# Predator-prey interactions in Arctic Peregrine Falcons

by

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# Abstract

Species interactions are thought to underlie the stability of ecosystems, and nowhere is studying such interactions more important than the rapidly changing Arctic. The foraging behaviour of generalist consumers is influenced by the abundance of multiple resources, and generalists are thought to confer stability to resource populations. Surprisingly, explicit treatment of the diverse prey communities that many predators encounter in nature has been relatively rare, with most studies confined to predator-prey pairs. My thesis investigates the relationships between predator and multiple prey in an Arctic ecosystem on the western coast of Hudson Bay from 2015-17, using Peregrine Falcons (*Falco peregrinus*) as a model species.

First, I set out to quantify prey abundance on the landscape using distance sampling for avian species and Arctic ground squirrels (*Urocitellus parryii*), and a combination of burrow counts and snap trapping for microtine rodents (lemmings and voles). Results of snap trapping indicated 2015 was a year of low microtine abundance, while abundance was highest in 2016 and slightly less high in 2017. Burrow counts and distance sampling data were analyzed using density surface modelling according to six habitat covariates, and results indicated that freshwater, productive vegetation, and low elevation were the most consistent predictors of avian abundance across species and groups. Terrain ruggedness positively influenced abundance for Arctic ground squirrels and microtine rodents, while Arctic ground squirrels specifically were more abundant at low elevation, in areas with little freshwater, and in areas with productive vegetation. Conversely, microtine burrow counts were higher in areas with freshwater that were far from the coast.

Second, I analyzed the abundance of the most common prey types for Peregrine Falcons in relation to distance from falcon nests to evaluate evidence for a "landscape of fear" that structured prey distribution. I found songbird and goose abundance to be positively related to distance from falcon nests, and in the case of songbirds, this relationship was present even during falcon incubation, when prey consumption is relatively low. This I argue, likely indicated avoidance of breeding Peregrine Falcons when songbirds arrived in the study area and established territories. Goose abundance was only lower near falcon nests in late summer, when vulnerable goslings entered the population. Unexpectedly, duck abundance was negatively influenced by distance from falcon nests in late summer, which I argue was likely due to similar nesting habitat selection between Peregrine Falcons and Common Eiders (*Somateria mollissima*), which were the dominant duck species detected in surveys.

Finally, I used distribution maps constructed using the aforementioned density surface models to fit a complex multispecies functional response model utilizing nearly 11,000 prey deliveries recorded by remote cameras placed at Peregrine Falcon nests. Considering uncertainty in prey identification, camera failures, and prey abundance estimates, the resulting model demonstrated negative impacts of microtine rodent (lemming and vole) abundance and food supplementation (from a concurrent experiment) on the consumption of other prey. This indicated a potential short-term mutualism between prey types as falcon diet shifted with the microtine rodent cycle, adding to a large body of literature demonstrating the indirect effects of microtine rodents on other Arctic fauna. Model predictions indicated a wide range of biomass consumption across nests. Predictions with a random effect of nest site-year combination differed substantially from those without, indicating potentially strong individual differences in foraging between breeding pairs in this population. Predicted biomass consumption was most strongly related to the abundance of small birds (songbirds and shorebirds), indicating Peregrine Falcon nestlings may face an energy shortage at nests with low local small bird abundance. Surprisingly, biomass

consumption by nestlings was generally unrelated to experimental food supplementation, providing context for a previous study demonstrating higher nestling survival at supplemented nests. Overall, my thesis provides insight into how Peregrine Falcons, as apex predators of the Arctic, provision their offspring and mediate indirect interactions among prey, and is a rare investigation of predator functional responses in a multi-prey context.

# Preface

Content contained in Chapter 2 of this thesis has been published as Hawkshaw, K. A.; L. Foote, and A. Franke, "Ecological determinants of avian distribution and abundance at Rankin Inlet, Nunavut in the Canadian Arctic" Polar Biology (DOI: https://doi.org/10.1007/s00300-020-02766-4), and as Hawkshaw, K. A.; L. Foote, and A. Franke, "Landscape-scale habitat associations of small mammals on the western coast of Hudson Bay" Canadian Journal of Zoology (DOI: https://doi.org/10.1139/cjz-2020-0304). I was responsible for the data collection and analysis as well as the manuscript composition. A. Franke and L. Foote were the supervisory authors and were involved with project conception and manuscript edits.

The remainder of this thesis (Chapter 1 and chapters 3-5) represents original work by Kevin Andrew Hawkshaw. This study was conducted using animal care and use protocol AUP00000042 approved by Animal Care and Use Committee Biosciences at the University of Alberta, and the study was permitted under Wildlife Research Permits (2015-036, 2016-033, 2017-034), approved annually by the Government of Nunavut.

*"For my part I know nothing with any certainty, but the sight of stars makes me dream."*

*-Vincent van Gogh*

# Acknowledgements

Conducting this research and writing this thesis over the last five years has been the most difficult and rewarding experience of my life. There have been highs and lows, breakthroughs and setbacks, periods of strong motivation and periods of struggle. Perhaps the greatest learning experience for me has been the realization that one cannot simply grind their way through a project for years on end. Time away, hobbies, and social interaction matter, even for one so introverted as me.

First, I'd like to thank my parents, Steve and Leslie, my brother Brian, and my sister Deborah. Without the camping, fishing and hiking trips of my childhood, I may never have developed an interest in science or nature. Allegedly I was obsessed with squirrels from the local woodlot in Toronto. Thank you for supporting me through the years and giving me the opportunity to pursue my dreams.

I'd like to thank my committee, Alastair, Lee, and Andy. I've appreciated your input and wise words over the years, which have played a large role in taking me from green undergrad, to functioning graduate student, to published author, and now to the completion of this degree and onwards. Al, thank you for always being ready to chat and for giving me the initial opportunity to go to Rankin, along with all of the other opportunities you have afforded me in the last five years.

I'd like to thank Dr. Kim Mathot and the Mathot lab for unofficially taking me in. I started this project very much lacking in lab mates and general social-academic experiences. The last few years since Kim began inviting me to lab meetings and extracurricular get-togethers have made a world of difference in my life as a graduate student and beyond.

On that note I'd also like to thank Erik Hedlin: friend, office mate and fellow Rankin researcher. Thank you for always being game to talk project ideas, for passing along all kinds of statistical tidbits to keep me sharp, and for the various birding trips and get-togethers over the years.

I'd like to thank all of the field technicians and fellow graduate students who worked with me during my time in Rankin Inlet. Alex Paiement, Mat Tetreault, Yannick Gagnon, Cameron Nordell, Nick Gulotta, Vincent Lamarre, Phil Galipeau, Rebekah McKinnon, and of course field guides Andy Aliyak, Silu Oolooyuk, and Jaden Sigurdson. Racking up hundreds of kilometers of walking, quadding, boating and snowmachining (and especially walking) never would have been so much fun without you.

Thank you as well to the entire community of Rankin Inlet, which has hosted the Peregrine Falcon project of which my thesis was a part for four decades. It has been an absolute pleasure and learning experience to spend so much of my time in such an incredible place and among such incredible people. I can't count how many times community members took pity on me while experiencing mechanical difficulties, or afforded me opportunities to join hunting or fishing trips, shared country food, or even just stopped by in the middle of the tundra for a friendly chat. Beyond being thankful, I'm also left with the realization of how much further researchers in the north must yet go, to ensure that local communities have input at all stages of the research process, and that the products of science, at least in part, serve those communities.

Lastly, I'd like to thank Alison Murata, who has been my partner in crime for the past year and a half, amidst all the trials and tribulations of this thesis and the larger COVID-19-stricken world. I can't even imagine what my life would have been like over that time without you. From the bottom of my heart I thank you.

# Table of Contents

# List of Tables

# List of Figures

# Abbreviations

**AICc** Akaike Information Criterion corrected for small sample size.

**CAFF** Conservation of Arctic Flora and Fauna (Arctic Council).

**CI** Confidence Interval.

**CrI** Credible Interval.

**DDT** Dichlorodiphenyltrichloroethane.

**DSM** Density surface model.

**MSFR** Multispecies functional response.

**NDVI** Normalized difference vegetation index.

**NDWI** Normalized difference water index.

**PEFA** distance to Peregrine Falcon nest.

**PI** Prediction Interval.

# Chapter 1

# Introduction

Predators consume other organisms, thus their fitness (survival, reproduction) is in large part determined by their ability to find, capture, kill, and consume prey. In turn, prey fitness largely depends on avoiding predation. The earliest models of population dynamics recognized this fundamental reality and that the populations of predators and prey are, absent additional factors, linked (Lotka 1925; Volterra 1926). Quantifying this link has been of longstanding theoretical and applied interest within ecology, with implications for management of endangered or invasive species (*e.g.,* DeCesare et al. 2010; Sinclair et al. 1998), and natural resource harvest (*e.g.,* May et al. 1979; Yodzis 1994).

This thesis is fundamentally about predator-prey interactions, and examines the issue from a spatiotemporal perspective, involving: 1) the distribution of prey species, particularly in relation to predator breeding locations, and 2) the influence of local variation in prey abundance on predator consumption rate. The implications of the latter relationship for biomass intake in predator offspring and the ability of predators to mediate indirect interactions between prey are also explored. I also discuss sampling methods and modelling approaches.

I have arranged my thesis into three data chapters, book-ended by (the current) introduction and concluding chapters. Chapter 2 examines the distribution of birds and small mammals at Rankin Inlet, Nunavut, Canada according to remotely sensed habitat covariates. This is followed by further examination of distribution of Peregrine Falcon (*Falco peregrinus*) prey types in a landscape of fear context in Chapter 3. In Chapter 4, I implement a multispecies functional response (MSFR) model for Peregrine Falcons and use it to examine how falcons mediate indirect interactions among their prey, as well as the ability for breeding Peregrine Falcons to provision offspring. In the remainder of this introduction, I give a proximate rationale for this thesis by introducing the reader to the Rankin Inlet study area and its history of scientific research.

## 1.1 The Rankin Inlet study area

Located on the western coast of Hudson Bay in the central Canadian Arctic (62.81° N, 92.09° W), the Rankin Inlet study area represents approximately 2500-km$^2$ of coastal tundra and marine habitat typical of the low Arctic, containing a diversity of wet meadows, dwarf shrubs, dry eskers, rocky ridges, tidal flats and sea cliffs. Figure 1.1 presents average temperature, precipitation and snow depth conditions from 1980-2010, as well as conditions during data collection for this thesis (2015-17). Scientific research at Rankin Inlet has spanned four decades and has focused on the area's Peregrine Falcons. When data collection began in the early 1980s, peregrines were of high conservation concern having been extirpated from eastern North America due to the bioaccumulative effects of chemical insecticides (Enderson et al. 1995; Kiff 1988; Ratcliffe 1967), which in part led to the banning of DDT in Canada in 1969 and the United States in 1972 (Fyfe et al. 1976).

Early on, data collection focused on basic natural history, including overall breeding densities, migration, phenology, diet, and population turnover (Court et al. 1989, 1988). Of note for my thesis were the apparent generalist foraging tendencies reported by Court et al. (1988), who described use of mammalian prey from remains collected at nests. In the Arctic, Peregrine Falcons have typically been described as specializing on avian prey, particularly small passerines or shorebirds (Dawson et al. 2011; Robinson

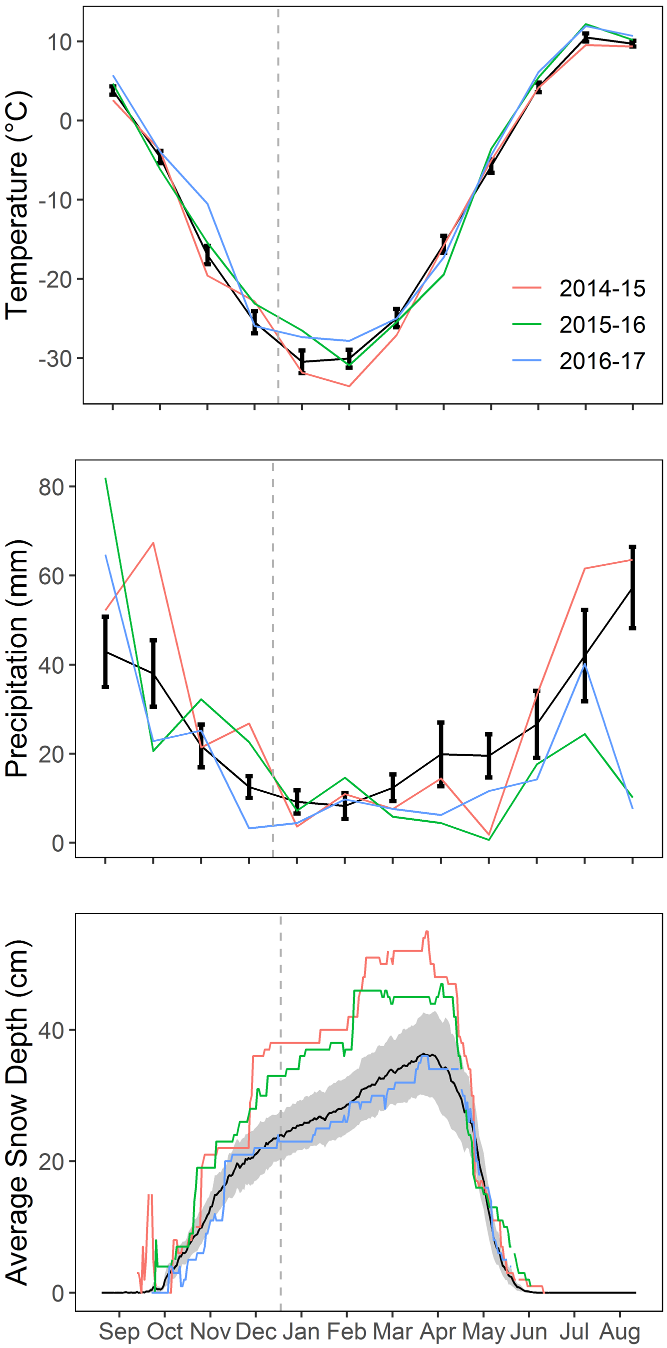


Figure 1.1: Monthly mean temperature (upper panel), total precipitation (middle panel) and snow depth (lower panel) in Rankin Inlet, Nunavut, Canada, with climate normals (1980-2010) represented by the black lines, error bars or shaded regions representing 95% confidence intervals, and coloured lines representing conditions during or preceding each season of sampling (May-August). The dashed vertical line represents January 1. Data collected at the Rankin Inlet airport by Environment and Climate Change Canada.

et al. 2015). Following this theme, Bradley and Oliphant (1991) noted the proportion of mammalian prey consumed by the population was unusually high, and remained high even in years of low microtine rodent (lemming and vole) abundance. Microtine rodents have long been noted for their large-amplitude population cycles, which have often exerted a strong effect on species above and adjacent to them in the food web (Bêty et al. 2001; McKinnon et al. 2014). Such cycles are a feature of the Rankin Inlet study area as well (Ehrich et al. 2020, Figure S1), but the small mammal community also includes Arctic ground squirrels (*Urocitellus parryii*), which may explain why falcons continued to consume substantial numbers of mammals even in low microtine years.

Bradley et al. (1997) focused on the effects of weather conditions on falcon breeding output. Like many species with altricial young, Peregrine Falcon nestlings have limited thermoregulatory ability and are vulnerable to severe weather conditions, particularly prior to the appearance of second down, and when brood size is small (Blix and Steen 1979; Whittow and Tazawa 1991). While Bradley et al. (1997) noted no significant association between seasonal precipitation and breeding output in their then-limited data, they did note the apparent deleterious effect of acute weather events. Franke et al. (2010) measured occupancy, reproductive performance and pesticide loads and showed that reproductive success of Peregrine Falcons in the study population had declined despite reductions in pesticide loads. They argued that changes in summer precipitation may have been a proximate cause for declining productivity. This study set the stage for later experimental work by Anctil et al. (2014), which involved sheltering a portion of the population from wet weather events using nest boxes. They found strong evidence for the negative effect of wet weather events across years (responsible for 38% of nestling deaths), and additionally found evidence that the frequency of severe rainfall events had increased in the study area since the beginning of monitoring. However, the authors noted that substantial mortality still occurred at sheltered nests, which sparked interest in food limitation as an additional source of nestling mortality.

Avian offspring in the Arctic face a short window in which to attain adequate size and physical condition to survive southward migration. Growth and plumage development are in part products of energy intake, thus the ability of breeding pairs to secure food for their young is a key component of successful reproduction (Perez et al. 2016; Suryan et al. 2002). In income-breeders, females must also secure adequate energy sources upon arrival on breeding territories to produce eggs (Klaassen et al. 2006). Lamarre et al. (2017) showed that female Peregrine Falcon body condition determined lay dates, a key predictor of offspring survival in many species (Daan et al. 1988; Perrins 1970). Most notably for the present thesis, in 2013 a five-year food supplementation experiment began (Hedlin 2015) in which a portion of broods received domestic quail (*Coturnix coturnix*) during nest visits. The goal was to assess food limitation in nestlings, and, given the findings of Anctil et al. (2014), to assess the potential for interactions between food limitation and precipitation. Supplemented nestlings had higher survival than those not supplemented, although effects on growth were less conclusive.

Supplementing 50% of nestling diet was perhaps *a priori* likely to produce a strong treatment effect on survival, but what kind of variation in food limitation existed under natural conditions? The observations of Anctil et al. (2014) suggested some nestlings were food limited, but a thorough investigation of the relationship between prey abundance and consumption was needed. Through the years of study at Rankin Inlet, a concentrated effort to measure prey abundance had never been undertaken.

Consumption is one of the mechanistic links between prey and predator populations, and is key to determining the precise nature of their interaction. Falcon diets in Rankin Inlet were recently investigated by L'Herault et al. (2013), but this study was conducted in the absence of knowledge of prey abundance. Instead, the terrestrial-marine gradient of individual nest sites was used as a proxy for local prey abundance, which was then compared to diet estimated via stable isotopes. The authors determined more marine prey (*e.g.,* Common Eiders *Somateria mollissima*, Black Guillemots *Cepphus grylle*) were consumed at nest sites with more local marine habitat, while terrestrial prey were consumed in greater amounts at sites with more terrestrial habitat. Terrestrial habitat was also associated with increased breeding productivity in the long-term data. While an improvement on historical diet studies conducted in Rankin Inlet (Bradley and Oliphant 1991; Court et al. 1988), this study still featured many unknowns. For example, prey abundance could be highly variable within the terrestrial and marine portions of the study area, as well as within the prey groupings determined from their stable isotope analysis (terrestrial herbivores included microtine rodents, known to have highly variable populations, as well as geese and Arctic ground squirrels). Findings from a study conducted in Igloolik, Nunavut indicated stable isotopes failed to accurately assess the contribution of lemmings to Peregrine diet (Robinson et al. 2018), and furthermore even if stable isotopes effectively described proportional diet contributions, they do not assess food limitation. Prey surveys, remote cameras, and the use of generalized functional response models offered potential improvements to investigating predator-prey interactions in this study area, and form the basis of my thesis.

Most recently, nest site occupancy and nestling productivity data for Peregrine Falcons in this study area were reported in Franke et al. (2020), and the population was deemed stable in terms of nest site occupancy, but with a gentle decline over time in productivity. Via the same publication, most Peregrine Falcon populations were described as stable across the Arctic.

To summarize, in the context of Rankin Inlet, my thesis fills a longstanding mechanistic knowledge gap by modelling prey distribution, explicitly linking prey distribution to falcon consumption, updating previous methodology in quantifying nestling diet, and posing new questions about the role of falcon predation in regulating and generating indirect relationships between prey.

## 1.2 Theoretical background

### 1.2.1 The functional response

What determines how many prey a given predator consumes? While many factors can be implicated, at a very elementary level consumption is related to prey abundance, with the simple rationale that the more prey there are on the landscape, the more likely a randomly-searching predator is to encounter them. The relationship between prey abundance and consumption by a predator is known as the functional response (Holling 1959a; Solomon 1949). Functional response models have been employed in a wide variety of circumstances, and have been subject to frequent modification (see Jeschke et al. 2002) and debate (*e.g.,* Abrams and Ginzburg 2000) through the latter half of the 20th century until today. As functional responses could be used to predict prey mortality resulting from predation, they became important components of predator-prey models, with the particular characteristics of the functional response leading to theoretically different dynamics (Murdoch and Oaten 1975). Given longstanding interest in the complexity and stability of ecosystems (May 1972; McCann 2000), functional responses present an obvious mechanism with which to explain the dynamics of ecosystems involving predators and prey.

What makes a generalist or specialist consumer? Labelling a species as such often belies a continuum of consumer behaviour and the highly context-dependent nature of foraging. For example, among raptors Snowy Owls (*Bubo scandiacus*) have long been known as a specialist on small mammals, particularly lemmings (Holt et al. 2020), but during winter, many Snowy Owls spend considerable time offshore at polynyas (Therrien et al. 2011), presumably feeding on seabirds. Rough-legged Hawks (*Buteo lagopus*) are similarly known as rodent specialists (Bechard et al. 2020), yet use of alternative prey can increase to the extent that breeding productivity is maintained in breeding seasons when lemming populations crash (Pokrovsky et al. 2013). The point is that predator diets are context-dependent, and prey community composition and abundance is a large part of that context. Many predators consume multiple prey species, and optimal foraging theory predicts that diet composition will change with (among other factors), prey abundance (Emlen 1966; Estabrook and Dunham 1976; MacArthur and Pianka 1966; Pulliam 1974). Though the strict "consume-always-or-not-at-all" behaviour often predicted by theory may not hold in nature for a variety of reasons (*e.g.,* information constraints that prevent predators from having complete knowledge of prey abundance and distribution), the more general point, that diet will change with prey abundance, is borne out by numerous studies (*e.g.,* Naef-Daenzer et al. 2000; Steenhof and Kochert 1988; Suryan et al. 2002).

The functional response literature however, has seen limited implementation of functional response models that explicitly allow consumption of one prey species to vary with the abundance of other prey species. The reasons for this are twofold: field logistics often preclude monitoring of more than just a single predator-prey pair (which itself has proven inadequate for modelling functional responses in some cases; Marshal and Boutin 1999; Novak and Stouffer 2021). Additionally, modelling approaches and computational tools (*e.g.,* Bayesian modelling software) allowing for the fitting of MSFRs have only become accessible to the general population of researchers recently. However, even in contemporary laboratory studies, where prey abundance is manipulated and quantified, it is still common to treat predators as though they were strict specialists with single predator-single prey feeding trials. In my opinion, this casts doubt on the ability for scientists to predict, for example, the potential impact of an invasive crayfish (Dalal et al. 2020; Linzmaier and Jeschke 2020) based on functional response models that neglect the multi-prey ecosystems that those omnivorous predators will almost inevitably encounter in nature. Chapter 4 is largely devoted to implementing a MSFR for Arctic Peregrine Falcons and discussing its implications for predator and prey.

### 1.2.2 Indirect interactions

Consumption of prey by predators is a form of direct interaction between species, but it has long been recognized that species may also interact through intermediary species, for example shared predators (Holt 1977; Holt and Bonsall 2017). In such indirect interactions, an increase in abundance of one prey species might deleteriously affect the population of another by inducing a positive numerical response in their shared predator (increase in population size), thereby increasing the mortality of the other prey item. Several notable examples of such "apparent competition" have emerged in recent decades, particularly in cases of invasive or introduced species (see examples in DeCesare et al. 2010), and examples extend to plant-pollinator (Carvalheiro et al. 2014), parasitoid-host (Frost et al. 2016) and plant-herbivore interactions (Morris et al. 2004). However, if predator populations are limited primarily by factors other than prey abundance, for example by density dependence, or if predators are able to switch to consume newly abundant prey, then increases in the abundance of a given prey species may benefit alternative prey by decreasing their mortality (Abrams and Matsuda 1996), a situation known as "apparent mutualism". Importantly, both apparent competition and mutualism may exist in a given system, but at different time scales (Holt 1977). For example, the invasion of a new prey species may benefit existing prey by replacing existing prey in the diets of resident predators, but long-term the availability of a new prey item may cause more predator individuals to recruit or immigrate into the population, leading to greater predation pressure on existing prey.

### 1.2.3 Non-lethal effects of predation

The "landscape of fear", coined by Laundré et al. (2010, 2001), is the spatial representation of how prey perceive predation risk (Gaynor et al. 2019). One obvious way prey may attempt to diminish this risk is through avoidance: prey may modify their habitat or space use to reflect areas of heightened predation risk (*e.g.,* where predator detection or escape is obstructed; Creel et al. 2005). Similarly, prey may modify their activity hours to avoid times when predators are most active (Haswell et al. 2020). If predator presence is concentrated around particular habitat features (*e.g.*, den or nest sites) prey distribution may reflect avoidance of such areas (Norrdahl and Korpimaki 1998; Thomson et al. 2006). Conversely, prey may continue to use areas and times occupied by predators, but instead increase vigilance behaviour or group with other individuals to decrease their own predation risk (Fuller et al. 2013). Whatever the strategy, anti-predator responses represent fitness trade-offs, where an individual trades risk of predation for foraging or breeding opportunities.

### 1.2.4 Research questions

The chapters in this thesis follow a logical progression: to know how prey affect predators in a spatiotemporal context, I first needed to know:

1. What prey are available to Peregrine Falcons in this system, and what drives their distribution and abundance? How do falcons themselves influence the spatial arrangement of prey?

These questions are the subjects of Chapters 2 and 3. Having quantified prey habitat associations and constructed predicted grids of their distribution across years, I then used these grids as inputs into a MSFR model for breeding Peregrine Falcons, with prey consumption data recorded at nests using remote cameras. Chapter 4 then investigates the following questions:

2. How is biomass consumption by Peregrine Falcon nestlings affected by prey abundance in the area surrounding a nest?

3. What evidence is there for indirect relationships (*i.e.,* apparent competition, apparent mutualism) between prey types, mediated by falcon predation? Specifically how does consumption of alternative prey types by falcons change with the abundance of microtine rodents, and with experimental food supplementation?

This thesis concludes with a discussion of potential improvements to the study, as well as logical extensions of the questions tackled here. Finally, I discuss Peregrine Falcons in the context of climate change in the Arctic. With that, I thank the reader in advance for their time and patience, and direct their attention to Chapter 2.

# Chapter 2

# Ecological determinants of avian and small mammalian distribution at Rankin Inlet, Nunavut

## 2.1 Introduction

Although wildlife studies are common in the Arctic, they are geographically clumped, and potentially cannot be generalized (Metcalfe et al. 2018). Significant knowledge gaps remain even for widespread ecosystem components, such as birds (Smith et al. 2020), microtine rodents (Oli 2019), and Arctic ground squirrels (*Urocetillus parryii*; Wheeler and Hik 2013). Baseline data and knowledge of habitat or climatic factors affecting populations of Arctic fauna are increasingly important given increased resource extraction in many areas (Haley et al. 2011) and climate change (Meredith et al. 2019).

An important aspect of effective wildlife surveys is accounting for detectability. Without this, abundance estimates can be biased, and, if detection varies spatially within a study area, abundance estimates can be biased spatially as well (Marques et al. 2007). Distance sampling is a well-known survey technique that accounts for detectability by modelling the relationship between observation distance and probability of detection (Buckland et al. 2015). Several extensions of distance sampling exist for spatiotemporal modelling of survey counts (*e.g.,* Bachl et al. 2019; Oedekoven et al. 2014), but one of the most common is density surface modelling (DSM; Miller et al. 2013), a two-stage approach that first fits a detection function to distance sampling data, and then models survey counts on the basis of spatial or temporal covariates. DSM has been used to model the abundance and distribution of a wide array of organisms, from cetaceans (Roberts et al. 2016) to seabirds (Winiarski et al. 2014) to ungulates (Valente et al. 2016) to benthic invertebrates (Katsanevakis 2007) to land birds (Camp et al. 2020), and has shown to be a flexible and effective alternative in species distribution modelling.

I investigated habitat associations of birds and small mammals breeding near the community of Rankin Inlet, Nunavut, Canada using distance sampling and DSM. I used multiple habitat measures from remotely sensed datasets to model habitat associations, including terrain ruggedness, elevation, distance from coast, freshwater, the normalized difference vegetation index (NDVI), and the normalized difference water index (NDWI), and accounted for changes in abundance across and within years. I also explored interactions between habitat and temporal covariates based on previous literature support and ecological rationale. NDVI is a widely used index of vegetation greenness that is correlated with vegetative biomass, cover and diversity in Arctic ecosystems (Laidler et al. 2008; Nilsen et al. 2013; Raynolds et al. 2006), and has been used in past investigations of avian habitat associations (Pellissier et al. 2013; Robinson et al. 2014). Arctic study areas are frequently characterized by saturated or intermittently flooded habitats, or those with very small water bodies (*e.g.,* ponds), which exist at scales finer than the resolution of satellite imagery (Muster et al. 2012). Because wet habitats are known to be frequented by Arctic birds (Latour et al. 2005; Slattery and Alisauskas 2007) and may influence small mammal distribution through risk of burrow flooding (Barker and Derocher 2010; Wheeler and Hik 2013), I also used the normalized difference water index (NDWI) in competing DSMs. NDWI is generally correlated with NDVI, but is further able to represent variation in vegetation water content (Gao 1996), which can reflect local differences in soil moisture and water table depth (De Alwis et al. 2007; Tagesson et al. 2013).

I expected the abundance of most birds and small mammals to increase with vegetative productivity, the availability of freshwater, and with low elevation or proximity to the coast. Vegetation represents potential forage for herbivores (Cadieux et al. 2005), nesting habitat for songbirds (Boal and Andersen 2005; Boelman et al. 2015; Peterson et al. 2014), and is also be correlated with invertebrate biomass for avian insectivores (Perez et al. 2016). Freshwater provides foraging and nesting habitat as well as refuges from predation for waterfowl (Lecomte et al. 2009; Stahl and Loonen 1998), and coastal or low elevation areas provide access to marine food sources (Eberl and Picman 1993). I predicted that songbirds and shorebirds would increase in abundance at low elevations near the coast later in the summer as individuals aggregated into post-breeding flocks and prepared for southward migration (Connors et al. 1979; Hussell and Montgomerie 2002; Wheelwright and Rising 2008). I also predicted that warm and dry summer conditions would lead to stronger associations between geese and freshwater (Robinson et al. 2014), and that geese would be more strongly associated with freshwater later in the summer to reduce predation risk to flightless juveniles and molting adults. I expected models of Arctic ground squirrel abundance containing NDVI to have greater support than those containing NDWI because squirrels would generally be expected to prefer drier habitats for burrowing. Similarly, I expected squirrels would also avoid freshwater to reduce the risk of burrow flooding (Barker and Derocher 2010; Wheeler and Hik 2013). I further expected Arctic ground squirrel abundance to be positively correlated with terrain ruggedness (*e.g.*, sloped terrain; Barker and Derocher 2010; Karels and Boonstra 1999).

Overall, my study provides habitat association data for nearly the full suite of avian and small mammalian life from a study area that is poorly represented in previous literature. My study contains species poorly represented in Arctic research (*e.g.,* Sandhill Cranes *Antigone canadensis*) and species of current conservation concern due to population declines (*e.g.,* shorebirds; Rosenberg et al. 2019; Smith et al. 2020).

## 2.2 Methods

### 2.2.1 Distance sampling

I used distance sampling transects (Buckland et al. 2015), each approximately 1-km in length, to estimate habitat associations of birds and small mammals. I generated random start points at the start of each field season and surveyed approximately two transects per day spanning the period from spring melt to the start of outward migration for many avian species. Among years, the sampling period was similar; in 2015 surveys were conducted from June 7-August 19, in 2016 from May 26-August 22, and in 2017 from May 29-August 21. Within each year, sampling was classified into two periods: period one included transects sampled prior to July 11, and period two included those sampled on or after (hereafter termed early and late summer, respectively). This date roughly corresponds to the division between incubation and brood rearing for most avian species and juvenile emergence in Arctic ground squirrels in my study area (*pers. obs.*), and thus was a logical cut-off when investigating how habitat associations and abundance might change within year. All transects were replicated before and after this date, and a small number of transects were sampled three times per season. In total, 498 distinct transect visits were made to 225 transect locations. Time of day of surveys ranged from 9:00 – 20:00. Although I sampled a different collection of transects in each year (Figure 2.1), data exploration revealed that the range of habitat covariates sampled was very similar. Species count data from these surveys can be found in Table A.1, Appendix A.

My analysis involved a two step process: 1) I modelled the probability of detection of each species or group as a function of distance and detection covariates, 2) I modelled spatiotemporal variation in my survey counts while accounting for the probability of detection estimated in step 1. The first step involved estimating the relationship between observation distance and probability of detection. I collected bearing and distance data for all observations using a compass and a laser rangefinder,

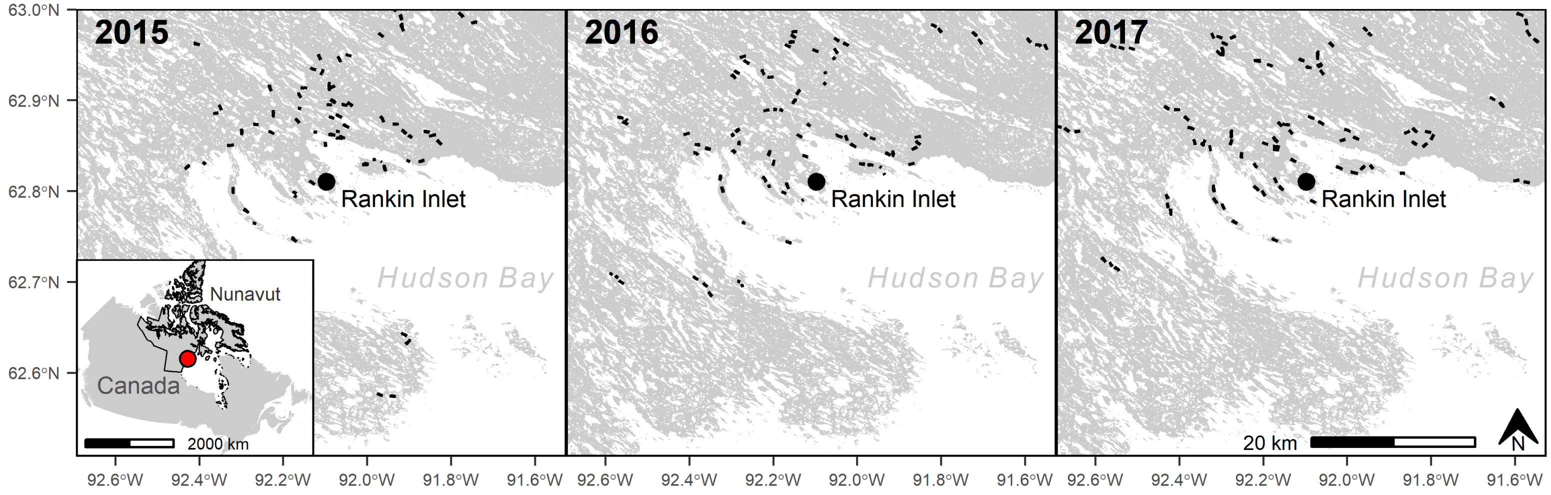


Figure 2.1: Maps of Rankin Inlet study area displaying the spatial distribution of distance sampling transects surveyed from 2015-17. ❙ represent individual transects, and note that each transect was repeated a minimum of twice during a season. Inset map displays the spatial location of the study area (●) within Nunavut, Canada.

and subsequently calculated perpendicular distance from the transect line (as recorded by handheld Global Positioning System: GPSmap 62s, Garmin Ltd.). I modelled only those species for which I had the recommended minimum 60 observations (Buckland et al. 2001), and in some cases combined species into groups to attain the minimum threshold. In other cases, I combined species into groups because I expected similar habitat associations (*e.g.,* gulls, loons *Gavia* spp., geese). For geese I dropped observations of >5 individuals observed in flight as they were presumed to be migrating through the study area and would have confounded my attempts to describe habitat associations.

I followed the recommendations of Thomas et al. (2010) and modelled combinations of key functions (half normal, hazard rate, uniform) and adjustment terms in my detection functions. Also included in candidate models were detection covariates, as follows: day of the year, time of day, terrain ruggedness (standard deviation in elevation; scale corresponded to that used in subsequent spatial modelling, see section 2.2.2), and wind speed on a 0-3 scale of increasing severity (upper limit $\sim$ 30-km/hr). I generally avoided sampling on days with poor weather conditions, but wind was difficult to avoid without creating large time gaps in sampling. I was responsible for all observations.

The best-fitting detection function for each species or group was selected by comparing Akaike's Information Criterion corrected for small sample size (AICc) for the suite of candidate models and selecting the competitive model ($\Delta$AICc <2) with the fewest parameters for subsequent spatiotemporal modelling. If detection functions with different covariates were competitive, I further fit a function including both covariates and retained it if it provided an improvement in AICc >2. Detection functions were fit using the package Distance (Miller et al. 2019) in the R statistical environment (R Core Team 2020).

### 2.2.2 Density surface modelling

I modelled the count data as a function of spatial and temporal covariates, and incorporated the previously estimated probability of detection into an offset term. Analyses were conducted using the R package dsm (Miller et al. 2020). Although I used all observations to fit detection functions, I restricted my spatiotemporal analyses to data collected between June 7 and August 19, as this was the consistent sampling period across all years.

I included combinations of six habitat variables in my candidate DSMs, as follows: ruggedness, NDVI, NDWI, proportion freshwater cover, distance from coast and elevation. All models included ruggedness and freshwater, as well as year, period and their interaction as factor covariates. I compared models containing NDVI to models containing NDWI, and models containing elevation to those containing distance from coast. Based on prior evidence and ecological rationale I also included interaction terms in candidate models as follows: for geese, freshwater x period and freshwater x year terms; for songbird species and shorebirds, elevation x period and distance from coast x period. Data exploration proceeded according to the protocol of Zuur et al. (2010), and I ensured collinearity among predictors included in a given model was $|R| \leq 0.6$. I standardized all continuous covariates prior to analyses.

Because habitat can vary along a line transect, during DSM analyses they are typically divided into smaller segments. In my study segment length corresponded to roughly twice the truncation distance used when modelling the detection function for a given species or group (Petersen et al. 2011), thus my sampling units were approximately square. For songbirds, shorebirds and Arctic ground squirrels segment length was approximately 250-m, for ducks, geese and gulls approximately 500-m, and for Tundra Swans (*Cygnus columbianus*), Sandhill Cranes, loons and Common Eiders (*Somateria mollissima*) transects were not split into segments unless a given transect was greater than 1050-m. I fit models with a full random effect structure corresponding to my sampling design, including random intercepts for a given transect visit and a given transect (segments were nested within transect visits, which were nested within transects). For Tundra Swans, Sandhill Cranes, loons and Common Eiders, a minority of transects were split into segments, and I therefore fit only random intercepts for transect identity. For the remaining species and groups I retained the full random effects structure in all models unless they produced poor diagnostics, in which case I reduced complexity and refit with a single random effect term for transect identity.

For each habitat index, data were extracted from 30-m resolution rasters. Ruggedness and elevation were extracted from a digital elevation map (original resolution: 16-m, vertical resolution: 5-m; Natural Resources Canada 2015), and I obtained NDVI and NDWI rasters derived from Landsat 8 images from Google Earth Engine (8-day composite images from July 12-20, 2018 in both cases; Gorelick et al. 2017). Freshwater cover was estimated using a surface water layer (resolution: 25-m; Natural Resources Canada 2016). Habitat variables were calculated over moving windows of size 270 x 270-m, 510 x 510-m and 990 x 990-m, which corresponded to the segment size used for each species or group. The goal was to ensure habitat covariates corresponded to individual transect segments with minimal overlap between segments. A distance from coast raster was calculated based on a land layer (resolution: 25-m; Natural Resources Canada 2019). Note that for distance from coast, inland areas have positive distances, while nearshore islands in Hudson Bay were assigned negative distances. Habitat covariates were then extracted at the midpoint of each transect segment. For NDVI and NDWI, I masked all water bodies prior to applying the roving window calculations.

Depending on model diagnostics I modelled segment counts with either negative binomial or Tweedie response distributions. I compared candidate models for each species or group by AICc and drew inference from competitive models ($\Delta$AICc $<2$). In the case of nested competitive models, I drew inference from the simplest nested model. The additional terms included in more complex, nested models are generally non-informative when AICc indicates statistical equivalence (Arnold 2010). Due to the large number of species and groups modelled here, in cases where there were multiple, non-nested competitive models but inference was identical between them, I present one model for brevity. Models to be compared by AICc were fit using Maximum Likelihood (ML), and competitive models were refit using Restricted Maximum Likelihood (REML) prior to presentation and interpretation (Zuur et al. 2009). I ensured good visual fit of my models using standard diagnostic plots, including quantile-quantile plots and plots of randomized quantile residuals (Dunn and Smyth 1996).

### 2.2.3 Microtine burrow counts

Microtine rodent burrows were counted within 1-m of distance sampling transects once per season during the post-July 11 period. Because burrows of different species could not be distinguished, and distinguishing inactive burrows from active can be difficult (Fauteux et al. 2018), I did not include year as a covariate in analyses. I modelled the total burrow count of each transect according to the habitat covariates described above, averaging values across segments within a given transect. The 270 x 270-m habitat covariate scale encompasses literature estimates of home range size for microtine rodents in the Arctic (Predavec and Krebs 2000; Rodgers and Lewis 1986). Observers varied across burrow counts, so I included a random effect for observer. I also included an offset term to account for variation in transect length (*e.g.*, due to water bodies or impassable terrain). Model selection followed the same procedures as for the distance sampling data.

## 2.3 Results

### 2.3.1 Detection functions

Overall I recorded 2942 observations and 6221 individual birds from 33 species (Table A.1, Appendix A.1), and an additional 549 observations of Arctic ground squirrels. Detection of American Pipits (*Anthus rubescens*), Horned Larks (*Eremophila alpestris*), Savannah Sparrows (*Passerculus sandwichensis*), shorebirds, geese, and Sandhill Cranes were affected by detection covariates in selected models, with pipits and Savannah Sparrows less detectable in more rugged terrain, larks less detectable later in the day and later in summer, shorebirds and cranes more detectable later in summer, and geese less detectable on surveys with higher wind scores (Table 2.1). Common Eiders were also less detectable later in summer, but there was minor overlap with zero of the 95% confidence intervals for this term. The best fitting detection function for Tundra Swans included a positive effect of ruggedness, but there was substantial overlap of the 95% confidence interval with zero for this term and a simpler model including no covariates narrowly missed the $\Delta$AICc $<2$ threshold ($\Delta$AICc $= 2.04$), so I retained the latter in DSMs.

### 2.3.2 Vegetation indices

Generally, NDVI rather than NDWI was present in competitive DSMs for avian species and groups. NDVI was positively related to Horned Lark, redpoll (*Acanthis* spp.; minor overlap of the 95% confidence interval with zero), Savannah Sparrow, and Sandhill Crane abundance and NDWI did not appear in competitive DSMs for any of these species (Figure 2.2, Table 2.2). Duck (not including Common Eider) abundance was positively related to NDWI (minor overlap of the 95% confidence interval with zero), and NDVI did not appear in competitive DSMs for ducks. For geese NDVI had no substantial effect on abundance and NDWI did not appear in the best-fitting DSM. For gulls, I found a small negative influence of NDVI on abundance

Table 2.1: Summary information for selected detection functions for species and groups surveyed at Rankin Inlet, Nunavut, Canada from 2015-17. Indicated is the species/group, number of observations (N), truncation distance, key function and adjustment terms added (Key + adj, with the number of adjustment terms indicated in parentheses), covariate term if present along with its coefficient estimates (Est) and their 95% confidence intervals (in parentheses), average probability of detection (Pdet) and 95% confidence intervals (in parentheses) across all surveys, and Cramer von Miser goodness of fit test *p*-value (CvM; >0.05 indicates good fit). Terms with 95% confidence intervals not overlapping zero are bolded. American Pipit (*Anthus rubescens*), Horned Lark (*Eremophila alpestris*), redpoll (*Acanthis* spp.), Lapland Longspur (*Calcarius lapponicus*), Savannah Sparrow (*Passerculus sandwichensis*), Tundra Swan (*Cygnus columbianus*), Sandhill Crane (*Antigone canadensis*), Common Eider (*Somateria mollissima*), Arctic ground squirrel (*Urocetillus parryii*).

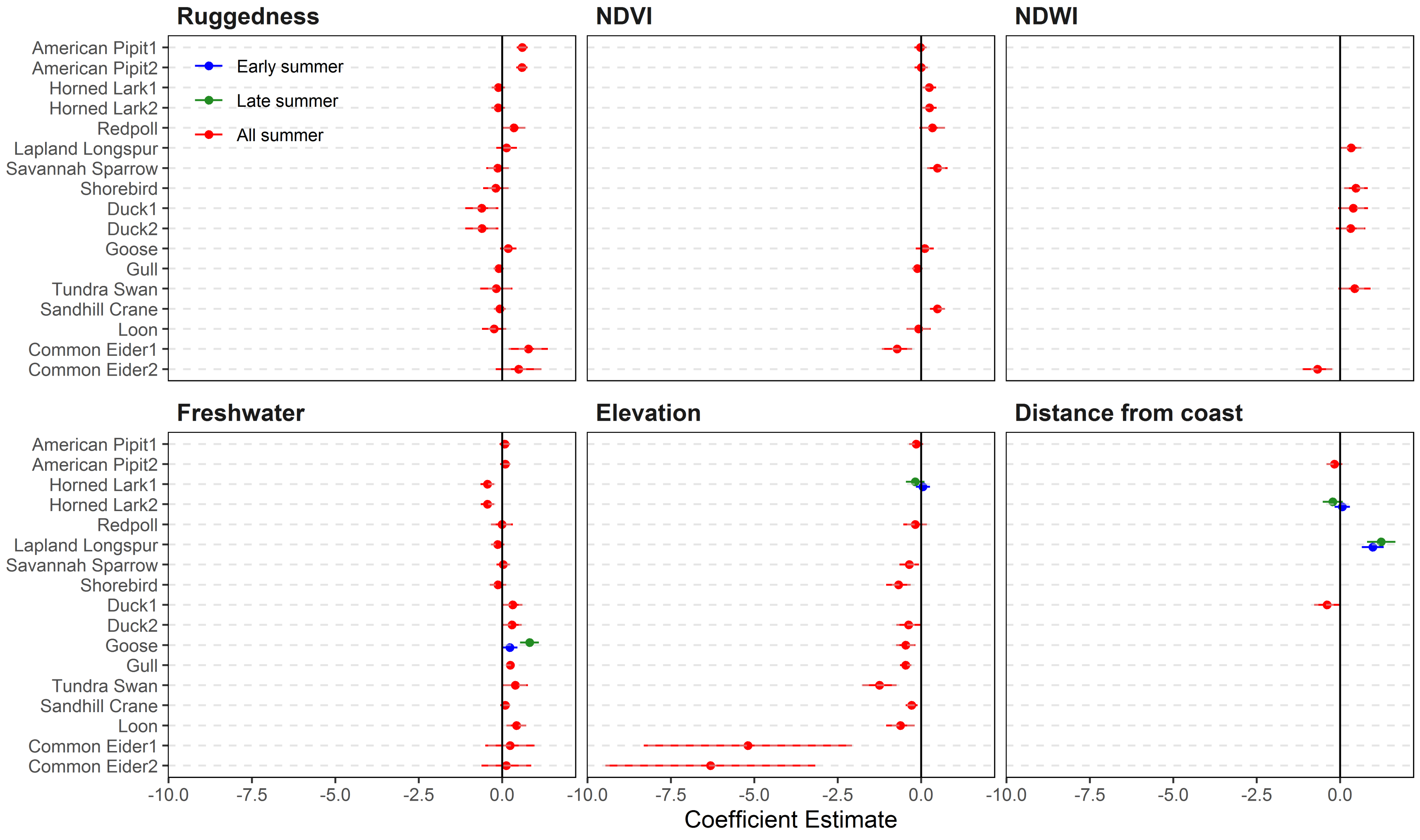
| **Species/group** | **N** | **Truncation (m)** | **Ind** | **Key + adj** | **Term** | **Estimate** | **Pdet** | **CvM** |
|---|---|---|---|---|---|---|---|---|
| American Pipit | 300 | 105 | 467 | half-normal | ruggedness | **-0.14 (-0.21, -0.07)** | 0.59 (0.54, 0.65) | 0.63 |
| Horned Lark | 298 | 110 | 448 | half-normal | time of day | **-0.20 (-0.37, -0.03)** | 0.60 (0.54, 0.65) | 0.71 |
| | | | | | day of year | **-0.13 (-0.24, -0.03)** | | |
| Redpoll | 83 | 130 | 153 | uniform + cos(1) | | | 0.55 (0.49, 0.62) | 0.35 |
| Lapland Longspur | 183 | 105 | 336 | uniform + cos(1) | | | 0.58 (0.53, 0.63) | 0.87 |
| Savannah Sparrow | 158 | 95 | 243 | half-normal | ruggedness | **-0.29 (-0.46, -0.12)** | 0.56 (0.49, 0.64) | 0.89 |
| Shorebird | 100 | 130 | 210 | hazard-rate | day of year | **0.38 (0.06, 0.70)** | 0.51 (0.37, 0.65) | 0.99 |
| Duck | 114 | 230 | 282 | half-normal | | | 0.68 (0.57, 0.80) | 0.77 |
| Goose | 314 | 250 | 1104 | half-normal | wind | **-0.20 (-0.33, -0.06)** | 0.57 (0.52, 0.62) | 0.24 |
| Gull | 314 | 250 | 964 | hazard-rate | | | 0.53 (0.45, 0.60) | 0.94 |
| Tundra Swan | 88 | 400 | 309 | half-normal | | | 0.73 (0.58, 0.88) | 0.81 |
| Sandhill Crane | 334 | 320 | 732 | half-normal | day of year | **0.12 (0.01, 0.23)** | 0.62 (0.56, 0.68) | 0.83 |
| Loon | 85 | 340 | 136 | half-normal | | | 0.59 (0.48, 0.70) | 0.73 |
| Common Eider | 69 | 330 | 298 | half-normal | day of year | -0.33 (-0.75, 0.09) | 0.56 (0.43, 0.68) | 0.73 |
| Arctic ground squirrel | 490 | 115 | 655 | uniform + cos(1) | | | 0.60 (0.56, 0.63) | 0.75 |

(minor overlap of the 95% confidence interval with zero) and NDWI did not appear in the best fitting DSM. Tundra swan, Lapland Longspur (*Calcarius lapponicus*) and shorebird abundance was positively related to NDWI (minor overlap of the 95% confidence interval with zero for swans), and NDVI did not appear in competitive DSMs for any of these species. Loon and American Pipit abundance was unrelated to NDVI or NDWI and Common Eider abundance was negatively related to both covariates. NDWI, rather than NDVI, was present in the best-fitting DSM for Arctic ground squirrels and was positively related to abundance (Figure 2.3, Table 2.2). Competitive models for microtine burrow counts contained both NDVI and NDWI, but confidence intervals for either had wide overlap of zero.

### 2.3.3 Elevation and distance from coast

Elevation was present more often in competitive DSMs than distance from coast. Savannah Sparrows, shorebirds, geese, gulls, Tundra Swans, Sandhill Cranes, loons, and Common Eiders were more abundant at low elevations, and distance from coast did not appear in competitive DSMs for any of these groups (Figure 2.2, Table 2.2). American Pipit abundance was also negatively related to both elevation and distance from coast (minor overlap of the 95% confidence interval with zero in both cases). Redpoll abundance was unrelated to elevation or distance from coast. Lapland Longspurs were more abundant inland and although the best fitting model included the interaction between distance from coast and sampling period, the 95% confidence interval for this term had wide overlap of zero. Elevation did not appear in competitive DSMs for longspurs. There was some evidence for a shift to lower elevation, coastal habitat in late summer for Horned Larks. Duck abundance was negatively related both to distance from coast and elevation. For mammals, elevation was negatively related to Arctic ground squirrel abundance, and distance from coast was positively related to microtine burrow counts (Figure 2.3, Table 2.2).

Figure 2.2: Parametric model coefficients and 95% confidence intervals for habitat covariates. Avian survey data collected during the summers of 2015-17 at Rankin Inlet, Nunavut, Canada. All covariates were standardized prior to analyses. Blue indicates a given estimate is specific to early summer, green is specific to late summer, and red indicates the estimate is pooled across the entire summer. Habitat covariates were modelled at the 270 x 270-m scale for songbird species and shorebirds, 510 x 510-m for ducks, geese and loons, and 990 x 990-m for Common Eiders, swans, cranes and loons. NDVI (normalized difference vegetation index), NDWI (normalized difference water index). In some cases there were multiple competitive DSMs for a given species or group, and these models are noted with a number. American Pipit (*Anthus rubescens*), Horned Lark (*Eremophila alpestris*), redpoll (*Acanthis* spp.), Lapland Longspur (*Calcarius lapponicus*), Savannah Sparrow (*Passerculus sandwichensis*), Tundra Swan (*Cygnus columbianus*), Sandhill Crane (*Antigone canadensis*), Common Eider (*Somateria mollissima*).



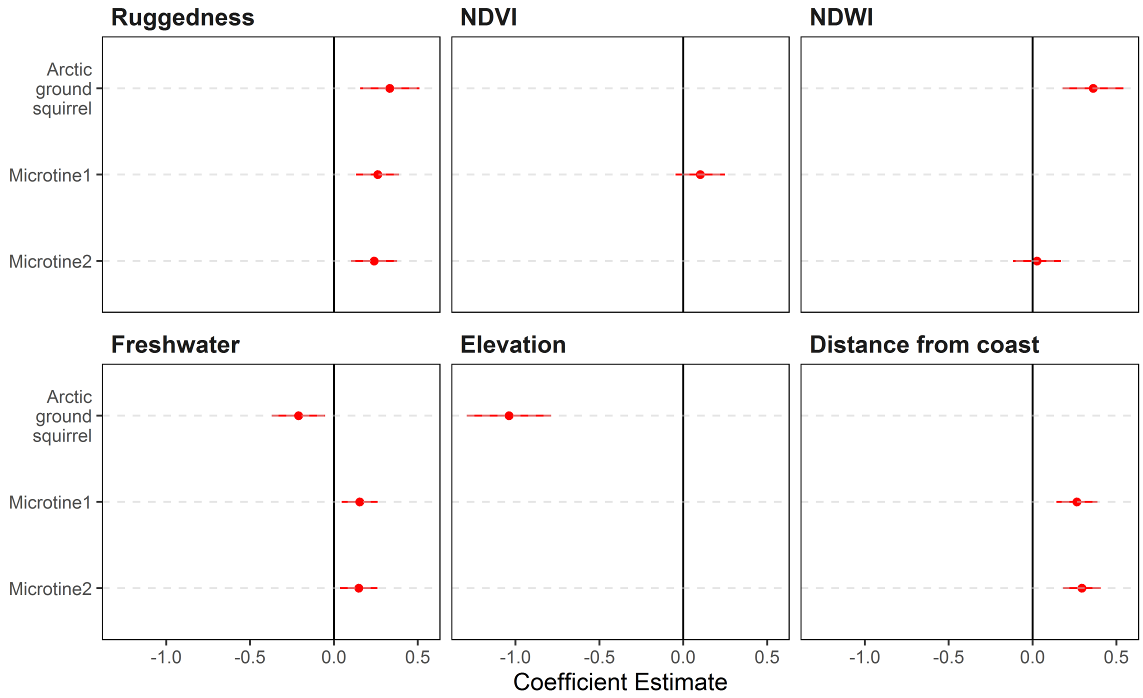


Figure 2.3: Parametric model coefficients and 95% confidence intervals for habitat covariates included in competitive models of Arctic ground squirrel (*Urocetillus parryii*) abundance and microtine burrow counts. All covariates were standardized before analyses. Habitat covariates were averaged at the 270 x 270-m scale. Survey data collected during the summers of 2015-17 at Rankin Inlet, Nunavut, Canada. For microtine burrows there were multiple competitive models (Microtine1 and Microtine2). NDVI (normalized difference vegetation index), NDWI (normalized difference water index).

### 2.3.4 Freshwater

Ducks, geese, gulls, Tundra Swans and loons were more abundant in areas with more freshwater (Figure 2.2, Table 2.2; minor overlap of the 95% confidence interval with zero for geese and one competitive duck model). Additionally, geese became more abundant in areas with more freshwater later in summer, and the interaction between freshwater and year did not appear in the best fitting DSM for geese. American Pipit, redpoll, Lapland Longspur, Savannah Sparrow, shorebird, Sandhill Crane, and Common Eider abundance was unrelated to freshwater. Horned Larks were less abundant in areas with more freshwater. Arctic ground squirrel abundance was negatively related to freshwater, while the reverse was true for microtine burrow counts (Figure 2.3, Table 2.2).

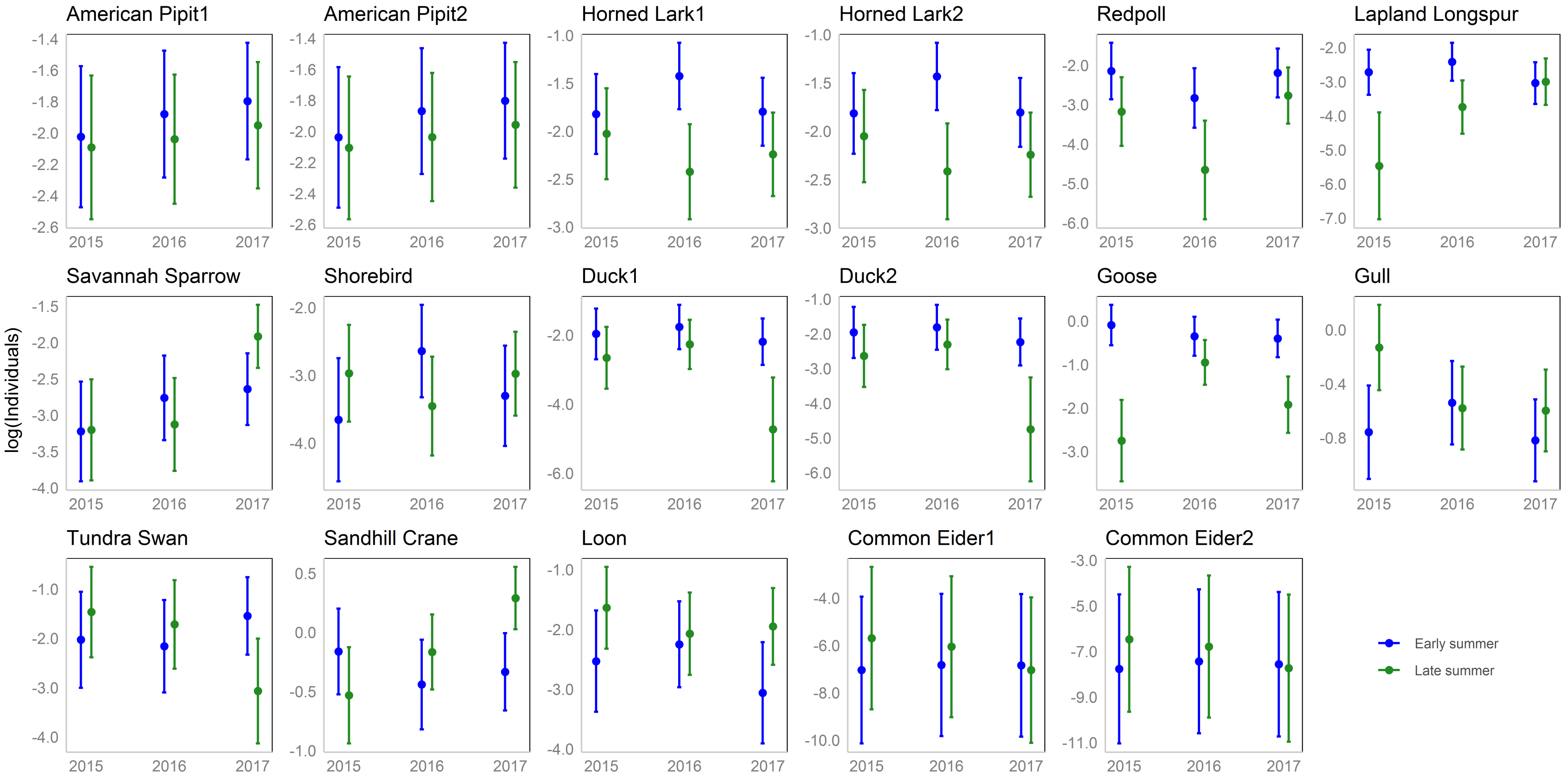
### 2.3.5 Ruggedness

American Pipits, redpolls and geese were more abundant in areas with rugged terrain, while ducks were more abundant in areas with flat terrain (Figure 2.2, Table 2.2; minor overlap of the 95% confidence interval with zero for geese). Lapland Longspur, Savannah Sparrow, Horned Lark, shorebird, gull, Sandhill Crane and loon abundance was unrelated to ruggedness. Competitive models for Common Eider abundance indicated differing effects of ruggedness; in the model including NDVI, eider abundance was positively related to ruggedness, while in the model including NDWI, this relationship was weakened considerably (minor overlap of the 95% confidence interval with zero). These differing effects are likely due to the fact that NDWI was correlated with ruggedness to a greater degree than NDVI. Arctic ground squirrel abundance and microtine burrow counts were positively related to terrain ruggedness (Figure 2.3, Table 2.2).

### 2.3.6 Temporal changes in abundance

American Pipit, shorebird, Common Eider and loon abundance was stable across all years and sampling periods (Figure 2.4). Horned Lark and redpoll abundance was lower in late summer 2016, while Savannah Sparrows and Sandhill Cranes were more abundant in late summer 2017. Lapland Longspurs were less abundant in late summer 2015 and to a lesser degree in late summer 2016 as well. Duck and Tundra Swan abundance was generally stable, but was lower in late summer 2017, while goose abundance was particularly low in late summer 2015 and late summer 2017. Gulls were more abundant in late summer 2015. In 2015, Arctic ground squirrel abundance was low compared to 2016 and 2017, and abundance also increased from early to late summer across all years (Figure 2.5).

Figure 2.4: Combined effects of year, period and their interaction on the abundance of avian species and groups, along with 95% confidence intervals, plotted on the scale of the linear predictor (*i.e.*, the logarithm of abundance when all other covariates in the model were set to their means, the effect of the random component of the model was removed, and for a transect segment of average size). Blue indicates early summer and green indicates late summer. Avian survey data collected during the summers of 2015-17 at Rankin Inlet, Nunavut, Canada. In some cases there were multiple competitive DSMs for a given species or group, and these models are noted with a number. American Pipit (*Anthus rubescens*), Horned Lark (*Eremophila alpestris*), redpoll (*Acanthis* spp.), Lapland Longspur (*Calcarius lapponicus*), Savannah Sparrow (*Passerculus sandwichensis*), Tundra Swan (*Cygnus columbianus*), Sandhill Crane (*Antigone canadensis*), Common Eider (*Somateria mollissima*).



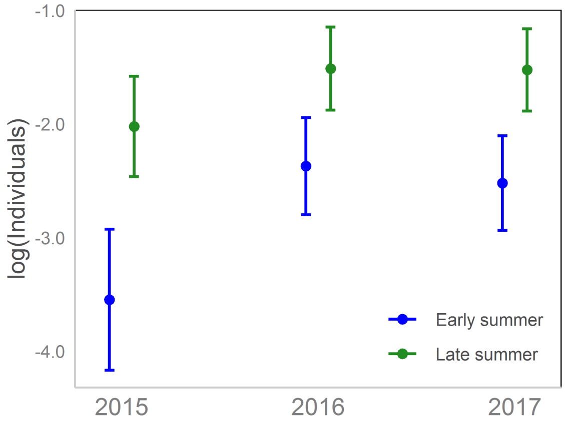


Figure 2.5: Combined effects of year, period and their interaction on the abundance of Arctic ground squirrels (*Urocetillus parryii*), along with 95% confidence intervals, plotted on the scale of the linear predictor (*i.e.,* the logarithm of abundance when all other covariates in the model were set to their means, the effect of the random component of the model was removed, and for a transect segment of average size). Blue indicates early summer and green indicates late summer. Figure was produced using the best fitting candidate model. Survey data collected during the summers of 2015-17 at Rankin Inlet, Nunavut, Canada.

## 2.4 Discussion

### 2.4.1 Habitat associations of avian species and groups in the Arctic

Among the general conclusions that can be drawn from my study is the importance of areas with high freshwater cover, low elevation and high vegetative productivity as habitat for breeding tundra birds, generally according with my predictions. For small mammals, I found a mixture of expected and unexpected results. As expected, Arctic ground squirrels were more abundant in areas with higher ruggedness and avoided areas with freshwater. Arctic ground squirrels were also associated with areas of high vegetative productivity. However, NDWI, rather than NDVI was present in the best fitting model for squirrel abundance, contrary to my predictions, and there was little effect of vegetative productivity on microtine rodent burrow counts. I now discuss these results in light of previous research.

### 2.4.2 Freshwater

The abundance of freshwater that characterizes many Arctic study areas provides foraging habitat for birds as well as refuges from predation (Petersen 1990; Ruggles 1994; Slattery and Alisauskas 2007; Stickney et al. 2002). Unsurprisingly, waterfowl such as ducks (not including Common Eiders), geese, and swans, as well as loons and gulls were all more abundant in areas with more freshwater. I also found that geese had stronger associations with freshwater later in summer, as adults were likely molting and juveniles remained flightless. This accords with the results of Stahl and Loonen (1998), who found Barnacle Goose (*Branta leucopsis*) habitat use with respect to freshwater during brood rearing to vary, in their case annually, with predation risk. Lecomte et al. (2009) showed that the availability of freshwater on the tundra is also important for providing nearby drinking water to incubating geese, and that nesting success with respect to freshwater varied with annual moisture conditions, raising the possibility that geese might respond to moisture conditions in terms of their annual habitat use as well (Robinson et al. 2014). However, I did not find strong evidence for shifts in annual habitat use with regards to freshwater. It is possible that the gradient in moisture conditions across years did not permit effective investigation of this phenomenon, and it is also possible that freshwater is less limiting in my study area, which is located on the generally low-lying Hudson Bay coast. Previous study has revealed a drying trend for high latitude ponds and lakes (Smol and Douglas 2007a), which would logically have adverse effects upon species relying on freshwater.

Perhaps surprisingly, I did not find positive associations between shorebirds and freshwater. My study area is coastal, and given the strong negative relationship between elevation and shorebird abundance, shorebirds in my study area may have associated with marine habitat instead. Additionally, the most common shorebird identified on my surveys, the Semipalmated Plover (*Charadrius semipalmatus*), is known to nest on dry, pebbled substrates (Nguyen et al. 2003; Nol and Blanken 2014) that likely decrease the probability of individuals being found near water. Lastly, much of the freshwater in the Arctic is below the scale generally captured in satellite imagery (Muster et al. 2012), and the positive relationship between shorebird abundance and NDWI hints at the possibility that shorebirds were associating with very small water bodies, or areas with wet soils. Only one bird species appeared to avoid areas with high freshwater cover, the Horned Lark, which generally accords with descriptions of its preferred habitat as dry or barren (Beason 1995).

I did not expect freshwater to influence microtine burrow counts largely because I was unable to distinguish between burrows of different species, and Arctic microtines generally distribute themselves along a gradient from wet to dry habitat (Ale et al. 2011; Batzli et al. 1983). The surprising positive relationship between microtine burrow abundance and freshwater may indicate that the microtine community is dominated by those preferring wet habitats, even though the collared lemming (*Dicrostonyx spp.*), the primary lemming in my study area, is known to prefer dry habitats (Ale et al. 2011; Batzli et al. 1983). Arctic ground squirrel abundance was negatively correlated with freshwater cover, as expected, likely due to the risk of burrow flooding (Wheeler and Hik 2013).

### 2.4.3 Elevation and distance from coast

The effects of elevation or distance from coast on avian abundance were almost universally negative. For species such as loons, gulls or Common Eiders, which utilize marine food sources, this association is intuitive, and gulls also exploit anthropogenic food sources (*e.g.,* landfill, discarded bycatch from fishing; Staniforth 2002; Weiser and Powell 2010) from the hamlet of Rankin Inlet itself, which is coastal within the study area (Figure 2.1). Higher abundance in low, coastal habitats is consistent with previous study on shorebirds (Saalfeld et al. 2013) and various waterfowl (Conkin and Alisauskas 2013), and it is likely this relationship is driven by the greater availability of suitable habitat in low, coastal areas, for example wetlands (bogs, fens), river deltas or tidal habitats.

Only a single bird species was positively associated with elevation or distance from coast, the Lapland Longspur, which accords with prior study by Andres (2006), which showed a heavily longspur-biased songbird population was more abundant at higher elevations in a study area on the Ungava Peninsula. While the mechanism for this association is unknown, it is possible this is a form of habitat partitioning, because other songbird species generally had negative responses to elevation or distance from coast. As these species all largely consume invertebrates during the breeding season (Beason 1995; Custer et al. 1986; Hendricks and Verbeek 2012; Hussell and Montgomerie 2002; Knox and Lowther 2000; Wheelwright and Rising 2008), competition may in part dictate their spatial distributions.

The use of coastlines by migrating birds has been long known (Alerstam and Pettersson 1977) and has been noted for some of the species modelled in my study (Connors et al. 1979; Hussell and Montgomerie 2002; Wheelwright and Rising 2008). However, only Horned Larks showed some evidence of a shift to lower, coastal habitats

Table 2.2: DSM results for species and groups surveyed in the Rankin Inlet, Nunavut, Canada study area from 2015-17. Included is the response distribution (Dist; tw for Tweedie and nb for negative binomial), proportion deviance explained (Dev), number of transect segments (N), and number of non-zero counts (N >0). Summary information for model terms is also included for each model, separated into fixed and random effects. For fixed effects, coefficient estimates are reported, along with their 95% confidence intervals (in parentheses). Random effects were modelled as smooth terms s() in the dsm package, so I report the estimated degrees of freedom of the smooth and the associated *p*-value (in parentheses). In some cases there were multiple competitive DSMs for a given species or group, and models are noted with a number. Fixed effects with 95% confidence intervals not overlapping zero are bolded. NDVI (normalized difference vegetation index), NDWI (normalized difference water index). American Pipit (*Anthus rubescens*), Horned Lark (*Eremophila alpestris*), redpoll (*Acanthis* spp.), Lapland Longspur (*Calcarius lapponicus*), Savannah Sparrow (*Passerculus sandwichensis*), Tundra Swan (*Cygnus columbianus*), Sandhill Crane (*Antigone canadensis*), Common Eider (*Somateria mollissima*), Arctic ground squirrel (*Urocetillus parryii*).

| **Model** | **Intercept** | **Ruggedness** | **NDVI** | **NDWI** | **Freshwater** | **Freshwater: late summer** |
|---|---:|---:|---:|---:|---:|---:|
| American Pipit1 | -12.40 (-12.85, -11.95) | **0.60 (0.44, 0.77)** | -0.02 (-0.21, 0.16) | | 0.08 (-0.08, 0.23) | |
| American Pipit2 | -12.42 (-12.87, -11.97) | **0.59 (0.42, 0.76)** | 0 (-0.20, 0.20) | | 0.09 (-0.07, 0.25) | |
| Horned Lark1 | -12.09 (-12.51, -11.67) | -0.11 (-0.31, 0.09) | **0.24 (0.04, 0.45)** | | **-0.44 (-0.65, -0.24)** | |
| Horned Lark2 | -12.08 (-12.50, -11.67) | -0.12 (-0.32, 0.08) | **0.25 (0.04, 0.46)** | | **-0.44 (-0.65, -0.24)** | |
| Redpoll | -12.58 (-13.30, -11.87) | **0.35 (0.01, 0.69)** | 0.33 (-0.05, 0.71) | | 0 (-0.33, 0.32) | |
| Lapland Longspur | -13.00 (-13.66, -12.34) | 0.13 (-0.18, 0.45) | | **0.33 (0.03, 0.63)** | -0.13 (-0.34, 0.07) | |
| Savannah Sparrow | -13.33 (-14.01, -12.64) | -0.14 (-0.48, 0.20) | **0.48 (0.18, 0.79)** | | 0.03 (-0.17, 0.23) | |
| Shorebird | -14.10 (-15.01, -13.19) | -0.19 (-0.57, 0.19) | | **0.47 (0.12, 0.83)** | -0.13 (-0.37, 0.12) | |
| Duck1 | -13.71 (-14.44, -12.97) | **-0.61 (-1.11, -0.12)** | | 0.39 (-0.06, 0.83) | **0.31 (0.02, 0.60)** | |
| Duck2 | -13.70 (-14.44, -12.97) | **-0.61 (-1.10, -0.11)** | | 0.31 (-0.13, 0.76) | 0.29 (0.00, 0.58) | |
| Goose | -11.78 (-12.25, -11.32) | 0.18 (-0.07, 0.43) | 0.11 (-0.16, 0.37) | | 0.23 (-0.01, 0.46) | **0.59 (0.29, 0.90)** |
| Gull | -12.36 (-12.71, -12.02) | -0.10 (-0.26, 0.05) | -0.11 (-0.27, 0.04) | | **0.24 (0.11, 0.38)** | |
| Tundra Swan | -14.88 (-15.85, -13.90) | -0.18 (-0.67, 0.31) | | 0.43 (-0.05, 0.91) | **0.39 (0.01, 0.77)** | |
| Sandhill Crane | -12.68 (-13.04, -12.31) | -0.07 (-0.25, 0.11) | **0.49 (0.26, 0.71)** | | 0.09 (-0.06, 0.24) | |
| Loon | -15.06 (-15.90, -14.21) | -0.24 (-0.60, 0.12) | -0.08 (-0.44, 0.29) | | **0.43 (0.13, 0.72)** | |
| Common Eider1 | -19.45 (-22.55, -16.35) | **0.78 (0.20, 1.37)** | **-0.72 (-1.18, -0.27)** | | 0.24 (-0.50, 0.98) | |
| Common Eider2 | -20.17 (-23.44, -16.91) | 0.49 (-0.19, 1.18) | | **-0.68 (-1.13, -0.24)** | 0.12 (-0.62, 0.87) | |
| Arctic ground squirrel | -13.96 (-14.58, -13.34) | **0.33 (0.16, 0.51)** | | **0.36 (0.18, 0.54)** | **-0.21 (-0.37, -0.05)** | |
| Microtine1 | -4.28 (-4.64, -3.92) | **0.26 (0.13, 0.39)** | 0.10 (-0.05, 0.25) | | **0.15 (0.05, 0.26)** | |
| Microtine2 | -4.27 (-4.63, -3.91) | **0.24 (0.10, 0.38)** | | 0.03 (-0.12, 0.17) | **0.15 (0.04, 0.26)** | |

*continued on following page*

| **Model** | **Elevation** | **Elevation: late summer** | **Coast** | **Coast: late summer** | **2016** | **2017** |
|---|---|---|---|---|---|---|
| American Pipit1 | -0.15 (-0.36, 0.06) | | | | 0.14 (-0.45, 0.74) | 0.23 (-0.35, 0.81) |
| American Pipit2 | | | -0.17 (-0.41, 0.07) | | 0.17 (-0.43, 0.77) | 0.24 (-0.35, 0.82) |
| Horned Lark1 | 0.05 (-0.16, 0.26) | -0.23 (-0.55, 0.09) | | | 0.40 (-0.14, 0.93) | 0.02 (-0.52, 0.56) |
| Horned Lark2 | | | 0.06 (-0.17, 0.29) | -0.28 (-0.61, 0.05) | 0.38 (-0.16, 0.92) | 0.01 (-0.53, 0.55) |
| Redpoll | -0.18 (-0.54, 0.17) | | | | -0.69 (-1.72, 0.35) | -0.05 (-1.00, 0.90) |
| Lapland Longspur | | | **0.98 (0.65, 1.31)** | 0.25 (-0.20, 0.71) | 0.31 (-0.54, 1.15) | -0.32 (-1.19, 0.56) |
| Savannah Sparrow | **-0.36 (-0.65, -0.07)** | | | | 0.46 (-0.43, 1.35) | 0.58 (-0.25, 1.42) |
| Shorebird | **-0.68 (-1.05, -0.32)** | | | | 1.01 (-0.10, 2.13) | 0.35 (-0.80, 1.51) |
| Duck1 | | | **-0.39 (-0.78, -0.01)** | | 0.20 (-0.75, 1.15) | -0.23 (-1.19, 0.74) |
| Duck2 | **-0.38 (-0.74, -0.02)** | | | | 0.15 (-0.80, 1.10) | -0.28 (-1.24, 0.69) |
| Goose | **-0.46 (-0.75, -0.18)** | | | | -0.26 (-0.90, 0.38) | -0.31 (-0.94, 0.32) |
| Gull | **-0.47 (-0.64, -0.30)** | | | | 0.22 (-0.24, 0.68) | -0.06 (-0.52, 0.40) |
| Tundra Swan | **-1.25 (-1.77, -0.73)** | | | | -0.13 (-1.44, 1.18) | 0.48 (-0.74, 1.71) |
| Sandhill Crane | **-0.28 (-0.46, -0.11)** | | | | -0.28 (-0.80, 0.24) | -0.17 (-0.66, 0.31) |
| Loon | **-0.62 (-1.05, -0.19)** | | | | 0.28 (-0.80, 1.36) | -0.53 (-1.70, 0.64) |
| Common Eider1 | **-5.19 (-8.31, -2.08)** | | | | 0.21 (-1.25, 1.68) | 0.20 (-1.24, 1.64) |
| Common Eider2 | **-6.32 (-9.46, -3.17)** | | | | 0.33 (-1.14, 1.81) | 0.21 (-1.24, 1.65) |
| Arctic ground squirrel | **-1.04 (-1.29, -0.79)** | | | | **1.18 (0.44, 1.91)** | **1.03 (0.30, 1.76)** |
| Microtine1 | | | **0.26 (0.14, 0.39)** | | | |
| Microtine2 | | | **0.29 (0.18, 0.41)** | | | |

*continued on following page*

| Model | Late summer | 2016: late summer | 2017: late summer | s(Transect visit) | s(Transect) | s(Counter) | Dist | N | N >0 | Dev |
|---|---|---|---|---|---|---|---|---|---|---|
| American Pipit1 | -0.07 (-0.62, 0.49) | -0.09 (-0.83, 0.65) | -0.09 (-0.82, 0.64) | 38.41 (0.15) | 72.28 (<0.001) | | tw | 1784 | 221 | 0.35 |
| American Pipit2 | -0.07 (-0.62, 0.49) | -0.10 (-0.84, 0.64) | -0.09 (-0.82, 0.64) | 38.89 (0.14) | 72.85 (<0.001) | | tw | 1784 | 221 | 0.36 |
| Horned Lark1 | -0.21 (-0.79, 0.38) | -0.79 (-1.61, 0.02) | -0.24 (-1.02, 0.54) | 67.57 (<0.001) | 46.23 (0.01) | | tw | 1784 | 226 | 0.33 |
| Horned Lark2 | -0.23 (-0.82, 0.35) | -0.75 (-1.57, 0.07) | -0.20 (-0.98, 0.58) | 67.66 (<0.001) | 46.17 (0.01) | | tw | 1784 | 226 | 0.33 |
| Redpoll | -1.03 (-2.15, 0.09) | -0.79 (-2.63, 1.04) | 0.46 (-1.01, 1.92) | 0 (0.99) | 0 (0.88) | | nb | 1784 | 67 | 0.11 |
| Lapland Longspur | **-2.75 (-4.34, -1.15)** | 1.42 (-0.27, 3.11) | **2.79 (1.13, 4.44)** | 37.65 (0.09) | 62.62 (0.01) | | tw | 1784 | 142 | 0.59 |
| Savannah Sparrow | 0.02 (-0.75, 0.80) | -0.39 (-1.46, 0.68) | 0.70 (-0.21, 1.61) | | 82.43 (<0.001) | | tw | 1784 | 126 | 0.40 |
| Shorebird | 0.69 (-0.25, 1.62) | **1.50 (-2.76, -0.23)** | -0.36 (-1.60, 0.88) | | 66.26 (<0.001) | | tw | 1784 | 85 | 0.45 |
| Duck1 | -0.69 (-1.70, 0.32) | 0.19 (-1.10, 1.47) | -1.85 (-3.70, 0.01) | | 59.07 (<0.001) | | tw | 1015 | 79 | 0.51 |
| Duck2 | -0.68 (-1.69, 0.33) | 0.18 (-1.11, 1.47) | -1.84 (-3.69, 0.01) | | 59.45 (<0.001) | | tw | 1015 | 79 | 0.51 |
| Goose | **-2.66 (-3.62, -1.70)** | **2.06 (0.97, 3.15)** | 1.14 (-0.02, 2.30) | | 77.46 (<0.001) | | tw | 1015 | 177 | 0.45 |
| Gull | **0.63 (0.21, 1.05)** | **-0.67 (-1.24, -0.09)** | -0.41 (-0.97, 0.16) | 0.02 (0.92) | 68.59 (<0.001) | | nb | 1015 | 350 | 0.29 |
| Tundra Swan | 0.56 (-0.73, 1.85) | -0.12 (-1.91, 1.66) | **-2.08 (-3.90, -0.27)** | | 13.37 (0.80) | | nb | 607 | 62 | 0.39 |
| Sandhill Crane | -0.37 (-0.87, 0.13) | 0.65 (-0.03, 1.32) | **-0.99 (0.37, 1.62)** | | 55.47 (<0.001) | | tw | 607 | 219 | 0.31 |
| Loon | 0.89 (-0.14, 1.93) | -0.72 (-2.11, 0.67) | 0.22 (-1.22, 1.66) | | 25.44 (0.10) | | nb | 607 | 67 | 0.36 |
| Common Eider1 | **1.35 (0.21, 2.49)** | -0.58 (-2.12, 0.96) | -1.55 (-3.16, 0.05) | | 27.53 (<0.001) | | tw | 607 | 45 | 0.80 |
| Common Eider2 | **1.30 (0.14, 2.46)** | -0.65 (-2.21, 0.90) | -1.47 (-3.08, 0.14) | | 28.31 (<0.001) | | tw | 607 | 45 | 0.80 |
| Arctic ground squirrel | **1.53 (0.93, 2.12)** | -0.67 (-1.37, 0.04) | -0.53 (-1.23, 0.17) | 0.01 (0.83) | 109.52 (<0.001) | | nb | 1784 | 303 | 0.57 |
| Microtine1 | | | | | | 4.93 (<0.001) | tw | 225 | 225 | 0.24 |
| Microtine2 | | | | | | 4.93 (<0.001) | tw | 225 | 225 | 0.23 |

later in summer. The general lack of a shift may reflect the fact that songbirds and shorebirds were already more abundant in low, coastal areas. Possibly this is also an artifact of my sampling design. I used July 11 as the division between early and late summer sampling, but it is likely that migratory flocking in most species occurs substantially later than this date, thus I was not able to detect coastward shifts in abundance.

Previous evaluations of small mammal habitat use in the Arctic have generally not examined the influence of elevation or distance from coast, however my study illustrates that these covariates should not be overlooked. Arctic ground squirrel abundance was negatively related to elevation, and microtine burrow abundance was also positively related to distance from coast. It is likely elevation and distance from coast were correlated with unmeasured habitat components, rather than directly influencing abundance *per se*. For example, well-drained substrates with a deep active layer permit burrow construction and support ground squirrel density (Batzli and Sobaski 1980; Carl 1971), and these conditions may be more abundant in low, coastal areas, particularly river deltas where sediment deposition is high. Future studies of Arctic ground squirrel and microtine rodent abundance should consider substrate suitability explicitly. My study area spans nearshore islands to areas >25-km inland, which may lead to differences in local climate due to the cooling influence of Hudson Bay (Rouse 1991). For microtines, areas inland may therefore represent advanced timing of snowmelt and leaf-out, increasing their access to new vegetation.

### 2.4.4 Vegetative productivity and water content

For both NDVI and NDWI, effects on abundance were generally positive or neutral, as expected. Surprisingly, I did not find positive associations between geese and NDVI or NDWI, despite their herbivorous diet and previously demonstrated associations with wet meadows and wetlands (Cadieux et al. 2005; Slattery and Alisauskas 2007). I suggest that this may be an idiosyncrasy specific to study areas where geese frequently nest on cliffs. These areas are generally low NDVI or NDWI because they contain bare rock or are otherwise sparsely vegetated. Geese in my study area are likely to divide their time among vegetated (where they forage) and non-vegetated (where they nest) areas, which would explain why I did not find an association with either measure of vegetation. On the other hand, I did find positive associations between NDVI and the generally herbivorous Sandhill Cranes, and also for three songbird species: Horned Larks, Savannah Sparrows and redpolls. Various vegetation types are used by songbirds; for example shrubs for nesting (Boelman et al. 2015; Peterson et al. 2014) and canopy-dwelling insect prey (Boelman et al. 2015; Perez et al. 2016), and seeds and berries are also important diet components when arthropods are less available (Custer and Pitelka 1978; Norment and Fuller 1997; White and West 1977).

To my knowledge this is the first usage of NDWI in modelling avian and mammalian habitat in the Arctic, although it has been used to characterize tundra vegetation in previous study (Riihimäki et al. 2019). Given there was more support for DSMs including NDWI rather than NDVI for some species and groups, NDWI may be an important variable to include in future studies of avian and mammalian distribution. There is some evidence that remotely sensed vegetation indices that utilize the shortwave infrared band of satellite sensors, such as NDWI, may be more effective at characterizing habitats with large amounts of senescent vegetation, such as tundra (Liu et al. 2017; Riihimäki et al. 2019). NDWI was particularly important in predicting abundance for Lapland Longspurs, shorebirds, ducks (excluding Common Eiders), Tundra Swans, and Arctic ground squirrels.

Quantity and structure of vegetation has implications for predation risk. Common Eiders have been shown to avoid nesting habitats with high levels of cover, even though nests in these habitats benefit from lower cost of thermoregulation (Fast et al. 2007), possibly because these habitats reduce predator detection (Noel et al. 2005). This may be reflected in their avoidance of areas with high NDVI and NDWI in my study. Similarly, Arctic ground squirrels inhabiting areas with tall vegetation (trees, shrubs) exhibit higher stress (Hik et al. 2016), and display higher giving-up densities when foraging (Flower et al. 2019; Wheeler and Hik 2014a). Relying mainly on visual predator detection, Arctic ground squirrels are likely more at risk of predation when their line of sight is obstructed. Accordingly, squirrel density declines where tundra transitions to forest (Barker and Derocher 2010; Donker and Krebs 2011). My study area is treeless and generally lacks tall shrubs (>1-m), thus squirrels were associated with areas of high NDWI, likely for forage.

The general trend for Arctic vegetation under climate warming has been towards general greening (Jenkins et al. 2019) and taller growth forms (Bjorkman et al. 2018). This is likely to have varying effects upon Arctic birds (Thompson et al. 2016), perhaps benefitting those that utilize shrub cover for nesting or foraging (Boelman et al. 2015). Based on the results of my study, Savannah Sparrows, redpolls, Horned Larks, Lapland Longspurs, Tundra Swans, shorebirds and ducks might be predicted to benefit from a greener Arctic on account of their positive relationships with vegetation indices. For Arctic ground squirrels, greening and the proliferation of tall vegetation are likely to have complex effects. Initially, greening may improve forage quantity for squirrels, but longer term, taller vegetation may cause increases in individual stress and decreased fitness (Hik et al. 2016), and reverse the current positive association with NDWI.

### 2.4.5 Ruggedness

Ruggedness can influence the distribution of birds and small mammals when vertical structure improves protection from terrestrial predators (Anderson et al. 2015). Geese (generally Canada Geese *Branta canadensis*; Table A.1, Appendix A) and Common Eiders were positively associated with rugged terrain, likely due to their use of cliffs for nesting. Arctic ground squirrels prefer well-drained slopes for burrowing and may also utilize raised areas as look-outs for detecting predators (Barker and Derocher 2010; Karels and Boonstra 1999), leading to positive associations with terrain ruggedness.

For microtines, rugged terrain may also contain greater abundance of rock cover, which, like tall vegetation (Predavec and Krebs 2000), may provide cover from predators. Ruggedness may also represent greater diversity of microhabitats, which may allow multiple microtine species to coexist in close proximity (Ale et al. 2011; Morris et al. 2000). Furthermore, ruggedness may also impact patterns of snow deposition and melt (Böhner and Antonić 2009), which in turn affect vegetation and soil moisture characteristics (Walker et al. 2001) and may therefore affect microtine distribution.

### 2.4.6 Temporal changes in abundance

Although summer represents the most favourable time of year in the Arctic for avian reproduction, abiotic factors can have a large impact on reproductive output (Chmura et al. 2018; Jehl Jr and Hussell 1966; Skinner et al. 1998). The patterns in abundance I found during my years of study were mixed relative to temperature and precipitation (Figure 1.1, 2.4), and in general there were few congruencies in abundance patterns across years and sampling periods among species and groups, which likely indicates that population drivers are species or group specific. For mammals, I found that Arctic ground squirrels were less abundant in 2015, the year with cool and wet conditions, but this interpretation is obviously tentative due to the low number of years considered and possible confounding factors (*e.g.,* microtine rodent abundance, which may also impact populations of mid trophic level consumers, was also low in 2015; Figure B.2, Appendix B).

Abundance of some songbirds declined from early to late summer, which is not intuitive given presumed brood production. Rather, this pattern may actually reflect declines in singing behaviour later in the year (Thompson et al. 2017), rather than a decline in abundance *per se*. Although my distance sampling analysis attempted to account for reduced detection later in the breeding season via detection distance, because detection of songbirds was primarily aural, non-singing birds may have been "unavailable" for detection, and thus the assumption of 100% detection on the transect line may have been violated (Bachler and Liechti 2007). For this reason, I did not present density estimates for the avian species and groups modelled here, and comparisons between early and late summer abundance for songbirds have to be interpreted in the context of possible variation in availability. For species that are large and more likely to be detected visually, this was less likely an issue, and additionally my line transect protocol resulted in many songbirds being detected as they flushed in front of the observer, perhaps maintaining this assumption. Future studies should explore variation in availability using double observer surveys or time removal protocol (Amundson et al. 2014; Buckland et al. 2015). In general, late season abundance was more variable than early season abundance across taxa (Figure 2.4), which may reflect the fact that late season abundance had considerable input from within-season breeding.

### 2.4.7 Conclusion

To conclude, I estimated habitat associations for birds and small mammals over three breeding seasons in the area surrounding Rankin Inlet, Nunavut, Canada. Low elevation, large amounts of freshwater, and high vegetative productivity were the most consistent determinants of high avian abundance, while abundance of Arctic ground squirrels and microtine rodents was related to terrain ruggedness. NDWI emerged as an alternative to NDVI for characterizing habitat for several species and groups. Analyses such as those demonstrated here offer necessary updates and new approaches to basic research questions (Conservation of Arctic Flora and Fauna (CAFF), see Christensen et al. 2013) regarding Arctic birds and small mammals and the biotic and abiotic drivers of their distribution and abundance. Although wildlife studies are lacking throughout large areas of the circumpolar Arctic (Metcalfe et al. 2018), available data suggest some Arctic-breeding birds are in decline (*e.g.,* shorebirds; Smith et al. 2020), and there are looming threats for small mammals as well, for example, shrub encroachment for Arctic ground squirrels (Wheeler and Hik 2013), and rain on snow events for microtines (Domine et al. 2018). My study provides information on habitat associations for some species that are underrepresented in previous literature in a geographic region that is equally poorly represented, addressing knowledge gaps and demonstrating methodological tools that can be widely applied across the Arctic.

# Chapter 3

# Accounting for predator effects in modelling the distribution of Peregrine Falcon prey

## 3.1 Introduction

Prey populations are often controlled, in part, by predators (Brown et al. 1999; Laundré et al. 2010), either through direct predation or the non-lethal effects of predation risk. Spatially, the distribution of predation risk as perceived by prey is known as the "landscape of fear" (Gaynor et al. 2019), the effects of which can manifest in several ways: altered habitat use (Creel et al. 2005), modified activity hours (Haswell et al. 2020), increased vigilance (Fuller et al. 2013), and increased stress (Clinchy et al. 2004). Ultimately, these effects can negatively affect population parameters, such as breeding productivity (Creel et al. 2007; DeWitt et al. 2019; Sheriff et al. 2009; Zanette et al. 2011). Non-lethal effects of predation can further manifest at the community level via trophic cascades whereby the lowest trophic levels of an ecosystem benefit from the presence of apex predators through control of mid-trophic level consumers (Matassa and Trussell 2011; Ripple and Beschta 2004; Suraci et al. 2016). Explicitly accounting for spatial variation in predation risk has the potential to alter species distribution models, improving identification of critical habitat, and may aid in predicting predator effects on the wider ecological community.

Central place foragers can have pronounced effects on prey distribution. They occupy fixed locations for extended periods of time, which can result in depletion of local prey populations (Ashmole 1963; Elliott et al. 2009). Additionally, in many avian systems, predators initiate breeding prior to their prey, and their spatial distribution can influence nest site selection by prey (Lima 2009). Accordingly, raptors have been found to reduce the abundance of avian prey surrounding their nest sites (Norrdahl and Korpimaki 1998; Suhonen et al. 1994). However, non-linear or positive relationships between raptor nests and avian prey have also been found (Monkkonen et al. 2007; Norrdahl et al. 1995; Thomson et al. 2006). Where prey face predation risk from multiple sources and that risk is concentrated on particular life stages, trade-offs exist that may result in optimal habitat use nearer to, or at intermediate distances from, predators. For example, raptors may, in the course of defending their own nests from potential predators, indirectly provide protection for prey nesting nearby (Quinn and Ueta 2008).

In Arctic-dwelling species, effects of nesting raptors on the local abundance of prey have previously been shown. Abundance of passerines was lower in the vicinity of Peregrine Falcon (*Falco peregrinus*) nests (Meese and Fuller 1989), while positive associations between nesting geese and raptors have also been found (Bêty et al. 2001; Kleef et al. 2007; Quinn and Kokorev 2002). Landscapes of fear have also been investigated in lemmings, with mixed results (Dupuch et al. 2014a,b), while in Arctic ground squirrels (*Urocitellus parryii*), predation risk is known to alter foraging behaviour and increase stress, leading to decreased population productivity (Hik et al. 2016; Wheeler and Hik 2014a,b). In summary, prey responses to the presence of predators are taxon-specific, varying in concert with the composition of the predator community, and whether predation risk is focused on nests, juveniles or adults.

I analyzed survey data from Chapter 2 in the context of a predator landscape where Peregrine Falcons were the apex predator. I hypothesized that Peregrine Falcons would depress prey abundance near their nests, either through predator avoidance, or direct predation, particularly for groups vulnerable to predation at multiple life stages. I limited analyses to common prey types for Peregrine Falcons (songbirds, shorebirds, Arctic ground squirrels, geese and ducks; Bradley and Oliphant 1991; Dawson et al. 2011; Robinson et al. 2015). In songbirds and shorebirds, both adults and juveniles are at risk of falcon predation, whereas in geese, ducks and ground squirrels, predation is concentrated on juveniles. For prey in which juveniles were most at risk, I expected a stronger response to Peregrine Falcon nests in late summer, when those individuals entered the population.

I considered the possibility that comparing prey responses to Peregrine Falcons between early and late summer may also distinguish predator avoidance from the effects of direct predation (Norrdahl and Korpimaki 1998). If prey abundance near Peregrine Falcon nests was lower in early summer, and then remained low in late summer, I interpreted this as evidence of predator avoidance during territory or nest site selection. If the effect of distance to Peregrine Falcon nests was stronger in late summer compared to early summer, this could be evidence of either direct predation, as falcons gradually depleted the prey population near their nest, or dispersal, as prey with vulnerable juveniles vacated areas near falcons after hatch. Arctic ground squirrels have limited dispersal capacity (Byrom and Krebs 1999), and are largely unable to spatially avoid nesting falcons, hence if I found lower abundance of squirrels near falcon nests, I took this as evidence of consumption. To accommodate for gradual dilution of predation risk (Forsman et al. 2001), I allowed the effect of distance to Peregrine Falcon nests to be non-linear. My study offers insights into how predation risk structures avian and small mammal communities in the Arctic, and highlights the importance of accounting for this risk in species distribution models.

## 3.2 Methods

### 3.2.1 Data collection

Data for this chapter are largely from Chapter 2, and distance sampling survey methods are already described in Section 2.2.

Peregrine Falcon nest sites were surveyed systematically prior to egg-laying to determine occupancy, and their spatial locations relative to distance sampling transects are shown in Figure 3.1. Three decades of prior surveys in this study area, as well as multiple visits to each historical nest site in each year of my study, provide some confidence that all occupied nests were found in each year (Franke et al. 2020), but this remained a study assumption. Nest fate was determined using a combination of remote cameras and nest visits. Occupied Peregrine Falcon nests were defined as those at which at least one egg was laid, and includes nests that subsequently failed during incubation or brood rearing. I repeated all analyses using only nests that were successful in fledging at least one young, meaning falcons were present for the full duration of prey sampling, but this did not alter my conclusions.

### 3.2.2 Analysis

The basic two-step analysis (1: model detection function, 2: model spatiotemporal distribution in survey counts) described in Chapter 2 is largely maintained here, but with some notable alterations. Prey were grouped into five types (songbirds, shorebirds, Arctic ground squirrels, geese and ducks) prior to analyses. Because prey can behave cryptically in the presence of predators (Lima 2009), I also included distance to the nearest Peregrine Falcon nest in candidate detection functions for each prey type. For songbirds, I knew *a priori* (Chapter 2) that detection functions varied by species, so I allowed for greater detection function complexity by testing all combinations of the above covariates, together with species, species x day of year and species x time of day. In Chapter 2, Common Eiders were modelled separately from

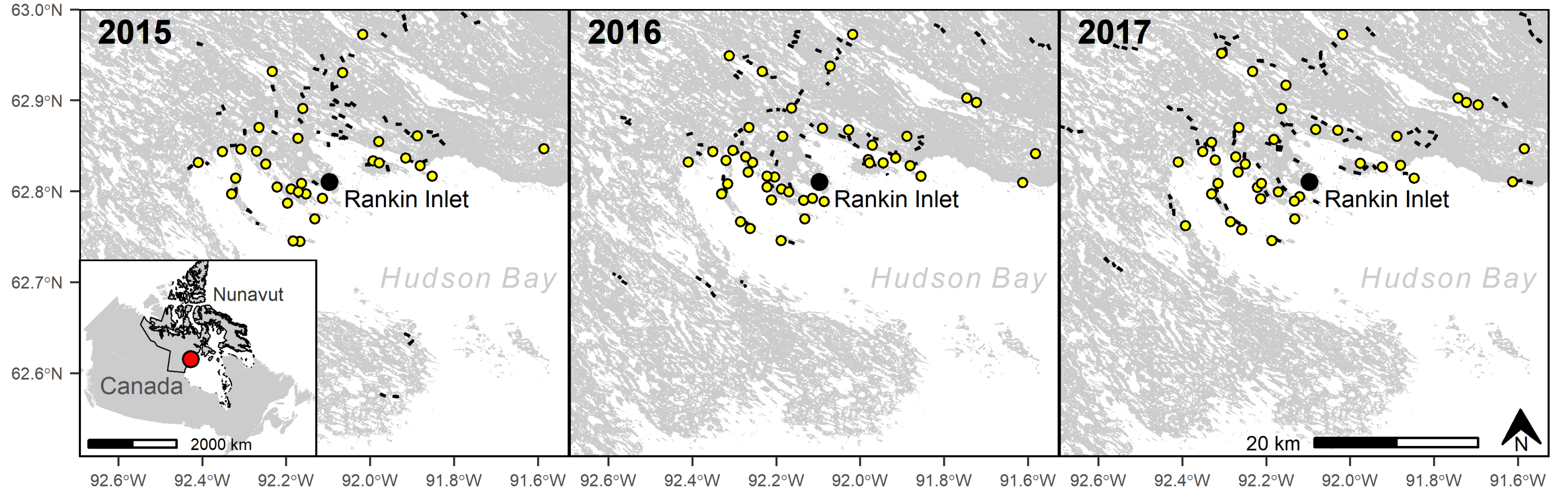


Figure 3.1: Maps of Rankin Inlet study area displaying the spatial distribution of distance sampling transects surveyed from 2015-17, along with the locations of occupied Peregrine Falcon (*Falco peregrinus*) nest sites (○). | represent individual transects, and note that each transect was repeated a minimum of twice during a season. Inset map displays the spatial location of the study area (●) within Nunavut, Canada.

other ducks. Here they are grouped with other ducks as I expected similar responses to Peregrine Falcon nests.

Habitat rasters were retained from Chapter 2, as it was necessary to control for habitat, in particular terrain ruggedness, while estimating responses to Peregrine Falcon nests.

Model selection for the density surface modelling (DSM) component of the analyses proceeded in two stages.

In stage one, all models included ruggedness and freshwater, as well as year, period, and their interaction as factors. I compared models containing NDVI to models containing NDWI, and models containing elevation to those containing distance from coast. Candidate models for geese included freshwater x period and freshwater x year terms, and for songbirds and shorebirds elevation x period and distance from coast x period. I compared habitat-only models for each group by AICc and selected the model with the lowest score. In the case of nested models with $\Delta$AICc $<2$, I selected the simplest model.

Having selected the best-fitting habitat model, I proceeded to stage two and compared three candidate models for the effect of distance to Peregrine Falcon nests: 1) the best fitting habitat model without any Peregrine Falcon related covariates; 2) a model including the effect of distance to the nearest occupied Peregrine Falcon nest; 3) a model allowing the effect of Peregrine Falcons to vary between early and late summer. Models compared during the second stage are displayed in Table 3.1. Distance to Peregrine Falcon nest terms were parameterized as penalized thin plate regression splines, with maximum five degrees of freedom to avoid overfitting. As in Chapter 2, depending on model diagnostics I modelled segment counts with either negative binomial or Tweedie response distributions. Models to be compared by AICc were fit using maximum likelihood, and best-fitting models were refit using restricted maximum likelihood prior to presentation and interpretation (Zuur et al. 2009). I ensured good visual fit of models using standard diagnostic plots, including

Table 3.1: AICc comparisons of candidate models for songbird, shorebird, Arctic ground squirrel (*Urocitellus parryii*), goose and duck abundances. Models including distance to Peregrine Falcon (*Falco peregrinus*) nest terms are compared to best fitting habitat-only models from the first stage of model selection. All models also contained an effect of year, period, and their interaction. The songbird and Arctic ground squirrel models contained random effects for transect and transect visit, while shorebird, duck, and goose models contained a random effect for transect. s() indicates the term was parameterized as a spline. NDVI (normalized difference vegetation index), NDWI (normalized difference water index), PEFA (distance to nearest Peregrine Falcon nest)

| | **Formula** | **AICc** | **$\Delta$AICc** |
|---|---|---|---|
| **Songbird** | Ruggedness + NDVI + Freshwater + Coast + Coast x Period + s(PEFA) | 4424.60 | 0 |
| | Ruggedness + NDWI + Freshwater + Coast + Coast x Period + s(PEFA) | 4425.13 | 0.53 |
| | Ruggedness + NDVI + Freshwater + Coast + Coast x Period + s(PEFA) x Period | 4425.29 | 0.69 |
| | Ruggedness + NDWI + Freshwater + Coast + Coast x Period + s(PEFA) x Period | 4425.78 | 1.18 |
| | Ruggedness + NDWI + Freshwater + Coast + Coast x Period | 4430.88 | 6.28 |
| | Ruggedness + NDVI + Freshwater + Coast + Coast x Period | 4430.92 | 6.32 |
| **Shorebird** | Ruggedness + NDWI + Freshwater + Elevation + s(PEFA) | 2100.64 | 0 |
| | Ruggedness + NDWI + Freshwater + Elevation | 2100.89 | 0.25 |
| | Ruggedness + NDWI + Freshwater + Elevation + s(PEFA) x Period | 2101.55 | 0.91 |
| **Arctic ground squirrel** | Ruggedness + NDWI + Freshwater + Elevation | 1938.11 | 0 |
| | Ruggedness + NDWI + Freshwater + Elevation + s(PEFA) x Period | 1938.80 | 0.69 |
| | Ruggedness + NDWI + Freshwater + Elevation + s(PEFA) | 1938.96 | 0.85 |
| **Duck** | Ruggedness + NDVI + Freshwater + Elevation + s(PEFA) x Period | 1654.26 | 0 |
| | Ruggedness + NDVI + Freshwater + Elevation | 1661.55 | 7.29 |
| | Ruggedness + NDVI + Freshwater + Elevation + s(PEFA) | 1663.1 | 8.84 |
| **Goose** | Ruggedness + NDVI + Freshwater+ Freshwater x Period + Elevation + s(PEFA) x Period | 2006.8 | 0 |
| | Ruggedness + NDVI + Freshwater + Freshwater x Period + Elevation + s(PEFA) | 2016.09 | 9.29 |
| | Ruggedness + NDVI + Freshwater + Freshwater x Period + Elevation | 2028.18 | 21.38 |

quantile-quantile plots and plots of randomized quantile residuals (Dunn and Smyth 1996).

## 3.3 Results

### 3.3.1 Detection functions

The best fitting detection function for songbirds included a negative effect of distance to Peregrine Falcon nest, however 95% confidence intervals (CI) for the term overlapped zero, and the model was separated from an otherwise identical model without the effect of distance to Peregrine Falcon nest by $\Delta$AICc <2, indicating the term did not substantially improve model fit. Choosing the model without distance to Peregrine Falcon nest did not meaningfully alter subsequent DSM results for songbirds. Songbirds were less detectable in rugged terrain (ruggedness: -0.10, 95% CI: -0.15, -0.05) and later in summer (day of year: -0.06, 95% CI: -0.11, -0.01). Probability of songbird detection within 110-m of the transect line (truncation distance) was 0.56 (95% CI: 0.54, 0.59). Best-fitting detection functions for shorebirds, Arctic ground squirrels, ducks and geese did not include distance to Peregrine Falcon nest. Thus, detection functions for shorebirds, Arctic ground squirrels and geese were those previously reported in Chapter 2. Duck detection was best described by a uniform key function without detection covariates, and detection probability within 270-m of the transect line (truncation distance) was 0.62 (95% CI: 0.55, 0.68).

### 3.3.2 Density surface models

For shorebirds and Arctic ground squirrels, DSMs including distance to Peregrine Falcon nest did not improve model fit over the best fitting habitat-only model (Table 3.1), and as modelling results for these species are already reported in Chapter 2 I do not reproduce them here. I note however that for shorebirds, in the model including the effect of distance to Peregrine Falcon nest pooled across the entire summer, the effect was directionally positive, though the 95% CI for the smooth overlapped zero.

For songbirds, inclusion of distance to Peregrine Falcon nest improved DSM fit (Table 3.1), and the effect was positive, indicating songbird abundance was lower in the vicinity of falcon nests (Figure 3.2). However, allowing the effect of distance to Peregrine Falcon nest to vary between early and late summer did not provide any additional improvement in model fit, indicating songbird distribution in late summer was not different compared to early summer. Songbirds were also more abundant in areas with rugged terrain, low freshwater, and were also more abundant near the coast later in summer (Table 3.2).

For geese, DSM fit was improved with the addition of distance to Peregrine Falcon nest, but in this case the best-fitting model allowed the effect to vary between early and late summer (Table 3.1). Although the effect of distance to Peregrine Falcon nest in early summer was negligible, in late summer goose abundance was lower near Peregrine Falcon nests (Figure 3.2). Coefficients for other terms in the best-fitting goose model were near identical to those reported in Chapter 2.

For ducks early season abundance was negligibly affected by distance to Peregrine Falcon nests, but abundance was higher near Peregrine Falcon nests in late summer (Figure 3.2). Duck abundance was also negatively related to NDVI, positively related to freshwater and negatively related to elevation (Table 3.2).

## 3.4 Discussion

I investigated the effect of distance to Peregrine Falcon nests on avian and mammalian prey distribution in an Arctic study area, and found taxon-specific responses. For songbirds, which are vulnerable to Peregrine Falcon predation as juveniles and adults, abundance was lower near Peregrine Falcon nests throughout the sampling period. I argue that this was due, at least in part, to avoidance of areas near Peregrine Falcon nests by prospective breeders upon arrival in the study area. Although songbird breeding phenology was not intensively studied, juvenile songbirds were first observed on surveys in early July, placing nest initiation in early to mid-June given

Table 3.2: Model results for avian groups surveyed at Rankin Inlet, Nunavut, Canada from 2015-17. Included information is the response distribution used in the modelling, proportion deviance explained, number of transect segments (N), and number of non-zero counts (N >0). Summary information for model terms is also included for each model, separated into fixed and random effects. For parametric fixed effects, coefficient estimates are reported, along with their 95% confidence intervals (in parentheses). For smooth terms s() I report the estimated degrees of freedom of the smooth and the associated *p*-value (in parentheses). Random effects are noted with an RE. For songbirds there were multiple competitive models (Songbird1 and Songbird2). Fixed effects with 95% confidence intervals not overlapping zero are bolded. NDVI (normalized difference vegetation index), NDWI (normalized difference water index), PEFA (distance to nearest Peregrine Falcon *Falco peregrinus* nest)

| | **Songbird1** | **Songbird2** | **Duck** | **Goose** |
|---|---|---|---|---|
| **Intercept** | -10.63 (-10.89, -10.38) | -10.64 (-10.89, -10.38) | -13.37 (-14.01, -12.73) | -11.84 (-12.29, -11.39) |
| **Ruggedness** | **0.27 (0.16, 0.38)** | **0.28 (0.17, 0.39)** | -0.09 (-0.36, 0.19) | **0.29 (0.04, 0.53)** |
| **NDVI** | 0.02 (-0.10, 0.14) | | **-0.70 (-0.97, -0.43)** | 0.13 (-0.13, 0.39) |
| **NDWI** | | 0.04 (-0.07, 0.16) | | |
| **Freshwater** | -0.10 (-0.19, 0.00) | **-0.10 (-0.20, -0.01)** | **0.28 (0.01, 0.54)** | 0.22 (-0.01, 0.45) |
| **Freshwater:late summer** | | | | **0.40 (0.08, 0.72)** |
| **Elevation** | | | -0.35 (-0.71, 0.01) | **-0.62 (-0.91, -0.33)** |
| **Coast** | 0.08 (-0.09, 0.24) | 0.07 (-0.09, 0.23) | | |
| **Coast:late summer** | **-0.21 (-0.39, -0.02)** | **-0.21 (-0.39, -0.02)** | | |
| **2016** | 0.15 (-0.19, 0.50) | 0.16 (-0.19, 0.50) | 0.33 (-0.50, 1.15) | -0.18 (-0.79, 0.43) |
| **2017** | 0.10 (-0.24, 0.44) | 0.10 (-0.24, 0.44) | 0.02 (-0.81, 0.85) | -0.23 (-0.84, 0.37) |
| **Late summer** | **-0.46 (-0.83, -0.09)** | **-0.46 (-0.83, -0.09)** | -0.49 (-1.34, 0.36) | **-2.42 (-3.36, -1.49)** |
| **2016:late summer** | -0.14 (-0.64, 0.35) | -0.15 (-0.65, 0.35) | -0.46 (-1.43, 0.52) | **1.67 (0.57, 2.76)** |
| **2017:late summer** | **0.54 (0.06, 1.02)** | **0.54 (0.06, 1.02)** | **-1.42 (-2.52, -0.33)** | 0.73 (-0.44, 1.90) |
| **s(PEFA)** | **1.83 (<0.001)** | **1.82 (<0.001)** | | |
| **s(PEFA):early summer** | | | 1.00 (0.29) | 1.00 (0.10) |
| **s(PEFA):late summer** | | | **1.00 (<0.001)** | **1.71 (<0.001)** |
| **s(Transect visit) RE** | 108.70 (<0.001) | 110.15 (<0.001) | | |
| **s(Transect) RE** | 28.08 (0.13) | 26.18 (0.16) | 72.67 (<0.001) | 67.37 (<0.001) |
| **Distribution** | Negative binomial | Negative binomial | Tweedie | Tweedie |
| **N** | 1784 | 1784 | 1015 | 1015 |
| **N >0** | 685 | 685 | 128 | 177 |
| **Deviance explained** | 0.25 | 0.25 | 0.57 | 0.46 |

typical incubation and brooding periods (Beason 1995; Hendricks and Verbeek 2012; Hussell and Montgomerie 2002; Wheelwright and Rising 2008). Because Peregrine Falcons typically arrive in the study area in mid-May (Court et al. 1988), ahead of most songbird species, adult songbirds were potentially able to account for the spatial distribution of Peregrine Falcons in selecting nest sites. While I cannot fully reject the possibility that songbirds which settled near Peregrine Falcon nests were consumed before prey surveys were conducted, I did not find evidence for a stronger response to Peregrine Falcon nests by songbirds in late summer, which would have resulted from falcons depleting the songbird population around their nest (Norrdahl and Korpimaki 1998), especially as their foraging requirements rapidly increased during brood rearing. Remote nest camera data (see Chapter 4) indicated that small birds (songbirds, shorebirds) were the most common prey items consumed during the brood rearing period for Peregrine Falcons, so one might have expected some signal of consumption in my results. In the candidate model for songbird abundance that allowed the effect of Peregrine Falcon nests to vary between early and late summer, the response was slightly stronger in late summer (not shown), but this did not improve model fit relative to the model with a pooled effect (Table 3.1). Perhaps this represents a minor effect of consumption, but it is also possible that spatial patterns of prey consumption may be more complex than simply declining with distance from a nest.

Chapter 2 noted potential violation of 100% detection on the transect line (Bachler and Liechti 2007), caused by temporal variation in songbird singing behaviour. Extended to the present study, songbirds may have sung less frequently in the vicinity of Peregrine Falcon nests, thus making them less “available” for detection, and depressing counts. Thus, I may have estimated a singing effect, rather than predator avoidance or consumption. However, Lima (2009) pointed out conflicting evidence on the nature of singing behaviour in the presence of predators, and furthermore, such studies are usually conducted with predators in close proximity to the subject (*e.g.*, Akçay et al. 2016; Duncan and Bednekoff 2006; Mougeot and Bretagnolle 2000), and therefore effects are found at small scales relative to the effects found in my study. I also included distance to the nearest Peregrine Falcon nest in candidate detection functions, but they offered no improvement in model fit for any of the groups modelled here.

Compared to songbirds and shorebirds, adult ducks, adult geese and adult Arctic ground squirrels are uncommon prey items for Peregrine Falcons in my study area, while predation on juveniles is common. Thus, I expected any effect of Peregrine Falcons to manifest in late summer after hatch or juvenile emergence. Accordingly, I found decreased goose abundance near Peregrine Falcon nests, but only in late summer (Figure 3.2). Ultimately, the degree to which this was caused by avoidance or consumption is unknown. Remote camera data indicated goslings were present in Peregrine Falcon diet, especially in late brood rearing, thus the effect found could be consumptive, but geese nesting near to Peregrine Falcons would also have incentive to move their broods away from falcons post-hatch. It could be argued that geese should simply avoid Peregrine Falcons during nest site selection, rather than move their broods post-hatch, but goose nests are also at risk from terrestrial predators such as Arctic foxes (*Vulpes lagopus*) and wolverines (*Gulo gulo*), which may constrain the availability of suitable nesting sites and necessitate, or incentivize, nesting near raptors. Canada Geese (*Branta canadensis*) frequently co-occupy cliffs with Peregrine Falcons in my study area (*pers. obs.*), and previous study has highlighted protective nesting associations (Bêty et al. 2001; Kleef et al. 2007; Quinn and Kokorev 2002). Nevertheless I did not expect to find evidence of this potential relationship because surveys were relatively sparse at the small spatial scales at which nesting associations are typically found.

Unexpectedly, results for ducks were opposite to those of geese: abundance was higher near Peregrine Falcon nests in late summer. Unlike geese, which are herbivorous and must forage on land, the majority of ducks sighted on surveys forage in marine

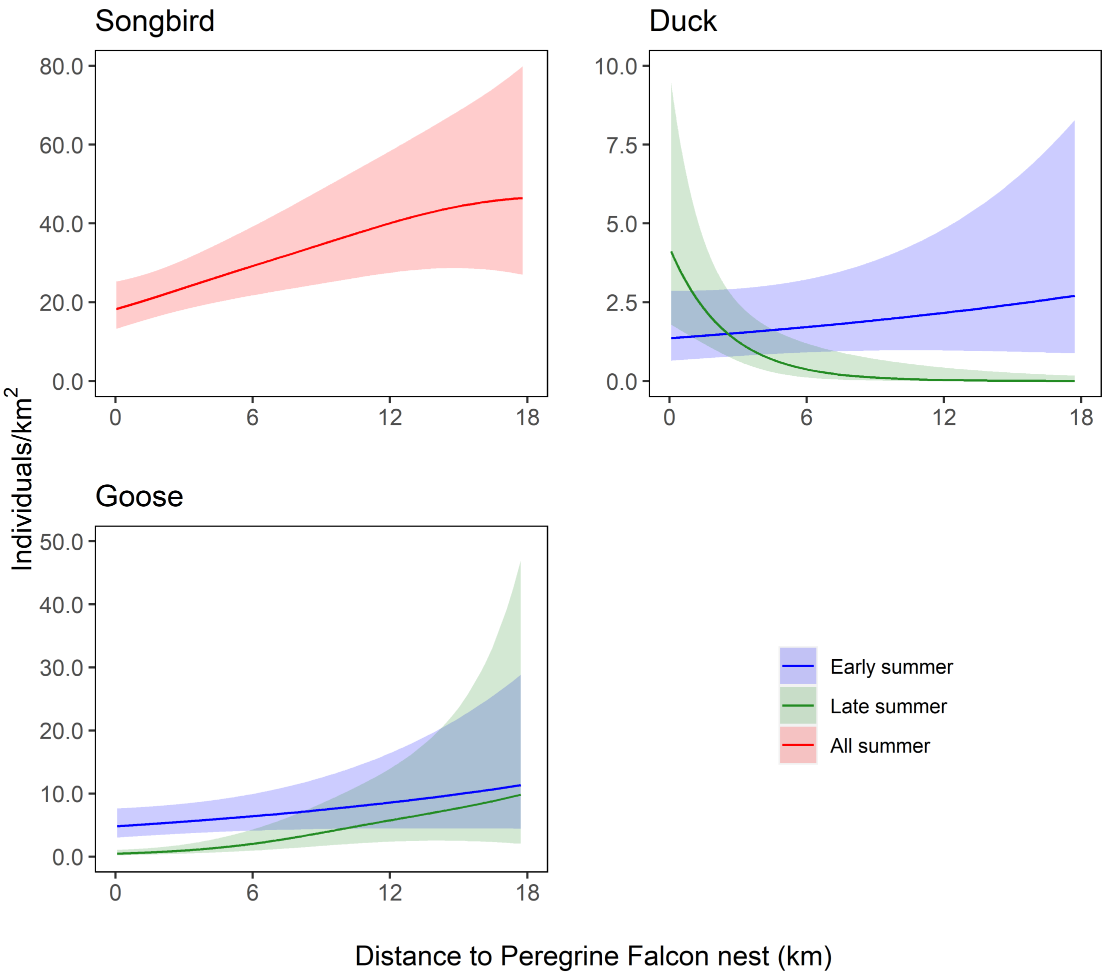


Figure 3.2: Effect of distance to Peregrine Falcon nest on songbird, duck and goose abundance. Predictions are shown for the reference year (2015), and other covariates were held to their means. Survey data collected during the summers of 2015-17 at Rankin Inlet, Nunavut, Canada. Blue indicates a given estimate is specific to early summer, green is specific to late summer, and red indicates the effect is pooled across the entire summer. For songbirds there were multiple competitive models including the effect of distance to Peregrine Falcons, however the effect was near identical in either case, thus one model is presented for brevity.

or aquatic habitats (*e.g.,* Common Eiders *Somateria mollissima*, Long-tailed Ducks *Clangula hyemalis*). Ducks commonly flee to open water when pursued by falcons or dive to evade attacks (Dekker 1987). This measure of protection afforded by water may allow ducks to frequent areas near Peregrine Falcons at limited risk, in contrast to geese which must spend time foraging on land. While this may explain why ducks would be less likely to avoid areas near Peregrine Falcon nests, it does not explain why they would preferentially select such areas. I suggest this may be due to similar habitat selection between Common Eiders and Peregrine Falcons, which are both commonly associated with offshore islands in my study area. The late summer sampling period occurred entirely after sea ice break-up, which coincides with Common Eider arrival and breeding (Freeman 1970; Schamel 1977), likely leading to more duck detections near Peregrine Falcon nests in late summer.

Peregrine Falcons in my study area consume unusually large numbers of mammalian prey, including Arctic ground squirrels (Bradley and Oliphant 1991), but I did not find an effect of Peregrine Falcon nests on ground squirrel distribution. As year-round residents of the study area with limited dispersal ability (Byrom and Krebs 1999), Arctic ground squirrels are less able to spatially avoid Peregrine Falcons compared to avian prey, thus, I expected any effects found would be due to consumption. Ground squirrels were more abundant in low elevation, coastal areas (Chapter 2), coinciding with areas of high Peregrine Falcon density (Figure 2.1). Juvenile emergence in these areas in early July may offset individuals lost to falcon predation, thus I did not find evidence of consumption in squirrel distribution. Additionally, a mammalian prey such as an Arctic ground squirrel may face stronger predation risk from non-falcon sources in this study area, for example Rough-legged Hawks (*Buteo lagopus*), which can be very abundant in the study area in some years. Additional predator species complicate the task of modelling landscapes of fear or consumption, and future study could potentially contrast the effects of distance to predator breeding locations of various types (*e.g.,* other raptor nests, fox dens, etc.).

Peregrine Falcons have been studied at Rankin Inlet for more than three decades, meaning knowledge of possible nesting locations is strong. Additionally, multiple visits to historical nest sites were conducted in the spring of each year of study, improving detection probability (Franke et al. 2020). Still, the possibility for undetected nests in the study area cannot be ignored, and could in theory have bearing on the results presented here. Undetected nests would on average lead to an inflation of the distance from each distance sampling survey to the nearest Peregrine Falcon nest in our study. However, the effect of this inflation with respect to songbirds and geese, for which abundance was lower near Peregrine Falcon nests, would be to make results more conservative, as it would mean that survey sites near undetected nest sites, which would have on average low abundance, would be assigned distances to nest sites that were too large. The reverse would be true for ducks, for which abundance was lower near Peregrine Falcon nests. For shorebirds and Arctic ground squirrels this could mean that I did not find an effect of distance to Peregrine Falcons when in fact there was. Overall however, it seems unlikely given the detailed nature of nest occupancy surveys that there were substantial numbers of undetected nests in any year of this study, and therefore any effect on results was likely minimal.

In summary, perception of predation risk can manifest itself spatially as a landscape of fear, which can influence prey distribution, behaviour, physiology, and ultimately fitness. My study indicates songbird abundance was reduced near the nest sites of an avian top predator, the Peregrine Falcon, and I argue that this was likely due to avoidance, rather than consumption. For geese, abundance was only reduced near Peregrine Falcon nests in late summer, after goslings, the age class most at risk of predation, entered the population. I believe these patterns are likely present in other Arctic study areas where breeding falcons are present, and future study should focus on integrating spatial data from additional predators (*e.g.,* Arctic foxes), to better understand the entire suite of risks faced by prey throughout the breeding season.

# Chapter 4

# The multispecies functional response of Arctic Peregrine Falcons (*Falco peregrinus*)

## 4.1 Introduction

The ability of predators to secure adequate quantities of prey for their offspring is key to their reproductive success, but they reside in landscapes where prey abundance is often patchy. For predators consuming multiple prey species, patchiness in prey abundance occurs along multiple dimensions, where low abundance of one prey species at a location may be compensated by greater abundance of another. Spatial heterogeneity in the prey community may, of necessity, drive individual diet specialization (Bolnick et al. 2003), potentially allowing individuals to secure adequate resources regardless of spatial location. Despite the importance of accounting for multiple prey types in studies of predator-prey interactions, simultaneously monitoring multiple prey, their individual consumption rates, in addition to a predator, is logistically difficult, and presents a barrier for understanding complex natural systems.

Species subjected to a common predator can exist in indirect relationship to one another, mediated by the response of the predator to their shared abundance. Apparent competition occurs when the consumption of one prey increases in response to an increase in the abundance of a second prey (Holt 1977). Conversely, apparent mutualism exists when the consumption of one prey declines in response to the increase in abundance of a second prey (Abrams and Matsuda 1996). The effect of indirect relationships on a given prey species can be pronounced (see DeCesare et al. 2010), thus accounting for alternative prey has implications for the dynamics of prey populations. The nature of indirect relationships between prey is determined by the numerical response (change in population size) and functional response (change in per capita consumption rates) of the predator to changes in prey abundance. The latter is the focus of the current study.

The functional response is a key component of predator-prey interactions, and its precise form is thought to contribute to the stability of prey populations (Oaten and Murdoch 1975; van Baalen et al. 2001). Beginning with early work by Holling (1959b), an enormous body of theoretical and empirical work on functional responses developed over the following decades (much of it reviewed in Jeschke et al. 2002). Holling's original descriptions included function types I, II and III. In a type I functional response, prey consumption is a positive linear function of prey abundance, which in some descriptions becomes instantly saturated at a particular prey abundance >0. Organisms with type I responses are not limited by the time required to handle and consume prey items. In contrast, a type II functional response describes a predator in which consumption saturates gradually with increasing prey abundance as a result of the time required for a predator to handle and consume prey items (*i.e.,* at high prey abundance, handling time limits further increases in consumption). A type III response is sigmoidal in shape, where consumption increases disproportionately at low prey abundance before saturating at high prey abundance. Behavioural mechanisms involving learning (*e.g.* search image or "niche" formation, Royama 1970; Tinbergen 1960) or prey switching in generalist predators (Murdoch 1969) have previously been proposed to explain the existence of such functional responses. Real (1977) unified these functional response types under a single framework with the following modification of Holling's disc equation:

$$\lambda = \frac{\alpha N^m}{1 + \alpha h N^m} \tag{1}$$

where $\lambda$ is the number of prey items consumed by an average predator, $\alpha$ is the attack rate, $N$ is the number of prey available, $h$ is the time it takes to handle one prey item, and $m$ is the shape parameter, where $m$ >1 generates the sigmoidal type III functional response.

This functional response has been generalized to the case of multiple prey items (Asseburg 2006; Koen-Alonso 2006):

$$\lambda_j = \frac{\alpha_j N_j^{m_j}}{1 + \sum_{k=1}^{s} \alpha_k h_k N_k^{m_k}} \tag{2}$$

where $s$ is the number of prey types and parameters are now prey-specific. The functional response to a given prey species is now dependent not only on the abundance of that prey, but also on the abundance of the $s$ - 1 alternative prey. This multispecies functional response (MSFR) model has been used in several recent studies (Baudrot et al. 2016; Critchley 2018; Smith and Smith 2020; Smout et al. 2010, 2013), presenting an effective approach to characterizing the functional responses of generalist predators. I utilize this model in describing the functional response of an Arctic top predator, the Peregrine Falcon (*Falco peregrinus*).

The Peregrine Falcon is a diurnal raptor found nearly worldwide. In the Arctic, they are generally characterized as consumers of insectivorous birds (Dawson et al. 2011; Robinson et al. 2018), however may consume substantial numbers of mammalian prey as well (Bradley and Oliphant 1991). Their ability to consume multiple prey types, in addition to central place foraging, which allows efficient monitoring of nestling diet, make Arctic peregrines an ideal species in which to investigate MSFRs. I sampled peregrine diet over three breeding seasons using remote cameras placed at nests, and conducted concurrent distance sampling surveys, burrow counts, and microtine rodent trapping to estimate the abundance of various prey types. I utilized a flexible Bayesian framework for modelling peregrine functional response, allowing for the incorporation of measurement error (prey abundance estimates, unknown prey items). The framework also allowed functional response parameters to vary according to the number and age of nestlings at the start of each day, and I generally expected more and older nestlings (representing increased demand for food) to increase the number of prey items delivered (Steen et al. 2012), either through higher attack rates, or lower handling times. The modelling of functional responses given varying levels of alternative prey is particularly important in an Arctic context given ongoing changes in climate (Meredith et al. 2019) that may result in species range alterations (Baltensperger and Huettmann 2015; Prost et al. 2013) and altered prey community composition.

My goals were: 1) to model the functional response of Arctic Peregrine Falcons in relation to the abundances of five food types, including supplemented domestic quail from a concurrent experiment, and, 2) determine the capacity for breeding pairs to provision offspring across the range of prey abundances around nests. Secondarily, the MSFR allowed for the comparison of consumption of a given prey type across a range of alternative prey densities, potentially providing insight into indirect relationships among prey. Variation in microtine rodent abundance across years influences the consumption rate of alternative prey by predators (Bêty et al. 2001; Hellstrom et al. 2014; McKinnon et al. 2014), and so I predicted that increases in abundance of microtine rodents would lead to decreased consumption rates of other prey types. I similarly predicted consumption of natural prey to be reduced at supplemented nests. In this study I highlight a dataset and approach that allows exploration of a complex predator-prey system, providing insight into the foraging behaviour of a widespread raptor, and shedding light on potential relationships between prey items.

## 4.2 Methods

### 4.2.1 Prey density

Data collection for estimating prey density in this study area are given in detail in Chapter 2. Briefly, I collected distance sampling data from 2015-17 using a collection of 225 line transects to which I made a total of 498 visits. I analyzed the data using density surface modelling (DSM; Miller et al. 2013), a two-stage method in which a detection function is first fit to data, followed by spatial modelling of abundance. Six habitat covariates (elevation, distance from coast, terrain ruggedness, normalized difference vegetation index, normalized difference water index, and freshwater), as well as distance to occupied Peregrine Falcon nests, year and sampling period (before or after July 11) were combined in candidate models, and the best-fitting models were selected by AICc. The best-fitting DSMs for the main prey types of Peregrine Falcons (songbirds, shorebirds, ducks, geese, and Arctic ground squirrels *Urocitellus parryii*) in my study area were used to calculate prey density within falcon pseudo-home ranges (see subsequent description). If there were multiple competitive models for a given prey type, predicted abundances from each model were averaged, and the unconditional standard error of prediction was calculated (Anderson 2007; Buckland et al. 1997), assuming equal model weights. Example distribution maps for prey can be seen in Figure B.1 in Appendix B.

Microtine rodent habitat associations were estimated across years using burrow counts conducted concurrently with distance sampling (Chapter 2). I also trapped microtine rodents using Museum Special snap traps to estimate an index of annual abundance. Three traps were placed at each of 20 stations spaced 15-m apart along five 300-m transects in two locations spaced several kilometers apart. Trap lines covered a mix of wet and dry habitat. Snap trapping results can be seen in Figure B.2 in Appendix B. Essentially, 2015 was a low year for microtine rodent abundance, while in 2016 and to a slightly lesser degree in 2017, abundance was high. Predicted burrow counts within falcon pseudo-home ranges were calculated as for other prey items, which was then multiplied by the trapping index in each year. This assumes that annual changes in microtine abundance were uniform throughout the study area.

To construct Peregrine Falcon pseudo-home ranges I simulated 1000 point locations using bivariate normal distributions (for $x$ and $y$ coordinates) centred on each nest site. Movement and home range data for this species is relatively sparse in the Arctic, but I endeavoured to construct home ranges that matched characteristics seen in previous study. The standard deviation of each coordinate distribution was set to 3500-m, which, when combined, led to point locations a maximum of 15-km from the nest site. This is somewhat smaller than the maximum distances seen in previous study (Sokolov et al. 2014; Tétreault 2019), however increasing this distance led to home range sizes that were well beyond the normal range of variation captured by previous study (20 - 260-km$^2$; Sokolov et al. 2014; Tétreault 2019), and it is not clear given the overall lack of data, whether such maximum distances represent outliers. Limited movement data from this study area indicated that falcon home ranges were concentrated over land (Tétreault 2019), even for birds nesting on islands several kilometers out to sea (*i.e.,* island-nesting birds commuted to the mainland regularly). To replicate this in pseudo-home ranges, I removed points located over water before calculating the 95% utilization distribution via a kernel density estimator (package adehabitatHR; Calenge 2006). Before calculating the utilization distribution, I simulated an equal number of points at the nest site, reflecting the fact that one adult bird (generally the female, as in many other raptors; Slagsvold and Sonerud 2007) is present at the nest site for much of the brooding period. The resulting home ranges were within the natural size variation seen in previous study and reflected increased use of terrestrial habitat. Furthermore, the MSFR model presented in this chapter using the above pseudo-home ranges had superior out-of-sample predictive accuracy to an equivalent model using circular 5-km pseudo-home ranges centred on each nest site, as measured by the Widely Applicable

Information Criterion (WAIC).

### 4.2.2 Peregrine Falcon diet

Motion-activated remote cameras (PC80, PC800, HC600; Reconyx Inc., Holmen, WI) were placed within 2-m of Peregrine Falcon nests from 2015-17 as part of ongoing monitoring of the Rankin Inlet population. Cameras were in place from the beginning of incubation in early June through mid August when young approached fledging age, barring nest failure at an earlier date. Cameras were set with medium to high sensitivity and took 1-5 pictures per trigger, with a quiet period (period after motion activation where the camera could not be re-triggered) of 0-30 seconds. Some variation in camera settings occurred to account for nest-specific conditions (*e.g.,* when cameras were placed particularly close to the nest, thus causing extremely frequent motion activation), which would otherwise have caused batteries to drain or memory cards to fill before subsequent nest visits. Nests were visited approximately every five days during the brood rearing period to replace camera batteries and memory cards, and to count and weigh nestlings.

During visits, supplemental food (frozen domestic quail) was also delivered to 10 randomly-selected nests in each year. Nestlings in the treatment group were provided domestic quail (*Coturnix coturnix*) at 5-day intervals in an amount corresponding to that required to suppress begging behaviour in captive nestlings of the same age (Hedlin 2015, L. Oliphant, *pers. comm., see*). The purpose of the supplementation experiment was to investigate food limitation within the peregrine population, and possible interactions between food limitation and annual weather conditions. For the purposes of the current study, the food supplementation experiment allowed us to test how the functional response of peregrines to their various prey might change given a large influx of readily available alternative food. The number of quail given was recorded during each nest visit or estimated in hindsight based on chick energetic requirements and available camera data. Because the maximum amount of quail ever given during a nest visit was 11, quail consumption had a large impact on the amount of quail available on subsequent days. For days following a supplementation visit, I calculated the number of quail available as the number available on the previous day minus the amount of quail eaten the previous day. Where this number was not available, I estimated the amount of quail eaten based on the number of deliveries observed and the average proportion eaten (see below) for quail across all nests. When this number was impossibly large based on the age of the nestlings, I substituted an approximate value for meal size according to the following equation:

$$\mu_{max} = \frac{170 \cdot c}{1 + e^{-0.3 \cdot (14-d)}} \tag{3}$$

Where $c$ is the number of nestlings in the nest and $d$ is the age of the eldest nestling. Essentially, this equation represents a logistic growth curve for nestling eating capacity which saturates at 170-g multiplied by the number of nestlings present, with an inflection point at age 14, which compares favourably with previously constructed nestling growth curves for this population (Hedlin 2015). The equation assumed that Peregrine nestlings had very small eating capacity during the first few days of life (Weaver and Cade 1991), but that eating capacity increased rapidly before saturating near adult eating capacity (I assumed this occurred as nestlings approached adult mass). Maximum adult eating capacity was assumed to be 170-g based on available literature (Barton 1992; Burnham et al. 2012).

Table 4.1: Frequency of deliveries of different prey types in the diets of Peregrine Falcons (*Falco peregrinus*) nestlings at Rankin Inlet, Nunavut, Canada from 2015-17. Frequencies are shown for nests receiving and not receiving supplemental food (frozen domestic quail, see text for description of protocol), with the sample size of nests indicated for each treatment group. Also shown is the mass distribution used in the calculation of nestling caloric intake (in grams). $N$: normal distribution(mean, standard deviation). Arctic ground squirrels (*Urocitellus parryii*).

| | **Unsupplemented (47 nests)** | | **Supplemented (34 nests)** | | | | |
|---|---|---|---|---|---|---|---|
| **Prey type** | **N** | **%** | **N** | **%** | **Mass dist.** | **Rationale** | **References** |
| **Arctic ground squirrel** | 862 | 14.31 | 538 | 11.90 | $N(350, 50)$ | juveniles <2 weeks of age | Kiell and Millar 1978; Poole 1987 |
| **Microtine** | 397 | 6.60 | 294 | 6.00 | $N(40, 4)$ | mean of species in study area | Legagneux et al. 2012 |
| **Other** | 75 | 1.25 | 54 | 1.10 | aggregate of squirrels, quail and waterfowl | most items were large | |
| **Quail** | 0 | 0 | 806 | 16.44 | $N(170, 10)$ | mean of provided quail | |
| **Small bird** | 2786 | 46.25 | 2083 | 42.48 | $N(30, 3)$ | mean of species in study area | various in Billerman et al. 2020 |
| **Unknown** | 1219 | 20.24 | 720 | 14.68 | | | |
| **Waterfowl** | 685 | 11.37 | 363 | 7.40 | $N(150, 25)$ | juveniles <2 weeks of age | Hollmén et al. 1999; Sedinger 1986 |

Nest photographs were used to extract phenological data (*i.e.,* lay dates, hatch dates, mortality dates), causes of mortality, adult identification (via unique alphanumeric bands) and feeding events. All feeding events observed on camera during the brood rearing period were recorded, identifying prey items to the lowest taxonomic level possible, as well as recording the number of nestlings present during feeding. Large prey items (*e.g.*, Arctic ground squirrels, waterfowl) were typically consumed over multiple feeding events, and thus it was necessary to estimate the proportion of the prey item consumed at each delivery (to the nearest 1/8th of a prey item). Items that could not be identified were classed as unknown. In total, I recorded nearly 11,000 prey deliveries from 81 individual nesting attempts with a camera present across my three years of study. In my analysis, I grouped prey into seven categories that were the most readily differentiable: small birds (including songbirds and shorebirds), waterfowl (mainly Canada Geese *Branta canadensis* and Common Eiders *Somateria mollissima*), Arctic ground squirrels, microtine rodents (collared lemmings *Dicrostonyx groenlandicus* and red-backed voles *Clethrionomys rutilus*), quail, unknown, and other, which included an assortment of rarely predated species such as Herring Gulls *Larus argentatus*, Black Guillemots *Cepphus grylle*, Arctic hares *Lepus arcticus*, Short-eared Owl *Asio flammeus*, and instances of cannibalism. As the "other" group was an aggregate of many species, their abundance was assumed to be constant across nests during analysis.

Temporal gaps in the camera dataset due to battery failures, camera shift, or nestlings moving out of the field of view were identified using the time stamps of photos, and failure was defined as gaps of 1 hour or more. I subtracted these gaps from a full 24-hour sampling period to create an offset term (see below) that accounted for variation in camera operation. Furthermore, I limited the dataset to days with at least 6 hours of camera monitoring to facilitate the calculation of consumption rates.

### 4.2.3 Multispecies functional response

I adopted a fully Bayesian approach using the modelling language Stan by way of the rethinking package (McElreath 2020a) and cmdstanr (Gabry and Cešnovar 2020) in R (R Core Team 2020). I assumed that the functional response of adult Peregrine Falcons on behalf of nestlings was reflected in the number of deliveries of each prey type to nests. The MSFR took the form described by (Smout et al. 2013), with some modifications to account for specific sources of uncertainty in the data:

$$P_{ji} \sim Poisson(\lambda_{jin})$$

$$\lambda_j = \frac{\alpha_j N_{jn}^{m_j+1}}{1+\sum_{k=1}^{s} \alpha_k h_k N_{kn}^{m_k+1}} \cdot o_{in} \cdot p_j \tag{4}$$

Where counts of prey deliveries $P_{ji}$ were assumed to be Poisson distributed with mean $\lambda_j$ (expected number of deliveries of prey $j$). For small birds, Arctic ground squirrels, and waterfowl, post-hoc model checking revealed that a Poisson distribution was unable to account for the number of zeros in the data. Deliveries for these prey types were therefore fit according to a zero-inflated Poisson distribution, with the zero-inflation factor assumed Bernoulli-distributed and modelled with an intercept specific to each prey type. $o_{in}$ was an offset term accounting for the time the camera at a nest was operating in a given day, and $N_{jn}$ was the abundance of prey type $j$ at nest $n$. $\alpha_j$, $h_j$ and $m_j + 1$ were the functional response parameters for the $j$th prey type (the attack rate, handling time and shape parameter, respectively). I added 1 to the shape parameter to ensure that, given a positively constrained $m_j$, the shape exponent would have a minimum value of 1 (values <1 imply consumption declines with increasing prey abundance, which was biologically implausible for this system). The denominator of the function accounts for the abundance of all $s$ prey types. $p_j$ were prey specific parameters estimated during model fitting corresponding to the proportion of prey items that were identified (1 - $p_j$ is thus the proportion of unidentified items of each prey type; Smout et al. 2013). The count of unknown items on each day was modelled as the sum of the unidentified items of each type (*i.e.,* replacing $p_j$ with (1 - $p_j$) in the equation for $\lambda_{jin}$).

I allowed the functional response parameter $\alpha_j$ (attack rate) to vary according to the following log-linear model:

$$log(\alpha_j) = \beta_{0j} + \beta_{1j} \cdot c_{in} + \beta_{2j} \cdot d_{in} + z_{jn} \tag{5}$$

where $\beta_{0j}$ are intercept terms and $\beta_{1j}$ and $\beta_{2j}$ are coefficients corresponding to the number of nestlings $c_{in}$ and their age $d_{in}$, and $z_{jn}$ are random effect terms, which account for non-independence of multiple prey delivery counts from the same nest site, as well as any innate differences in attack rate unexplained by local prey abundance. I further allowed $h_j$ (handling time) to vary according to a similar log-linear model as for attack rate, but without the random effect term.

Because predicted prey abundance estimates for each group were subject to uncertainty, during model fitting I sampled prey abundances $N_{jn}$ from log-normal distributions using variance estimates from DSM predictions (Smout et al. 2013). Each abundance draw was scaled between zero and 100 to ease presentation of results and improve fitting performance.

### 4.2.4 Meal size

To predict the biomass consumed by nestlings, it was necessary to model the proportion consumed of each prey item delivered to the nest. The proportion of a prey item eaten at each feeding event was modelled as the following:

$$M_x \sim logNormal(\mu, \sigma)\ T[0, 1]$$

$$\mu = \omega_{0j} + \omega_{1j} \cdot c_{in} + \omega_{2j} \cdot d_{in} \tag{6}$$

Where meal sizes $M_x$ were assumed log-normally distributed with mean $\mu$ and standard deviation $\sigma$. The distribution was truncated at one, matching the distribution of the data, which were proportions. $\mu$ was then modelled according to a generalized linear model with the number $c_{in}$ and age $d_{in}$ of the nestlings as covariates. Before modelling I removed data where the proportion eaten multiplied by the mean prey mass (Table 4.1) was higher than nestlings could physically consume according to Equation 3.

### 4.2.5 Model priors and implementation

I used regularizing (weakly informative) priors for all model parameters, following recommendations of Lemoine (2019). I selected normal priors (with mean and standard deviation) for all model coefficients involving functional response parameters, zero-inflation factors, and meal size ($N(0,\ 5)$ for attack rate, handling time, and meal size intercepts, $N(0,\ 1)$ for covariate effects, $N(0,\ 2)$ for zero-inflation factor intercept). Beta priors (which require two shape parameters) $Beta(2,\ 2)$ were used for $p_j$. Random effects in the attack rate models were drawn from $N(0,\ 1)$ distributions. All standard deviation parameters and the switching parameter $m_j$ were assigned half-normal priors $HN(0,\ 1)$. My approach in prior selection was to both constrain parameters to possible ranges and to be gently skeptical of extreme values. I verified these priors were consistent with the data by conducting prior predictive simulations (Gabry et al. 2019).

The MSFR and meal size model were fit using Hamiltonian Monte Carlo with 5000 iterations on each of 3 chains, with 1000 of those iterations as warm-up. I verified proper sampling of the chains visually using trace plots, and stable estimation of model parameters using reported effective sample sizes and $\hat{R}$ statistics (McElreath

2020b). Finally, I simulated data from each model and compared their distribution to the observed data. Diagnostics for each model can be found in Appendices C and D.

## 4.3 Results

### 4.3.1 Probability of prey identification

Parameter estimates from the MSFR indicated that probability of correctly identifying a prey item was highest for small birds at 0.98 (95% credible interval (CrI): 0.94, 1) and lowest for "other" at 0.21 (95% CrI: 0.14, 0.32) (Table C.1, Appendix C). Microtines were the next least likely to be correctly identified at 0.54 (95% CrI: 0.45, 0.65), followed by waterfowl at 0.83 (95% CrI: 0.7, 0.95) and Arctic ground squirrels at 0.91 (95% CrI: 0.85, 0.95). In general, more common items were more readily identified in nest camera images.

### 4.3.2 Functional response shapes

Model parameters indicated a moderately sigmoidal functional response shape for small birds, quail and Arctic ground squirrels; $m_j = 1.40$ (95% CrI: 1.09, 1.73), 1.42 (95% CrI: 1.22, 1.62) and 1.69 (95% CrI: 1.14, 2.24), respectively (Table C.1 in Appendix C). However, sigmoidal shape was only visually apparent for Arctic ground squirrels (Figures 4.1-4.8).

### 4.3.3 Effect of age and number of nestlings

At constant abundances of alternative prey, the number of prey deliveries to Peregrine Falcon nestlings of waterfowl, Arctic ground squirrels, microtine rodents and supplemented quail increased with the number of nestlings in the nest, while number of small bird deliveries generally did not vary with the number of nestlings (Figures 4.1-4.8). Prey deliveries to peregrine nestlings of small birds and waterfowl increased with nestling age, while deliveries of Arctic ground squirrels, microtine rodents and supplemented quail declined with nestling age.

For meal size, proportion eaten of Arctic ground squirrels, quail and waterfowl increased with both nestling age and number (Table D.1, Appendix D).

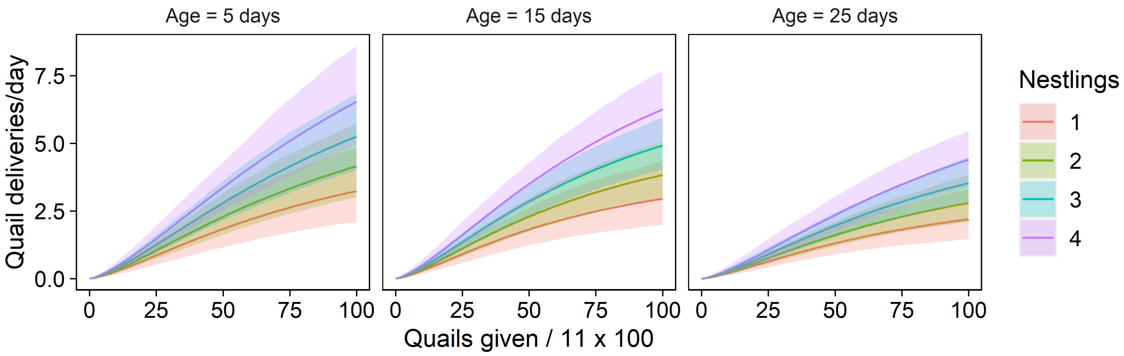


Figure 4.1: Mean and 95% prediction interval for 1000 functional response curves of Peregrine Falcon (*Falco peregrinus*) nestlings to supplemented quail. Separate curves are shown for broods of 1-4 nestlings at 5, 15, and 25 days of age. On the x-axis quail given were scaled to the maximum number of quail given during the study (11). Abundance of alternative prey were held constant at 50% of their maximum value, and "other" prey were held at constant value of 100. Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Nest camera and prey abundance data used to fit the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

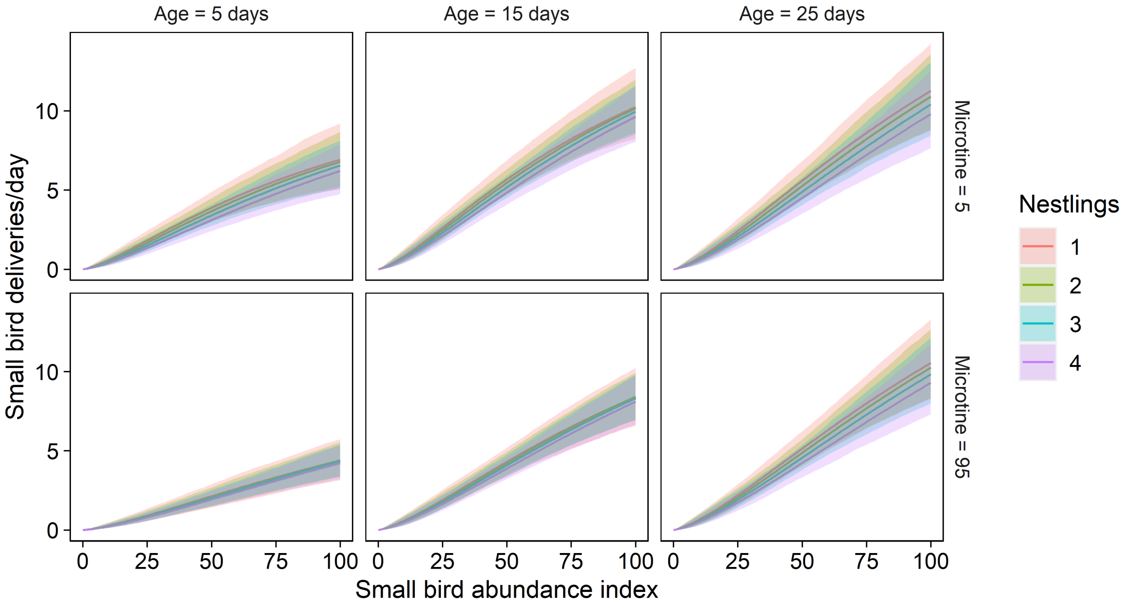


Figure 4.2: Mean and 95% prediction interval for 1000 functional response curves of Peregrine Falcon (*Falco peregrinus*) nestling to small birds at nests with low (upper panel) or high (lower panel) microtine rodent abundance. Separate curves are shown for broods of 1-4 nestlings at 5, 15, and 25 days of age. Abundance of alternative prey were held constant at 50% of their maximum value, while "other" prey were held at constant value of 100, and nests were assumed unsupplemented (no quail given). Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Nest camera and prey abundance data used to fit the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

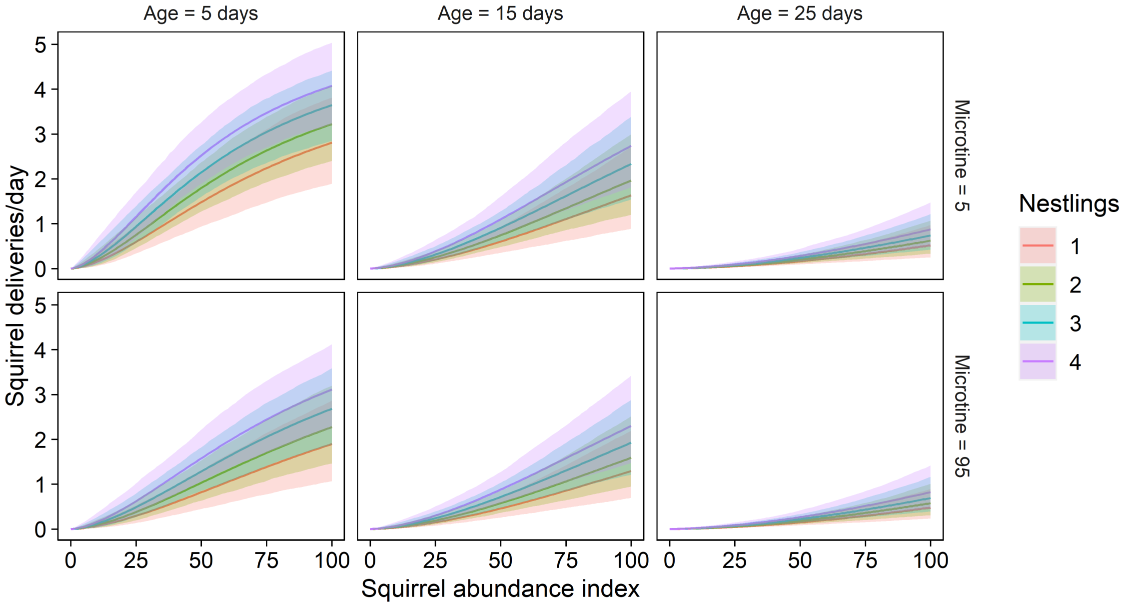


Figure 4.3: Mean and 95% prediction interval for 1000 functional response curves of Peregrine Falcon (*Falco peregrinus*) nestlings to Arctic ground squirrels (*Urocitellus parryii* at nests with low (upper panel) or high (lower panel) microtine rodent abundance. Separate curves are shown for broods of 1-4 nestlings at 5, 15, and 25 days of age. Abundance of alternative prey were held constant at 50% of their maximum value, while "other" prey were held at constant value of 100, and nests were assumed unsupplemented (no quail given). Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Nest camera and prey abundance data used to fit the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

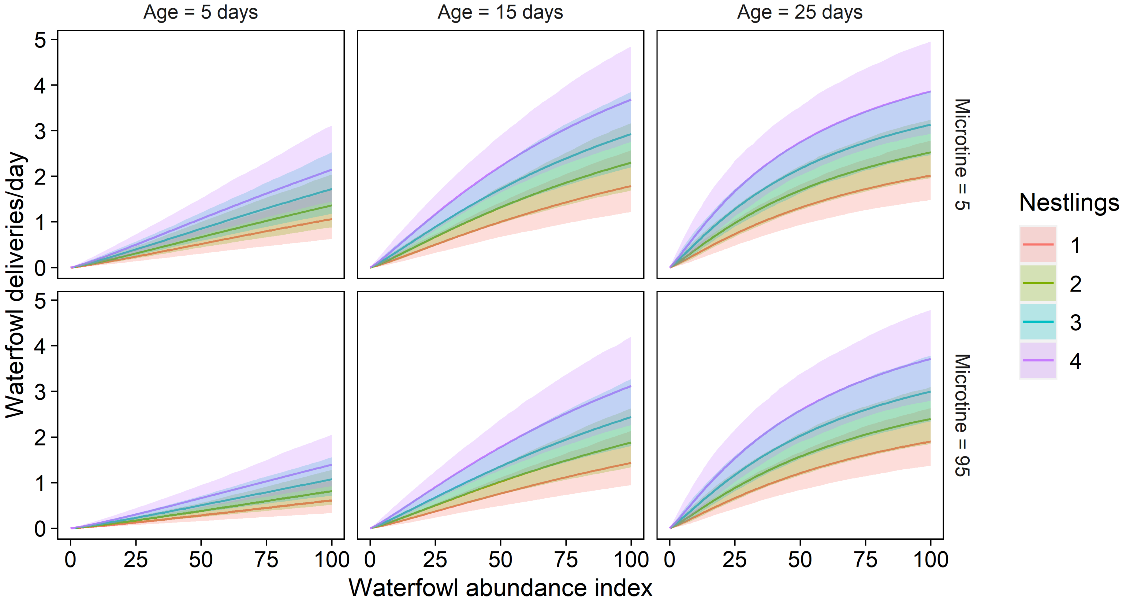


Figure 4.4: Mean and 95% prediction interval for1000 functional response curves of Peregrine Falcon (*Falco peregrinus*) nestlings to waterfowl at nests with low (upper panel) or high (lower panel) microtine rodent abundance. Separate curves are shown for broods of 1-4 nestlings at 5, 15, and 25 days of age. Abundance of alternative prey were held constant at 50% of their maximum value, while "other" prey were held at constant value of 100, and nests were assumed unsupplemented (no quail given). Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Nest camera and prey abundance data used to fit the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

### 4.3.4 Effect of microtine rodent abundance

I constructed functional responses for each prey type given high or low microtine abundance, keeping the abundance of other prey constant at 50% of their maximum ("other" were held constant at their reference value of 100 and no quail were given). For each prey type, increasing the abundance of microtine rodents (consistent with the change in abundance between crash and peak phases of their cycle) decreased deliveries of each alternative prey type (Figures 4.2-4.4). This effect was strongest when nestlings were young, which was when microtines were most often delivered to nests.

### 4.3.5 Effect of experimental food supplementation

For the effect of supplemental quail, I constructed two sets of predictions. In the first, quail were provided according to nestling age and number in accordance with 50% of their predicted energy requirement for one day. Predicted number of prey deliveries given this protocol displayed negligible differences compared to deliveries at an unsupplemented nest (Figures 4.5-4.8; upper and middle panels). In the second set of predictions, quail were provided according to nestling age in accordance with 50% of their energy requirement for the previous five days. This is in line with how quails were provided in the field, at five day intervals. Unsurprisingly, supplementing quail in this manner caused more substantial declines in consumption of each prey type (Figures 4.5-4.8; upper and lower panels), particularly for larger broods.

In general, the differences seen in the two sets of predictions indicate that Peregrine Falcons had a response to quail in the immediate aftermath of a five-day supplementation visit (when quail were "abundant"), which decreased consumption of natural prey, but this subsided as quail were consumed, and supplementing merely 50% of their single day energetic requirement would have had a muted impact on consumption of natural prey.

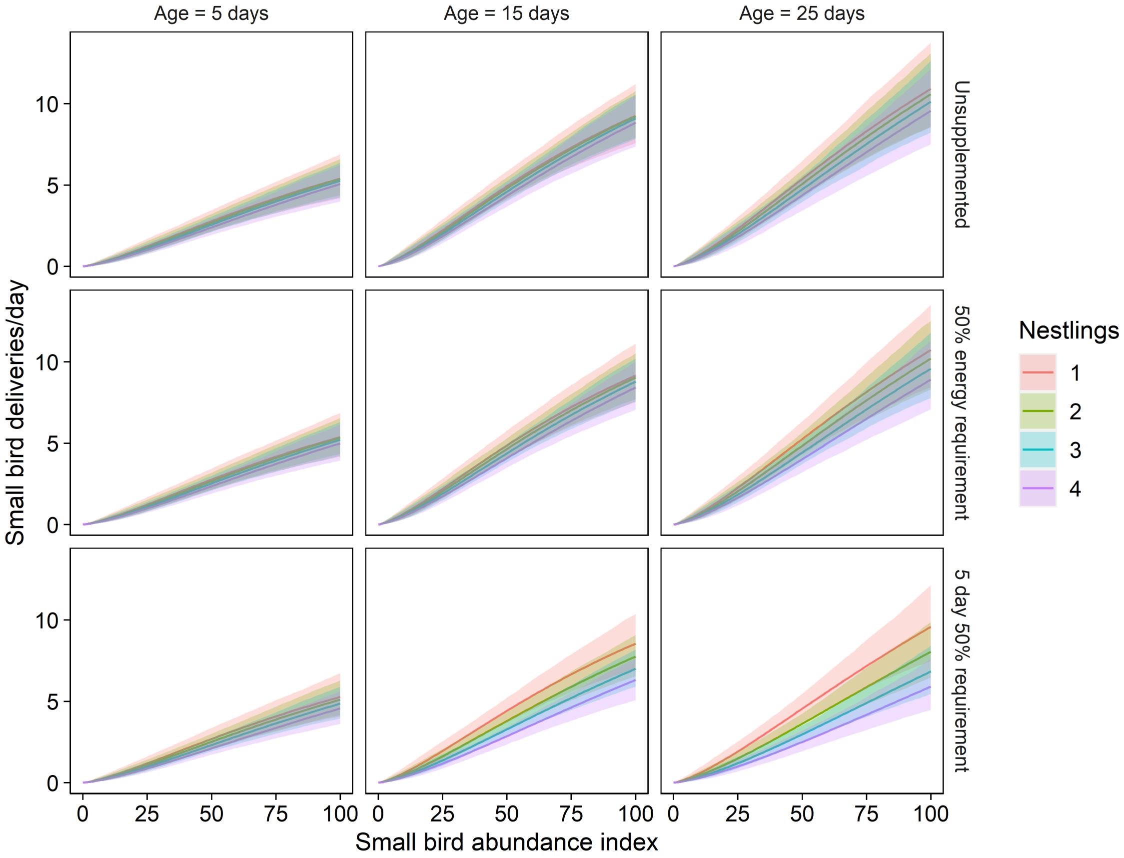


Figure 4.5: Mean and 95% prediction interval for 1000 functional response curves of Peregrine Falcon (*Falco peregrinus*) nestlings to small birds at nests provided with supplementary food and controls (upper panel). Separate curves are shown for broods of 1-4 nestlings at 5, 15, and 25 days of age. The middle panel displays predictions for nests provided with 50% of their energy requirement for one day based on the number of nestlings and their age. The lower panel displays predictions for nests provided with 50% of their energy requirement for five days, and thus predicts consumption in the direct aftermath of a nest visit per experimental protocol (supplementary quail were provided every five days). Abundance of alternative prey were held constant at 50% of their maximum value, and “other” prey were held at constant value of 100. Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Nest camera and prey abundance data used to fit the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

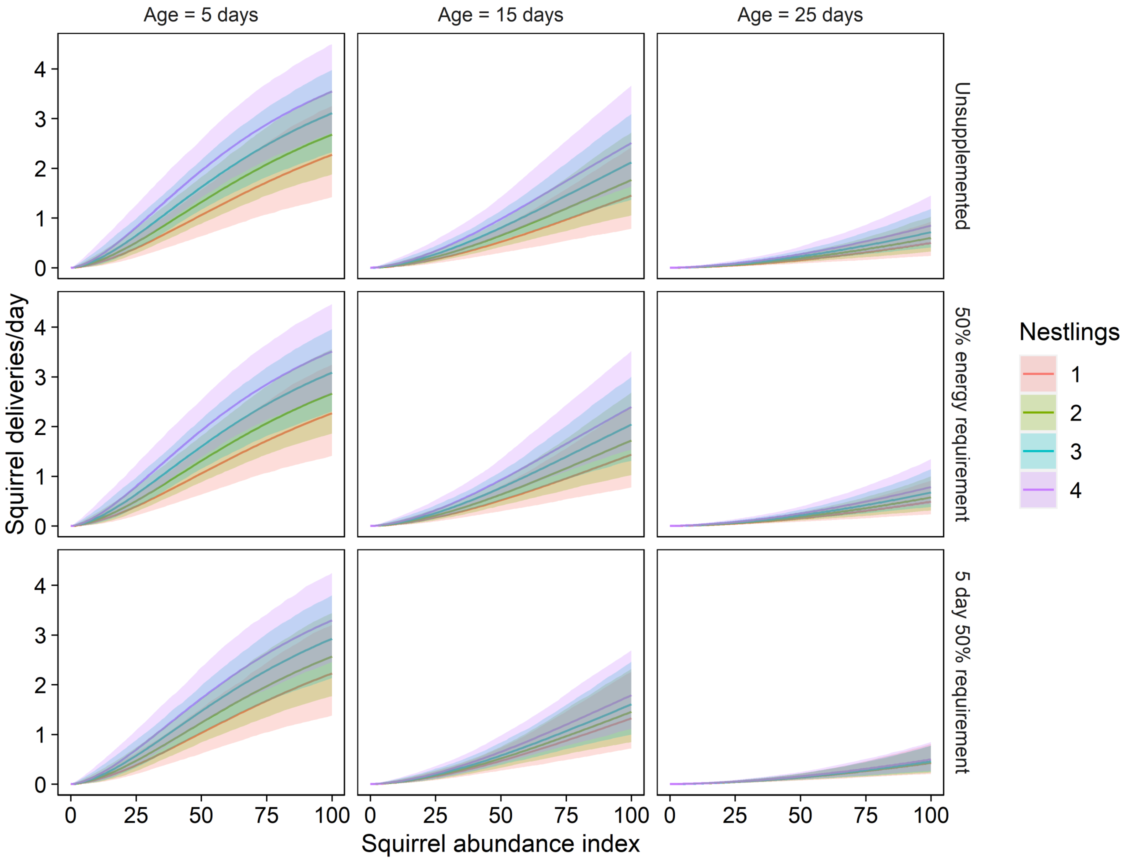


Figure 4.6: Mean and 95% prediction interval for 1000 functional response curves of Peregrine Falcon (*Falco peregrinus*) nestlings to Arctic ground squirrels (*Urocitellus parryii*) at nests provided with supplementary food and controls (upper panel). Separate curves are shown for broods of 1-4 nestlings at 5, 15, and 25 days of age. The middle panel displays predictions for nests provided with 50% of their energy requirement for one day based on the number of nestlings and their age. The lower panel displays predictions for nests provided with 50% of their energy requirement for five days, and thus predicts consumption in the direct aftermath of a nest visit per experimental protocol (supplementary quail were provided every five days). Abundance of alternative prey were held constant at 50% of their maximum value, and “other” prey were held at constant value of 100. Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Nest camera and prey abundance data used to fit the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

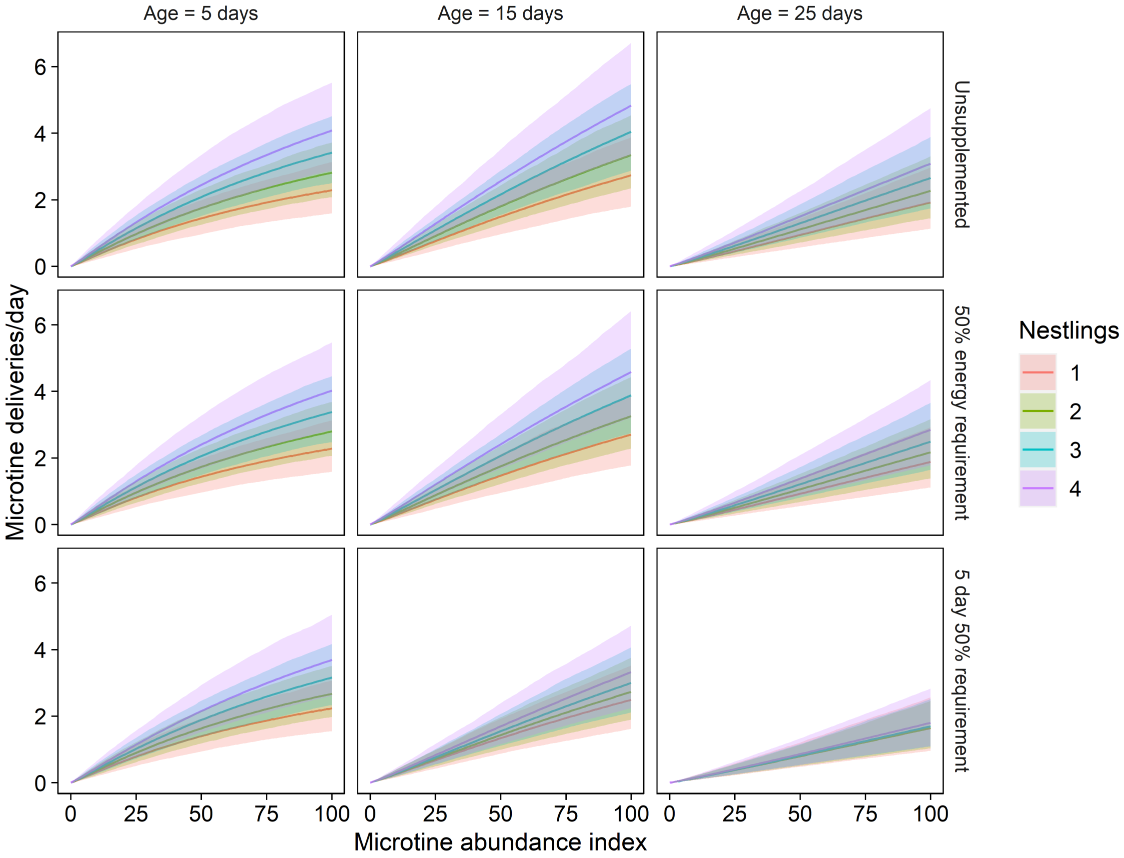


Figure 4.7: Mean and 95% prediction interval for 1000 functional response curves of Peregrine Falcon (*Falco peregrinus*) nestlings to microtine rodents at nests provided with supplementary food and controls (upper panel). Separate curves are shown for broods of 1-4 nestlings at 5, 15, and 25 days of age. The middle panel displays predictions for nests provided with 50% of their energy requirement for one day based on the number of nestlings and their age. The lower panel displays predictions for nests provided with 50% of their energy requirement for five days, and thus predicts consumption in the direct aftermath of a nest visit per experimental protocol (supplementary quail were provided every five days). Abundance of alternative prey were held constant at 50% of their maximum value, and "other" prey were held at constant value of 100. Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Nest camera and prey abundance data used to fit the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

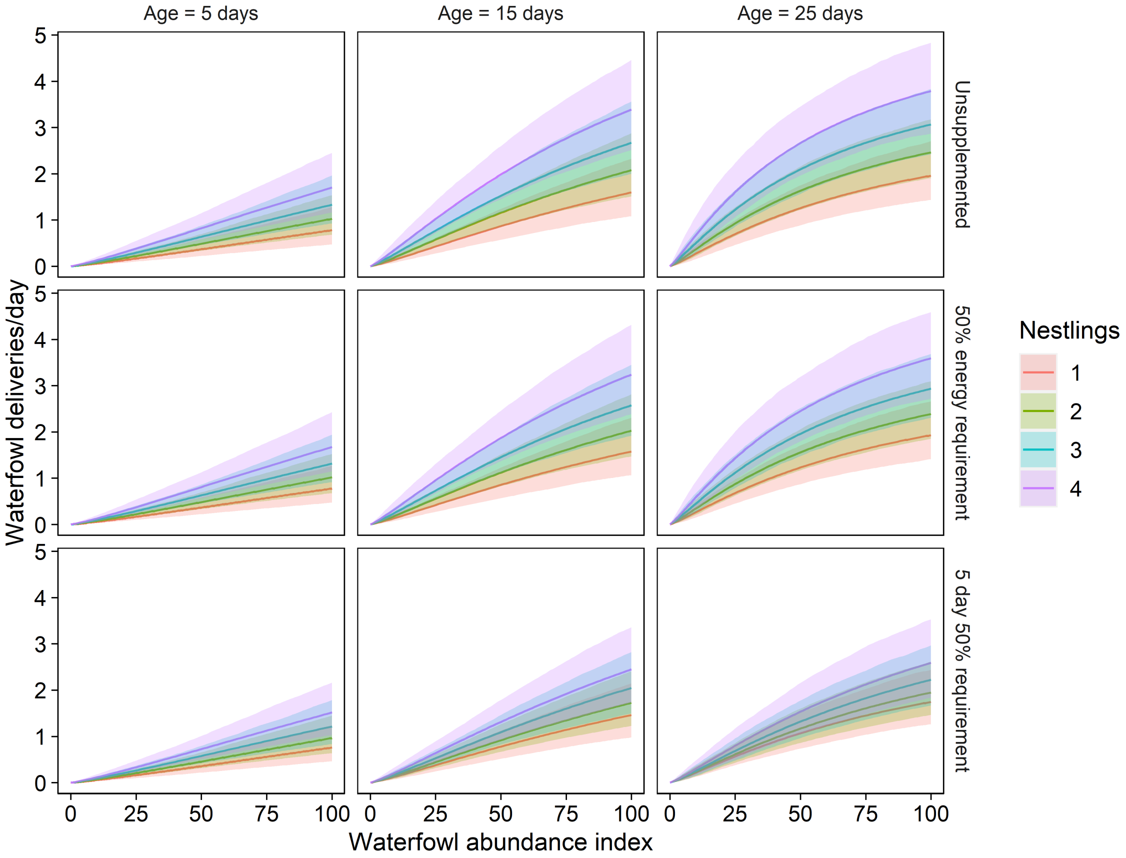


Figure 4.8: Mean and 95% prediction interval for 1000 functional response curves of Peregrine Falcon (*Falco peregrinus*) nestlings to waterfowl at nests provided with supplementary food and controls (upper panel). Separate curves are shown for broods of 1-4 nestlings at 5, 15, and 25 days of age. The middle panel displays predictions for nests provided with 50% of their energy requirement for one day based on the number of nestlings and their age. The lower panel displays predictions for nests provided with 50% of their energy requirement for five days, and thus predicts consumption in the direct aftermath of a nest visit per experimental protocol (supplementary quail were provided every five days). Abundance of alternative prey were held constant at 50% of their maximum value, and "other" prey were held at constant value of 100. Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Nest camera and prey abundance data used to fit the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

### 4.3.6 Prey biomass consumed by nestlings

Computing predictions for biomass consumed at individual nest sites required combining predictions from the MSFR, meal size model, as well as the mass distribution of each prey type (Table 4.1). This was accomplished through 1000 simulations from each model at each predicted data point. In the first set of predictions I omitted the influence of random effects, thus, predictions correspond to the foraging behaviour of an average breeding pair in the population. The second set of predictions included the influence of random effects, thus, they reflect innate abilities or preferences in prey capture, space use that did not correspond to the pseudo-home ranges used in the analysis, or other unaccounted for factors that may have influenced the prey consumption of individual nests. Food supplemented nests were provisioned every five days as in the experimental protocol, and quail were depleted as they were consumed. Whenever the average meal size exceeded that defined by Equation 3, the prediction was reset to that value. Primarily, this affected predictions early in brood rearing.

Invariably, the predicted pattern of biomass consumption by nestlings given nestling age was a saturating curve, with larger broods saturating more quickly and at a higher level than smaller broods. Figure 4.9 visualizes such a curve for an example nest. Although predicted consumption was higher for larger broods at all ages, the effect was not proportional as nestlings aged. In other words, broods of two were not fed twice as much food as broods of one, broods of three were not fed three times as much as broods of one, and broods of four were not fed four times as much as broods of one.

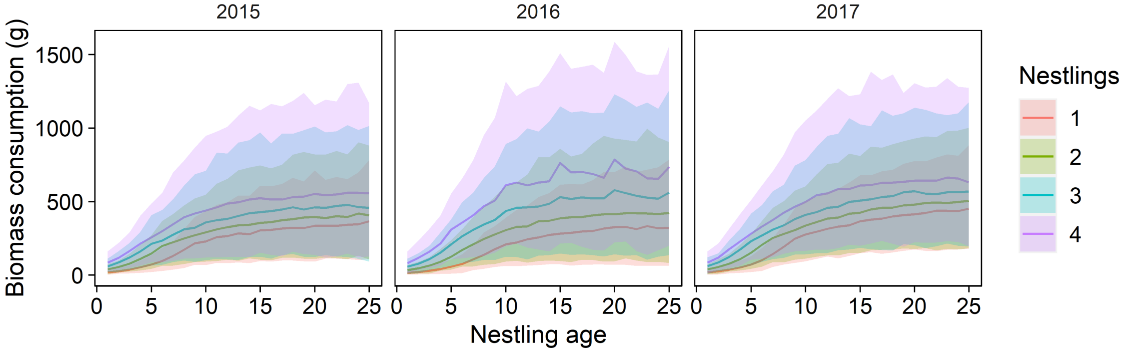


Figure 4.9: Mean and 95% prediction interval for 1000 simulated daily biomass consumption estimates for Peregrine Falcon (*Falco peregrinus*) nestlings at an example nest from 1-25 days of age. Separate curves are shown for broods of 1-4 nestlings. Predictions are generalized for the study population, meaning they omit the influence of random intercepts for nest site-year combination. Predictions also assumed a complete camera monitoring period (24 hours / day) and that all prey were correctly identified. Predictions were constructed by multiplying simulated prey deliveries from the multispecies functional response (MSFR) by simulated proportion consumed estimates from the meal size model, and then multiplying by random draws from the prey mass distributions in Table 4.1. Uncertainty in the mean represents uncertainty in parameter estimation, as well as sampling uncertainty from the response distributions of the MSFR and meal size model. Nest camera and prey abundance data used to fit the models were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

For predictions both omitting and including the influence of random effects, there was substantial variation in biomass consumption among nests. Inclusion of random effects either increased or decreased the predicted biomass consumed during the first 25 days of life (Figure 4.10). For predictions including the influence of random effects, biomass consumption for a brood of two nestlings ranged from 4.78-kg (95% prediction interval (PI): 3.3, 6.48) to 10.16-kg (95% PI: 8.19, 12.44), thus predicted biomass consumption varied more than two-fold across nests, and this difference was similar across brood sizes.

On a per-nestling basis, predicted biomass consumption ranged from 3.49-kg (95% PI: 2.36, 4.68) to 8.19-kg (95% PI: 6.57, 10.11) in broods of a single nestling and from 1.96-kg (95% PI: 1.38, 2.63) to 4-kg (95% PI: 2.93, 5.23) in broods of four.

Plots of predicted biomass consumption versus prey abundance within the pseudo-home range of each nest revealed that biomass consumption was positively related to the abundance of small birds (Figure 4.11). Conversely, biomass consumption appeared weakly or unrelated to microtine rodent, Arctic ground squirrel or waterfowl abundance, and was also generally unrelated to experimental food supplementation with quail, with perhaps a slight positive relationship for broods of four.

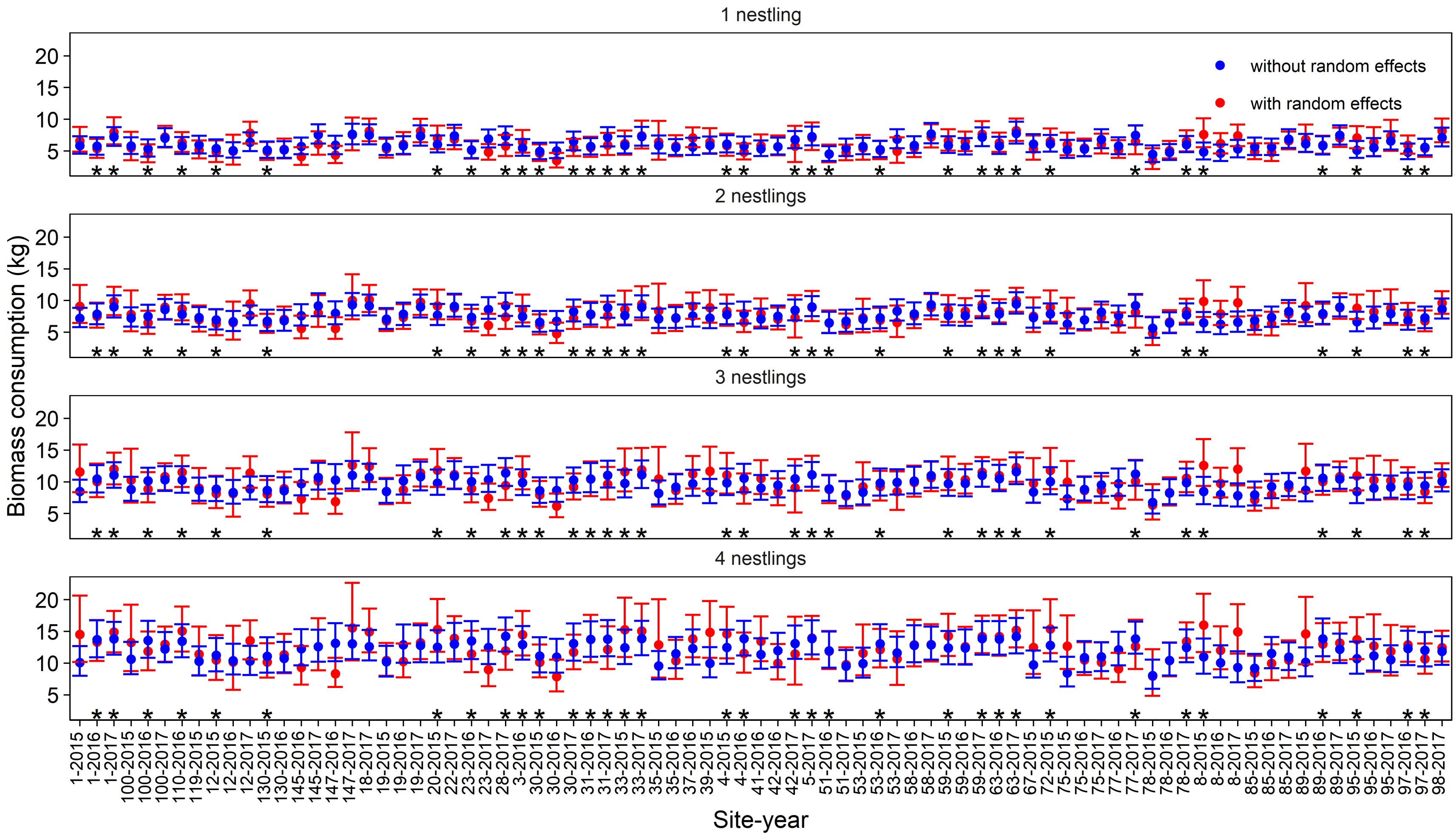


Figure 4.10: Mean and 95% prediction interval for 1000 simulated biomass consumption estimates for Peregrine Falcon (*Falco peregrinus*) nestlings at all nests during the first 25 days of brood rearing. Biomass consumption estimates include all prey types. Separate predictions are shown for broods of 1-4 nestlings, and with and without the influence of random effects from the multispecies functional response (MSFR). Nests marked with an asterisk were food supplemented. Predictions also assumed a complete camera monitoring period (24 hours) and that all prey were correctly identified. Predictions were constructed by multiplying simulated prey deliveries from the MSFR by simulated proportion consumed estimates from the meal size model, and then multiplying by random draws from the prey mass distributions in Table 4.1. Uncertainty in the mean represents uncertainty in parameter estimation, as well as sampling uncertainty from the response distributions of the MSFR and meal size model. Nest camera and prey abundance data used to fit the models were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

## 4.4 Discussion

### 4.4.1 Peregrine Falcons as mediators of indirect interactions between prey

The alternative prey hypothesis (Lack 1954) has been invoked to explain synchrony between populations of microtine rodents and various mid-trophic level Arctic consumers (*e.g.,* Summers 1986). Evidence has accumulated that such synchrony is due to variation in predation pressure from generalist predators, typically Arctic foxes ( *Vulpes lagopus*; Bêty et al. 2001; McKinnon et al. 2014), which replace alternative prey with microtines in their diet when microtines become abundant, leading to an apparent mutualism between microtines and alternative prey. My study provides evidence that Peregrine Falcon functional responses shift in a similar fashion with microtine rodent abundance. However, the total effect of a predator population on a prey population is a combination of numerical and functional responses. The numerical response has two components with respect to migratory birds: how many pairs attempt to breed in a given season, and how many young are produced per breeding pair. The Peregrine Falcon population at Rankin Inlet, Nunavut has been stable since monitoring began in the early 1980s, with probability of occupancy of monitored sites fluctuating in a narrow band around 0.75 (Franke et al. 2020). This indicates that peregrines in my study area have not shown the large aggregative responses to prey abundance that are characteristic of other Arctic predators, for example Snowy Owls (*Bubo scandiacus*; Bêty et al. 2001) and Rough-legged Hawks (*Buteo lagopus*; Potapov 1997). Reliance on a broad prey base, as confirmed by my study, may allow peregrines to maintain breeding density as prey abundance fluctuates, meaning that their breeding density may be regulated more strongly by other factors, perhaps competition for nest sites, or low juvenile recruitment (Newton 1980; Newton 2003). Franke et al. (2020) also presented productivity data for this population, which showed greater variability than occupancy, but it is likely this variability is due to the impact of severe weather events, which can decimate breeding output in any given season (Anctil et al. 2014). With relatively consistent breeding densities, and reproductive output largely determined by severe weather events, the influence of Peregrine Falcons on prey populations in this study area is likely to be mediated mainly by their functional responses. Increases in microtine rodent abundance caused declines in the consumption of other prey types, which may indicate apparent mutualism between microtines and other prey types (Abrams et al. 1996).

One caveat with regards to my results comes from the grouping of prey species. The impossibility of consistently identifying prey delivered to nests at the species level necessitated grouping prey into broader categories. While species within groups likely experience somewhat similar predation risk from Peregrine Falcons, there is heterogeneity among species within groups across a wide range of traits (*e.g.,* singing phenology of songbirds Thompson et al. 2017), and their populations may vary independently of one another, both in response to predation, and more broadly via other factors (*e.g.,* conditions on wintering grounds). I therefore caution readers that, for example, while the results of my analysis pertain to small birds as a whole, they may not for Lapland Longspurs (*Calcarius lapponicus*) or other individual species.

Additionally, falcons are only one of a suite of predators in this study system, all of which have their own functional and numerical responses to the array of prey types included here. Multiple predators can have additive effects on prey populations (Latham et al. 2011; Latham et al. 2013, *e.g.*), and may also interact, such as when apex predators mediate the distribution or behaviour of mesopredators (Haswell et al. 2020; Suraci et al. 2016). In my system, microtine rodent specialist Rough-legged Hawks (*Buteo lagopus*) breed in large numbers in years when microtine rodents are at high abundance. If hawks also incidentally consume Arctic ground squirrels for example, then squirrel mortality via hawks will increase in years when microtine abundance is high (apparent competition). Should this effect be strong enough, the net effect of microtines on squirrel could be negative, despite the mutualistic effect of

Peregrine Falcons supported by my study.

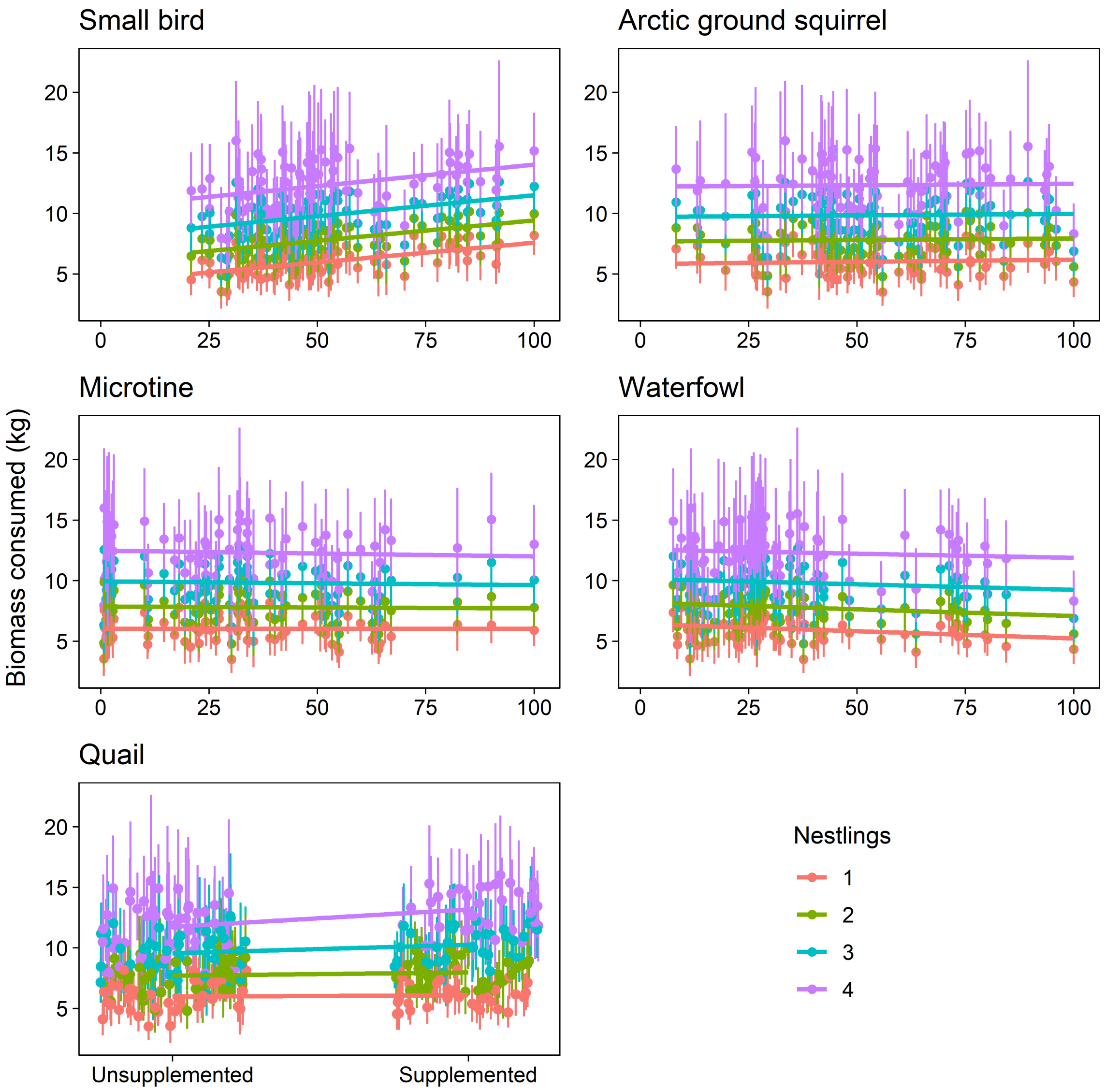


Figure 4.11: Predicted mean and 95% prediction interval for 1000 simulated biomass consumption estimates for Peregrine Falcon (*Falco peregrinus*) nestlings at Rankin Inlet, Nunavut, Canada during the first 25 days of brood rearing, plotted against the abundance of five prey types. Biomass consumption estimates include all prey types. A simple line of best fit is shown. Separate estimates are shown for broods of 1-4 nestlings. Predictions assumed a complete camera monitoring period (24 hours / day) and that all prey were correctly identified. For quail, estimates are shown for supplemented and unsupplemented nests, while for other prey types the x-axis represents abundance scaled from 1-100. Points are jittered to avoid overlap. Predictions were constructed by multiplying simulated prey deliveries from the multispecies functional response (MSFR) by simulated proportion consumed estimates from the meal size model, and then multiplying by random draws from the prey mass distributions in Table 4.1. Uncertainty in the mean represents uncertainty in parameter estimation, as well as sampling uncertainty from the response distributions of the MSFR and meal size model. Nest camera and prey abundance data used to fit the models were collected from 2015-17.

### 4.4.2 Experimental food supplementation

In contrast to microtine rodent abundance, the effect of supplemented quail on nestling diets was more muted. Nestlings certainly consumed some of the provided quail (Table 4.1), but the MSFR predicted that substantial numbers of quail in the diet were generally found in the short-term after larger numbers of quail were left at the nest every five days. The predicted impact of supplying 50% of one day's worth of energy in quail to a brood was negligible on consumption of other prey types. Similarly, predicted biomass consumption of prey by a given number of nestlings did not differ on average between food supplemented nests and controls, even when provisioned at five-day intervals. Study limitations, such as uncertainty in the amount of quail consumed by nestlings (and therefore the amount of quail leftover for subsequent days), as well as adult consumption of quail (which could not be seen on camera), may have bearing on this result. However, the lack of increase in biomass consumed by supplemented nests also provides context to previous results showing that nestling growth was negligibly affected by food supplementation in this population (Hedlin 2015), despite strong effects on nestling survival.

While it is common for food supplementation to benefit juvenile growth (Boutin 1990), increased survival within the brood also increases energy demand, and having more mouths to feed lowers the amount of food available to each nestling. Byholm and Kekkonen (2008) found that food supplementation increased survival in Northern Goshawk (*Accipiter gentilis*) nestlings, but also decreased body condition at fledging. Thus, trade offs may exist between nestling survival and growth or body condition. Past study has also indicated that parents may decrease hunting effort in response to the extra food (Dawson and Bortolotti 2002), highlighting that parents and offspring may both benefit from provided food, as suggested by parent-offspring conflict (Trivers 1974). My study also adds to this line of evidence by showing that deliveries of quail were at least partially offset by fewer deliveries of natural prey.

Nestlings need not consume large quantities of the extra food to derive benefit from it. For example, while reducing hunting effort, adults may increase their nest attendance, which could deter predators or allow offspring to be brooded more often, lowering their thermoregulatory burden. As previous study on nestling survival by Hedlin (2015) excluded nest predation events, increased brooding by supplemented adults remains a possible mechanism for improved nestling survival. As adults decrease hunting effort, they may improve their own body condition, and increase the chance that they survive the migration and non-breeding seasons to breed the following year. Brood enlargement (which increases the breeding season burden placed on parents) is known to decrease adult survival (Daan et al. 1996), and the opposite may therefore be true of food-supplemented parents.

### 4.4.3 Biomass consumption by Peregrine Falcon nestlings

Clearly, my models predict that smaller broods are advantaged from a prey intake perspective, which is not an uncommon result in birds (Barba et al. 2009; Olsen et al. 1998; Robinson and Hamer 2000). Lower per-nestling food intake in larger broods may be partially offset by lower thermoregulatory requirements due to increased huddling with siblings (Royama 1966). Although nestling survival was not analyzed here, among my years of study, of 36 nests that hatched at least four young, only eight still contained four young at 25 days after hatch. Figure 4.9 indicated that the lower per-nestling intake of larger broods is potentially most acute for older broods. Thus, barring a home range with exceptional prey abundance, parents may struggle to adequately provision large broods as they age, resulting in increased probability of active brood reduction by parents or simply nestling starvation.

Estimates of the dietary requirements of wild peregrine nestlings are rare. Redpath and Thirgood (1997) calculated a daily intake of 222-g of food per nestling from hatch until fledging (42 day period), which yields a total estimate of 9.3-kg. Ratcliffe (2010) provided an estimate of 7-kg for a 33-day brooding period including wastage, while

Boulet et al. (2001) gave much lower estimates for a 32-day brooding period of 1.9-3.6-kg, determined via tritiated water turnover. All of these estimates were derived from warmer study locations, but at the very least, estimates provided by my study for the first 25 days of brood rearing are plausible in light of prior research.

Biomass consumption predictions that included the influence of random effects in the MSFR in some cases provided different estimates of total biomass consumption, which may have implications for individual diet specialization. In theory, random effect estimates for site-year combination represent variation in Peregrine Falcon foraging that are inexplicable by local prey abundance, and may therefore represent individual hunting ability or preference. This interpretation largely hinges on how accurate my constructed pseudo-home ranges were in imitating Peregrine Falcon space use (and therefore prey availability in the MSFR) and how accurate my DSMs were in describing the distribution of prey. The irregular shape of some estimated Peregrine Falcon home ranges in prior research (*e.g.,* Tétreault 2019) suggests that my largely circular or elliptical home ranges may be poor approximations of falcon space use in some cases, and therefore some of the variation explained by the random effects in the MSFR may reflect foraging outside of my constructed pseudo-home ranges rather than diet specialization on prey available within home ranges. Furthermore, although DSMs accounted for a large proportion of variability in abundance of various prey types (Table 3.2), much variation remained unexplained. Individual diet specialization due to intrinsic differences in prey preference or hunting ability between breeding pairs within this population remains an intriguing possibility that may act to diminish competition between closely-spaced breeding pairs, but future research will have to integrate data on space use to investigate this idea.

Plots of predicted biomass consumption versus prey abundance indicated that consumption was related to small bird abundance, but not the abundance of other prey types. Although there was a mean population functional response to all prey types in my study, this appears to be largely overridden by the influence of site-year random effects for prey types other than small birds. Indeed, the variance term for random effect estimates was smallest for small birds (Table C.1, Appendix C), indicating more consistent responses to their abundance than for other prey types. Among identified prey, small birds were delivered three times more often than the next most frequent prey type (Table 4.1), so any potential signal of abundance of other prey types may have been diminished. My study indicates that peregrine broods with low small bird abundance within their home range may face food shortages as large as 2-kg during the first 25 days of life. Effects of such shortages on fitness remain to be explored.

### 4.4.4 Future considerations

Recent reviews (*e.g.,* Novak and Stouffer 2021) have highlighted the prevalence of consumer density dependence in functional responses. To date, this has seen limited application in a MSFR context (Baudrot et al. 2016), and is therefore an area in need of further empirical study. Peregrine Falcon home ranges commonly overlap (Sokolov et al. 2014; Tétreault 2019), even though nest sites show distinct spacing (minimum nearest neighbour distance $\sim$ 400-m over my three years of study), so there is potential for neighbouring pairs to interfere with each other through agonistic encounters or simply by depleting shared resources. Comparing functional response models that omit predator interference to models that include it would shed light on the degree of competition for resources that occurs in this population. Additionally, given the multi-predator nature of my study area, falcons may also face competition from other species, for example Arctic foxes or Rough-legged Hawks, which may also play a role in structuring falcon functional response.

In my study, prey abundance was assumed constant within season, which neglects possible prey increases during the peregrine brooding period as a result of juvenile recruitment or perhaps immigration, or, conversely, decreases as a result of prey depletion. Suryan et al. (2002) showed that Black-legged Kittwakes (*Rissa tridactyla*) can respond almost instantly to changes in prey abundance surrounding their breeding colonies, with consequences for reproductive output, demonstrating that within-season changes in prey abundance are an important source of variation for future studies to consider. Estimating abundance continuously through the growing season is a daunting task given the logistical challenges of data collection by small field teams in a remote location, but perhaps this represents an opportunity for passive acoustic monitoring, if such methods can accurately estimate abundance during the post-hatch period, when auditory cues may decline (Thompson et al. 2017). Additionally, it is likely that prey breeding phenology plays a large role in their susceptibility to predation (*e.g.,* the vast majority of waterfowl consumed are ducklings and goslings), so abundance may not accurately reflect prey availability to breeding falcons. Accounting for this would require additional monitoring of prey breeding phenology and output, which may not be feasible on a large spatial scale. Fortunately, because nestling age was included in log-linear models for attack rate and handling time parameters, temporal shifts in diet composition were accounted for in the model, however, the degree to which this was due to changes in prey availability versus changes in Peregrine Falcon prey selection as nestlings grew is unknown. I suspect, given likely prey phenology for the species in my study area, that Peregrine Falcons are largely opportunistic hunters, taking advantage of successive influxes of juvenile prey during brood rearing, particularly Arctic ground squirrels, which are consumed mainly early in the brood rearing period, and waterfowl, which are consumed mainly late in brood rearing. They also take advantage of microtine rodents in years when microtine abundance is high. Overall though, my study indicates that the abundance of small birds is the most consistent driver of biomass consumption by Peregrine Falcon nestlings in my study area.

Previous work has criticized the use of nestling prey deliveries to characterize the functional responses of central place foragers, due to lack of data on the prey consumption of adults (Sonerud 1992). In short, central place foraging predicts that items brought back to the nest site will be larger than those consumed out on the landscape due to travel costs, thus nestling consumption will be biased towards large prey and the true functional response of the species will be overestimated relative to large prey and underestimated relative to small prey. Subsequent study pointed out that this prediction may not hold in practice for a variety of reasons (Korpimaki 1994), including the fact that raptors frequently partially consume prey items before delivering them to nestlings (most notably removing the head; Steen et al. 2010), thus diminishing any differences between adult and nestling diets. Nest attendance and nestling feeding are largely done by the adult female through the early portion of brood rearing (Sonerud et al. 2014), meaning her diet is likely supplied by the male during this time, so if there is any load size bias in items brought to the nest, it will be reflected in the diets of adult females as well. Nonetheless, I cannot discount the possibility that adult and nestling diets are substantially different (Catry et al. 2016; Masman et al. 1986), and acknowledge that even if they are not, the functional response for the entire population will be greater than that estimated here, due to adult consumption, including periods outside of brood rearing.

To conclude, despite multiple sources of uncertainty, the MSFR was able to replicate observed delivery rates for five prey types and, in combination with a model for meal size, produced plausible estimates of biomass consumption for nestlings, showing that it is generally robust to unknowns common to functional response studies in natural populations. The diets of Peregrine Falcon nestlings reflected local variation in prey abundance, as well as nestling age and number. Increases in microtine rodent abundance decreased consumption of alternative prey, highlighting potential indirect mutualisms between prey types. The effects of food supplementation were similar, if more muted, and highlighted possible parent-offspring conflict over extra food, and most importantly, did not increase prey biomass consumed at nests. My study demonstrates the importance of accounting for alternative prey in determining the functional response of generalist predators, and, following from a limited selection of other MSFRs in the literature, provides a blueprint that other researchers can use to implement such models.

# Chapter 5

# Conclusions, recommendations, and future work

This thesis has focused on the relationship between predator and prey in an Arctic ecosystem, spanning topics such as: the habitat associations of prey species (as well as incidentally observed non-prey species; Chapter 2), the influence of an apex predator, the Peregrine Falcon, on prey distribution in a landscape of fear framework (Chapter 3), and 3), in-depth exploration of foraging and nestling diet in Peregrine Falcons via a multispecies functional response (MSFR) model (Chapter 4). In this concluding chapter, I will briefly summarize the main findings of the three data chapters, highlight remaining areas of uncertainty, suggest future improvements, and then comment on ongoing changes to the species and ecosystems that are the subjects of this thesis, particularly in light of climate change.

### 5.0.1 The habitat associations of Arctic birds and small mammals

The intent of Chapter 2 was to comprehensively describe the habitat associations of birds and small mammals in the Rankin Inlet study area, and the overarching findings were the importance of freshwater, along with low elevation and vegetative productivity, in constituting habitat for the above species. I was able to survey and model the distributions of essentially the full suite of avian and small mammalian life in the Rankin Inlet study area, excepting raptors and corvids. NDWI emerged as an important covariate not seen in previous study.

### 5.0.2 Survey protocol and analysis methods for multispecies surveys: one size fits all, or none?

Chapters 2 and 3 featured distance sampling and density surface modelling (DSM), two widely-used survey and analysis techniques for estimating species populations. Though the efficiency and comprehensive nature of the dataset I was able to amass are clear points in favour of the methodology, there were nevertheless issues encountered.

First, any kind of terrestrial line transect or point count survey is perhaps likely to encounter issues when sampling species that reside primarily in aquatic or marine habitats. I made considerable effort to ensure that coastlines and islands were adequately sampled during my study, but sampling was still restricted to larger islands >1-km in diameter, which likely neglected smaller islands which could easily serve as important resting or breeding locations for ducks and seabirds such as Common Eiders (*Somateria mollissima*) and Black Guillemots (*Cepphus grylle*). Secondly, as the detection radius of my surveys was limited to a maximum of 400-m (more or less the limit of reliable bird detection), birds that were physically on the water outside of this distance went unsampled. For ducks and seabirds, for which a large proportion of the population at any given time is beyond 400-m from the nearest shoreline, estimating abundance accurately was impossible. In particular, I did not accumulate enough observations to estimate Black Guillemot distribution.

Conducting distance sampling surveys in study areas with a large amount of lakes, rivers, ponds and saltwater is additionally problematic because water and land are used in different amounts by the species surveyed. For a small terrestrial bird, such as a Lapland Longspur (*Calcarius lapponicus*), area covered by water is unavailable to them, and the opposite is true for aquatic or marine species (large areas of terrestrial habitat are unavailable to them). The main problem this creates is a shift in the average detection distance of a given species and therefore potential bias in abundance estimates. To illustrate this, consider a terrestrial line transect. This line transect will never traverse water (for the safety of the observer), thus any water bodies in the survey area will be some distance from the transect. If a species, for example a Long-tailed Duck (*Clangula hyemalis*), is only likely to be physically on water, this means that all, or at least a large majority of detections will likely be biased away from the transect line. This is not unlike well-known observer or linear feature avoidance that occurs in some species, where distance sampling surveys reveal a dearth of detections at close range (Marques et al. 2010). Unaccounted for, this will result in abundance estimates that are biased low. The reverse will be true for obligate terrestrial species like Lapland Longspurs. Properly accounting for this bias requires prior information on the true distribution of organisms with respect to the transect line (Marques et al. 2013). Conversely, one could select their distance sampling points to avoid areas with water, but this could obviously hamper the investigator's ability to estimate species distribution with respect to water, or estimate the abundance of aquatic or marine species at all.

While tundra is an open landscape with few obstacles to visual detection, particularly for songbirds and shorebirds, a large proportion of birds are detected aurally. As noted in the Chapter 2 Discussion, this may mean that non-singing birds are unavailable for detection, and the assumption of 100% detection on the transect line may be violated (Bachler and Liechti 2007). Therefore, temporal trends in singing behaviour (Thompson et al. 2017) have the potential to bias abundance estimates. Similarly, for Arctic ground squirrels, for which a proportion of the population will be underground at any given time, line transect surveys will underestimate abundance and require a correction factor.

For all the reasons noted above, I was skeptical of the abundance estimates generated by my models and generally chose not to present them (some estimates are shown in Figure 3.2 in Chapter 3 and Figure B.1 in Appendix B as the relationships depicted in these figures are non-linear and thus presentation on the true response scale was necessary for communicating the correct forms of the relationships to readers). That being said, I am confident in model results as relative estimates of abundance, both spatially and across years. If and where the above biases are present, they are likely present across the study area, and unlikely to change markedly across years. To summarize, while my methodology was adequate for the main task at hand (estimating the distribution and habitat associations of a wide variety of avian and mammalian life), they were inadequate for estimating true abundance, particularly for aquatic or marine species. Sampling and modelling refinements may improve future attempts.

Estimating the abundance of wildlife populations, though a simple problem conceptually, remains a difficult task. From my experience conducting distance sampling surveys and analyzing the resulting data using DSM, the following advice may be useful to future practitioners:

- I suggest adapting protocol or analysis to try to accommodate violation of 100% detection on the transect line. On the sampling side, double observer surveys or time removal protocol are potential solutions (Amundson et al. 2014; Buckland et al. 2015). On the analysis side, a Bayesian approach with multiple hierarchies (availability, detection, abundance) may be another avenue to accommodate such violations.

- For multispecies surveys I would advocate the community approach of Goyert et al. (2016), Monroe et al. (2021), and Sollmann et al. (2016), which allows for modelling the distribution and abundance of rare species for which not enough detections are accumulated to model individually.

- The use of acoustic recorders in avian surveys is becoming increasingly popular (Sugai and Llusia 2019). They offer many advantages to traditional line transect or point count methods, including more standardized sampling across "observers", simultaneous monitoring of multiple survey points, and lower human sampling effort in the field. Recently implemented machine learning algorithms (*e.g.,* Oliver et al. 2018) for automatic song recognition, and integration with distance sampling methods for estimating abundance by sound level (Yip et al. 2020) add to the advantages in passive acoustic monitoring. Where possible, I recommend the use of acoustic monitors in Arctic study areas as well, but I note that acoustic recorders, like my terrestrial distance sampling surveys, are unlikely to be effective for all species and at all times of year.

- Developing high quality land cover products for tundra regions should be a priority. In preparing the analyses of Chapter 2, I attempted to secure land cover products describing vegetation and substrate cover for the Rankin Inlet, Nunavut study area, but ultimately found them lacking due to extensive cloud cover over the region of interest (Campbell et al. 2012) or lack of ground-truthing in the Arctic (Latifovic et al. 2017).
- Lastly, comparisons across study areas using similar methodology should be a key research focus in the future. In reviewing literature for Chapter 2, it was apparent how fragmented and disconnected past research on the habitat use of Arctic fauna has been. In many cases, it is not a lack of information that limits synthesis, but rather heterogeneity in methodology, covariates considered, scale, and comprehensiveness. Given habitat loss and change are the largest causes of biodiversity declines worldwide (Millennium Ecosystem Assessment 2005), and the potential for climate change to alter Arctic habitats in particular (Bjorkman et al. 2020; Smol and Douglas 2007b), studies that consider habitat associations across the range of a species, and use standardized methods, are needed to provide robust conclusions and predictions.

### 5.0.3 Landscapes of fear, or death?

Chapter 3 described the relationship between abundance and proximity to Peregrine Falcon nests for five common prey types. Songbird and goose abundance were lower near Peregrine Falcon nests (goose abundance was specifically lower in late summer), while shorebird and Arctic ground squirrel abundance was unaffected by distance to Peregrine nests, and duck abundance was higher near peregrine nests, but only in late summer. While I pointed to lines of evidence and reasoning supporting lower abundance near falcon nests as an avoidance effect, I acknowledged that it is possible the effects described could be due to the effects of consumption, or else short-term behavioural adjustments, such as declines in singing.

Truly determining the relative roles of consumption and fear in structuring the prey community would require additional study. For example, experimental work using falcon audio playback or taxidermy units would shed light on the existence of short-term behavioural adjustments of prey that may have diminished their availability during surveys. Data on arrival and territory establishment in prey may indicate whether prey individuals settle near falcon nests, and are subsequently killed, or whether they avoid falcons altogether. Physiological data from prey may indicate whether proximity to falcons increases stress (Clinchy et al. 2004) or impacts hatching or fledging success. For Common Eiders and Canada Geese (*Branta canadensis*), nest survival at varying distances from falcon nests could be monitored, perhaps providing an indication of any protective benefits to nesting near falcons (Quinn and Ueta 2008). Finally, marking prey offspring and then subsequently searching pellets and prey remains at falcon nest sites may indicate how large an impact falcon consumption has on reproductive output in prey.

### 5.0.4 Prey abundance and Peregrine Falcon prey consumption

Chapter 4 demonstrated implementation of a MSFR model for Peregrine Falcon nestling prey consumption. Peregrine Falcons responded functionally to each prey type, and potentially mediated indirect mutualism among prey by consuming more microtine rodents as they became abundant, while at the same time decreasing consumption of alternative prey. In combination with a model of meal sizes and distributions of prey masses, the MSFR was able to produce estimates of biomass consumed by Peregrine Falcon nestlings, including saturating prey consumption with nestling age and proportionally greater per-nestling prey intake in smaller broods. Variation in small bird abundance around nests resulted in large differences in predicted biomass intake.

### 5.0.5 Multispecies functional response: improvements and further questions

From a data collection perspective, a better method of accounting for prey size than I was able to implement here would be useful for future study. Estimating proportion eaten of each prey item neglected sometimes large size discrepancies between prey, even within prey types. For example, Arctic ground squirrels triple in mass during their first summer (Kiell and Millar 1978). I accounted for this variation by drawing prey masses from plausible mass distributions when making predictions, but better still would be to estimate prey size during a delivery. Comparing the size of delivered prey items to a model item of known size in the field of view of the nest camera is one such method that may benefit future study (*e.g.,* Steen 2010).

Future study might consider joint estimation of the number of prey deliveries and meal sizes at nests. My study assumed these components are independent, conditional on the number and age of nestlings, which are present in either model, but there could still be unmodelled correlation between meal size and number of deliveries that could have bearing on results. An approach featuring a single response variable (*e.g.,* daily biomass consumed) would have been ideal, however such data would be continuous and positive, but also feature many zeros, for which modelling options are currently limited, and it was not clear how the assumptions of such options (*e.g.,* zero-inflated gamma response distribution) match the data-generating process of prey consumption by falcon nestlings. Additionally, it was not clear how unknown prey items, whose size and proportion eaten were unknown, and whose unit was therefore in deliveries, would be integrated in such a framework.

Turning back to biology, findings from Chapter 4 beg numerous additional questions within the Rankin Inlet, Nunavut study area. Most notably, how does prey consumption translate into reproductive success? Disparities in predicted biomass consumption at individual nests were large, reflecting differences in prey abundance as well as the influence of site-year random effects. Boulet et al. (2001) suggested that nestlings could survive and grow on a wide range of prey intakes, so the link between prey intake and reproductive success may not be obvious. The most logical extension of my study would be to investigate the relationship between prey consumption and nestling survival or growth.

Results of my study also have bearing on the food supplementation experiment that took place in Rankin Inlet from 2013-17. In particular, future questions should focus on the mechanism by which nestlings exhibit greater survival when provided extra food. Model results suggested overall biomass intake was not impacted by food supplementation, which may mean adults decreased their hunting effort in response to the extra food, which could lead to nestlings benefiting from food supplementation through increased nest attendance. A follow-up study on nest attendance could examine this possibility. Furthermore, parent-offspring conflict may lead to adults deriving benefit from food supplementation, and a follow-up study could investigate adult survival during the non-breeding season via re-sightings of marked individuals.

Future study could also collect movement data on Peregrine Falcons to delineate home ranges, which would lead to more accurate estimates of the prey available to each nest than I was able to manage here. This in turn would lead to better delineation of the effects of prey availability versus innate differences between individual breeding pairs in hunting ability or prey preference. Individual diet specialization has been recognized as widespread (Bolnick et al. 2003) and may be a factor affecting community dynamics and species evolution (Bolnick et al. 2011). Delineation of home ranges may also shed light on the potential for predator interference in the MSFR, which was noted in the Chapter 4 Discussion as another avenue of potential study.

Finally, there is considerable interest in how climate change may alter species interactions (Gilg et al. 2012), and previous study by Robinson et al. (2017) indicated that biomass delivered to Peregrine Falcon nestlings declined in a year with cool, wet weather conditions, independent of changes in prey abundance. Wet weather may reduce time spent hunting by adult Peregrine Falcons or else make prey less active or available. Increased frequency and severity of precipitation are among the predicted changes to climate in many Arctic locations (Meredith et al. 2019), thus, incorporating weather variables into the MSFR, particularly into the linear models for attack rates would be another avenue of future study.

### 5.0.6 Peregrine Falcons in a changing Arctic

Franke et al. (2020) presented Peregrine Falcon occupancy and productivity data from across the Arctic, with considerably heterogeneity noted across study areas. Many study areas showed both greater variability, long-term temporal trends, and perhaps, in some cases, possible cyclic dynamics, not present at Rankin Inlet. While some of long-term increases in population parameters are likely evidence of recovery following declines due to organochloride contaminants (Enderson et al. 1995), and comparisons across study areas are fraught with differences in survey methodology, prey abundance and the ecological role Peregrine Falcons play in each study area is another possible explanation for variation in population dynamics. While typically cited as a specialist on avian prey, particularly passerines and shorebirds, my study adds to previous lines of evidence that peregrines can function as generalist consumers. Peregrine populations with less diverse prey communities compared to Rankin Inlet may be more subject to fluctuations in the abundance of any one prey, and may have more variable populations as a result. However, despite consuming multiple prey, small birds were the only prey type that predicted biomass consumption at nests in my study area, indicating that local abundance of small birds may impact the Rankin Inlet population, regardless of changes in the rest of the prey community. A synthesis of foraging behaviour in light of population dynamics in Peregrine Falcons across the Arctic and the world would shed light on the ecological role they play across their range and the factors affecting their populations.

With the climate of the Arctic changing rapidly (Meredith et al. 2019), peregrine distribution is expected by some to shift northwards, and to contract overall (Gu et al. 2021) due to loss of open tundra. Determining the role peregrines play and the impact they have upon prey populations may simultaneously shed light on their ability to invade established ecosystems, displace competitors, deplete sensitive prey populations, and also the impact of their removal from systems of which they are currently a part. Studies such as my own also highlight the potential impact of range expansion in the prey community; the invasion of a new potential prey source into the Rankin Inlet ecosystem may be analogous to the food supplementation experiment, or the change in microtine abundance between peak and crash phase. If that were the case, then I would predict that a substantial prey invasion would decrease the impact of Peregrine Falcon predation upon the prey community already in place. Clearly, there are many moving parts in Arctic ecosystems at present (Gilg et al. 2012), which is a source of both uncertainty and potential for observational and experimental studies highlighting species interactions and community dynamics. This thesis was one attempt at capturing some of that uncertainty.

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# Appendix A: Supplementary data for avian distance sampling

Table A.1: Species and counts recorded during distance sampling surveys from 2015-17 at Rankin Inlet, Nunavut, Canada. Reproduced from Online Resource 1 in Hawkshaw et al. (2021).

| | **Observations** | **Individuals** | **Species** | **%Ind** |
|---|---|---|---|---|
| Songbird | 1271 | 1966 | American Pipit (*Anthus rubescens*) | 25.8 |
| | | | Redpoll (*Acanthis* spp.) | 8.2 |
| | | | Horned Lark (*Eremophila alpestris*) | 24.0 |
| | | | Lapland Longspur (*Calcarius lapponicus*) | 17.9 |
| | | | Savannah Sparrow (*Passerculus sandwichensis*) | 12.9 |
| | | | Snow Bunting (*Plectrophenax nivalis*) | 4.2 |
| | | | White-crowned Sparrow (*Zonotrichia leucophrys*) | 1.0 |
| | | | Songbird spp. | 6.1 |
| Shorebird | 109 | 236 | American Golden Plover (*Pluvialis dominica*) | 4.8 |
| | | | Least Sandpiper (*Calidris minutilla*) | 6.7 |
| | | | Pectoral Sandpiper (*Calidris melanotos*) | 8.1 |

(Continued on next page)

|  | Observations | Individuals | Species | %Ind |
|---|---|---|---|---|
|  |  |  | Red-necked Phalarope (*Phalaropus lobatus*) | 2.9 |
|  |  |  | Semipalmated Plover (*Charadrius semipalmatus*) | 37.6 |
|  |  |  | Semipalmated Sandpiper (*Calidris pusilla*) | 9.5 |
|  |  |  | Shorebird spp. | 30.5 |
| Loon | 87 | 140 | Common Loon (*Gavia immer*) | 11.0 |
|  |  |  | Pacific Loon (*Gavia pacifica*) | 76.5 |
|  |  |  | Red-throated Loon (*Gavia stellata*) | 12.5 |
| Swan | 88 | 309 | Tundra Swan (*Cygnus columbianus*) | 100.0 |
| Gull | 545 | 1085 | Glaucous Gull (*Larus hyperboreus*) | 1.1 |
|  |  |  | Herring Gull (*Larus argentatus*) | 98.1 |
|  |  |  | Long-tailed Jaeger (*Stercorarius longicaudus*) | 0.1 |
|  |  |  | Parasitic Jaeger (*Stercorarius parasiticus*) | 0.6 |
| Goose | 313 | 1129 | Canada/Cackling Goose (*Branta canadensis/B. hutchinsii*) | 84.8 |
|  |  |  | Snow/Ross' Goose (*Anser caerulescens/A. rossii*) | 9.3 |
|  |  |  | Greater White-fronted Goose (*Anser albifrons*) | 5.9 |
| Duck | 192 | 617 | Common Eider (*Somateria mollissima*) | 51.2 |

(Continued on next page)

|  | Observations | Individuals | Species | %Ind |
|---|---|---|---|---|
|  |  |  | Common Goldeneye (*Bucephala clangula*) | 1.7 |
|  |  |  | Green-winged Teal (*Anas crecca*) | 1.2 |
|  |  |  | King Eider (*Somateria spectabilis*) | 0.7 |
|  |  |  | Scaup (*Aythya* spp.) | 1.0 |
|  |  |  | Long-tailed Duck (*Clangula hyemalis*) | 23.0 |
|  |  |  | Northern Pintail (*Anas acuta*) | 15.5 |
|  |  |  | Red-breasted Merganser (*Mergus serrator*) | 3.0 |
|  |  |  | Duck spp. | 2.6 |
| Crane | 337 | 739 | Sandhill Crane (*Antigone canadensis*) | 100.0 |

# Appendix B: Prey distribution maps and snap trapping results

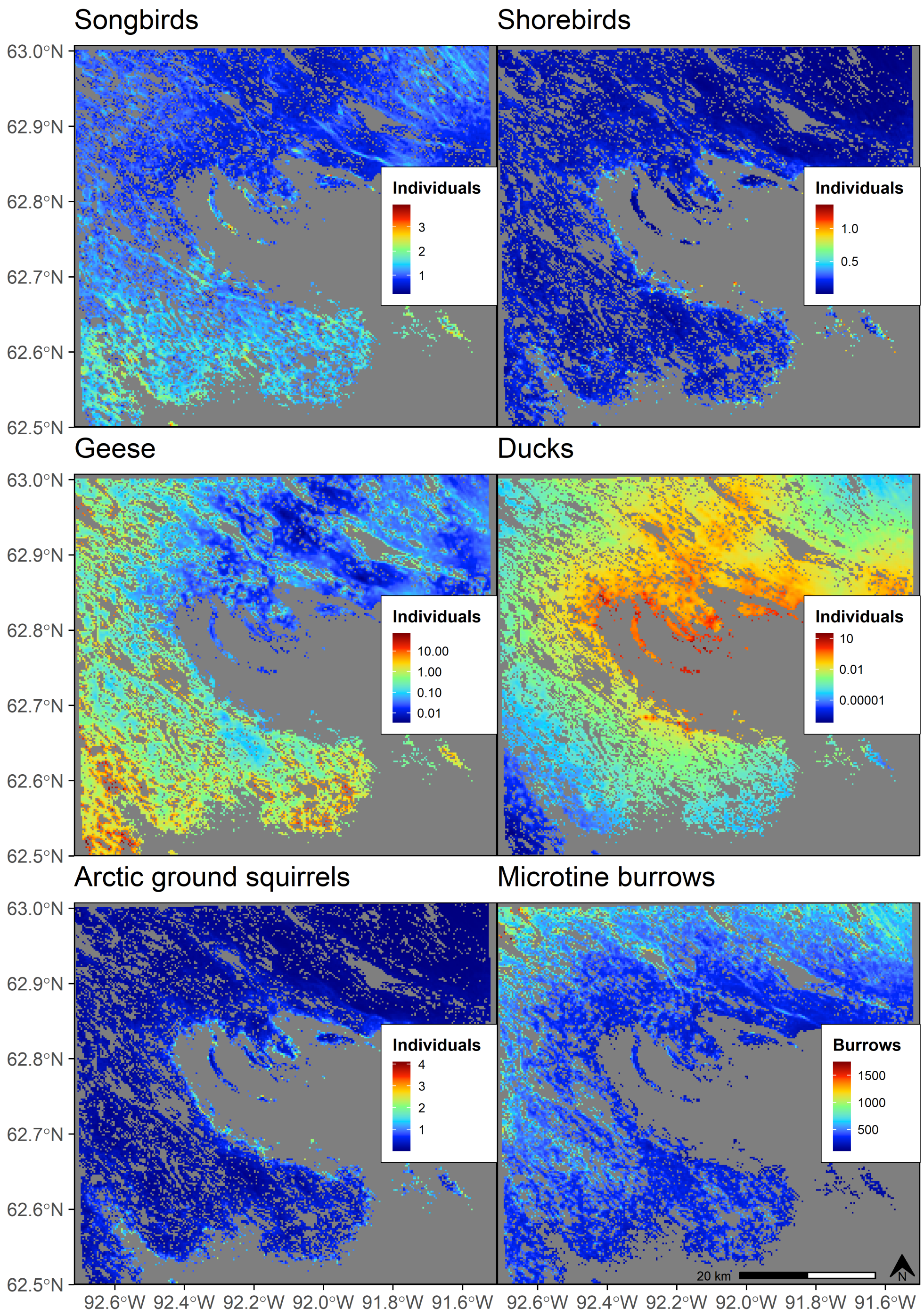

Figure B.1: Example distribution maps for Peregrine Falcon (*Falco peregrinus*) prey at Rankin Inlet, Nunavut, Canada. Maps display the number of individuals predicted to occur in 240 x 240-m grid cells for each prey type. Maps are shown for late summer (Peregrine Falcon brooding period) 2015. $\log_{10}$-transformed colour scales are shown for geese and ducks due to outliers that would otherwise mask patterns. Models used to construct the maps were the best-fitting models described in Chapter 3 for avian prey and Arctic ground squirrels (*Urocitellus parryii*), and in Chapter 2 for microtine burrows. Distance sampling data and burrow counts used to construct the maps were collected from 2015-17.

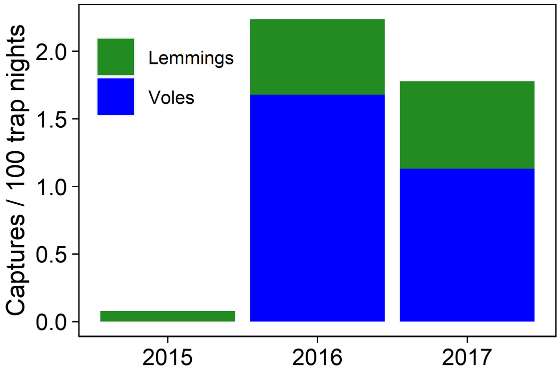

Figure B.2: Snap trapping results for lemmings (*Dicrostonyx*) and red-backed voles (*Clethrionomys rutilus*) at Rankin Inlet, Nunavut, Canada from 2015-17. Index is expressed as captures per 100 trap nights, which was the number of traps set each night, minus the number of misfires and broken traps when traps were checked each morning.

# Appendix C: MSFR model parameters and diagnostics

Table C.1: Parameter estimates and diagnostics from the multispecies functional response model described in Chapter 4. Displayed are the parameter name, its meaning, mean and 95% credible interval of the posterior, the effective sample size, and $\hat{R}$ statistic. Prey consumption by Peregrine Falcon (*Falco peregrinus*) nestlings and prey abundance data for the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

| **Parameter** | **Meaning** | **Estimate** | **N_eff** | $\hat{R}$ |
|---|---|---:|---:|---:|
| tt_ot | "other" handling time | 14.42 (9.54, 22.22) | 2700.55 | 1 |
| zero_wf | waterfowl zero-inflation intercept | -2.54 (-4.16, -1.61) | 5130.28 | 1 |
| zero_sq | Arctic ground squirrel zero-inflation intercept | -2.51 (-3.53, -1.86) | 5510.57 | 1 |
| zero_sb | small bird zero-inflation intercept | -5.08 (-6.94, -3.87) | 9163.33 | 1 |
| pp_ot | "other" probability of identification | 0.21 (0.14, 0.32) | 3014.92 | 1 |
| pp_mt | microtine probability of identification | 0.54 (0.45, 0.65) | 2920.26 | 1 |
| pp_wf | waterfowl probability of identification | 0.83 (0.7, 0.95) | 2354.29 | 1 |
| pp_sq | Arctic ground squirrel probability of identification | 0.91 (0.85, 0.95) | 5993.93 | 1 |

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| **Parameter** | **Meaning** | **Estimate** | **N_eff** | $\hat{R}$ |
|---|---|---:|---:|---:|
| pp_qu | quail probability of identification | 0.9 (0.83, 0.96) | 9114.82 | 1 |
| pp_sb | small bird probability of identification | 0.98 (0.94, 1) | 7274.34 | 1 |
| alpha_ot_aa | "other" attack rate intercept | 2.35 (1.22, 3.49) | 4902.32 | 1 |
| alpha_qu_tt | quail handling time intercept | 1.57 (0.8, 2.31) | 10232.56 | 1 |
| alpha_qu_aa | quail attack rate intercept | 3.57 (2.4, 4.74) | 5058.35 | 1 |
| alpha_mt_tt | microtine handling time intercept | 2.26 (1.22, 3.03) | 3600.33 | 1 |
| alpha_mt_aa | microtine attack rate intercept | 4.26 (3.13, 5.36) | 5231.65 | 1 |
| alpha_wf_tt | waterfowl handling time intercept | 1.24 (0.35, 2.11) | 4498.7 | 1 |
| alpha_wf_aa | waterfowl attack rate sub model intercept | 2.09 (0.82, 3.31) | 4346.15 | 1 |
| alpha_sq_tt | Arctic ground squirrel handling time intercept | 1.76 (1.36, 2.15) | 8730.01 | 1 |
| alpha_sq_aa | Arctic ground squirrel attack rate intercept | 2.05 (0.1, 3.98) | 2528 | 1 |
| alpha_sb_tt | small bird handling time intercept | 0.81 (-0.37, 1.73) | 2755.38 | 1 |
| alpha_sb_aa | small bird attack rate intercept | 3.69 (2.27, 5.06) | 1860.39 | 1 |
| mm_qu | quail switching parameter | 0.42 (0.22, 0.62) | 12469.9 | 1 |
| mm_wf | waterfowl switching parameter | 0.19 (0.01, 0.46) | 3255.64 | 1 |
| mm_sq | Arctic ground squirrel switching parameter | 0.69 (0.14, 1.24) | 1881.47 | 1 |

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| **Parameter** | **Meaning** | **Estimate** | **N_eff** | $\hat{R}$ |
|---|---|---:|---:|---:|
| mm_mt | microtine switching parameter | 0.09 (0, 0.28) | 7693.05 | 1 |
| mm_sb | small bird switching parameter | 0.4 (0.09, 0.73) | 1265.4 | 1 |
| beta_ot_aa_age | “other” attack rate coefficient for nestling age | 1.29 (0.17, 2.42) | 3247.66 | 1 |
| beta_qu_tt_age | quail handling time coefficient for nestling age | 0.92 (-0.09, 1.93) | 7247.26 | 1 |
| beta_qu_aa_age | quail attack rate coefficient for nestling age | -0.47 (-1.38, 0.47) | 4662.83 | 1 |
| beta_wf_tt_age | waterfowl handling time coefficient for nestling age | 1.07 (0.13, 2.01) | 4848.7 | 1 |
| beta_wf_aa_age | waterfowl attack rate coefficient for nestling age | 2.23 (1.32, 3.14) | 4147.32 | 1 |
| beta_mt_tt_age | microtine handling time coefficient for nestling age | -2.93 (-4.53, -1.05) | 5105.32 | 1 |
| beta_mt_aa_age | microtine attack rate coefficient for nestling age | -0.79 (-1.7, 0.12) | 4271.22 | 1 |
| beta_sq_tt_age | Arctic ground squirrel handling time coefficient for nestling age | -1.44 (-2.51, -0.5) | 3382.91 | 1 |
| beta_sq_aa_age | Arctic ground squirrel attack rate coefficient for nestling age | -3.45 (-4.35, -2.56) | 4435.24 | 1 |
| beta_sb_tt_age | small bird handling time coefficient for nestling age | -1.43 (-3.45, 0.44) | 2422.89 | 1 |

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| Parameter | Meaning | Estimate | N_eff | $\hat{R}$ |
|---|---|---:|---:|---:|
| beta_sb_aa_age | small bird attack rate coefficient for nestling age | 1.19 (0.35, 2.03) | 3945.04 | 1 |
| beta_ot_aa_nestling | “other” attack rate coefficient for number of nestlings | -0.75 (-1.77, 0.28) | 6060.67 | 1 |
| beta_qu_tt_nestling | quail handling time coefficient for number of nestlings | -1.58 (-2.54, -0.59) | 10227.83 | 1 |
| beta_qu_aa_nestling | quail attack rate coefficient for number of nestlings | 0.23 (-0.86, 1.34) | 7175.91 | 1 |
| beta_wf_tt_nestling | waterfowl handling time coefficient for number of nestlings | -0.8 (-1.63, 0.06) | 6817.36 | 1 |
| beta_wf_aa_nestling | waterfowl attack rate coefficient for number of nestlings | 0.73 (-0.27, 1.73) | 6236.34 | 1 |
| beta_mt_tt_nestling | microtine handling time coefficient for number of nestlings | -1.23 (-2.29, -0.14) | 8855.97 | 1 |
| beta_mt_aa_nestling | microtine attack rate coefficient for number of nestlings | 0.26 (-0.77, 1.29) | 5898.1 | 1 |
| beta_sq_tt_nestling | Arctic ground squirrel attack rate coefficient for number of nestlings | -0.25 (-0.87, 0.38) | 8814 | 1 |
| beta_sq_aa_nestling | Arctic ground squirrel handling time coefficient for number of nestlings | 0.41 (-0.61, 1.45) | 6075.62 | 1 |
| beta_sb_tt_nestling | small bird attack rate coefficient for number of nestlings | -0.33 (-1.25, 0.6) | 7169.51 | 1 |

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| **Parameter** | **Meaning** | **Estimate** | **N_eff** | $\hat{R}$ |
|---|---|---:|---:|---:|
| beta_sb_aa_nestling | small bird handling time coefficient for number of nestlings | -0.86 (-1.73, 0.01) | 4946.04 | 1 |
| sigma_ot | "other" random effect variance | 0.69 (0.46, 0.99) | 2054.21 | 1 |
| sigma_un | unknown random effect variance | 0.54 (0.43, 0.67) | 3402.56 | 1 |
| sigma_mt | microtine random effect variance | 0.9 (0.68, 1.17) | 3753.04 | 1 |
| sigma_wf | waterfowl random effect variance | 0.93 (0.7, 1.2) | 2744.92 | 1 |
| sigma_sq | Arctic ground squirrel random effect variance | 1.76 (1.43, 2.16) | 2420.49 | 1 |
| sigma_qu | quail random effect variance | 0.51 (0.26, 0.78) | 1435.91 | 1 |
| sigma_sb | small bird random effect variance | 0.35 (0.06, 0.58) | 413.46 | 1.01 |

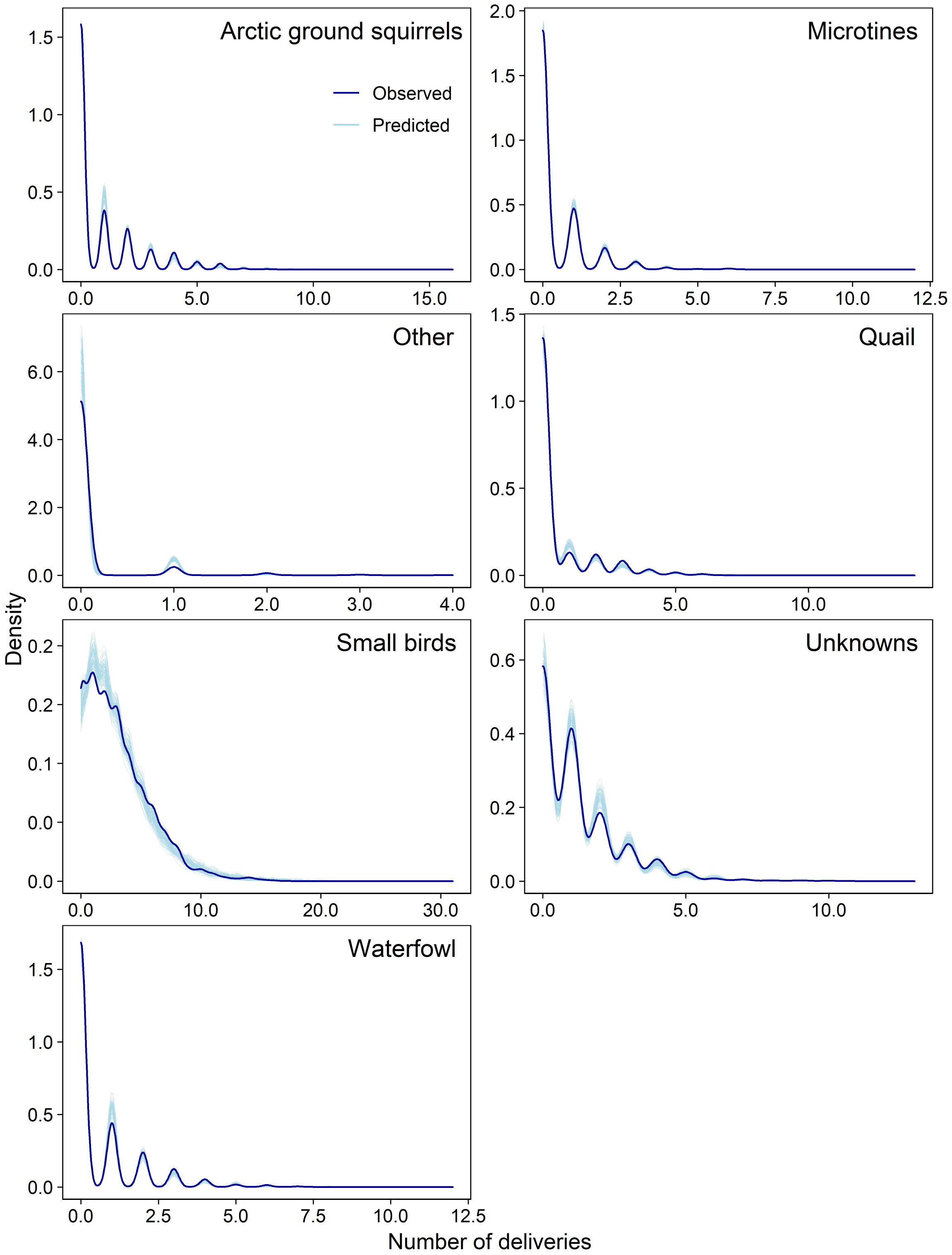

Figure C.1: Distribution of observed delivery counts of prey to monitored Peregrine Falcon (*Falco peregrinus*) nests at Rankin Inlet, Nunavut, Canada, from 2015-17, along with 100 simulated datasets from the multispecies functional response model described in Chapter 4. Observed data are displayed in dark blue, while simulated data are displayed in light blue. Generally, observed data falls within the ranges of the simulated data, indicating that the model could predict the data relatively well.

# Appendix D: Meal size model parameters and diagnostics

Table D.1: Parameter estimates and diagnostics from the meal size model described in Chapter 4. Displayed are the parameter name, its meaning, mean and 95% credible interval of the posterior, the effective sample size, and $\hat{R}$ statistic. Peregrine Falcon nestling prey consumption data for the model were collected from 2015-17 at Rankin Inlet, Nunavut, Canada.

| **Parameter** | **Meaning** | **Estimate** | **N_eff** | $\hat{R}$ |
|---|---|---:|---:|---:|
| alpha_qu | quail intercept | -2.09 (-2.53, -1.66) | 6038 | 1 |
| alpha_sq | Arctic ground squirrel intercept | -2.75 (-3.06, -2.44) | 5642 | 1 |
| alpha_wf | waterfowl intercept | -2.73 (-3.13, -2.32) | 5541 | 1 |
| beta_age_qu | quail coefficient for nestling age | 2.14 (1.72, 2.58) | 8336 | 1 |
| beta_age_sq | Arctic ground squirrel coefficient for nestling age | 1.81 (1.42, 2.21) | 8204 | 1 |
| beta_age_wf | waterfowl coefficient for nestling age | 2.58 (2.15, 3.04) | 6894 | 1 |
| beta_nestling_qu | quail coefficient for number of nestlings | 0.87 (0.35, 1.4) | 7003 | 1 |
| beta_nestling_sq | Arctic ground squirrel coefficient for number of nestlings | 0.96 (0.58, 1.34) | 6769 | 1 |
| beta_nestling_wf | waterfowl coefficient for number of nestlings | 1.86 (1.4, 2.32) | 6753 | 1 |

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| **Parameter** | **Meaning** | **Estimate** | **N_eff** | $\hat{R}$ |
|---|---|---:|---:|---:|
| sigma | standard deviation for log-normal distribution | 0.66 (0.62, 0.69) | 12511 | 1 |

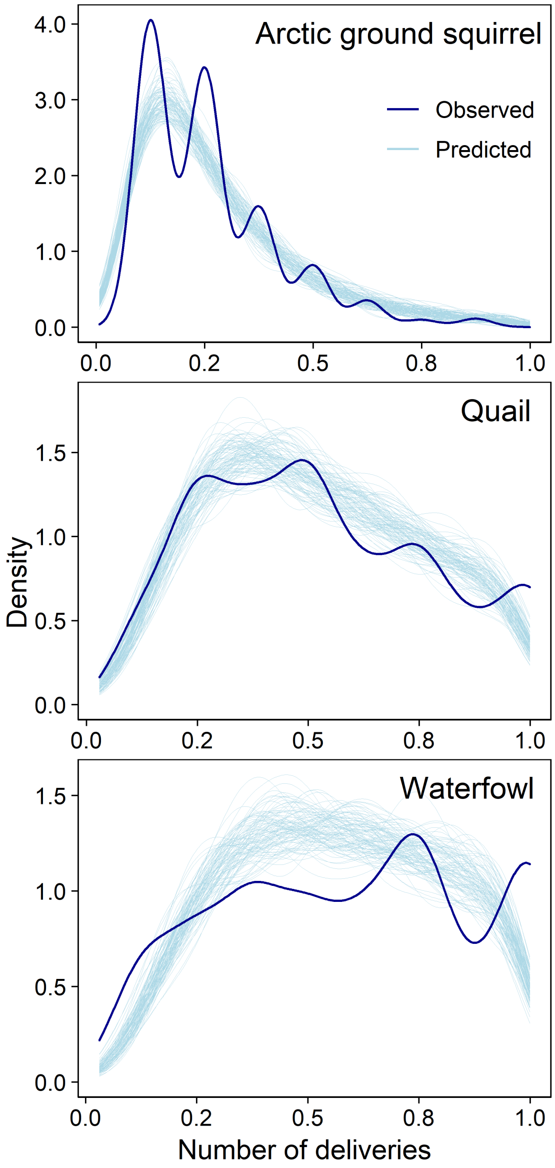

Figure D.1: Distribution of meal sizes (proportion of prey item) consumed by Peregrine Falcon (*Falco peregrinus*) nestlings at Rankin Inlet, Nunavut, Canada, from 2015-17, along with 100 simulated datasets from the meal size model described in Chapter 4. Observed data are displayed in dark blue, while simulated data are displayed in light blue. The apparent multimodal nature of the observed data is a measurement artifact of the discrete intervals in which observers estimated the proportion of a prey item eaten (see Section 4.2.2). Otherwise, the distribution of simulated data matches the observed fairly well.