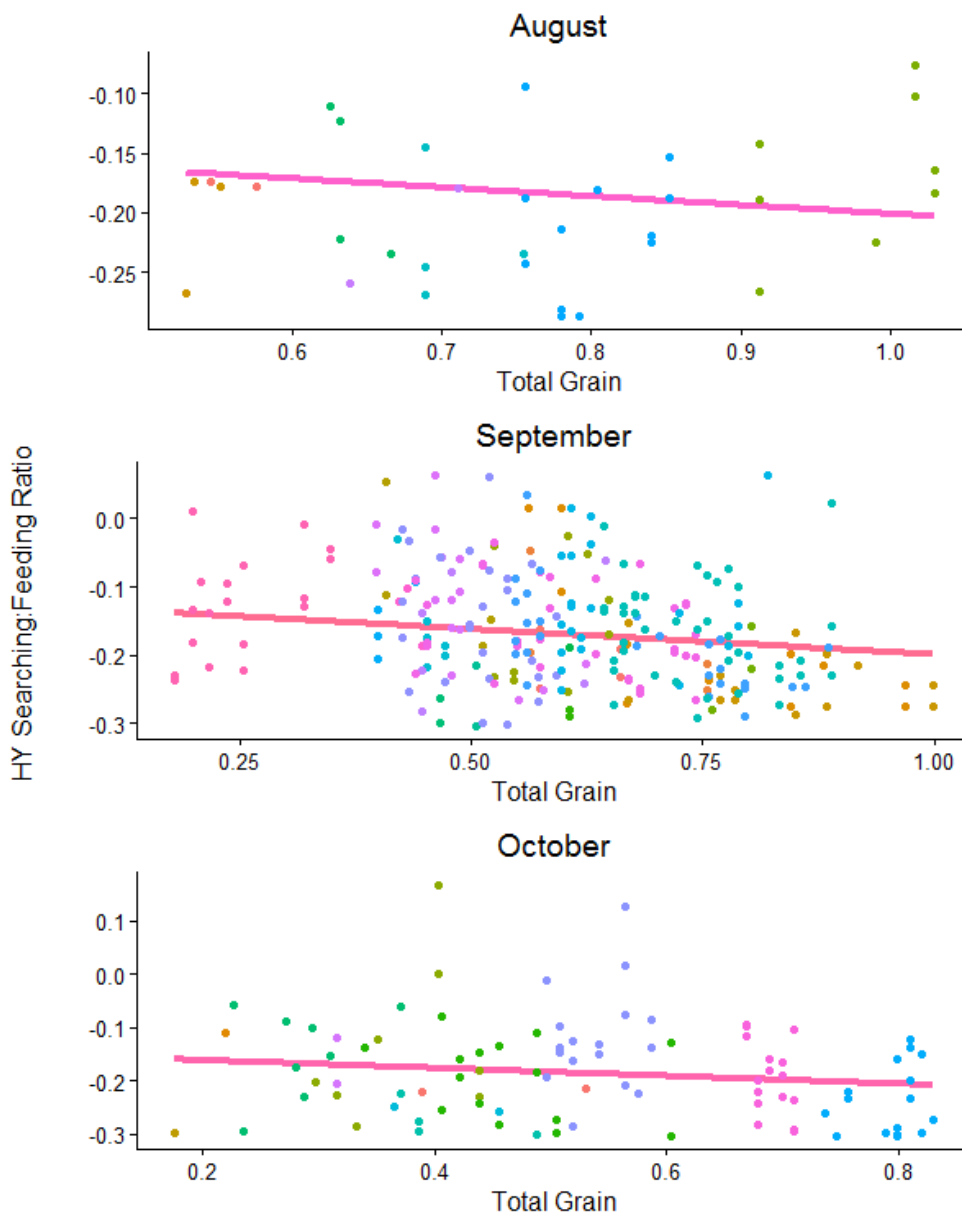
Figure 3.14 Predicted lines for retained predictor variables (Total Grain; kg) from linear mixed-effects modelling plotted against log-transformed foraging efficiency of juvenile (HY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other continuous predictor variables were set to mean values at all levels of categorical predictors to isolate predictor-specific effects. Dot colours show field/year combinations. Data were collected from cranes in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

3.3.4 *Experimental Behaviour*

As with observational behaviour data collection, I attempted to collect approximately equal sample sizes between age classes in my experimental observations. During the ~20-day experiment, I recorded a total of 65 observation events in experimental plots from AHY ($n = 39$) and HY ($n = 26$) cranes. I omitted three AHY observations and one HY observation where cranes did not spend any time feeding. Thus, my final sample size was reduced to 61 observation events in experimental plots ($n = 36$ and 25 AHY and HY, respectively; Table 3.14).

I found no significant difference ($\alpha = 0.05$) in foraging efficiency amongst experimental grain density treatments or age classes (two-way ANOVA with replication; Figure 3.15).

Table 3.14 Number of observation events ("n"; $n = 65$ total) by experimental treatment and age (AHY = adult or HY = juvenile) used to collect experimental foraging behaviour data from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) using experimental plots in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2012. Experimental treatment (Treatment) labels denote high (H), medium (M), low (L), and control (C) grain densities (kg/ha). Observation where cranes did not feed were omitted from the analysis ($n = 3$ AHY and 1 HY).

Age Class	Treatment	*n*
	H	10
	M	9
AHY	L	15
	C	5
	Total	**39**
	H	10
	M	10
HY	L	4
	C	2
	Total	**26**

Figure 3.15 Mean (±SE) age-specific foraging efficiency (searching:feeding ratio; SF) under varying experimental grain density treatments. Lesser SF values indicate greater foraging efficiency. Shaded bars represent juvenile (HY) cranes and open bars represent adult (AHY) cranes. Data were collected from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) feeding in experimental plots in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2012.

The top model in fitting my experimental behavioural observation dataset (Mod2) included the following additive effects: treatment level, crane age, and log-transformed variation (CV). Model Mod2 received 51% of the available support per AIC weight calculations (Table 3.15). The second-best model (Modnull, containing no predictor variables other than the random effect of Field_ID) received 22% of the available support. Backwards single term deletion for the top model suggested removing the experimental treatment and crane age terms (in that order) to improve model performance (Table 3.16). Parameter estimates (Table 3.16) and plots of predicted values from my reduced top model (Figure 3.16) suggested a decrease in foraging efficiency as grain became more variable.

Table 3.15 Candidate linear mixed-effects models used to analyze Eastern Population Greater Sandhill Crane (*Antigone canadensis tabida*) experimental foraging behaviour related to grain density and variation at Manitoulin Island, Ontario, Canada in autumn 2012. Model names (Model) and structures (Structure), number of parameters (K), degrees of freedom (df), and Akaike's Information Criterion scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown.

Model	Structure†	K	df	AIC	ΔAIC	^{W}AIC
Mod2	FE = 1+2+4	4	8	-135.4	0.0	0.51
Modnull	FE = null	1	3	-133.7	1.2	0.22
Mod4	FE = 1+(2*4)	4	9	-133.5	1.9	0.21
Mod1	FE = 1+2+3	4	8	-130.1	2.0	0.04
Modfull	FE = 1+(2*3*4)	5	13	-128.3	2.0	0.01
Mod3	FE = 1+(2*3)	4	9	-128.2	26.7	0.01

† **FE** = foraging efficiency (searching:feeding ratio), **1** = treatment (H, M, L, or C), **2** = age class, **3** = grain density, **4** = grain variation (CV).

Table 3.16 Top (Mod2) and reduced (Mod2.1 and Mod2.2) linear mixed-effects model used to analyze Eastern Population Greater

Sandhill Crane (*Antigone canadensis tabida*) experimental foraging behaviour with grain density and variation at Manitoulin Island,

Ontario, Canada in autumn 2012. Model names (Model), number of parameters (K), degrees of freedom (df), Akaike's Information

Criterion score (AIC), random effect variance (RV; Field_ID), and coefficient estimates (±SE) are given. TreatH, TreatM, and TreatL

represent changes in the response variable from the Control to the High, Medium, and Low experimental treatment categories,

respectively. AgeHY represents changes in the response variable from the adult (AHY) to juvenile (HY) age categoriees.

Model	K	df	AIC	RV	Intercept	TreatH	TreatM	TreatL	AgeHY	CV
Mod2	4	8	-135.4	<0.0001	0.629±0.27	0.074±0.06	0.075±0.05	0.091±0.05	0.009±0.02	1.800±0.61
Mod2.1	3	5	-137.7	<0.0001	0.381±0.18	--	--	--	0.006±0.02	1.150±0.36
Mod2.2	2	4	-139.5	<0.0001	0.376±0.18	--	--	--	--	1.134±0.36
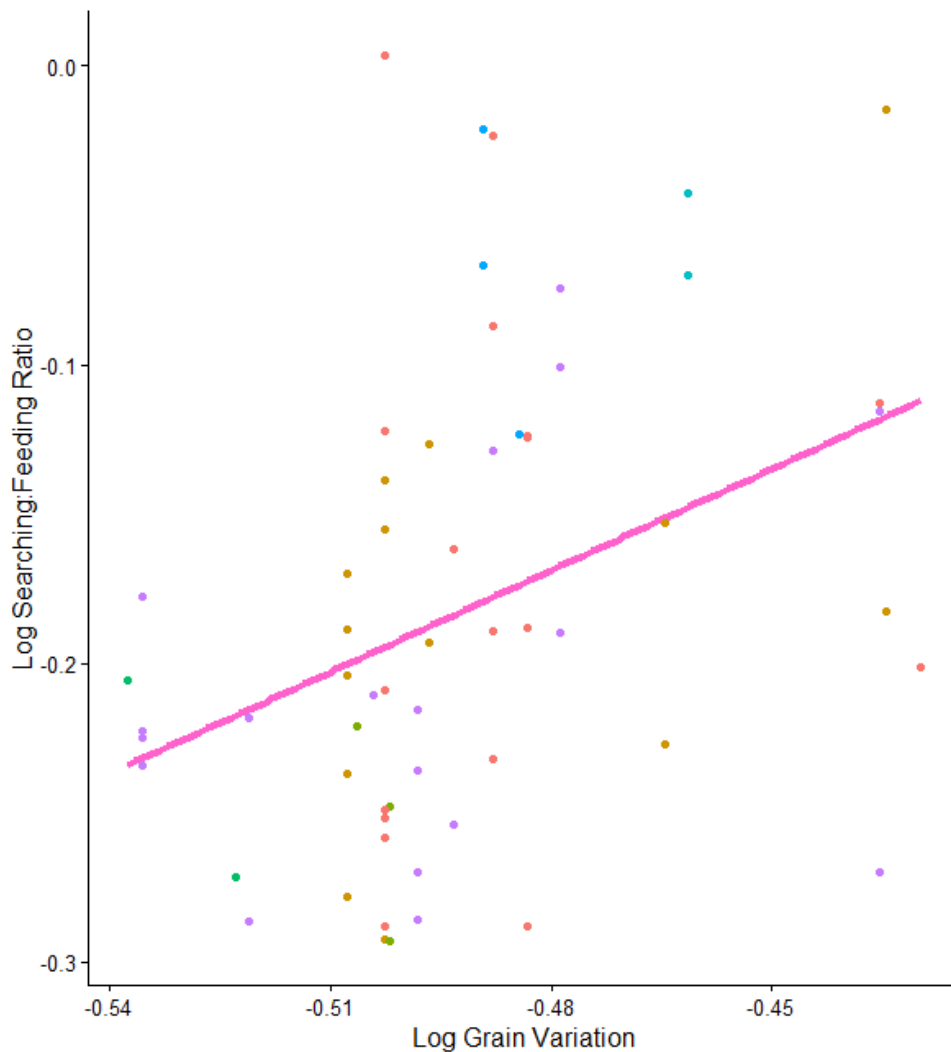
Figure 3.16 Predicted line for retained predictor variable (Grain Variation; coefficient of variation) from linear mixed-effects modelling plotted against log-transformed foraging efficiency of adult (AHY) Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Dot colours show field/treatment combinations. Data were collected from cranes feeding in experimental plots in harvested agricultural grain fields at Manitoulin Island, Ontario, Canada in autumn 2012.

3.4 Discussion

3.4.1 General Findings

My prediction that HY cranes feed less efficiently than AHY conspecifics (i.e., spend relatively more time looking for food compared to feeding) was not supported by my behavioural data collected in observational fields. In fact, I found evidence for marginally greater foraging efficiency amongst HY cranes in observational fields. I also did not find support for my prediction that AHY cranes would forage more efficiently in experimental plots. I predicted that AHY cranes would forage more efficiently than HY cranes in experimental plots because I controlled grain density and variation effects by emulating natural grain depletion and distributed experimental grain homogeneously. Therefore, because I did not detect an age-specific effect on foraging efficiency in my experimental analysis, the relationship that I found in my observational analysis may be an artifact of the sample I collected in the field. However, I offer alternate explanations to account for the marginally greater foraging efficiency I detected in HY cranes.

Grain variation had a negative effect on foraging efficiency in both HY and AHY cranes (in both observational fields and experimental plots). This finding provides support for my prediction that foraging efficiency decreases with more variably distributed grain. Conversely, total abundance of grain had a minor positive effect on foraging efficiency. Thus, if cranes are facing pressure to optimize foraging behaviour (*sensu* Pyke *et al*. 1977), they should focus on patches with less variable grain and, to a lesser extent, fields with a greater total abundance of grain.

Finally, I found that cranes moderately increased their foraging efficiency in observational fields as autumn staging progressed. This finding aligns with my prediction and is consistent with the hypothesis that cranes increasingly optimize foraging behaviour through autumn, as HY cranes learn to feed on agricultural grain and as both age classes face increasing pressure to prepare for departure.

3.4.2   Age-specific Foraging Efficiency

Differences in physiological status (e.g., size in fish; Thygesen *et al.* 2016) and age class (e.g., life stage in fish; Labeelund *et al.* 1993) affect foraging behaviour in other taxa. However, I found no substantial difference in AHY and HY crane foraging efficiency. The lack of a substantial age-specific effect on foraging efficiency could be the result of one or both of two potentially important factors that were not quantified in my study; 1) the social context in which HY cranes were observed and 2) the true novelty of grain as a food source to HY cranes.

Like other avian groups, cranes (*Gruidae*) show considerable social complexity (Aviles 2003, Panov *et al.* 2010, Zhou *et al.* 2010), which can influence foraging behaviour. For example, Yang *et al.* (2016) reported a negative relationship between individual proportion of time spent in vigilant behaviour while foraging and flock composition and size in wintering Black-necked Cranes (*Grus nigricollis*). Specifically, Yang *et al.* (2016) provided evidence for differences in behaviour related to social context by comparing individual behaviour between larger composite flocks and smaller (family) flocks of related individuals. Moreover, flock size effects on foraging efficiency have been reported in captive Skylarks (*Alauda arvensis*; Powolny *et al.* 2012).

Similarly, in terms of the relationship between social context and age and foraging behaviour, Stöwe *et al*. (2006) studied age- and social context-specific effects on novel object/food exploration in hand-raised Common Ravens (*Corvus corax*). That study showed consistent responses to different novel objects within individuals at different ages (three and six months old) but interactive effects on novel object exploration with social context (various dyadic sex/dominance groupings). Hence, the ability of HY cranes observed in my study to adjust to a novel food source like agricultural grain may have been related to the social context (e.g., small family flock, large mixed group, etc.). Furthermore, extended parental care (Alonso *et al.* 2004, Dinets 2015) likely allows HY cranes to learn more quickly by being exposed to their parents during autumn. Thus, the social context of the HY forager could offset the lack of individual experience, resulting in similar foraging efficiency between HY and AHY cranes.

HY cranes are likely continuing to learn foraging behaviour from their parents, siblings, and unrelated conspecifics during autumn staging. Foraging behaviour specific to agricultural grain is likely learned when HY cranes encounter harvested grain fields during autumn. In Ontario, most EP cranes first encounter grain fields near the forested-cleared land interface during autumn migration (e.g., my study site). A seminal study of animal learning by Marchetti & Drent (2000) tested individual variation in ability to learn foraging behaviour from conspecifics in Great Tits (*Parus major*). In that study, the behaviour of a group of known relatively slow and fast explorers faced with a novel foraging situation (novel bird feeder design) was compared in the absence and presence of a tutor bird (trained on the novel feeder design). Slow birds did not copy the behaviour of the tutors whereas fast birds did thereby providing support for the producer-

scrounger model (Barnard & Sibly 1981) wherein individuals either obtain food primarily from interaction (scrounger) or active foraging (producer).

Not surprisingly, scrounger behaviour is more profitable (in terms of food items gained) when producers are present, regardless of group composition; however, there is an asymptote to the positive relationship between scrounger profitability and producer density, likely relative to the distribution, density, and nature of the food item being targeted. Therefore, individual variation in learning behaviour, specifically related to foraging, exists amongst other avian taxa. Moreover, HY cranes in my study were likely of varying exploratory propensities and feeding in different social contexts such that the foraging challenge presented by the novelty of agricultural grain could have varied between individuals. Thus, age-specific differences in foraging efficiency may have been obfuscated by the underlying social contexts and behavioural differences in my HY crane sample, especially considering that I did not study known (e.g., marked) individuals.

Determining the novelty of a food source/item to a population is necessarily difficult without experimentation. Typically, novelty is used to describe items not previously presented in studies involving captive animals, where previous encounters are controlled and thus known (e.g., Stöwe et al. 2006). Barley grains, for example, are somewhat similar to the seeds of sedges and grasses that HY cranes may encounter during the nestling and fledgling stages in natal areas. Thus, if anything, the density, spatial distribution, and setting (harvested fields) associated with barley are likely most novel for HY cranes during autumn. Furthermore, most of the cranes I observed likely fed on grain at my study site before being included in my sample. Nevertheless, the degree of novelty represented by agricultural grain as a food source did not result in detectable reduction of

foraging efficiency in HY cranes when compared to AHY conspecifics. In fact, a marginally opposite effect was detected.

As an alternate explanation, the marginally greater foraging efficiency I detected in HY cranes in observational fields could be the result of age-specific differences in selective pressure to optimize foraging behaviour. Primary amongst the six assumptions of optimal foraging theory described by Pyke (1984) is a link between fitness and foraging behaviour. Therefore, AHY cranes may have sufficient energetic reserves during autumn such that they face less selective pressure to forage optimally. HY cranes, however, may face greater selective pressure to optimize foraging behaviour because of their differing physiological constraints (e.g., continued growth of long bones and muscles). In short, foraging behaviour may be more strongly linked to fitness in HY than AHY cranes during early autumn staging.

Weathers & Sullivan (1991) postulated that adult Yellow-eyed Juncos (*Junco phaeonotus*) reduced foraging efficiency because constraints associated with energy and/or time budgeting were temporarily relaxed. Furthermore, the authors discussed two possible causes for reduced pressure to forage more efficiently in adults, namely: 1) temporally negligible costs associated with foraging less efficiently and 2) alternate hidden costs or risks related to foraging relatively more efficiently (e.g., increased exposure to predators while foraging). Moreover, Wheelwright & Templeton (2003) experimentally demonstrated convergence of foraging efficiency in older juvenile (30-42 days old) and adult Savannah Sparrows (*Passerculus sandwichensis*) approximately coinciding with cessation of parental care in the wild. Collectively, these related studies

provide an ecological context whereby AHY cranes may not need to forage as efficiently as HY conspecifics during autumn staging.

Although the interpretations of my findings described above are well founded, a more parsimonious explanation may be appropriate. Namely, in the context of age-specific foraging efficiency, learning to forage for grain may be a relatively quick process when compared to the other motile (e.g., insects) and sessile prey items (e.g., native seeds) that HY cranes likely consume before arriving at autumn staging sites. Therefore, foraging efficiency may have been similar between AHY and HY cranes because foraging for grain is relatively easy.

3.4.3   Grain Density & Variation Effects

The relationship between environmental variability and animal foraging behaviour has been studied in many contexts. These studies include the use of social and non-social information by Blue Jays (*Cyanocitta cristata*; Heinen & Stephens 2016), trade-offs between growth and predation risk in American bullfrog (*Rana catesbeiana*) tadpoles (Anholt & Werner 1995), and seasonally-shifting conifer seed diets in crossbills (*Loxia* spp.) that track conifer species-specific peak seed profitability (Benkman 1987). How animals optimize foraging behaviour is governed generally by optimal foraging theory (Werner & Hall 1974) and, in relation to feeding within patches, marginal value theorem (Krebs 1974, Charnov 1976). These theories describe the mechanisms by which foraging behaviour is modulated to best suit varying environmental conditions with the assumed goal of maximizing fitness. In terms of crane foraging behaviour, variation in spatial distribution and density of agricultural grain represents a form of environmental

variability in food resources. My finding that grain variation had the most important effect on foraging efficiency aligns with previous experimental research on animal foraging behaviour that has documented behavioural effects from changes in the spatial distribution of food through time (e.g., Berger-Tal *et al*. 2014). Although grain is a sessile prey item and its distribution typically does not change substantially relative to post-harvesting conditions, concurrent consumption by con- and heterospecifics, and sprouting, can alter the spatial distribution and density in each field. Thus, there is likely a selective advantage for cranes to perceive grain density and distribution at a specific scale within fields. Integrating this type of information may allow cranes to avoid feeding in fields where variation in the spatial distribution of grain might negatively affect net energy acquisition.

3.4.4   Temporal Foraging Efficiency

The relationships discussed heretofore have concerned age-specific crane foraging ecology in relation to the density and spatial distribution of grain food resources without consideration of within-season changes related to migratory preparedness. However, the energetic requirements of migration in birds affects foraging behaviour prior to and during migration (Weber 2009, Smith & McWilliams 2014). Accordingly, I expected that the variables shown to affect foraging efficiency in my study would become increasingly important as autumn progressed (i.e., a survey month effect on foraging efficiency) because the impetus to prepare for migration grows stronger during staging (Hupp & Robertson 1998, Prop *et al*. 2003). Granivorous migratory birds like cranes consume grain because it is relatively abundant, accessible, energy-dense, and readily

converted into lipid reserves (McWilliams *et al*. 2004) necessary for migration (Sherfy *et al*. 2011). Daily maximum fat deposition rates influence how staging birds utilize food resources. These daily maximum values are particularly limiting in smaller, long-distance migratory birds whereas larger birds likely cannot reach this upper limit due to the intrinsic relationship with body mass (Lindstrom 1991). Cranes likely do not reach the upper limit of maximum fat deposition rate dictated by their size. If foraging efficiency is related to migratory preparedness, it should continue to increase until departure. Thus, the increase in foraging efficiency I detected in both HY and AHY cranes, especially in 2011, may be explained by proximity to migratory departure.

3.4.5   Research & Management Implications

Although I described variation in age-specific foraging at multiple temporal scales, I only modelled temporal effects by month to avoid developing overly complex models that may have prevented analysis via LME. However, because energetic reserve acquisition may vary on a shorter temporal scale (e.g., Schaub & Jenni 2001, Schaub *et al.* 2008), future research should attempt to model effects at multiple temporal scales (e.g., by day, week, and month). Such an analytical approach would likely provide the resolution necessary to better detect temporal changes in behaviour related to migratory preparedness during staging.

The abundance and distribution (at multiple spatial scales) of grain available for cranes during autumn migration may vary spatially and temporally as commodity values and harvesting equipment change (Pearse *et al*. 2010). The implications of these perturbations for crane foraging and migratory ecology can be better understood using the

findings presented in my study because I concurrently studied foraging behaviour and food availability, as has often been lacking in similar research with dabbling ducks (*Anas* spp.; Callicutt *et al*. 2011). At present, grain is likely less variable at my study site than the theoretical threshold above which foraging is not energetically-sustainable (i.e., cranes continued to utilize fields at my study site). However, increasingly variable grain distribution driven by changes in agricultural practices (e.g., technological advances in harvesting equipment; Sherfy *et al.* 2011) could render the staging area an energetic sink. Cranes might initially stop at a staging area because of behavioural experience yet incur a net loss in energetic reserves leading up to migratory departure due to suboptimal foraging conditions. Furthermore, cranes may be forced to skip the staging area completely, travelling further south earlier in autumn. Earlier migration could have negative effects on HY cranes that may have hatched late or otherwise be less prepared for substantial migratory movement. Pending patterns in grain availability and distribution at migratory stopovers further south, such changes could lead to reduced productivity and, ultimately, bear cross-seasonal population-level effects (Davis *et al*. 2014, Sedinger & Alisauskas 2014). Future EP management decisions should consider potential changes in agricultural grain production at this study site and other important staging areas given the link to foraging behaviour that I presented here.

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4 Roost site use by Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) during autumn staging

4.1 Introduction

Communal roosting behaviour has been described and studied amongst a diverse group of taxa including, for example, bats (Agosta 2002), geese (Si *et al*. 2011, Jankowiak *et al*. 2015), fish (Clough & Ladle 1997), and insects (Vulinec 1990, Grether & Switzer 2000). Multiple factors likely result in selection for communal roosting behaviour and can be grouped into three general categories: 1) thermoregulatory benefits, 2) reduced predation risk, and 3) increased foraging efficiency (Beauchamp 1999). Despite the simplicity of these groupings, studying the evolutionary pressure to roost communally at the individual level, where selection is often strongest, remains difficult in practice, and so researchers have often made efforts via theoretical and empirical modelling (Laughlin *et al*. 2014).

Because some birds roost communally to reduce predation risk and increase foraging efficiency, it is expected that variation amongst these factors, in part, determines how individuals choose and utilize roost sites. However, although animals may gain thermoregulatory benefits from roosting communally (du Plessis *et al*. 1994), the associated selective pressure may not impact roost site selection if competing roost sites offer comparable protection and/or insulative properties. Amongst cranes (*Gruidae*), communal roosting may be a strategy to minimize predation risk and time spent in vigilant behaviours, as there is greater safety and security in larger groups (Lambertucci & Ruggiero 2013). Communal roosting may also serve to increase foraging efficiency in

cranes during autumn staging by enhancing social transmission of foraging information (Beauchamp 1999). If communal roosting does increase foraging efficiency in cranes, it likely results in greater net energy gains during staging (Sparling & Krapu 1994). For granivorous, migratory birds, energetic reserves acquired from agricultural grain at staging sites are particularly important (Reinecke & Krapu 1986, Krapu *et al.* 2004, Anteau *et al.* 2011, Pearse *et al.* 2011, Sherfy *et al.* 2011).

Birds may interpret anthropogenic disturbance similar to the risk of predation at roost (Webb & Blumstein 2005) and feeding (Gill *et al.* 1996, Klaassen *et al.* 2006) sites. Generally, anthropogenic disturbances at roost sites can have negative effects on migratory birds by directly and/or indirectly causing depletion of energetic reserves critical for migration (Végvári & Barta 2015, Lilleyman *et al.* 2016). Roost site disturbance can also lead to greater risk of predation and various forms of accidental injury (e.g., flying into power lines; Janss 2000, flying into wind turbines; Pearse *et al.* 2016). Thus, avian roost sites are likely selected, at least in part, to minimize disturbance (i.e., perceived predation risk) and thereby conserve energetic reserves (Zabala *et al.* 2012, Lambertucci & Ruggiero 2013). Though the risk of predation is relatively minimal during autumn migration in cranes (Sparling & Krapu 1994), roost use is still likely affected by disturbance.

Typically, anthropogenic disturbance at avian roost sites has been studied using parameters describing human presence (Lilleyman *et al.* 2016) or, especially for waterfowl, hunting pressure (Végvári & Barta 2015). However, anthropogenic disturbance effects on the behaviour and distribution of wildlife can come in many different forms, including marine (Albuquerque *et al.* 2015) and automobile traffic

(McLeod *et al*. 2013, Wolf *et al*. 2013). Therefore, various forms of anthropogenic disturbance can influence avian behaviour. In agricultural landscapes often used by granivorous birds during staging, wetland roost sites may be located in habitat mosaics, often bisected by networks of primary and secondary roads (Ditmer *et al*. 2015, Beatty *et al*. 2016). If roads facilitate ecologically-relevant forms of disturbance for avian species roosting in agricultural landscapes (e.g., human presence, automobile traffic, etc.), related behaviour may be affected by the proximity of roost sites to roads. This relationship may be especially important for species that roost communally in relatively isolated locations. Therefore, understanding effects of anthropogenic disturbance on roost use could aid in future development and conservation project planning.

Communal roosting has often been considered a mechanism by which foraging information is exchanged and aggregated between individuals or groups, in particular amongst both birds and bats (Marzluff *et al*. 1996, Beauchamp 1999, Kerth *et al*. 2001, Kerth & Reckardt 2003). This phenomenon is described generally by the information-center (IC) hypothesis (Ward & Zahavi 1973). In the context of avian foraging behaviour, the IC hypothesis posits that birds at communal breeding, loafing, or roosting sites might exchange information on the day's foraging experiences. However, a review by Mock *et al*. (1988) demonstrated that very few studies in the intervening 15 years provided support for the IC hypothesis. To refine tests of the evolutionary validity of the IC hypothesis and associated benefits, Richner & Heeb (1999) highlighted eight necessary conditions, namely: 1) patchy and/or volatile food resources, 2) locally abundant food resources, 3) food patches which last long enough for information transfer between conspecifics, 4) return to the colony after encountering new patches, 5) the

ability to communicate successful encounters, 6) return to new patches after returning to

the colony, 7) foraging success disparity between individuals is governed by chance or

differing abilities to forage, not competition or variation in rates of exploitation, and, 8)

following successful foragers on subsequent foraging bouts increases foraging success

compared to not following previously successful foragers. Further to these IC hypothesis

prerequisites, application is often complicated by the complexity of the sociobiological

predispositions of the participants (Torney *et al*. 2011) and so the ecological and

evolutionary mechanisms perpetuating the behaviour remain poorly understood (Evans *et

al*. 2016).

Correspondingly, research findings remain somewhat divided amongst those that

provide support for the IC hypothesis (Thiebault *et al*. 2014, Bijleveld *et al*. 2015) and

those that do not (Giraldeau *et al*. 2002, Racine *et al*. 2012). Nonetheless, studies of

some gregarious avian species (e.g., the Pink-footed Goose, *Anser brachyrhynchus*),

demonstrate selection of foraging sites closer to roosts during migration (Chudzińska *et

al*. 2015). Such findings, however, likely offer support more specifically to the central-

place foraging (CPF) model (Orians & Pearson 1979). Under the CPF model, the

probability of use for given foraging locations declines with distance from the focal point

(e.g., a central roost site; Rosenberg & McKelvey 1999), to a point where otherwise

attractive food resources are completely ignored because they are beyond a threshold

commuting distance for a given species in a certain ecological context (Rainho &

Palmeirim 2011).

In populations of migratory Sandhill Cranes (*Antigone canadensis*), the interaction

between roost site characteristics, including disturbance and proximity to food sources,

and use/selection has been studied extensively, mostly in the context of applied management and conservation (Sidle *et al*. 1993, Sparling & Krapu 1994, Kinzel *et al*. 2009, Kessler *et al*. 2011). This research interest is primarily due to the fact that some of these populations sustain annual recreational harvest and because roost sites represent relatively important and potentially limiting habitat components during both spring and autumn staging (Folk & Tacha 1990, Ivey *et al*. 2015). Moreover, an understanding of roost site ecology, including how cranes make decisions with regards to roost use, is critical for planning population surveys and making informed management decisions (Fronczak *et al*., In press).

Conversely, disturbance and food effects on roost use have not received substantial attention amongst Eastern Population (EP) Greater Sandhill Cranes (*A. c. tabida*; cranes herein). This lack of research attention may be a result of recreational harvest only recently being permitted in two states (Tennessee and Kentucky; Dubovsky 2016). Thus, the objective of my study was to analyze the concurrent effects of roost disturbance and agricultural grain on roost use in EP cranes. I digitized satellite imagery of focal roost wetlands and measured the area and perimeter of each for inclusion in my analysis. I used a spatial analysis of primary and secondary roads near focal roost wetlands as an index of roost disturbance and measured grain density in surrounding focal fields to include in models describing variation in crane roost use at my study site during autumn staging.

I predicted that grain density within a radius equal to mean foraging flight distance (distance flown from roost wetland to feeding site, FFD) would be the most important determinant of roost use because nutrient acquisition is particularly important during

autumn staging. Furthermore, I predicted that anthropogenic disturbance from primary and secondary roads would have a moderate negative effect on roost use because communally roosting birds often respond negatively to various forms of roost site disturbance. Thus, my study is designed to provide understanding of food resource and anthropogenic disturbance effects on roosting behaviour in relatively unstudied EP cranes. The results of my study will also assist researchers and managers in designing future population surveys as well as in informing habitat conservation efforts involving EP cranes by providing a means to evaluate wetland suitability for crane roosting based on surrounding habitat features.

4.2 Methods

4.2.1 Study Area

All field components of my study were conducted at Manitoulin Island (Manitoulin herein), Ontario, Canada (UTM Zone 17 N, 0394968 E, 5065491 N; see Figure 1.2 in Chapter 1). Manitoulin is the largest freshwater island in the world at 2,766 km^2 (Chapman & Putnam 1973, Kraus *et al*. 2009) and is located at the northern end of Lake Huron. The landscape varies from coastal alvar and wetland habitats (i.e., swamps, fens, and bogs) to upland deciduous forest and cleared agricultural fields. Please refer to Section 2.3.1 in Chapter 2 for a description of the ecological context of Manitoulin as it relates to cranes in my study.

4.2.2   Grain Sampling & Quantification

To quantify grain availability around each roost site, at the start of each field season (early August), I assessed and classified all fields in my study area per crop type (i.e., grain vs. non-grain) and sampled grain in a focal subset of fields, as described in Section 2.2.2 in Chapter 2.

I thawed and weighed grain samples in the lab after the completion of each field season to quantify spatial and temporal variation in density and distribution, as described in Section 2.2.3 in Chapter 2.

4.2.3   Roost Use Observations

I identified six primary roost wetlands (Figure 4.1) using historical information provided by local naturalists, pilot data collected via fixed-wing aircraft surveys during autumn 2009, and GPS tracking data collected during autumn 2010-2012 (see Section 4.2.5.3). I initiated roost surveys starting 15 and 6 September in 2011 and 2012, respectively. I returned to roosts on a seven- or eight-day schedule, visiting each roost six times during each autumn.

I determined the number of cranes using each roost by counting flocks flying into (evening surveys) or leaving roost wetlands (morning surveys) from strategic vantage points. I recorded flock sizes onto data sheets while making observations in the field or immediately after surveys using data narrated into Sony digital voice recorders (Model ICDUX533s, Sony Corporation, Tokyo, Japan). I added all flocks recorded to calculate the total number of cranes per roost per survey.

I conducted morning surveys from one half hour before sunrise to one hour after sunrise and evening surveys one hour before sunset to one half hour after sunset. I used these survey windows following personal observations made at roost sites where I could determine with certainty when all cranes had departed in the morning and the time before which no cranes were present in the evening. I used spotting scopes (Spacemaster 15-45× – 60 mm, Bushnell Outdoor Products, Overland Park, KS, USA) and binoculars (Viper 10× 42 mm, Vortex Optics, Middleton, WI, USA) to enumerate cranes when landcover and/or topography forced observation from greater distances. I used both morning and evening counts to ensure all roosts were counted on the same day to minimize the potential for double-counting cranes that switched roosts between surveys.
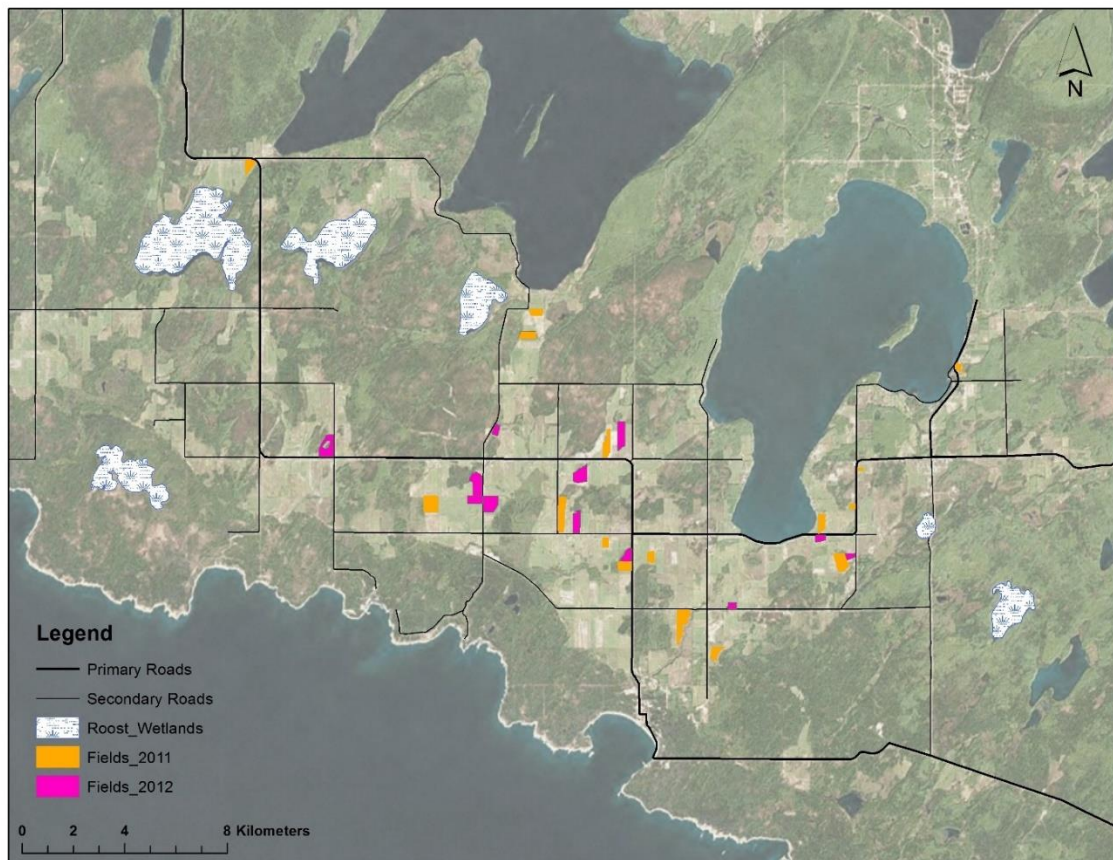
Figure 4.1 Location of roost wetlands and focal grain fields used to study disturbance and food effects on the roosting behaviour of Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

4.2.4   Crane Capture & GPS Deployment

During July and August 2010, I captured cranes to deploy GPS transmitters primarily as part of a larger study of EP migratory chronology (Hanna *et al*. 2014, Fronczak *et al*. 2015, In press). However, the resulting data were also used to inform my data collection methodology, calculate FFDs, and validate the roost use models developed in my study. All capture and banding activities were sanctioned under Western University Animal Use Protocol #2010-213 (Appendix I) and Canadian Wildlife Service Scientific Permit to Capture and Band Migratory Birds #10787 D (with rocket net authorization; Appendix II). For a comprehensive description of crane capture and GPS deployment methods, please refer to Section 2.2.5 in Chapter 2.

4.2.5   Data Handling & Analysis

4.2.5.1   Spatial Analysis

I digitized and analyzed spatial features using ArcGIS 10.4 (V10.4.0.5524, ESRI 2015). I digitized satellite imagery (Landsat 2008 imagery) of the primary roost wetlands in my study area ($n = 6$) and calculated area, in square-metres ("Area"), and perimeter, in metres ("Perimeter"), for each.

I established two spatial buffers (≤ 6 km and ≤ 12 km) to represent potential scales at which cranes could interpret the nutritional landscape based on the mean FFD as calculated from GPS tracking data (see Section 4.3.2). Within each year of the study, I determined which fields were within the 6-km (Figure 4.2) and 12-km (Figure 4.3) spatial scales (polygon edge to polygon edge) using Buffer analysis from the Geoprocessing

toolbox. Fields included in the ≤6 km category were also included in the ≤12 km category.

Because roosts were located relatively close together (mean = 13.7 ± 7.89 km), there was potential for spatial autocorrelation amongst both the 6- and 12-km grain density buffers during each roost survey period ($n = 6$ per year, 12 total) within each spatial buffer ($n = 2$). Therefore, I calculated Moran's Index (Moran 1950) with inverse spatial weighting for each of the survey week by spatial buffer by year combinations ($n = 24$ total) and found no significant spatial autocorrelation ($\alpha = 0.05$).

I estimated mean grain density by summing density values amongst all fields at each spatial scale and dividing by the number of fields to produce a unique grain density value for each roost ("X6km_Density" and "X12km_Density"). Because fields were harvested on different dates during roost and grain data collection, two roosts (Mud and Saigheon) had zero values for <6 km grain density at different points in time. Therefore, I added 100 as a constant to all <6 km grain density values to permit log transformation of this parameter.

I also digitized satellite imagery (Landsat 2008 imagery) of primary and secondary roads within my study area to quantify potential roost use effects from anthropogenic disturbance relating to automobile traffic. I defined primary and secondary roads based on surface type (i.e., paved vs. gravel, respectively). I calculated straight line distances (m) from roost borders to nearest primary ("D.PRoad") and secondary ("D.SRoad") roads using Proximity analysis from the Geoprocessing toolbox. Because one roost (Yonge) had a secondary road running through the wetland basin, I added 100 as a constant to

both the distance to primary and secondary road measurements for all roosts to allow for

log transformation of these parameters.
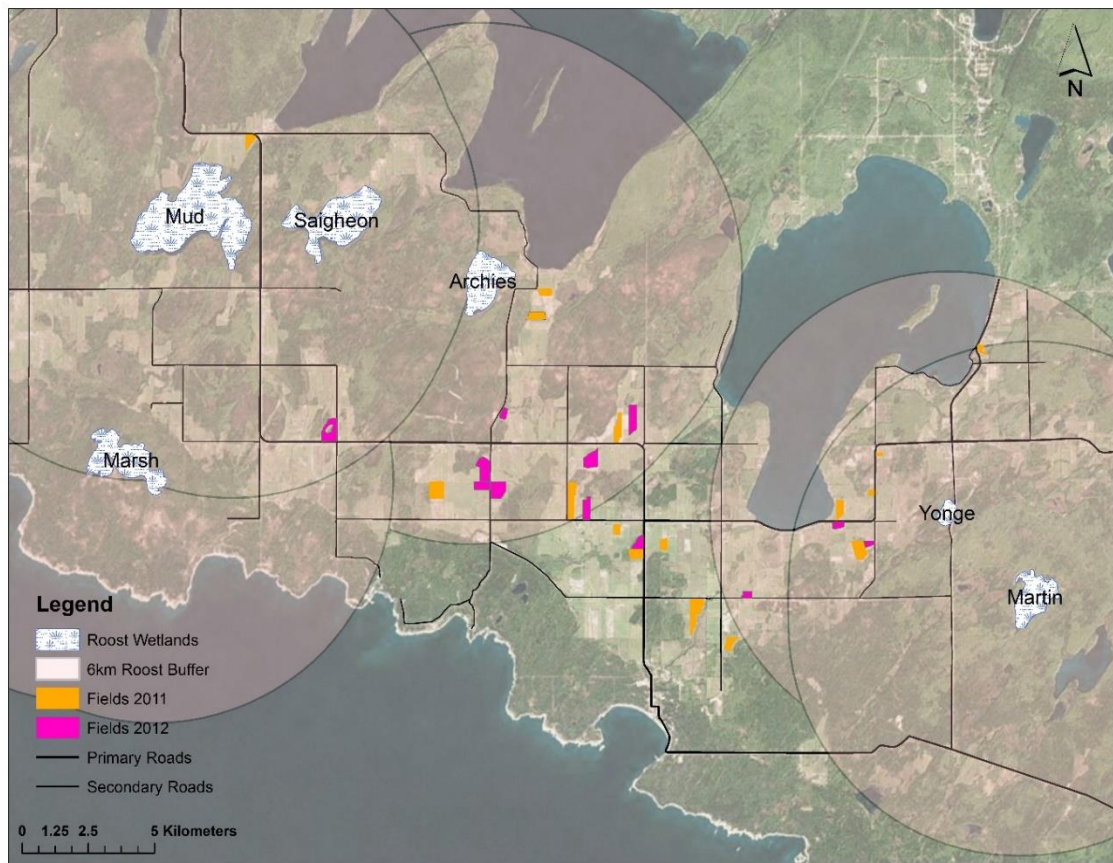
Figure 4.2 Six-kilometre buffers around roost wetlands used to analyze effects of agricultural grain and disturbance on roost use in Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.
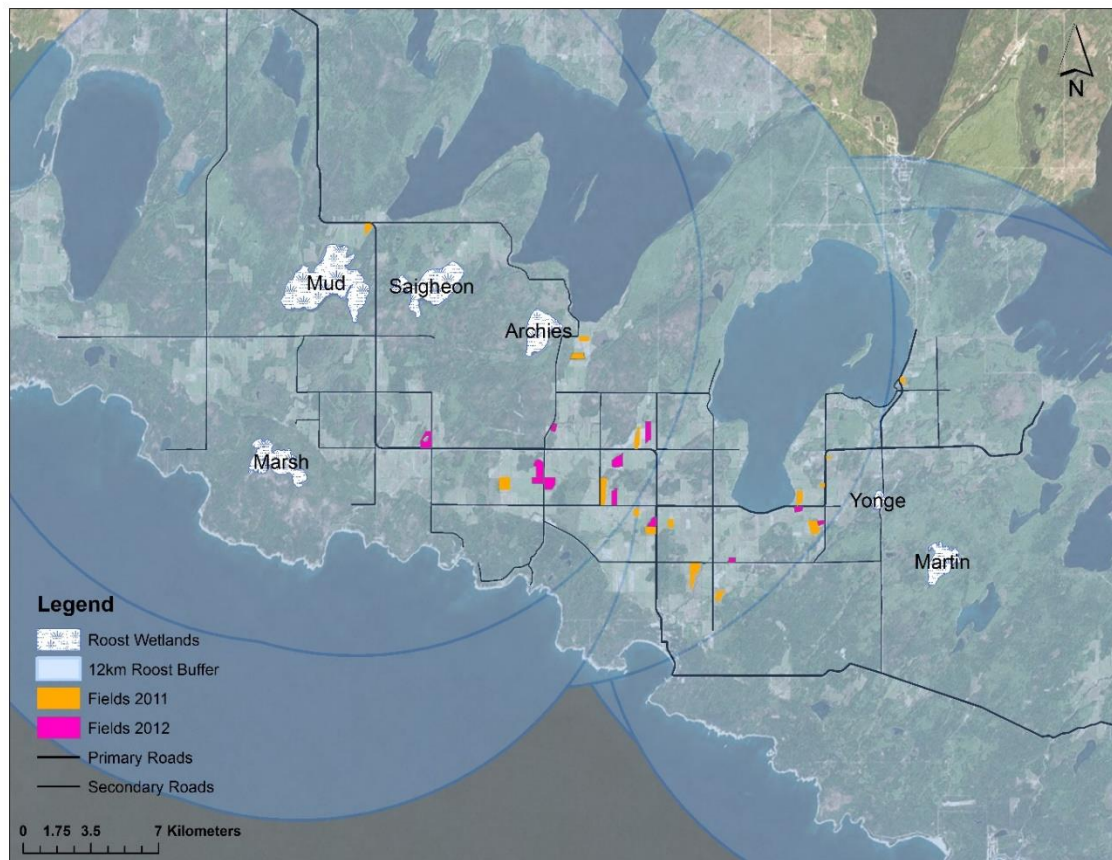
Figure 4.3 Twelve-kilometre buffers around roost wetlands used to analyze effects of agricultural grain and disturbance on roost use in Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

4.2.5.2 Estimating Grain Density

Because my behavioural observations were collected on days that I did not collect grain density samples, I needed to estimate field-specific daily values. I estimated field-specific daily values for grain density using linear mixed-effects (LME) models with maximum likelihood estimation in the *lme4* package (function: *lme*; Bates *et al*. 2015) in R Studio (V3.3.0, R Core Team 2016). For a comprehensive description of my grain density estimation approach, please refer to Section 2.2.6.2 in Chapter 2.

4.2.5.3 Foraging Flight Distance

I used GPS tracking data collected from marked cranes in 2011 and 2012 ($n = 8$ and 5 cranes, respectively) to estimate mean FFD at my study site. I used the same protocol to estimate mean FFD as described in Section 2.2.6.3 in Chapter 2.

4.2.5.4 Roost Use Analysis

Using the spatial data and grain density values estimated from the modelling procedures described above, I built negative binomial generalized linear mixed-effects models (GLMM) in the *lme4* package (function: *glmer.nb*; Bates *et al*. 2015) in R Studio (V3.3.0, R Core Team 2016) to analyze the effects of roost characteristics, grain food resources, and roost disturbance on crane roost use (see Table 4.1 for a description of all predictor variables). I first attempted to run Poisson GLMMs but found that negative binomial GLMMs were a better fit to my actual data. I used a GLMM approach with maximum likelihood (Laplace approximation) to fit models. I used the number of cranes using a given roost on a given day as a count response variable representing roost use. I

inspected data for outliers using scatterplots and boxplots prior to building models. I

used log transformations to improve predictor variable distributions where outliers were

detected. I ran a candidate set of seven models (Table 4.2) and compared AIC values to

select the most parsimonious model. I calculated Akaike differences (ΔAIC) and

normalized their values to sum to 1.0 to assess the relative support for each of my

candidate models. I selected the model with the lowest AIC value as the best from the

candidate set.

Because overparameterization in GLMMs can cause convergence issues during

parameter estimation, I attempted to develop models with a minimal number of predictor

variables (other than the fully saturated model) and, where necessary, increased the

number of iterations to 100,000 (default = 10,000 in *glmer.nb*). If convergence warnings

were returned and increasing iterations did not resolve the issue, I calculated and

compared gradient and Hessian equivalent values for models that initially produced

convergence warnings. As suggested by designers of the *lme4* package (Bates *et al*.

2015), if the calculated value was <0.001, I retained the model, whereas I did not proceed

with interpreting results from models exceeding the <0.001 tolerance threshold.

Table 4.1 Descriptions of predictor variables used to model grain food resource and roost

disturbance effects on roost use in Eastern Population Greater Sandhill Cranes (*Antigone*

canadensis tabida) at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

Variable Name	Description	Specific Use
Roost.ID	Roost name and survey year	Roost name/year combination unique identifier with 12 levels (random effect)
Area	Area of roost wetland (m^2)	Fixed continuous predictor; metric of roost size effects
Perimeter	Perimeter of roost (m)	Fixed continuous predictor; metric of roost size effects
D.PRoad	Straight line distance from roost edge to nearest primary road (m)	Fixed continuous predictor; metric of disturbance effects
D.SRoad	Straight line distance from roost edge to nearest secondary road (m)	Fixed continuous predictor; metric of disturbance effects
X6km_Grain	Mean grain density from fields at 6-km spatial scale (kg/ha)	Fixed continuous predictor; metric of spatial scale/grain density effects
X12km_Grain	Mean grain density from fields at 12-km spatial scale (kg/ha)	Fixed continuous predictor; metric of spatial scale/grain density effects

I developed an *a priori* candidate set of models based on what I thought would best describe the relationships contained in my data given my existing knowledge of the species' roost use during autumn staging. I built the candidate set of models shown in Table 4.2 using the following approach.

I included roost area (Area) in most candidate models because I wanted to model the relative importance of wetland size in determining roost use. Specifically, I included area to control for the fact that larger roosts may attract greater numbers of cranes due to increased space and/or the possibility of enhanced predator avoidance. Though I measured roost perimeter (Perimeter), I did not include the variable in my models because of the degree of positive correlation with roost area. I included roost identifier (fRoost.ID) as a random variable in all models to preserve roost-level effects.

I created Modnull and Modfull for comparison as per standard information-theoretic model selection procedure (Burnham & Anderson 2002) while observing the limitations of GLMM analysis. I included all additive (random and fixed) effects in Modfull. I built Mod1 to account for the singular effects of roost area on roost use. I added proximity to primary roads (D.PRoad) and secondary roads (D.SRoad) to Mod2 to create a model that could singularly account for roost size and anthropogenic disturbance effects on roost use. In Mod3, I included mean grain density at the 6-km (X6km_Density) and 12-km (X12km_Density) scales to model food density effects on roost use at both spatial scales in isolation of roost size and anthropogenic disturbance effects. In Mod4, I included additive and interactive effects from roost size and mean grain density at the 6-km scale on roost use to account for interaction between roost size and grain food resources at the 6-km scale. Finally, in Mod5 I considered the additive and interactive effects from roost

size and mean grain density at the 12-km scale on roost use to account for interaction between roost size and grain food resources at the 12-km scale.

In aggregate, I developed these models to investigate effects of anthropogenic disturbance and distance to and quality of feeding fields on roost use by cranes during autumn staging while also accounting for roost size effects.

Table 4.2 Candidate set of negative binomial generalized linear mixed-effects models used to analyze food and roost disturbance effects on roost use of Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Variables written with an "L" (e.g., LArea) were log transformed. Variables written with an "f" (e.g., fRoost.ID) were treated as factors. All models listed below included Roost.ID as a random effect.

Model	K	Structure
Modnull	1	1
Mod1	2	LArea
Mod2	3	LD.PRoad + LD.SRoad
Mod3	3	LX6km_Grain + LX12km_Grain
Mod4	3	LArea * LX6km_Grain
Mod5	3	LArea * LX12km_Grain
Modfull	6	LArea + LD.PRoad + LD.SRoad + LX6km_Grain + LX12km_Grain

I used an identical approach for model selection (AIC), reduction (backwards single term deletion), and evaluation (Pearson residuals) as described in Subsection 2.2.6.4 in Chapter 2.

I also analyzed the individual contribution of each retained fixed, continuous predictor variable using a similar simulation and prediction approach to that described in Subsection 2.2.6.4 in Chapter 2.

4.2.5.5   Model Validation with GPS Data

I used known individual crane (n = 5 and 8 in 2011 and 2012, respectively) roost use data calculated via GPS tracking technology to validate the observational roost use dataset. I only included fixes that were acquired via GPS technology as they are more accurate than locations estimated via Doppler technology ($\sim$ 20 m and $\sim$ 250 m maximum accuracy, respectively). I only used one GPS location per crane/roost/night to avoid pseudoreplication. I treated each GPS fix as an observation in each roost on a given day and calculated predictor variable values for that observation in the same way I did for my roost use dataset collected in the field. This procedure yielded observations with values for the same predictor variables used to model roost use as described above.

I constructed kernel density plots for the predictor variables included in my final reduced model using both my GPS roost use dataset and my observational roost use dataset to qualify the accuracy of the data I used in the modelling procedures described above. I considered the GPS roost use dataset independent from field survey data and thus expected to find similar relationships between my response and predictor variables in both datasets if both were relatively accurate representations of roosting behaviour (i.e., unbiased estimates of crane roost use).

4.3   Results

4.3.1   Grain Density Estimation

I selected the random intercept and slope days since cut (DSC) predictor model for use in estimating daily grain density values. For a comprehensive summary of grain density estimation results, please refer to Section 2.3.1 in Chapter 2.

4.3.2   Foraging Flight Distance

I estimated mean FFD (km $\pm$ SE) at 6.36 $\pm$ 0.153 km for September and October of 2011 and 2012 combined. For a comprehensive summary of FFD results, please refer to Section 2.3.2 in Chapter 2.

4.3.3   Roost Use Analysis

I collected roost use observations at six roost wetlands for six consecutive weeks in both 2011 and 2012 resulting in a balanced dataset ($n = 72$ roost counts total; Figure 4.4).

The top model in fitting my roost use data (Modfull) included the following terms (no interactive effects): roost area, distance to primary road, distance to secondary road, mean grain density at the 6-km scale, and mean grain density at the 12-km scale. Modfull received 43% of the available support per AIC weight calculations (Table 4.3). The second-best model (Mod2) received 35% of the available support and included the distance to primary road and distance to secondary road terms. Backwards single term deletion for Modfull first suggested removing the mean grain density at the 6-km scale term to improve model performance (i.e., decrease the AIC score). Dropping the 6-km

scale term (Modfull.1) improved the AIC score by 2.0 units (AIC = 981.1 and 979.1, respectively). Backwards single term deletion for Modfull.1 suggested removing the roost area term to improve model performance. Dropping the roost area term (Modfull.2) improved the AIC score by 2.0 units (AIC = 977.1). Backwards single term deletion for Modfull.2 suggested removing the distance to secondary road term to improve model performance. Dropping the distance to secondary road term (Modfull.3) improved the AIC score by 1.1 units (AIC = 976.0). Subsequent single term deletion would not improve model performance so I stopped the procedure.

Parameter estimates (Table 4.4; Figure 4.5) and plots of predicted values from the final reduced top model suggested an increase in roost use with distance to primary road and mean grain density at the 12-km scale. Specifically, the number of cranes using a given roost increased by 9.21 for every one-unit increase in distance (log km) from a primary road and by 4.15 for every one-unit increase in mean grain density (log kg/ha) in fields within 12 km.

I plotted standardized (Pearson) residuals with observed values for all predictor variables to inspect for patterns. I detected heteroscedasticity in plots for mean grain density at both the 6- and 12-km scale. These patterns were not remedied by data transformations. However, because negative binomial models are relatively robust to heteroscedasticity and my modelling results (term deletions and parameter estimates) appear consistent with my ecological knowledge of the system, I consider my results valid.
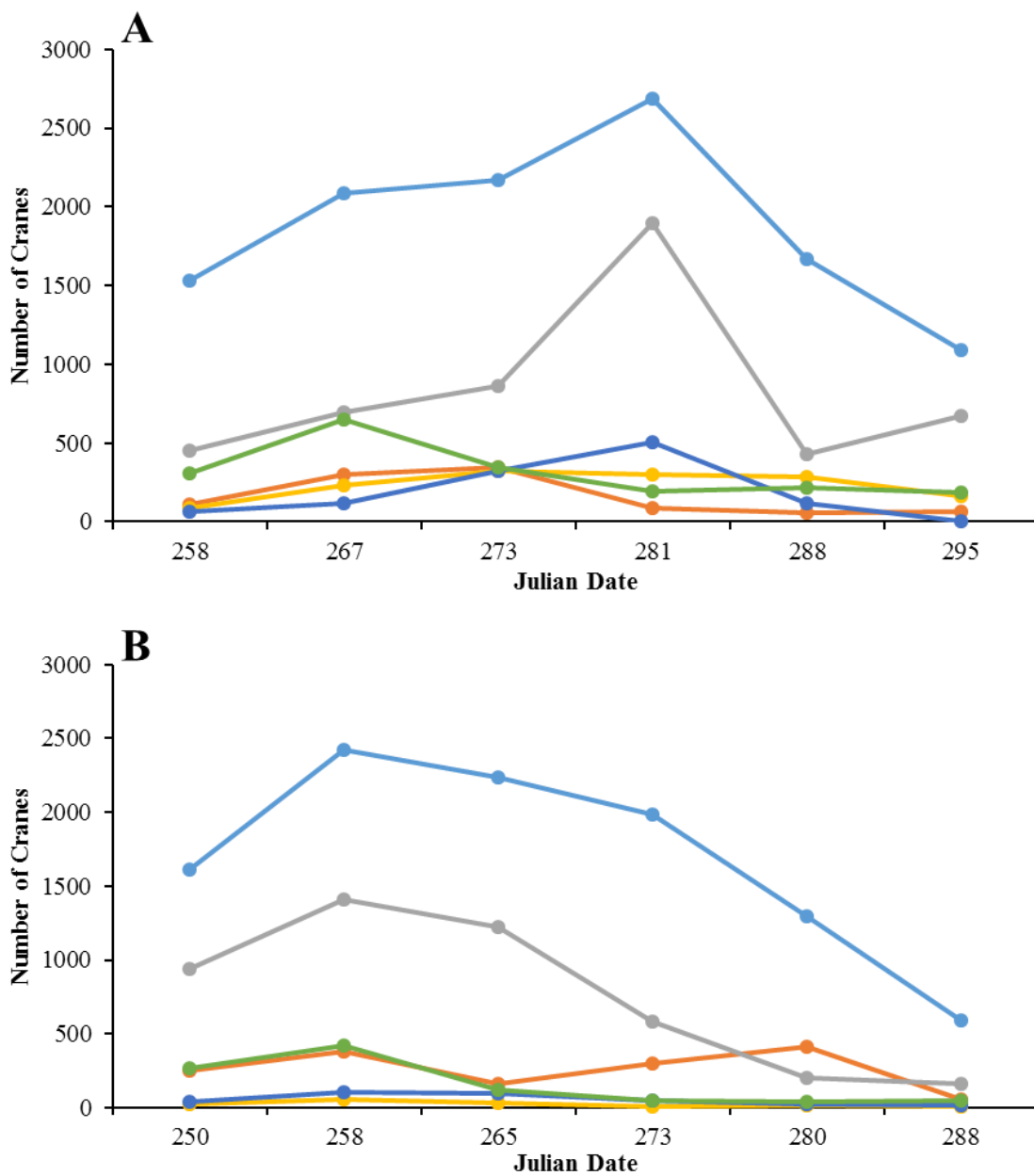
Figure 4.4 Number of cranes counted (*n* = 72 sampling events) in a study of roost use of Eastern

Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario,

Canada in autumn 2011 (A) and 2012 (B). Archies (light blue), Martin (grey), Yonge (green),

Marsh (orange), Mud (yellow), and Saigheon (dark blue) roost sites are shown. Julian date 258 =

15 September in 2011 (A); Julian date 250 = 6 September 2012 (B).

Table 4.3 Candidate negative binomial generalized linear mixed-effects models used to analyze roost use in Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Model names (Model) and structures (Structure), number of parameters (K), sample size (*n*), degrees of freedom (df), and Akaike's Information Criterion scores (AIC), differences (ΔAIC), and weights (^{W}AIC) are shown.

Model	Structure†	K	df	AIC	ΔAIC	^{W}AIC
Modfull	RU = 1+2+3+4+5	6	8	981.05	0.0	0.43
Mod2	RU = 2+3	3	5	981.48	0.4	0.35
Mod5	RU = 1*5	3	6	984.46	3.4	0.08
Mod3	RU = 4*5	3	5	984.66	3.6	0.07
Mod4	RU = 1*4	3	6	985.00	3.9	0.06
Modnull	RU = null	1	3	989.67	8.6	0.01
Mod1	RU = 1	2	4	990.30	9.2	0.00

† **RU** = roost use (number of cranes), **1** = roost area, **2** = distance to primary road, **3** = distance to secondary road, **4** = 6-km grain density, **5** = 12-km grain density.

Table 4.4 Top (Modfull) and reduced negative binomial generalized linear mixed-effects models (Modfull.1, Modfull.2, and Modfull.3) used to analyze roost use in Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Model names (Model), number of parameters (K), degrees of freedom (df), Akaike's Information Criterion score (AIC), theta (Θ), random effect variance (Random Var; Roost.ID), and coefficient estimates ± standard errors are given. Top model was reduced via backwards single term deletions.

Model	K	df	AIC	Θ	Random Var	Intercept	Area	D.Proad	D.SRoad	X6m_Grain	X12km_Grain
Modfull	6	8	981.1	2.199	0.599	-6.09±6.5	1.04±4.3	10.04±3.1	1.90±3.5	-0.60±3.2	4.42±2.1
Modfull.1	4	7	979.1	2.195	0.594	-6.22±6.3	1.03±4.3	9.97±3.1	1.93±3.5	---	4.18±1.7
Modfull.2	3	6	977.1	2.197	0.600	-4.80±2.7	---	9.50±2.5	2.48±2.6	---	4.22±1.7
Modfull.3	2	5	976.0	2.195	0.646	-3.00±1.9	---	9.21±2.5	---	---	4.15±1.7
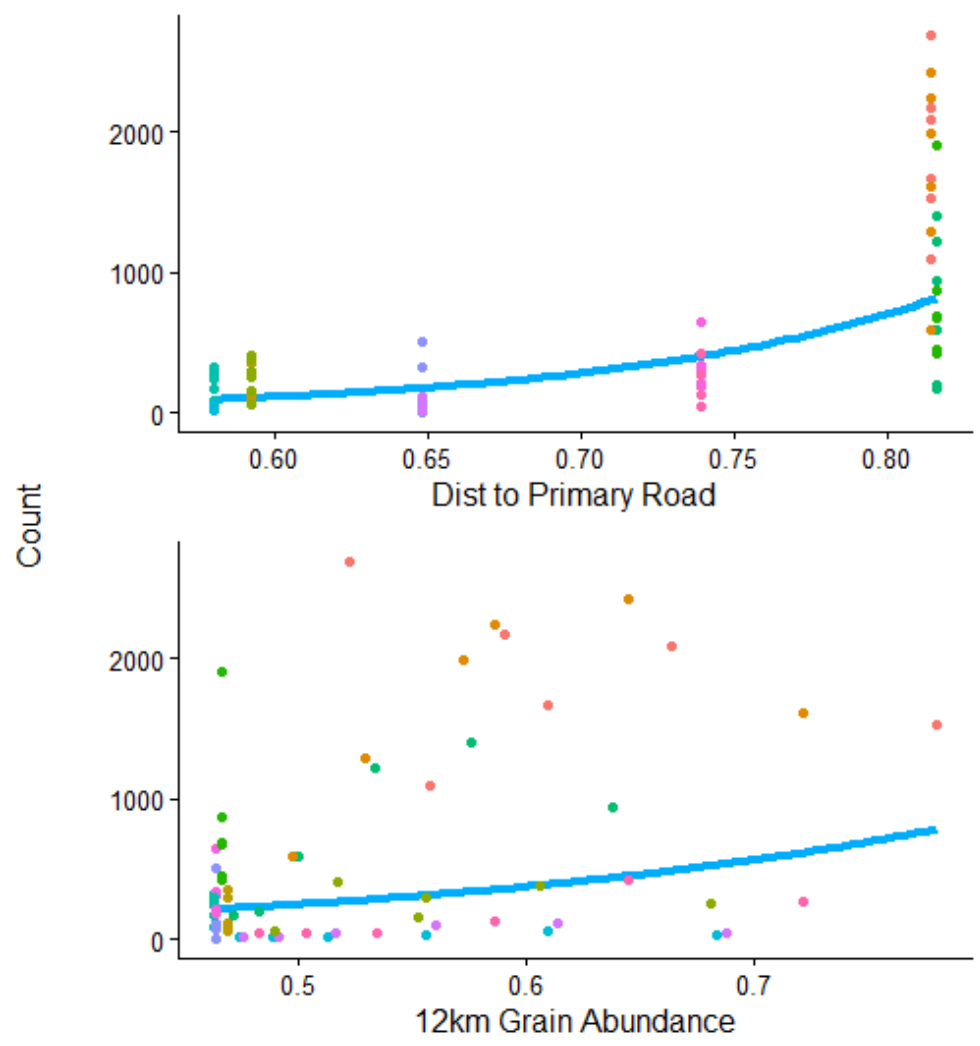
Figure 4.5 Predicted lines for retained predictor variables (backwards single term deletions) from negative binomial generalized linear mixed-effects modelling plotted against observed roost use by Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*). Other predictor variables were set to mean values to isolate predictor-specific effects. Dot colours show roost/year combinations. Data were collected from cranes at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012. Distance to primary road (log km) and mean grain density (log kg/ha) within a 12-km radius of roost sites are shown.

4.3.4   Model Validation with GPS Data

Because I deployed GPS transmitters in 2010 ($n = 9$), some transmitters were offline during autumn 2011 and 2012, reducing my sample of marked cranes ($n = 8$ and 5, respectively). My GPS tracking data yielded 1,188 GPS fixes in focal roosts in 2011 and 2012 combined ($n = 660$ and 528, respectively; Figure 4.6 and 4.7). I omitted fixes in 2011 ($n = 159$) and 2012 ($n = 66$) that were collected by the same transmitter in the same roost during the same night reducing my sample size ($n = 567$ and 396, respectively). I also omitted fixes from 2011 ($n = 322$) and 2012 ($n = 325$) that were outside the roost survey windows reducing my final sample size to 316 roost GPS fixes ($n = 245$ and 71, respectively).

Comparison of kernel density plots generated for predictor variables retained in my reduced top models based on field observation data demonstrated relatively consistent agreement between GPS tracking data and the observational roost use dataset (Figure 4.8). My GPS tracking density plots suggested that marked cranes used roosts that were further from primary roads than those suggested from my field observation data. Furthermore, GPS-marked cranes appeared to have a greater tolerance for decreasing grain density at the 12-km scale.
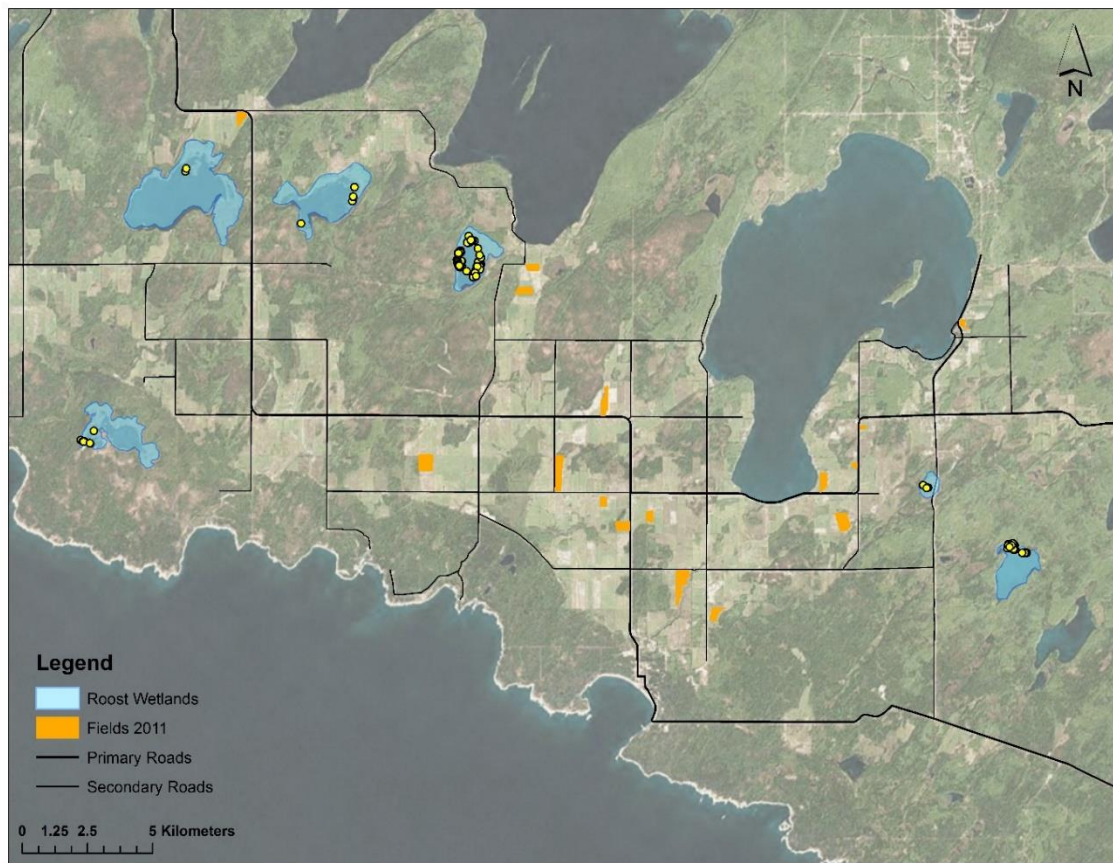
Figure 4.6 GPS fixes collected in focal roost wetlands used to analyze effects of grain and disturbance on roost use in Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2011.
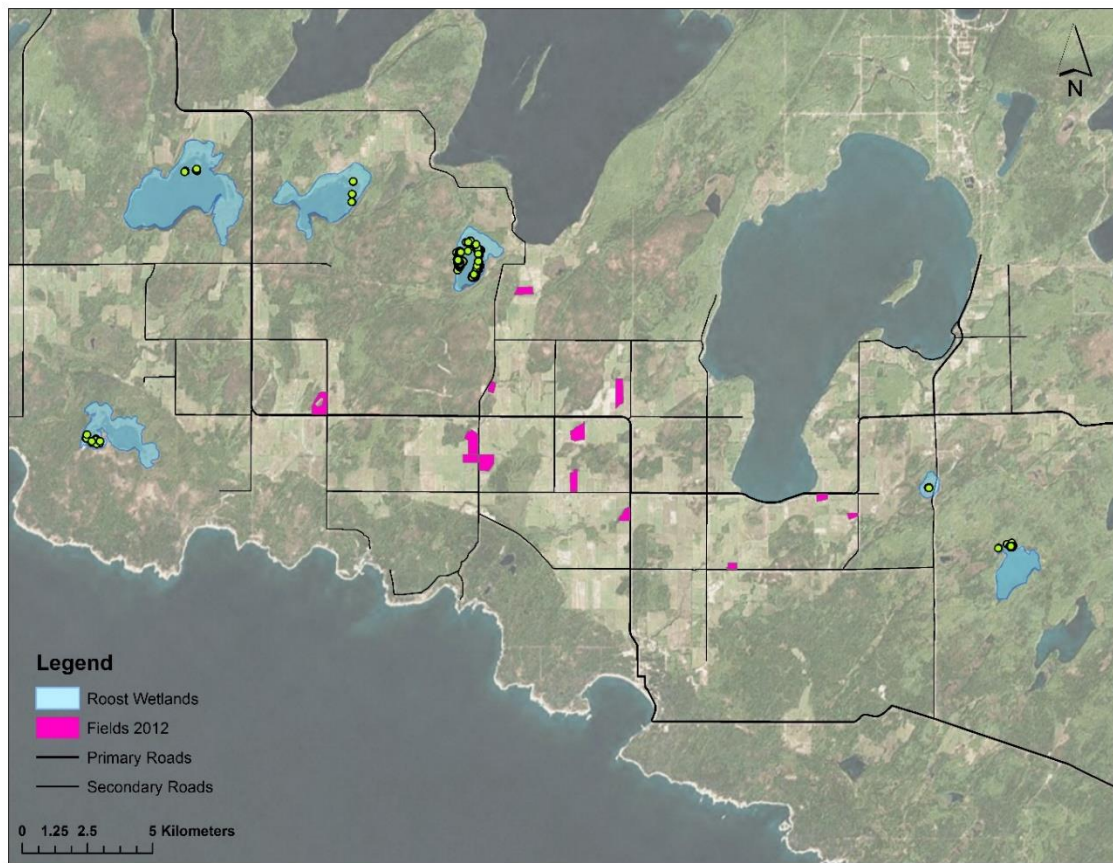
Figure 4.7 GPS fixes collected in focal roost wetlands used to analyze effects of grain and disturbance on roost use in Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) at Manitoulin Island, Ontario, Canada in autumn 2012.
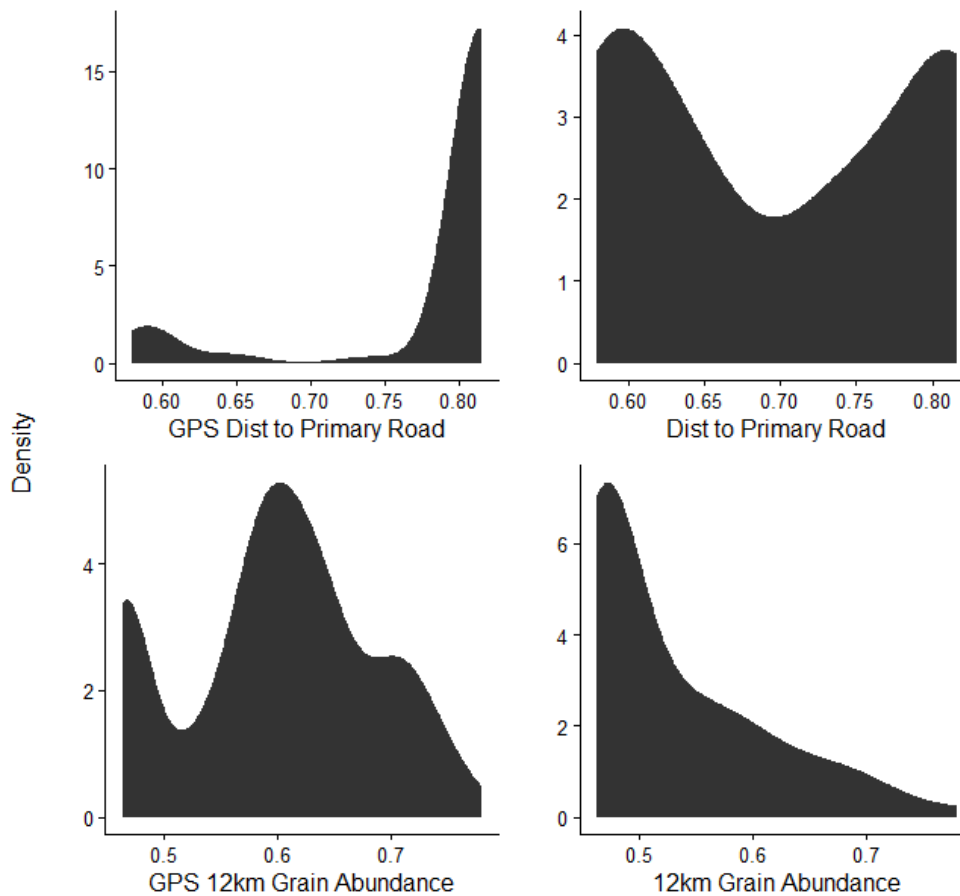
Figure 4.8 Comparison of kernel density plots generated for predictor variables retained in reduced top negative binomial generalized linear mixed-effects models based on roost use observations (right column) and GPS tracking (left column). Data were collected from Eastern Population Greater Sandhill Cranes (*Antigone canadensis tabida*) roosting in wetlands at Manitoulin Island, Ontario, Canada in autumn 2011 and 2012.

4.4   Discussion

4.4.1   *General Findings*

Colonial roosting behaviour in birds is influenced by multiple factors, generally aggregated as 1) thermoregulatory benefits, 2) reduced predation risk, and 3) increased foraging efficiency (Beauchamp 1999). Though the absolute importance of these factors varies interspecifically, the relative importance of each varies spatially and temporally within a given species (Zheng *et al*. 2015). In my study of EP cranes, I demonstrated the relative importance of avoiding anthropogenic disturbance while maintaining proximity to sufficient food resources in determining roost site use during autumn staging. Optimizing behaviour considering the potential energetic trade-offs associated with each of these factors is required to successfully complete (survive) migration (Hedenström & Alerstam 1997).

Specifically, my prediction that anthropogenic disturbance, as measured by distance to primary and secondary roads, would have a moderate negative effect on roost use was partially supported. I made this prediction because cranes utilized roosts that were relatively spatially isolated at my study site, often apparently avoiding roosts that were less isolated. Although distance to secondary roads was removed from the final roost use model, distance to primary roads (assumed greater traffic levels) was retained and contributed the most explanatory power of the two terms remaining following model reduction. These results suggest that roost disturbance may play an important role in crane roost use decisions.

My second prediction, that grain density within the mean FFD (6-km scale) would be the most important determinant of roost use, was not supported. I assumed that there was a proportionate functional link between mean FFD (6.4 ± 0.15 km at my study site) and crane roost site use. In fact, I selected my spatial scales for modelling potential grain density effects on roost use using the mean FFD that I calculated from GPS-marked cranes. However, grain density at the 12-km scale had a stronger effect than at the 6-km scale. Furthermore, the 12-km scale grain density effect on roost use was less than 50% of the magnitude of the anthropogenic disturbance effect (distance to primary roads) in my final reduced model, suggesting cranes may have to balance competing pressure to roost away from anthropogenic disturbance while remaining relatively close to quality food resources.

4.4.2 Roost Disturbance

Although cranes likely face minimal predation risk during autumn (Sparling & Krapu 1994), they appeared to use roost sites that were further from primary roads in my study. In fact, proximity to primary roads had an effect size more than twice that of the most important food density parameter. It is important, however, to consider the ecological context of my study site for the species when interpreting this finding. Manitoulin is one of the more northern agricultural staging areas for this segment of EP cranes. The agriculturalized landscape at the staging area is likely the first encountered during the southward autumn migration for cranes that summer in northcentral Ontario.

As Chudzińska *et al.* (2016) demonstrated in Pink-footed Geese, reaction to risk of predation/disturbance varies along the migratory route, likely because of temporal

proximity to impending physiological tasks (e.g., reproduction, migration, wintering, etc.). Indeed, anecdotal observation of field-foraging cranes at my study site demonstrated aversion to many forms of disturbance including agricultural equipment, off-highway vehicles, hunters pursuing waterfowl in nearby fields, bird watchers, and Bald (*Haliaeetus lecocephalus*) and Golden Eagles (*Aquila chrysaetos*) flying overhead. Thus, at northern staging areas encountered earlier in autumn migration, when food is likely more abundant (Alonso *et al.* 1994), cranes may be able to afford to avoid more disturbed roost sites.

In contrast, cranes may become less sensitive to roost site disturbance encountered at lower latitudes later during autumn migration. Furthermore, the relatively unique behavioural and physiological requirements of juvenile cranes (Krapu & Johnson 1990, Curro *et al*. 1996, Nowald 2001) may interact with latitude in determining how cranes respond to perceived levels of roost disturbance. Juvenile cranes likely become less vulnerable to predation at roost sites as they grow. Thus, if roost site disturbance is perceived as a predation risk, family groups may become less sensitive thereto further south during autumn migration. Future research should investigate latitudinal variation in the effects of disturbance on roost and field-feeding site use in EP cranes by quantifying aversion to such factors at multiple locations along the migratory route (*sensu* Chudzińska *et al*. 2016).

My study explicitly assumed that vehicular traffic and thus primary and secondary roads are perceived as predation risks by cranes. The distinction between primary and secondary roads was made based on road surface (i.e., paved vs. gravel, respectively) because quantitative data describing traffic patterns for the roads included in this analysis

were not available. Other studies have presented more precise models of vehicular traffic

and distance to road effects on animal behaviour by actively quantifying traffic while

collecting behavioural data (Ciuti *et al*. 2012, D'Amico *et al*. 2016). I did not collect

similar data in my study; however, given the importance of proximity to primary roads in

this analysis, subsequent studies of disturbance effects on crane behaviour would be wise

to implement modern advances in traffic (foot and vehicular) counting technology.

Advanced counting technology would provide data that are of greater precision and

temporally coincide with behavioural observations. Nevertheless, cranes at my study site

appeared to avoid roosting near primary roads, and the most parsimonious explanation for

this finding is that cranes were avoiding roads with greater vehicular traffic.

4.4.3   *Grain Effects on Roost Use*

The effects of food availability and distribution on roost site use and selection have

been studied in a diverse group of taxa (e.g., bats, Agosta 2002; geese, Si *et al*. 2011,

Jankowiak *et al*. 2015; etc.). Amongst avian species, the scale at which these effects are

most prominent varies by species and ecological context, ranging from <2 km in Barnacle

Geese (*Branta leucopsis*) in The Netherlands (Si *et al*. 2011) to 5-50 km in Bean (*Anser

fabalis*) and Greater White-fronted (*A. albifrons*) Geese in Poland (Jankowiak *et al*. 2015)

to approximately 12-km in EP cranes during autumn staging in my study. Amongst

cranes (*Gruidae*), similar relationships have been considered from studies of the Mid-

Continent Population (MCP; Pearse *et al*. 2010). Those studies have proposed grain

harvesting practices and watercourse management as means to prevent required daily

FFDs from approaching a theoretical energetically-sustainable maximum. Exceeding

such a threshold would effectively render some roost sites energetic sinks (Pearse *et al*. 2010), potentially causing negative population level effects, especially during spring migration (Krapu *et al*. 2014).

The concurrent study of roost use and food resources in colonially roosting avian species is informative because colonial roosts have been considered "information hubs" (Beauchamp 1999) whereby the day's foraging experiences can be exchanged between individuals to improve the success of subsequent foraging bouts (i.e., the IC hypothesis). In this way, the benefits of improved foraging success may result in selection for colonial roosting. However, because the IC hypothesis has been supported (Bijleveld *et al*. 2015) and refuted (Racine *et al*. 2012) in studies of other avian taxa, Buckley (1996) tested alternate (but not mutually exclusive) explanations, including: the assembly-point hypothesis (promotion of foraging groups) and the spatial-concentration hypothesis (concentrating birds in space). In Buckley (1996)'s study of Turkey (*Cathartes aura*) and Black Vulture (*Coragyps atratus*) foraging behaviour, the formation of foraging groups led to improved foraging efficiency. Thus, the formation of foraging groups is possibly one of the selective advantages of communal roosting in cranes.

My study did not collect the data necessary to describe the formation of social groups. However, food resource abundance within twice the mean FFD was an important factor in determining how many cranes used individual roost sites. If cranes use communal roosting to increase foraging efficiency, this finding may represent the functional link between habitat characteristics and selection for communal roosting. Comparison of flock sizes arriving at the roost in the evening to those departing in the morning, as well as flocks foraging in fields during the day, could allow tests of a mechanism similar to the

assembly-point hypothesis in cranes (Sarangi *et al*. 2014). Even still, my study presents

the first evidence for a positive effect from food proximity and density on roost use by EP

cranes during autumn staging. My findings provide a benchmark for future studies of

food density and proximity and communal roosting in cranes by indicating potential

spatial scales at which to test for behavioural effects.

4.4.4   Management Implications

Collectively, my study of crane roost use in relation to anthropogenic disturbance and

proximity to quality food resources provides information concerning a potentially

sensitive habitat type for EP cranes during autumn staging (e.g., Franco *et al*. 2000).

Although further disturbance of the landscape at my study site via agriculture or road

construction does not seem likely at present, other forms of disturbance, including

recreation and aggregate resource extraction, could alter patterns of roost use by cranes

(Végvári & Barta 2015). Thus, legal protection of these roost sites may be necessary in

the future (Krapu *et al*. 2014). Furthermore, roost wetlands at staging sites further south

are often located in more volatile landscapes due to anthropogenic activities. With

knowledge of the spatial scale at which disturbance might affect crane roosting

behaviour, especially during staging, managers can incorporate scale-dependencies into

conservation planning (Jankowiak *et al*. 2015).

Similarly, the distance between roost and feeding sites, and the quantity and quality of

food at feeding sites, may affect roost site suitability. Folk & Tacha (1990) studied roost

site suitability and stressed the importance of maintaining suitable roosting habitat for

MCP cranes migrating through the North Platte River Valley in Nebraska, USA. Ivey *et*

al. (2015) recommended that conservation habitat planners should consider all habitats within 5 km of known Central Valley Population (CVP) *A*. *c*. *tabida* roosts based on their findings from CVP cranes wintering in California. Similarly, my study provides initial identification and description of the spatial scales of two important factors affecting roost use, thereby allowing for the classification and management of suitable roosting habitat for EP cranes during autumn staging.

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5   General Discussion

5.1   Ecological Context of Study

The central objective of my study was to investigate the relationship between the behavioural ecology of Eastern Population (EP) Greater Sandhill Cranes (*Antigone canadensis tabida*; cranes herein) and agricultural waste grain as a food resource during autumn staging. This objective was important to address because 1) EP cranes are of interest to managers because they were extirpated from much of their historic range within the last century and now present potential opportunity for recreational harvest; 2) little information describing the behavioural ecology of EP cranes during autumn staging exists; 3) cranes are a relatively large, conspicuous species with extended juvenile growth and development, making them a good model in which to study age-specific behavioural differences; and 4) EP cranes utilize a locale (Manitoulin Island) ideal for studying food effects on behaviour because of the small number of potential feeding sites that allow for sampling a relatively large proportion of the available feeding sites and the few, isolated roost wetlands that are relatively easy to survey. Manitoulin was also a good site for this study because it is likely where cranes first encounter agricultural grain fields in the fall (first time in life for juveniles). Thus, I asked if spatial and temporal variation in grain food resources influenced foraging behaviour in my study system.

I predicted that spatial and temporal variation in grain density and distribution would have a strong influence on crane behaviour. I made this prediction because granivorous, migratory birds often adjust foraging behaviour to exploit relatively abundant, accessible, and energy-rich grain resources preceding and during migration (Littlefield 1986,

Reinecke & Krapu 1986, Kaminski *et al*. 2003, Stafford *et al*. 2006, Galle *et al*. 2009, Anteau *et al*. 2011, Sherfy *et al*. 2011). More specifically, I sought to quantify the effect of spatial and temporal variation in grain on foraging scale/numerical response, foraging efficiency, and roost use, considering age-/demographic-specific differences in behaviour where possible. I interpreted my results in the context of the selective pressure to optimize behaviour involving the acquisition of food resources (i.e., classical optimal foraging theory; Werner & Hall 1974).

To test my central prediction, I first studied the age-/demographic-specific foraging scale and numerical response of field-feeding cranes to spatial and temporal variation in grain density and distribution between fields at multiple spatial scales (Chapter 2). I then focused my efforts on quantifying variation in grain density and distribution effects on age-specific (i.e., adult vs. juvenile behaviour) foraging efficiency within fields (Chapter 3). Lastly, I studied the effects of grain density at multiple spatial scales and anthropogenic disturbance on the use of communal wetland roost sites (Chapter 4). In aggregate, I employed GPS tracking (Chapters 2, 4) and field observation (Chapters 2, 3, 4) and experimentation (Chapter 3) to collect data at a relatively important autumn staging site for EP cranes located at Manitoulin Island, Ontario, Canada during autumns 2010-2012.

5.2 Foraging Scale & Numerical Response

In Chapter 2, I tested for age-/demographic-specific effects on foraging scale and numerical response related to spatial and temporal variation in grain density and

distribution. I predicted that changes in within-field grain density and distribution determine the age-specific numerical response of field-feeding cranes such that family group behaviour is different from non-breeding AHY conspecifics.

I first attempted to collect samples of non-parental AHY cranes and family groups to test for effects on foraging behaviour from the behavioural inexperience and energetic requirements of juvenile (hatched during the current calendar year or "hatch year", HY herein) cranes during autumn. However, due to difficulties in distinguishing and tracking family groups in the field, I instead collected a sample of HY and adult cranes (hatched prior to the current calendar year or "after hatch year", AHY herein). Because I treated the HY sample as an index of family group behaviour, I expected to find a difference between AHY and HY models if juvenile effects on family groups resulted in behavioural differences. I developed and compared sets of candidate models developed to represent how AHY and HY cranes navigate their nutritional landscape. I assumed cranes sought to maximize fitness, in part, by optimizing energy intake. Finally, I used data collected from GPS-marked cranes to validate my models based on field observations of foraging behaviour.

In this portion of my study, I found partial support for my prediction. Cranes appeared to respond most strongly to relative grain density at the 5-km scale (i.e., within-field grain density compared to that of focal fields within a 5-km radius). However, I did not detect differences between my AHY and HY models. That is, even though AHY and HY cranes have different behavioural experience and energetic requirements, these differences did not result in disparity in foraging scale and numerical response between non-breeding and family groups as predicted. Moreover, my estimate of foraging scale

and numerical response using data collected from GPS-marked AHY cranes generally validated my observational data analyses, indicating that cranes may use a spatial scale beyond individual fields to decide where to forage. The similarity I found in my results from these analyses suggests that I collected unbiased samples of field use behaviour through field observation.

The scale at which I detected relative grain density effects on numerical response may be indicative of a link between mean foraging flight distance (FFD) and the foraging scale of a given species. I estimated mean FFD (km ± SE) for EP cranes at 6.4 ± 0.15 km (Table 2.7). Thus, the spatial scale at which relative grain density was most important in my analyses approximates my estimate of mean FFD. Furthermore, estimates of mean FFD for ecologically-similar species/subspecies, including dabbling ducks (5.1 ± 4.4 km; Johnson *et al*. 2014), cranes (*A. c. tabida* and *A. c. canadensis*) wintering in California, USA (4.5 ± 0.01 km; Ivey *et al*. 2015), and all three migratory crane subspecies migrating along the Platte River in Nebraska, USA during spring (6.8 ± 3.8 km; Sparling & Krapu 1994), are similar.

These findings suggest that cranes travelling to fields located beyond the 5-7 km range may incur a prohibitive energetic cost. In this way, my description of the relationship between field use and spatial and temporal variation in grain density and distribution offers insight that can inform future landscape management and crane conservation decisions in North America by improving understanding of the spatial scale that might be most relevant to foraging cranes (Pearse *et al*. 2010).

Finally, given the treatment of giving-up densities (GUD) in many studies of waterfowl foraging ecology (e.g., Hagy & Kaminski 2012), it was surprising that I did

not detect a more prominent within-field effect of grain density on field use (i.e., a result that would indicate a link between field use and GUD in cranes). Other researchers have noted, however, the importance of exercising caution when studying GUD because oversight of apparently minor parameters (e.g., energetic state of the forager, group foraging effects, patch predictability, etc.) can bias results (Bedoya-Perez *et al*. 2013).

Investigations relating to GUD in waterfowl have typically considered only those resources available in the focal feeding unit (e.g., field, wetland impoundment, experimental plot, etc.; e.g., Hagy & Kaminski 2015). However, my study capitalized on the essentially closed setting of my field site (i.e., a large island with relatively few feeding sites concentrated in space and time) by considering concurrent effects from feeding sites at multiple spatial scales. Thus, my findings suggest that future foraging scale and GUD studies should consider the behaviour (e.g., mean FFD) and geographical setting of the focal species in conceptualizing experimental designs. In doing so, the scale at which data are collected will align with the scale at which organisms likely interpret their nutritional environments (i.e., foraging scale).

Sampling the landscape at scales which are most convenient or apparent to human interpretation (e.g., field, wetland, etc.) may entirely overlook the true connectivity between food resources that cranes and other species perceive and exploit. For instance, a field likely represents only a patch in a mosaic of potential feeding sites for cranes, and perhaps other species as well. Striving for alignment between sampling design and an organism's foraging scale will improve practical and theoretical application of the results yielded by related studies (e.g., Beatty *et al*. 2015).

5.3 Age-/Demographic-specific Foraging Efficiency

In Chapter 3, I studied the relationship between age-specific foraging behaviour and grain density and distribution at the within-field scale. I predicted that AHY cranes would forage more efficiently than HY conspecifics and that grain density would be the most important predictor of foraging efficiency. Because AHY cranes have more experience feeding on harvested agricultural grain than HY cranes, I expected to find that AHY cranes spend less time searching for than consuming food (i.e., greater foraging efficiency). Furthermore, I expected that my models would include grain density as a top predictor for both the AHY and HY datasets if cranes were adjusting foraging behaviour to exploit changes in grain availability. I compared separate sets of candidate models for both the AHY and HY age classes built from observational and experimental datasets to describe factors affecting age-specific foraging efficiency. I assumed cranes maximize fitness, in part, by modulating foraging behaviour. I also assumed that cranes respond to spatial and temporal variation in grain density and distribution to optimize energy intake.

Analyses of observational and experimental datasets did not detect greater foraging efficiency in AHY cranes compared to HY conspecifics (i.e., no substantial age class effect). Interestingly, I found an opposite effect in my observational analysis where HY cranes foraged marginally more efficiently than AHY cranes. I did not find greater foraging efficiency amongst AHY cranes in my experimental analysis. Furthermore, both AHY and HY cranes appeared to respond most prominently to variation in the spatial distribution of grain instead of grain density as I predicted. My observational models provided insight into these behavioural responses by quantifying how grain distribution affects foraging efficiency; cranes foraged less efficiently when grain distribution was

more variable. Cranes showed similar declines in foraging efficiency as grain became distributed more variably in experimental plots. Taken together, my observational and experimental data provide insight concerning how AHY and HY cranes might adjust foraging behaviour to exploit spatial and temporal variation in grain food resources to optimize energy intake.

The lack of a strong age-specific effect on foraging efficiency could be related to either social context or the true novelty of grain as a food resource for HY cranes during autumn. Given that cranes (*Gruidae*) are relatively socially advanced (Aviles 2003, Panov *et al*. 2010, Zhou *et al*. 2010), and that social context effects on foraging behaviour have been reported in other avian species (e.g., Common Ravens, *Corvus corax*; Stöwe *et al*. 2006), including cranes (e.g., Black-necked Cranes, *Grus nigricollis*; Yang *et al*. 2016), I may have missed part of the age-specific foraging behaviour equation by not quantifying the social contexts in which I observed cranes. For example, Yang *et al*. (2016) demonstrated an inverse relationship between proportion of time spent in vigilant behaviour while foraging and flock type/size in Black-necked Cranes during winter. Therefore, if HY crane foraging behaviour was linked to flock type and/or size at my study site, including such parameters in analyses would likely improve the explanatory power of associated behavioural models.

Beyond differences in social context, individual animals have varying propensities to explore or to follow in terms of foraging behaviour (Barnard & Sibly 1981). Although individual differences in behaviour are problematic to study in unmarked, wild animals, consideration should be given to effects on foraging behaviour. These effects may be

especially important in terms of interaction with the social context of the individual forager because behaviour may change in relation to flock size and/or composition.

Whereas the social context of crane foraging behaviour could be described and quantified in the field relatively easily, determining the novelty of grain as a food resource to HY cranes during autumn proved more challenging. I assumed that HY cranes arriving from natal grounds at greater latitudes must learn how to forage in harvested agricultural grain fields such that their foraging efficiency would at least initially be less than that of AHY conspecifics. Accordingly, if cranes were facing selective pressure to maximize net energy intake, HY cranes would be at a disadvantage. I expected that such a disadvantage would be especially prominent at those staging areas encountered earlier during autumn migration when HY cranes are still growing and learning foraging behaviour (e.g., my study site at Manitoulin Island). However, one of the central conditions of optimal foraging theory is a direct link between foraging behaviour and fitness (Pyke 1984). While HY cranes may have been optimizing foraging behaviour out of necessity (i.e., to support continued growth of muscles and long bones; Krapu & Johnson 1990, Curro *et al.* 1996, Nowald 2001), AHY cranes may not be facing such selective pressure during early autumn migration.

Similar temporary suspension of constraints associated with energy and/or time budgeting in adults, but not juveniles, has been reported in other avian taxa (e.g., Yellow-eyed Juncos, *Junco phaeonotus*; Weathers & Sullivan 1991). Description of age-specific differences in foraging behaviour that may be linked with disparate selective pressures provides a unique insight into how the optimal foraging equation changes through the life stages of an individual.

Lastly, foraging for grain may not be difficult compared to other motile (e.g., insects) and sessile prey items (e.g., native seeds) which cranes consume. Thus, HY cranes may learn to forage on grain relatively quickly during autumn staging, resulting in comparable foraging efficiency between age classes.

Select field studies have quantified spatial and temporal variation in how organisms optimize behaviour to exploit food resources. However, few studies have advanced understanding of age-specific differences in foraging behaviour optimization. The insight offered by my study advances the latter. My study of age-specific foraging behaviour in cranes will provide direction for experimental design in future studies of optimal foraging behaviour. Moreover, my findings will help guide future decisions relating to landscape management and crane conservation by describing the effects of grain food resources on crane foraging behaviour during autumn staging.

5.4   Grain Density & Anthropogenic Disturbance Effects on Roost Use

In Chapter 4, I studied the effects of grain density and anthropogenic disturbance on roost use during autumn staging. I predicted that grain density in feeding fields within a radius equal to the mean foraging flight distance (FFD) would be the most important predictor of roost use. I made this prediction because cranes may optimize their energetic budgets by minimizing FFD. Such behaviour would allow for maximizing the energy gained via foraging, which is especially important for granivorous, migratory birds during migration (Littlefield 1986, Reinecke & Krapu 1986, Kaminski *et al*. 2003, Krapu *et al*. 2004, Stafford *et al*. 2006, Galle *et al*. 2009, Anteau *et al*. 2011, Pearse *et al*. 2011,

Sherfy *et al*. 2011). Furthermore, I predicted that anthropogenic disturbance from both primary and secondary roads would have a moderate negative effect on roost use because birds tend to respond negatively to such disturbances near roost sites (Végvári & Barta 2015, Lilleyman *et al*. 2016). I built candidate models describing scenarios wherein food resources at different spatial scales and different forms of anthropogenic disturbance might affect roost use behaviour. Finally, I used data collected from GPS-marked cranes to validate my models based on field observations of roost use.

My study did not provide support for my prediction that grain density within the mean FFD of roost sites would be the most important predictor of roost use. This result was unexpected because I predicted a spatially proportionate, functional link between the distance at which food resources would affect crane roost use and the mean FFD (km $\pm$ SE) estimated from GPS-marked cranes (6.4 ± 0.15 km). However, there was partial support for my secondary prediction that anthropogenic disturbance from both primary and secondary roads would have a moderate negative effect on roost use. I found that distance to secondary roads was not an important factor in determining roost use but that distance to primary roads had an effect size (number of cranes $\pm$ SE) more than two times that of the most important food density parameter (9.21 ± 2.5 and 4.15 ± 1.7 cranes, respectively). Finally, while there was general agreement between the trends in my GPS and observational roost use analyses, there were minor differences in the magnitude of both main effects. Thus, my estimate of crane roost use behaviour may have been biased or GPS-marked cranes may have exhibited different roost use behaviour than my observational sample due to unknown factors beyond the scope of my study.

Although I found that grain density at a scale twice that of mean FFD (i.e., 12 km) was a more important predictor of roost use than at a scale equal to mean FFD (i.e., 6 km), there exists some precedent for such a finding from previous research. Other studies have reported food availability and distribution effects on roost site use and selection over substantial spatial gradients; including distances ranging from <2 km in Barnacle Geese (*Branta leucopsis*) in The Netherlands (Si *et al*. 2011) to 5-50 km in Bean (*Anser fabalis*) and Greater White-fronted (*A. albifrons*) Geese in Poland (Jankowiak *et al*. 2015). Differences in the spatial scales of these effects are likely linked to ecological context. For example, because intra- and interspecific competition for food resources (Guillemain & Fritz 2002, Sherry *et al.* 2005) and energetic demands (e.g., thermoregulatory costs; Livolsi *et al.* 2015) often increase during winter in migratory birds, proximity to quality feeding fields may become increasingly important in determining roost site use in EP cranes later in autumn migration. That is, the selective pressure to optimize behaviour may increase as birds continue along migratory routes to wintering grounds, and thus, the relative importance of the distance between roost sites and food sources may vary by location, or, perhaps more accurately, latitude.

Colonial roost sites have been considered "information hubs" by other researchers (Ward & Zahavi 1973, Beauchamp 1999) whereby the day's foraging experience can be exchanged between individuals to improve subsequent foraging efforts. More specifically, the formation of foraging groups at communal roost sites can lead to improved foraging efficiency (e.g., the assembly-point hypothesis; Buckley 1996). Although quantifying the formation of foraging groups at roost sites was beyond the scope of this study, the evidence that I presented for a grain proximity effect (i.e., at least

two times mean FFD) on roost use indicates the potential benefit necessary for selection and thus conservation of communal roosting behaviour. If subsequent researchers desire to test these mechanisms (e.g., the assembly-point hypothesis), a simple comparison of flock sizes arriving at roosts in the evening with the size of those departing in the morning, and in relation to foraging flock sizes observed in fields during the intervening days, could prove useful (Sarangi *et al.* 2014).

Finally, anthropogenic disturbance, namely distance to primary roads, was the most important predictor of EP crane roost use at my study site. Although anthropogenic disturbance was an important factor in the spatial and temporal context of this study, how birds respond to perceived threats of predation/disturbance can vary along the migratory route (Chudzińska *et al*. 2016). Specifically, variation in behavioural response to threats is likely associated with changing nutritional demands. Moreover, latitudinal variation in response to disturbance may interact with differences in physiological requirements between AHY and HY cranes (Krapu & Johnson 1990, Curro *et al*. 1996, Nowald 2001). Because my findings suggest that human activities can affect roost use in EP cranes, future researchers should consider quantifying real-time disturbance (e.g., measure traffic levels) while collecting concurrent observations of roost use (Ciuti *et al*. 2012, D'Amico *et al*. 2016). Collecting targeted data of this nature may prove useful as landscapes become increasingly divided by road networks and traffic levels increase.

5.5   Modern Agriculture & Crane Ecology

The landscape in much of North America changed from woodland and short-, mixed-, and tall-grass ecosystems to largely agricultural fields within an ecologically short timeframe (i.e., 200-300 years). Moreover, the recent agrarian revolution in North America (i.e., last 50-100 years) has led to essentially unrestricted energetic winter carrying capacities for some migratory, granivorous birds (Fox & Abraham 2017). Thus, it is important to consider the implications of the timing and speed of this change for the behaviour of migratory birds that now rely on modern agricultural grain resources. For example, the findings presented here were interpreted assuming that either cranes have had sufficient evolutionary time to adapt to modern grain food resources (relatively unlikely) or that these modern food resources are sufficiently similar to those that existed prior to conversion of the landscape to agriculture, such that cranes were able to effectively modulate their behaviour (more likely).

Other species of granivorous, migratory birds, including Tundra Swans (*Cygnus columbianus*; Nagel 1965, Tate & Tate 1966, Petrie *et al*. 2002, Petrie & Wilcox 2003) and Snow Geese (*Chen caerulescens*; Alisauskas & Ankney 1992), have also recently adjusted their migratory and foraging behaviour to exploit modern grain resources. Perhaps not surprisingly, some swan and goose populations increased substantially following their relatively recent switch to consuming grain resources during winter and migration (e.g., Serie & Bartonek 1991, Ankney 1996, Fox & Madsen 2017), and a similar population increase has been observed in EP cranes that also coincides with this change in food resource availability (Kruse & Dubovsky 2015, Fronczak *et al*., In press).

Historically, cranes would likely not have had discrete feeding patches similar to those presented by modern agricultural fields, and thus may have relied more on the seeds of aquatic plants. Food resources made available from modern agriculture likely shape much of what is now considered natural crane behaviour during winter and migration. Specifically, between-field variation in food availability and quality on the modern landscape, primarily driven by crop type and farming practices (e.g., fertilization regime and harvesting equipment), is likely greater than what may have existed historically between patches, and has implications for the behavioural ecology of species that target such food sources (Fox *et al.* 2017).

If there is greater variation between modern feeding sites, selection should favour being more selective when deciding between fields/patches. That is, finding and exploiting the best field may have a proportionally greater benefit compared to finding and exploiting the best patch historically. In the context of grain field use, cranes appear to consider food resources at a spatial scale that approximates mean FFD (Chapters 2 & 4), and adjust foraging behaviour (Chapter 3) and roost site use (Chapter 4) to aid in exploiting the most profitable fields within that range.

Because of the relative importance of grain food resources to cranes (and many other migratory, granivorous birds), variation in the quality, quantity, and spatial distribution of grain can affect crane behaviour (Chapters 2, 3, & 4, Anteau *et al.* 2011) and habitat suitability (Pearse *et al.* 2010). For example, if grain resource availability changes substantially, cranes may need to increase FFDs to continue to utilize preferred foods or shift to alternate food types or habitats (Fox *et al.* 2017). To some degree, increasing FFDs may be a suitable behavioural response, but there would likely be a particular

spatial threshold beyond which the energy gained from foraging would not offset the energy expended flying (Pearse *et al*. 2010). To this end, research from a key staging site for the Mid-Continent Population in Nebraska, USA implicates both harvesting equipment and post-harvest practices in relatively substantial decreases in grain availability over the last several decades (Sherfy *et al*. 2011).

Should similar changes in grain availability occur at key EP staging sites, cranes may need to continue to adjust foraging behaviour to match their relatively dynamic nutritional landscape. Thus, researchers should continue to monitor grain availability at key staging and wintering sites (Sherfy *et al.* 2011) to allow for relatively early detection and response to substantial decreases in grain availability to prevent negative population-level effects (Krapu *et al.* 2004, Pearse *et al.* 2010).

5.6   Future Research

My research has identified several potential avenues of investigation that would contribute to the understanding of how spatial and temporal variation in grain food resources might affect EP crane foraging and migratory behaviour, and, potentially, population dynamics. Following, I offer possible approaches to studying a selection of these topics.

As identified in Chapter 2, understanding of the foraging scale for cranes during autumn staging provides a benchmark for subsequent study of foraging sites and habitat use. However, my study only considered grain density and distribution effects at the within-field, 1-km, and 5-km scales. Thus, although the 5-km scale was the most

important predictor of crane field use, I was not able to determine the precise scale at which cranes interpreted the nutritional landscape – only that it was likely at least at a 5-km radius. I suggest that future studies consider similar effects at spatial scales extending to at least a 10-km radius to identify the foraging scale in this system with greater precision. Increasing the precision of the estimate of such a spatial scale would allow for more effective conservation efforts concerning habitat procurement and management for staging cranes because strategies could be designed to align more accurately with the foraging scale of the species.

In Chapter 3, I assumed that prey capture efficiency was consistent between foraging cranes. However, other studies have reported variation in capture efficiency amongst avian conspecifics (Maccarone *et al.* 2012, Brzorad *et al*. 2015). If capture efficiency varies between AHY and HY cranes, comparison of foraging efficiency between these age classes, as calculated by searching to feeding time ratios, may be misleading. To test this assumption, researchers may consider attempting to quantify capture efficiency with a smaller sample of targeted, close-range observational trials wherein the number of food items consumed per time spent feeding could be estimated per age class. Comparison of capture efficiency between AHY and HY cranes would determine if the assumption of equal capture efficiency between age classes is appropriate, thereby providing further insight towards my findings.

Finally, in Chapter 4, I assumed that primary roads had more traffic than secondary roads when cranes were using nearby wetlands as overnight refugia. I made this assumption because primary roads were paved whereas secondary roads were gravel-covered. Given that my findings identified distance to primary roads as an important

determinant of roost site use, I recommend quantifying road traffic while collecting behavioural data at roost sites (e.g., Ciuti *et al.* 2012, D'Amico *et al.* 2016) to ensure disturbance by vehicle traffic is a suitable predictor of crane roost use. Quantifying road traffic in this way would also allow for a more robust test of whether cranes perceive road traffic as a predation risk (i.e., roost disturbance). Traffic surveys at sunrise and sunset may provide a measure of disturbance as perceived by cranes arriving at and departing roost wetlands. Alternatively, because road traffic likely decreases overnight, when cranes are using roost wetlands, it may be particularly useful to quantify overnight road traffic if anthropogenic disturbance effects on roost use occur over a longer timescale.

5.7   Closing Remarks

While grain food effects were relatively important in the studies presented here, I did not find evidence for the ubiquitous effect I predicted, especially concerning roost use, where anthropogenic disturbance appeared to be more important than grain. Moreover, my foraging efficiency study suggested that AHY cranes may not be maximizing efficiency during early autumn staging. Therefore, I conclude that cranes are likely modulating behaviour in response to spatial and temporal variation in grain to maximize net energy acquisition (i.e., optimal foraging) but that other less or equally important factors also shape behaviour during autumn staging.

Nevertheless, in aggregate, my findings represent the first comprehensive study of behavioural ecology in EP cranes during autumn staging. My work offers increased understanding of applied and theoretical concepts of avian behaviour that can be used for subsequent research, conservation, and management of a recreationally-harvested species.

I described the specific contributions of each of my studies to behavioural ecology and wildlife management in the preceding subsections (i.e., 5.2-5.4), as well as in greater detail in Chapters 2, 3, and 4. Therefore, in closing, I offer a summary of five of the most important findings arising from my research:

1. EP cranes did not appear to respond to within-field changes in grain abundance as documented in similar studies of field-feeding waterfowl (i.e., traditional GUD), but instead appeared to use a spatial scale greater than a given field to optimize feeding field use. Notably, this spatial foraging scale appeared to align with the mean FFD estimated from GPS-marked cranes.

2. Behavioural and physiological differences associated with HY cranes during autumn staging did not appear to have a substantial effect on family group foraging behaviour. Non-parent AHY and family group cranes seemed to respond to spatial and temporal changes in grain similarly.

3. Variation in the spatial distribution of grain appeared to be more important than grain density in terms of its negative relationship with foraging efficiency amongst AHY and HY cranes.

4. AHY cranes may face less selective pressure to optimize foraging behaviour than HY conspecifics, especially earlier in autumn migration, such that they do not need to forage as efficiently in harvested agricultural grain fields.

5. Both distance to and density of grain food resources may affect EP crane roost use, but anthropogenic disturbance effects were ultimately more than two times stronger in this study.

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Appendices

Appendix I – UWO Animal Use Protocol 2010

May 14, 2010

This is the Original Approval for this protocol
A Full Protocol submission will be required in 2014

Dear Dr. Petrie:

Your Animal Use Protocol form entitled: Population size, fall recruitment, habitat use, and migratory habits of Eastern Population Sandhill Cranes (Grus canadensis) staging and breeding along the North Shore of Lake Huron, Ontario. Funding Agency: Long Point Waterfowl; Canadian Wildlife Service; Wildlife Habitat Canada

has been approved by the University Council on Animal Care. This approval is valid from **May 14, 2010 to May 31, 2011.** The protocol number for this project is **2010-213.**

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
   If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
4. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

ANIMALS APPROVED FOR 4 Years

Species	4 Year Total Numbers Estimated as Required	List All Strain(s)	Age / Weight
Other	10	Sandhill Crane	AHY/10-12lbs.

REQUIREMENTS/COMMENTS

Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.
The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

c.c. Approval   - S. Petrie, E. Hanna, S. Waring

The **University** *of* **Western Ontario**
Animal Use Subcommittee / University Council on Animal Care
Health Sciences Centre, ● London, Ontario ● CANADA – N6A 5C1
PH: 519-661-2111 ext. 86770 ● FL 519-661-2028 ● www.uwo.ca / animal

AUP Modification #1   **12/2/2010 #2010-213 Petrie**

PI / PROTOCOL INFORMATION

PI Name: Dr. Scott Petrie	**Protocol Number: 2010-213**

Protocol Title: Population size, fall recruitment, habitat use, and migratory habits of Eastern Population Sandhill Cranes (Grus canadensis) staging and breeding along the North Shore of Lake Huron, Ontario.

1. REQUESTED MODIFICATIONS TO PREVIOUSLY APPROVED ANIMAL USE PROTOCOL

Identify all requested changes to the AUP identified above

AUP Ref. #	Form Elements	
7, 8, 9, 10, 11, 13	Acute & Chronic Elements, PAU, Animal Groups Overview, Species Number, Source, Strains, Justification	C ☒

2.PROVIDE JUSTIFICATION FOR PROPOSED CHANGES OUTLINED IN THIS PROTOCOL MODIFICATION

Because funding for only 10 GPS units was secured prior to the 2010 field season, the original AUP proposed the capture/use of only 10 birds. However, given that multiple birds would often feed on bait sites at one time and that only one bird from each rocket net deployment was eligible to receive a GPS transmitter, surplus birds were captured and marked with standard aluminium Canadian Wildlife Service leg bands in addition to the 10 GPS transmitter-marked birds. In total, seven (n=7) surplus birds were captured and marked with standard aluminium leg bands in 2010.

4.INVESTIGATOR DECLARATION

I.   All animals used in this research project will be cared for in accordance with the recommendations of the Canadian Council on Animal Care and the requirements of the provincial legislation entitled, "The Animals for Research Act," of the Province of Ontario.

II.   I confirm that this *Animal Use Protocol* accurately represents the proposed animal use.

III.   I accept responsibility for procedures performed on animals in this project.

IV.   I will ensure that any individual who will perform any animal-related procedure(s) within this protocol will complete all related mandatory training AND will be made familiar with the contents of this document.

2010-213 Petrie 12.02.10 Modification #1 Approved.doc

AUP Modification #1   **12/2/2010 #2010-213 Petrie**

V. I confirm that all identified external approvals, including Institutional Safety Permits and Scientific Peer approvals, represent the stated intention of animal use within this _Animal Use Protocol_.

1. **I support the above declaration - YES ☒**   **Today's Date** _mm/dd/yy_: 12/01/10

2. **By checking 'YES' in this section, I authorize the submission of this form and its electronic delivery to auspc@uwo.ca YES ☒ NO ☐**

3. **I authorize** Everett E. Hanna **(PI Designate) to submit this form and to receive a copy of authorization via email on my behalf. Today's Date** (_mm/dd/yy_): 12/01/10

AUS APPROVAL - _AUS Office Use Only_ -

Veterinary Authorization by Dr. Gatchell Authorization Date (mm/dd/yy) **12/02/10**	Signature:

10. CHANGES TO SPECIES NUMBER & STRAINS – See Section 10, AUP Reference

Species	4 Year Total Numbers Estimated as Required	List All Strain(s)	Age / Weight	Is This Strain Genetically Altered?	IF Genetically Altered Animals are COMMERCIALLY AVAILABLE — Insert VENDOR STRAIN INFO URL	IF Genetically Altered Animals are from a NON-COMMERCIAL SOURCE		
						Provide Genetic Source	Describe the NATURE of the genetic modification in heterozygous and homozygous animals	Identify the SYSTEMS AFFECTED and SPECIAL CARE required
Other	17	Grus canadensis tabida	AHY/10-12lbs.	☐ Yes ☒ No				

Appendix II – CWS Banding Permit and Rocket Net Authorization

Environment Canada | Environnement Canada

Canadian Wildlife Service | Service canadien de la faune

Bird Banding Office
Canadian Wildlife Service
National Wildlife Research Centre

████████████████████████

May 26, 2010

Everett Hanna
Long Point Waterfowl

████████████████████

Dear Everett,

Enclosed is your new bird banding sub-permit (10787 D) under Long Point Waterfowl & Wetlands Res Fund station permit as requested.

Upon receipt, please review and sign your permit. If there are any questions or concerns about the authorisations please contact me.

Please note that a federal banding permit may be only one of several permits require for your project and is only valid in conjunction with other necessary permits. Banders are responsible for ensuring that they have all necessary permits for their project. Please contact provincial and territorial authorities where your permittee intends to band to ensure they have all necessary permits in place. Visit the BBO website for more information on permits http://www.cws-scf.ec.gc.ca/nwrc-cnrf/default.asp?lang=En&n=B197CA34-1.

Thank you for your co-operation.

████████████████

Louise Laurin
Senior Bird Banding Administrator

████████████████████

cc : Scott Petrie

Canadä

I✦I Environment   Environnement
Canada   Canada

Environmental   Service de la conservation
Conservation Service   de l'environnement

SCIENTIFIC PERMIT TO CAPTURE AND BAND MIGRATORY BIRDS
PERMIS DE CAPTURE ET DE BAGUAGE D'OISEAUX MIGRATEURS

In the Province(s) - Dans la (les) province(s) Ontario	Permit No N° de permis 10787 D
Name and Address - Nom et adresse **EVERETT E. HANNA** **LONG POINT WATERFOWL**	Issued under Migratory Bird Regulations. Emis en vertu du règlement concernant les oiseaux migrateurs.
	Section Article **4 and 19**
	Issue Date Date d'émission **2010/05/21**
	Expiry Date Date d'expiration **2010/12/31**

Signature of Holder - Signature du détenteur	For the Minister - Pour le Ministre Name (Print) - Nom (Lettres moulées) **L. LAURIN**	Signature

AUTHORIZATIONS - AUTORISATIONS

Authorized to:

- Band waterbirds Sandhill Crane (SACR) (2060) only
- Use Rocket nets
- Use Satellite Transmitter on Sandhill Crane (SACR) (2060)
  PTT attached to a 3" BLK/WHI alpha-num (K/0 to K/9) pvc plastic band on 10 adults (north shore of Lake
  Huron) (SATELLITE TRANSMITTER USE MAY REQUIRE CERTIFICATION OF THE DEVICE BY
  INDUSTRY CANADA)   (IF IN POSSESSION OF A CURRENT ANIMAL CARE COMMITTEE APPROVAL) in
  Ontario

SEE GENERAL CONDITIONS ON REVERSE SIDE / VOIR CONDITIONS GÉNÉRALES AU VERSO
061 - 1744 (12/01)

Curriculum Vitae

Name:	Everett Edward Hanna, RPBio, CWB®
Place of Birth:	Toronto, Ontario, Canada
Date of Birth:	13 December 1985

Post-secondary Education:

Western University (3.95 GPA)
London, ON, Canada
2010-2017, Ph.D., Biology

Trent University (3.58 GPA)
Peterborough, ON, Canada
2007-2009, B.Sc., Biology

Sir Sandford Fleming College (3.74 GPA)
Lindsay, ON, Canada
2006-2007, Advanced Diploma, Fish & Wildlife Technology

Sir Sandford Fleming College (3.43 GPA)
Lindsay, ON, Canada
2004-2006, Diploma, Fish & Wildlife Technician

Honours & Awards:

Vice-President Academic's Contract Faculty Award for Excellence in Teaching
Sir Sandford Fleming College
2014/15 Academic Year

Western Graduate Research Scholarship
Western University
2010-2015

Graduate Student Research Grant
Long Point Waterfowl
2009-2013

Provincial Fish & Wildlife Research Grant
Ontario Federation of Anglers & Hunters
2009-2012

Wildlife Research Grant (Zone G)
Ontario Federation of Anglers & Hunters
2010 and 2011

Honours
& Awards (cont.):
Top Student Presentation Award (poster)
Fifth North American Duck Symposium
2009

Dean's Honour Roll
Trent University
2007-2009

President's Honour Roll
Trent University
2007-2009

National Entrance Scholarship
Trent University
2007

Letter of Academic Achievement
Sir Sandford Fleming College
2004-2007

Research
Experience:
Doctoral Researcher
Long Point Waterfowl/Western University
London and Manitoulin Island, ON, Canada
2010-2017

Senior Wildlife Biologist/Project Ecologist
Great Bear Environmental Consulting, Ltd.
Central and Western Canada
2012-Present

GIS/Data Management Specialist
DSS Management Consultants, Inc.
Pickering, ON, Canada
2013-2015

Field Biologist
Long Point Waterfowl
Port Rowan and Algoma Region, ON, Canada
2009

Wildlife Research Technician
Colorado Division of Wildlife
San Luis Valley, CO, USA
2009

Research Experience (cont.):	Undergraduate Researcher Trent University and Ducks Unlimited Canada Hill Spring, AB, Canada and Peterborough, ON, Canada 2008
	Waterfowl Research Technician Ducks Unlimited Canada Medicine Hat and Hill Spring, AB, Canada 2006 and 2008
	Mourning Dove Bander/Wildlife Technician North Dakota Game and Fish Department Harvey, ND, USA 2007
Teaching Experience:	College Professor, Fisheries & Wildlife Science Portage College, Natural Resources Technology Program Lac La Biche, AB, Canada 2015-Present
	College Professor, Applied Biological Science Sir Sandford Fleming College, Fish and Wildlife Programs Lindsay, ON, Canada 2013-2015
	Instructor, Wildlife Ecology and Management Western University, Department of Biology London, ON, Canada 2014 (Winter Term)
	Teaching Assistant Western University, Department of Biology London, ON, Canada 2010-2015
	Teaching Assistant Trent University, Department of Biology Peterborough, ON, Canada 2008

Technical Publications:

Hanna, EE, Petrie, SA, Rubin, BD. Sandhill crane numerical response and foraging scale in harvested agricultural grain fields. In preparation.

Hanna, EE, Petrie, SA. Age-specific autumn foraging ecology of greater sandhill cranes (*Antigone canadensis tabida*). In preparation.

Hanna, EE, Petrie, SA. Roost site use by eastern population sandhill cranes (*Antigone canadensis tabida*) during autumn staging. In preparation.

Hanna, EE. A novel and inexpensive technique for monitoring duck incubation behaviour. In preparation.

Hanna, EE, Palumbo, MD, Van Zyl, J, Petrie, SA. Starvation thresholds and heavy metal burdens in waterfowl wintering on the Great Lakes. In preparation.

Fronczak, DL, Andersen, DE, **Hanna, EE**, Cooper, TR. In press. Distribution and migration chronology of eastern population sandhill cranes. The Journal of Wildlife Management.

Hanna, JE, **Hanna, EE**. 2016. Integrating natural capital in planning: benefit-cost analysis. DSS Management Consultants Inc. prepared for Credit Valley Conservation, 77 *pp*.

Hanna, JE, **Hanna, EE**. 2015. Grand River Watershed case study: phosphorus management benefit/cost analysis - phase II report. DSS Management Consultants Inc. prepared for Environment Canada, 118 *pp*.

Hanna, EE, Schummer, ML, Petrie, SA. 2015. Evaluation of a vacuum technique to estimate abundance of waste barley. Journal of Fish and Wildlife Management **6(2)**: 430-436.

Fronczak, DL, Andersen, DE, **Hanna, EE**, Cooper, TR. 2015. Annual survival rate of satellite-transmitter-marked eastern population greater sandhill cranes. Journal of Fish and Wildlife Management **6(2)**: 464-471.

Hanna, EE, Schummer, ML, Petrie, SA. 2014. Migratory chronology, autumn recruitment, and population size of eastern population sandhill crane (*Grus canadensis*). Long Point Waterfowl; prepared for Ontario Ministry of Natural Resources, Ontario Region of the Canadian Wildlife Service, and various stakeholder groups, 14 *pp*.

Santomauro, D, **Hanna, EE**. 2014. Liard 3D seismic Environmental Sampling and Monitoring Program, Fort Nelson, BC, Canada. Great Bear Environmental Consulting; prepared for Apache Oil Canada, 143 *pp*.

Technical Publications (cont.):

Santomauro, D, **Hanna, EE**, Kaytor, B, Randall, J. 2013. Corvidae Vantage Pipeline construction - environmental impact assessment: South Dakota, USA to Edmonton, Alberta, Canada. Corvidae Environmental Consulting and Great Bear Environmental Consulting; prepared for Vantage Pipeline, 76 *pp*.

Hanna, JE, **Hanna, EE**. 2013. Grand River Watershed case study: phosphorus management benefit/cost analysis - phase I report. DSS Management Consultants Inc. prepared for Environment Canada, 81 *pp*.

Hanna, EE. 2009. Incubation rhythms and nest success of mallards (*Anas platyrhynchos*) and northern pintails (*Anas acuta*) in southwestern Alberta, Canada. Undergraduate Honours Thesis, Trent University, Peterborough, ON, Canada, 22 *pp*.

Popular Publications:

Ontario Field Ornithologists' Newsletter 2015
Long Point Waterfowl Annual Newsletter 2009-2014
Manitoulin Expositor Newspaper 2009-2010, and 2012
Cottage Country Magazine 2010
The Unison Call Magazine 2010
Port Rowan Good News Newspaper 2010

Technical Presentations:

Hanna, EE, Schummer, ML, Petrie, SA. 2014. Autumn foraging and migratory ecology of sandhill cranes (*contributed; oral*). Great Lakes Partners Forum. Port Clinton, OH, USA.

Hanna, EE, Schummer ML, Petrie, SA. 2014. Eastern population sandhill crane migratory ecology and information needs in Ontario (*invited; oral*). North American Sandhill Crane Information Needs Workshop. Lafayette, LA, USA.

Hanna, EE, Schummer, ML, Petrie, SA. 2014. Autumn foraging and migratory ecology of sandhill cranes (*contributed; oral*). North American Crane Working Group Meeting. Lafayette, LA, USA.

Hanna, EE, Schummer, ML, Petrie, SA. 2014. Evaluation of a vacuum technique for the sampling of agricultural grain (*contributed; poster*). North American Crane Working Group Meeting. Lafayette, LA, USA.

Hanna, EE. 2013. Autumn foraging and staging ecology of sandhill cranes (*invited; oral*). Academic Lecture, Sir Sandford Fleming College. Lindsay, ON, Canada.

Technical Presentations (cont.):

Hanna, EE. 2013. Autumn foraging and migratory ecology of sandhill cranes (*invited; oral*). Academic Lecture, Western University. London, ON, Canada.

Hanna, EE, Schummer, ML, Petrie, SA. 2013. Evaluation of a vacuum technique for the sampling of agricultural grain (*contributed; poster*). Sixth North American Duck Symposium. Memphis, TN, USA.

Hanna, EE. 2012. Autumn migratory ecology of eastern population sandhill cranes (*invited; oral*). Academic Lecture, Long Point Waterfowl REC. Turkey Point, ON, Canada.

Hanna, EE. 2012. Physiology, behaviour, and habitat use of sandhill crane family groups during autumn migration (*contributed; oral*). Waterfowl and Wetlands Research, Management, and Conservation in the Lower Great Lakes: Partners Forum 2012. Turkey Point, ON, Canada.

Hanna, EE, Schummer, ML, Petrie, SA. 2012. Physiology, behaviour, and habitat use of sandhill crane family groups during autumn migration (*contributed; oral*). OFAH 2012 National Fish and Wildlife Conservation Congress. Ottawa, ON, Canada.

Hanna, EE. 2012. Physiology, behaviour, and habitat use of sandhill crane family groups during autumn migration (*invited; oral*). Academic Lecture, Western University. London, ON, Canada.

Hanna, EE. 2011. Physiology, behaviour, and habitat use of sandhill crane family groups during autumn migration (*invited; oral*). Academic Lecture, Long Point Waterfowl REC. Turkey Point, ON, Canada.

Hanna, EE, Schummer, ML, Petrie, SA. 2011. Exogenous and endogenous factors affecting sandhill crane migratory chronology (*contributed; oral*). Waterfowl and Wetlands Research Management, and Conservation in the Lower Great Lakes: Partners Forum 2011. Pointe Mouillée State Game Area, MI, USA.

Fronczak, DL, **Hanna, EE**. 2011. The use of satellite telemetry to evaluate migration chronology and breeding, migration, and wintering distribution of the eastern population of sandhill cranes (*contributed; poster*). North American Crane Working Group & Waterbird Society Meeting. Grand Island, NE, USA.

Hanna, EE, Schummer, ML, Petrie, SA. 2011. Habitat use, migratory behaviour, and vital rates of sandhill cranes on the North Shore of Lake Huron, Ontario (*invited; oral*). North American Crane Working Group & Waterbird Society Meeting. Grand Island, NE, USA.

Technical Presentations (cont.):

Hanna, EE, Badzinski, SS, Petrie, SA. 2010. Habitat use, migratory behaviour, and vital rates of sandhill cranes on the North Shore of Lake Huron, Ontario (*contributed; oral*). International Association of Great Lakes Research Conference. Toronto, ON, Canada.

Hanna, EE, Emery, RB. 2009. Incubation rhythms and nest success of prairie nesting mallard and northern pintail (*contributed; poster*). Fifth North American Duck Symposium. Mississauga, ON, Canada.

Hanna, EE. 2009. Incubation rhythms and nest success of prairie nesting mallard and northern pintail (*oral*). Trent University Thesis Seminar. Peterborough, ON, Canada.

Public Presentations:

Hanna, EE, Schummer, ML, Petrie, SA. 2012. Autumn foraging and migratory ecology of sandhill cranes (*invited; oral*). Sudbury Naturalists Club Meeting. Laurentian University - Living with Lakes Centre, Sudbury, ON, Canada.

Hanna, EE. 2012. The wonderful world of the sandhill cranes (i*nvited; oral seminar*). Auberge Inn Crane Spotting Extravaganza Weekend. Providence Bay, ON, Canada.

Hanna, EE, Schummer, ML, Petrie, SA. 2012. Autumn foraging and migratory ecology of sandhill cranes (*invited; oral*). Manitoulin Nature Club. Mindemoya, ON, Canada.

Hanna, EE, Schummer, ML, Petrie, SA. 2012. Migratory and reproductive ecology of sandhill cranes on Manitoulin Island, Ontario (*invited; oral*). Ontario Nature, Friends of Misery Bay, and Manitoulin Nature Club. Misery Bay, ON, Canada.

Hanna, EE, Schummer, ML, Petrie, SA. 2012. Physiology, behaviour, and habitat use of sandhill crane family groups during autumn migration (*invited; oral*). Georgian Bay Stewardship Council Meeting. Parry Sound, ON, Canada.

Hanna, EE, Schummer, ML, Petrie, SA. 2012. Physiology of migration in sandhill crane family groups during autumn (*invited; oral*). Hamilton Naturalists Club - Bird Study Group. Burlington, ON, Canada.

Hanna, EE, Schummer, ML, Petrie, SA. 2012. Physiology, behaviour, and habitat use of sandhill crane family groups during autumn migration (*invited; oral*). Ontario Federation of Anglers and Hunters, Zone D Annual Meeting. Sudbury, ON, Canada.

Hanna, EE, Petrie, SA. 2009. Population dynamics and habitat use of eastern population sandhill cranes (*invited; oral*). Massey Naturalists Club. Massey, ON, Canada.