Foraging ecology of the Arctic peregrine falcon (*Falco peregrinus tundrius*)

by

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Abstract

Specialist predators with a limited diet may be less adaptable to environmental change than generalists, which consume a diversity of prey. As the climate changes, ecological homogenization is occurring, where generalist species outcompete specialists, reducing ecosystem complexity. In Arctic ecosystems, temperatures are rising at almost twice the rate of the rest of the planet and summer rainfall has increased significantly over the last century. Arctic peregrine falcons (*Falco peregrinus. tundrius*) breeding throughout the circumpolar regions of Canada, the USA, and Greenland have a diversity of prey species to choose from, but little is known about how they select for these resources as prey populations fluctuate. To fully appreciate the potential implication of climate change on Arctic peregrine falcon populations, research investigating prey selection and the potential for peregrines to switch to alternative prey is needed. In this dissertation I studied an Arctic tundra ecosystem around Igloolik, Nunavut, and related spatiotemporal variations in all prey species consumed by peregrines to annual variation in weather, while simultaneously monitoring peregrine diet and reproductive output. First, I investigated the relationship between annual variation in weather and spatiotemporal variation in the abundance of multiple avian guilds: songbirds (Passeriformes), shorebirds (Scolopacidae and Charadriidae), gulls (Laridae and Sternidae), loons (Gaviiformes), geese and ducks (Anatidae), and black guillemots (*Cepphus grylle*). I spatially stratified my study area and conducted distance sampling to estimate strata-specific densities of each guild during the summers of 2010-2012 while also monitoring temperature and rainfall. Shorebirds, songbirds and gulls were less abundant in 2012, which was a cool and wet summer, relative to 2010 and 2011. I monitored annual variation in lemming abundance using snap trapping and assumed spatial variation in lemming density was proportional to spatial variation in the density of lemming burrows observed while surveying distance sampling transects. Lemming density was at least 25 times higher in 2011 than in 2010 and 2012. I quantified peregrine nestling diet using a combination of two methods: direct observations from motion-sensitive cameras at nest sites and stable isotope analysis. I developed a novel method of incorporating unidentified food items from nest camera images into diet estimates and quantifying error around these estimates for individual nests, which were used as informative prior hypotheses in Bayesian mixing models predicting nestling diets. I used stable isotope signatures of falcon nestling plasma and prey tissues samples as inputs for Bayesian mixing models. When informative priors were included, the resulting diet estimates from mixing models had narrow credible intervals and generally reflected the prior hypotheses. Nestling diets were dominated by songbirds and shorebirds (insectivorous birds), which generally contributed > 80% of total diet. The use of ducks and marine prey (gulls and black guillemots) was somewhat limited, but these prey contributed up to 50% of nestlings' diet in nests with more access to marine habitat. Lemmings were generally not used while they were scarce in 2010 and 2012, but they contributed 20-50% of nestlings' diet during the lemming peak in 2012. Next, I investigated whether peregrines switched to alternative prey when their primary prey of insectivorous birds declined by examining the functional response of falcons to changes in prey density. I also compared peregrine nestling survival across all years of the study to determine if reproductive output was influenced by prey density and prey intake rates. Peregrine falcons exhibited a functional response to lemmings, ducks and total prey density: intake rates decreased when prey densities declined in 2012. The number of fledglings produced per nest also declined in 2012, indicating there was a fitness consequence of declining prey densities and intake rates. Finally, I compared the proportional availability of each prey type to its proportional contribution to peregrine falcon diets and calculated selection ratios for each prey type. Peregrine falcons selected for insectivorous birds and avoided lemmings. There was no evidence that peregrines switched to alternative prey when insectivorous birds declined. Results from my research indicated that Arctic peregrine falcons specialize on insectivorous birds and use alternative prey only opportunistically to supplement their diet.

Preface

This dissertation contains original work by Barry Glen Robinson. A version of Chapter 2 has been published as:

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For these publication, B. G. Robinson designed and implemented the field program, analyzed the data, and wrote the majority of the manuscript. A. Franke and A. E. Derocher provided logistic, in kind, and monetary support for the field work and provided valuable input and feedback throughout the implementation of the field work and writing of the manuscript.

All methods used to collect data for this dissertation were in accordance with the guidelines put forth by the Canadian Council on Animal Care and were approved by the University of Alberta's BioSciences Animal Care and Use Committee (protocol #738).

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Table of Contents

1 Introduction 1

1.1 Generalist and specialist predators in multi-prey systems 1

1.2 Influence of climate on predator-prey interactions 2

1.3 The Arctic peregrine falcon: generalist or specialist? 4

1.4 Dissertation outline 7

1.5 Study area 9

2 The influence of weather and lemmings on spatiotemporal variation in the abundance of multiple avian guilds in the Arctic 12

2.1 Introduction 12

2.2 Methods 15

2.2.1 Spatiotemporal stratification 15

2.2.2 Distance sampling design 18

2.2.3 Statistical analysis of spatiotemporal variation 20

2.3 Results 22

2.3.1 Detection functions 22

2.3.2 Spatiotemporal variation 22

2.4 Discussion 23

3 Estimating nestling diet with cameras: quantifying uncertainty from unidentified food items 37

3.1 Introduction 37

3.2 Methods 38

3.2.1 Nest monitoring 38

3.2.2 Estimating diet along with uncertainty 39

3.3 Results 42

3.4 Discussion 43

4 Estimating the diet of predators with stable isotopes: using priors in Bayesian mixing models to reduce uncertainty 49

4.1 Introduction 49

4.2 Methods 52

4.2.1 Peregrine falcon monitoring 52

4.2.2 Prey tissue collection 53

4.2.3 Stable isotope analysis 54

4.2.4 Developing informative priors 55

4.2.5 Implementing mixing models in the SIAR package 55

4.3 Results 57

4.4 Discussion 59

5 Weather-mediated prey depletion causes a functional response for a top predator ... 68

5.1 Introduction 68

5.2 Methods 71

5.2.1 Spatiotemporal variation in prey density 71

5.2.2 Estimating prey available to foraging peregrine falcons.............................. 72

5.2.3 Prey delivery rates and nestling survival... 74

5.2.4 Functional response.. 74

5.3 Results 75

5.3.1 Spatiotemporal variation in prey density 75

5.3.2 Functional response.. 75

5.4 Discussion 76

6 Conclusion 93

6.1 Diet preferences of the Arctic peregrine falcon 93

6.2 Influence of diet on Arctic peregrine falcon reproductive output 97

6.3 The sensitivity of Arctic peregrine falcons to severe weather and the potential implications of climate change 98

6.4 Future directions: indirect effects of climate change and the importance of monitoring multiple trophic levels.. 101

Literature cited 108

Appendices.. 142

List of Tables

Table 2.1. *A priori* hypotheses predicting the relationship between the abundance of different avian guilds and three landscape metrics. 29

Table 2.2. Values of the landscape metrics for each of the 8 strata used to stratify the 2030 km^2 study area at the northern tip of the Melville Peninsula, Nunavut, Canada. 30

Table 2.3. Detection function model forms determined to be most parsimonious (AIC_c^b) for each avian guild. 31

Table 2.4. Top log-linear Poisson models predicting the counts of bird clusters observed along transects within 16 different strata. 32

Table 3.1. Data from four nest cameras monitoring peregrine falcon nestlings in Nunavut, Canada, showing the frequency of prey items within each category delivered to nestlings during the observation period. 45

Table 3.2. All of the possible outcomes (*j*) of allocating the 7 unidentified prey items from nest site 2 in 2010 (Table 3.1) to either the unidentified avian or lemming categories, along with the probability of each outcome occurring (Po_j). 46

Table 3.3. The probability of an unidentified prey item being within each prey category for each year. Probabilities are based on the proportion of identified prey items within each prey category across all nests for a given year. 47

Table 3.4. An example of 10 samples of possible outcomes simulated from the probability space shown in Table 3.2, demonstrating how the frequency of identified prey items in each prey category (site 2, 2010, in Table 3.1) were modified by allocating the unidentified. 48

Table 4.1. The taxonomic classification of each prey type, along with the mean and standard deviation of the carbon and nitrogen concentrations within their tissues, and the mass assumed for individual prey deliveries of each type. 64

Table 5.1. Functional response model forms relating prey delivery rates (D g/nestling/day) to prey density (P g/km^2); *a* and *b* are parameters. The performance of model forms was compared separately for each prey type and nestling age class using AIC$_c$. 82

Table 5.2. Detection function model forms determined to be most parsimonious (AIC$_c$) for each marine guild. 83

Table 5.3. Marine prey density estimates and 95% confidence intervals for each year. Estimates were produced from distance sampling data. 84

Table 5.4. Mean density of lemming burrows observed along distance sampling transects and strata-specific estimates of lemming density for each year. Abundance estimates from snap trapping on strata 8 each year were transformed into density estimates assuming variation in lemming density was proportional to variation in burrow density. 85

Table 5.5. Results from AIC$_c$ analysis comparing various functional response model forms (Table 5.1) relating peregrine falcon prey delivery rates to prey density, treating each peregrine nestling age class and prey type separately. Bolded models were assumed to represent the functional response. Model forms not shown for a given age class and prey type did not converge during parameterization. 86

Table 5.6. Estimates, standard errors (SE) and *P*-values for the parameters of a linear regression model predicting total prey delivery rates to peregrine falcon nestlings (g/nestling/day) as a function of year, nestling age class and an interaction between these variables. Year 2012 and age class 10-14 days were used as reference categories. 88

Table 6.1. AIC$_c$ analysis comparing generalized linear models (Poisson) predicting the number of fledglings produced by peregrine falcon nests as a function of the density of different types of prey available within falcon home-ranges. 104

List of Figures

Figure 1.1. Study area location near Igloolik, Nunavut, Canada. Black dots represent Arctic peregrine falcon nests monitored from 2010-2012. Numbers are unique identities for nest sites used throughout this dissertation. 11

Figure 2.1. Spatial distribution of the strata used to estimate the density of various avian guilds using distance sampling. Strata were based on a Terrain Ruggedness Index (TRI), the amount of standing fresh water, and the Normalized Difference Vegetation Index (NDVI).34

Figure 2.2. Mean monthly temperature and total monthly rainfall in the Igloolik study area. Data from 2010-2012 were collected during this study using a remote weather station located on the Coxe Islands. The 20-year mean is based on data from 1980-2000 collected by Environment Canada at the Igloolik airport (http://www.weather.gc.ca)............................. 35

Figure 2.3. Guild-specific density estimates in relation to summer weather and landscape metrics. For each guild (A – songbirds, B – shorebirds, C – geese, D – gulls, E – loons) only landscape metrics found to significantly influence the number of individuals observed along transects were used (Table 2.4). The binomial landscape metrics (low (L) or high (H)) include the proportion of area made up of standing freshwater (water), terrain ruggedness (rugged) and vegetation productivity (NDVI). Note the scale on the density axis is different for each guild. Error bars show the 95% confidence interval around each density estimate. 36

Figure 4.1. The mixing space geometry for the Bayesian mixing models used to estimate peregrine falcon diet. Shown are the mean and standard deviations of the isotopic values for each prey type (corrected for diet-blood fractionation) relative to the isotopic values of each nestling peregrine plasma sample. Contour lines and colour ramp show how variation in the isotopic value of peregrine falcon plasma (mixture) would influence the probability that a

mixing model using the prey types (sources) shown could be reasonably solved (Smith et al. 2013). Peregrine plasma samples outside the outer 5% probability contour were not used in my mixing models. 65

Figure 4.2. A comparison of the posterior distribution of dietary proportions for each prey type consumed by peregrine falcons estimated with uninformed mixing models (left column), motion-sensitive cameras (center column; priors), and informed mixing models (right column), which incorporated priors into the uninformed models. Each row of graphs represents a single nest. The influence of priors on the informed model changes as the error around priors increases from a-d. Nest-years shown are site 5, 2010 (a); site 8, 2011 (b); site 13, 2011 (c); and site 5, 2011 (d); see Figure 1.1 for geographic location of sites. 66

Figure 4.3. A comparison of the posterior distribution of dietary proportions for each prey type consumed by peregrine falcons estimated with uninformed mixing models (left column), motion-sensitive cameras (center column; priors), and informed mixing models (right column), which incorporated priors into the uninformed models. Each row of graphs represents a single nest. The influence of priors on the informed model changes as the distribution of prey types within the diet becomes more even from a-d. Nest-years shown are site 2, 2010 (a); site 13, 2010 (b); site 2, 2011 (c); and site 14, 2011 (d); see Figure 1.1 for geographic location of sites. 67

Figure 5.1. Home-ranges of adult female peregrine falcons represented by the 95% isopleth of utilization distirbutions (dashed line). The solid lines represent the minimum convex polygon around each 95% isopleth, which is the area assumed to be available to foraging peregrine falcons. 89

Figure 5.2. Functional responses for different prey types and falcon nestling age classes (indicated in upper right corner of each graph) showing the relationship between prey density within peregrine falcon home-ranges and prey delivery rates to falcon nestlings (red = 2010, green = 2011, blue = 2012). Blue curves represent the models found to best represent each functional response using AIC_c analysis (Table 5.5). Graphs with no curve indicate the null model was best. 90

Figure 5.3. Mean (± standard error) prey delivery rates (total prey biomass) to different age classes of peregrine falcon nestlings during each year of this study. 92

Figure 6.1. Proportional contribution of each prey type to the diet of nestling peregrine falcons in relation to proportional availability of each prey type within peregrine falcon home ranges. Dashed lines represent no selection; points above the dashed line indicate peregrines were selecting for that prey type, while points below indicate peregrines were avoiding it (red = 2010, green = 2011, blue = 2012). Solid lines for insectivorous birds and lemmings are merely to help visualize the relationship; functions represented by these lines were parameterized using non-linear regression, but no model selection techniques were applied. 105

Figure 6.2. Selection ratios for each prey type estimated for the entire population of peregrine falcons (Manly et al. 2002) for each year of the study. A selection ratio of 1 indicates no selection and ratios > or < 1 indicate selection or avoidance, respectively. Error bars represent Bonferroni confidence intervals. 106

Figure 6.3. Number of fledglings within a nest surviving to 25 days old in relation to the density of insectivorous birds within the home-range surrounding the nest. The black line represents

a generalized linear model parameterized with a Poisson error distribution and a log link function. 107

1 Introduction

1.1 Generalist and specialist predators in multi-prey systems

Optimal foraging theory predicts that prey selection is driven by the energetic costs and benefits associated with encountering, capturing and consuming each prey item (Krebs 1978). Under this theory, a generalist predator will primarily consume their preferred prey type when it is abundant, but switch to alternative prey as their preferred prey declines (Murdoch 1969, Pyke 1984, van Leeuwen et al. 2013). Conversely, a specialist predator will consume their preferred prey type regardless of prey abundance because they possesses adaptations that make them more efficient at encountering, capturing and/or consuming their preferred prey, relative to alternative prey (Krebs 1978)

The concept of specialization is an important component of predator-prey dynamics because the dietary breadth of a predator can influence prey population demographics. Specialist predators can cause populations of their primary prey to cycle (Fryxell and Lundberg 1994, Gilg et al. 2006, Therrien et al. 2014). As the primary prey population grows, so too does the specialist predator, increasing predation pressure on the prey, eventually causing the prey population to crash. Specialist predators cannot be sustained by alternative prey, so their populations subsequently crash, starting the cycle over again (Hanski et al. 1991). In contrast, generalist predators, which are able to subsist on a diversity of prey, tend to have a stabilizing effect on prey populations (Gleeson and Wilson 1986). If both specialist and generalist predators are competing for the same prey type, the prey population may continue to cycle, but the amplitude of prey peaks and the period between peaks may decline (Hanski et al. 2001).

The degree of dietary specialization also has implications for predator populations because specialized and generalized diets both have costs and benefits (Remold 2012).

MacArthur (1972) described a potential mechanism driving the evolution of specialization with the phrase “a jack of all trades is the master of none”. Under this hypothesis, a generalist can never be as efficient as a specialist at consuming any one prey type. The evolution of specialists is, therefore, likely to occur in stable environments with a reliable source of a specific prey type, present either consistently or cyclically (Futuyma and Moreno 1988, Remold 2012). Generalists, in contrast, are better suited for stochastic environments, where prey populations are variable and a flexible diet is advantageous (Kassen 2002). Because of their restricted diet, specialists may be less adaptable to environmental change than generalists (Devictor et al. 2010). It has been long predicted that rapid, anthropogenically-induced, environmental change could lead to ecological homogenization where generalist species outcompete specialists, reducing ecosystem complexity (McKinney and Lockwood 1999). Indeed, a worldwide decline in specialist species has been observed, which is reducing biodiversity, altering ecosystem function and reducing ecosystem goods and services (Clavel et al. 2011). Along with habitat destruction, global climate change is one of the leading causes of ecological homogenization, which will likely perpetuate the widespread loss of ecological specialists (Warren et al. 2001).

1.2 Influence of climate on predator-prey interactions

Global climate change caused by the emission of greenhouse gases into the atmosphere is now a widely accepted phenomenon with pervasive ecological consequences. Surface and ocean temperatures have increased, the global water cycle has been altered with increases in precipitation throughout the Northern Hemisphere, ocean acidification is occurring, the Greenland and Antarctic ice sheets and glaciers around the world have decreased in mass, causing a rise in sea level, and annual mean Arctic sea-ice extent has decreased (IPCC 2014).

Predator-prey interactions can be altered by these rapid changes in climate because each trophic level responds differently to annual variation in weather (Petchey et al. 1999, Pounds et al. 1999, Post and Forchhammer 2008). More specifically, the rate of change in phenology, the timing of life-history events, is generally higher at lower trophic levels (Hoye et al. 2007, Møller et al. 2008, Both et al. 2009, Thackeray et al. 2010). Asynchrony in phenological change across trophic can create a mismatch between the timing of peaks in prey availability and the nutritional demand of predators, a phenomenon known as the mismatch hypothesis (Cushing 1969). For example, Visser et al. (1998) found that spring laying date of great tits (*Parus major*) did not change to match the advance of peak caterpillar abundance, their most important prey, which was driven by a warming climate. Specialist predators relying solely on pulses in the abundance of specific prey may be particularly susceptible to phenological mismatch. Growing evidence of climate-change-related mismatches, particularly in avian species, are being documented in a diversity of ecosystems (Visser et al. 2004, Møller et al. 2008, Both et al. 2009)

The influence of climate change on lower trophic levels unrelated to phenology can also have cascading effects up the food chain. Even if predators are not affected directly, fluctuations in prey abundance associated with climate change can affect predator population dynamics (Bowler et al. 2014). For example, a climate-induced reduction in prey density could lead to functional and numerical responses (Holling 1959b): decreases in prey densities reduce predator encounter rates with prey, subsequently reducing predator consumption rates (functional) and population density (numerical). For generalist predators, the presence of alternative prey can buffer the effects of reductions in their primary prey. Unlike specialists, generalists may exhibit a multi-species functional response, where prey consumption rates are a function of the relative abundance of multiple prey populations (Oaten and Murdoch 1975, Smout et al. 2010, Hellström et al. 2014).

Knowledge of whether a predator is a specialist with a narrow diet or a generalist with a variety of potential prey types is essential to determine the extent to which climate change will influence predator-prey interactions. Although dietary studies of predators are widespread, relating diet to prey availability to determine how predators select from an assortment of prey are less common. Without knowledge of the prey preferences of a predator, it is impossible to determine how fluctuations in prey abundance will impact predator populations. Determining the influence of climate change on predator-prey interactions through functional and numerical responses is difficult because it requires simultaneous monitoring of weather (as a proxy for climate change over longer periods), prey density, and predator density and diet. Long-term studies encompassing temporal fluctuations in weather, prey and predators are ideal, but costly. However, short-term studies relating weather variables to spatiotemporal variation in prey densities, and predator diet and demography can provide insight into the potential long-term effects of a changing climate (Berteaux et al. 2006). Case studies involving short and simple food webs with limited amounts of competition among predators and few alternative prey provide a good starting point for the evaluation of the influence of climate change on predator-prey interactions.

1.3 The Arctic peregrine falcon: generalist or specialist?

Peregrine falcons (*Falco peregrinus*) are a top predator often considered to be generalists because of their vast global distribution which ranges from Arctic tundra to tropical rain forests, where local populations are assumed to feed primarily on the most abundant avian prey species (Baker 1967, Ratcliffe 1993). However, the degree of dietary specialization observed in peregrine falcons varies across different habitats. Studies suggests that peregrines breeding in temperate regions have specialized diets, while those breeding in more extreme habitats, such as deserts, tundra, and boreal forests, are more generalized (Jenkins and Avery 1999, Jenkins and Hockey 2001), which supports the notion that stochastic environments promote a more generalized diet (Kassen 2002). However, peregrines breeding in boreal forests appear to consume shorebirds and water birds in greater proportion to their availability, indicating peregrines in boreal regions may be specialists (Hunter et al. 1988, Dawson et al. 2011). Studies have also shown that the foraging efficiency of peregrines is higher in open habitats with high perching cliffs (Jenkins 2000), suggesting they may select foraging sites based on factors other than prey abundance. Inferences made from use-availability data should, therefore, be treated with caution if specific foraging sites are not identified when measuring prey availability. For example, Hunter et al. (1988), considered all habitat within a 3 km radius of nest sites to be available to foraging peregrines, regardless of habitat type. If peregrines select specific habitat types for foraging based on habitat structure, many prey species documented by Hunter et al. (1988) may have been unavailable, which could skew the interpretation of their use-availability data .

Arctic peregrine falcons (*F. p. tundrius*) breeding throughout the circumpolar regions of Canada, the USA, and Greenland, have a diversity of prey species to choose from, but little is known about how they select for these resources. Arctic peregrines are exposed primarily to open tundra, but the suitability of habitat for foraging may be spatially heterogeneous due to spatial variation in topography (Jenkins 2000). The phenologies of Arctic-breeding birds are tightly synchronized because of the short, productive, summer season (Careau et al. 2008). As a result, peregrines are exposed to annual pulses in resources, first as different prey species arrive on the breeding grounds, and again as these species fledge young (Jenkins and Hockey 2001). The general diet of Arctic peregrines is well documented, consisting of primarily insectivorous songbirds (Passeriformes) and shorebirds (Charadriiformes), but few studies have examined temporal trends in prey use compared to fluctuations in availability (Burnham and Mattox 1984, Court et al. 1988, Rosenfield et al. 1995, Reid et al. 1997). Food supply can limit population productivity and the distribution and density of nesting pairs of other subspecies of peregrines (Bond 1936, Hickey 1942, Ratcliffe 1993, Jenkins and Hockey 2001). Without information on prey selection, it is impossible to determine how Arctic peregrines mitigate fluctuating prey availability and the extent with which these fluctuations influence population productivity.

As the climate continues to change, fluctuations in the Arctic peregrine falcon's primary prey, insectivorous birds, are likely to become more pronounced. Many regions throughout the Canadian Arctic are predicted to receive more precipitation falling as rain in the summer months (Kattsov et al. 2005, Collins et al. 2013, Bintanja and Selten 2014), which will likely reduce the activity and abundance of arthropods (Bolduc et al. 2013) and decrease the growth and survival of juveniles shorebirds (Schekkerman et al. 2003, Kendall et al. 2011). Further, Arctic-breeding songbirds are primarily insectivorous (Custer and Pitelka 1978, Montgomerie and Lyon 2011) and may also experience declines associated with increases in summer rainfall.

Arctic peregrine falcons have a diversity of alternative prey ranging from lemmings (Cricetidae) to ducks (Anatidae), gulls (Laridae, Sternidae and Stercorariidae) and black guillemots (*Cepphus grille*) (Court et al. 1988, Rosenfield et al. 1995), which could supplement their diet when insectivorous birds are scarce. Peregrine falcons in Australia, for example, switched to alternative prey after their primary prey species declined (Olsen et al. 2008). Peregrine falcons in Yukon Territory, Canada, may diversify their diet when limited amounts of their preferred prey are unavailable (Dawson et al. 2011). To fully appreciate the potential implication of climate change on Arctic peregrine falcon populations, research investigating prey selection and the potential for peregrines to switch to alternative prey is needed.

The objectives of my PhD dissertation were to relate spatiotemporal variation in all prey species consumed by peregrines to annual variation in weather, while simultaneously monitoring peregrine falcon diet and reproductive output. If Arctic peregrine falcons are true generalists, they should switch to alternative prey when their primary prey declines, without reducing reproductive output. Alternatively, if Arctic peregrine falcons are specialists that rely on adequate densities of insectivorous birds to successfully breed, they are likely vulnerable to continued changes in climate, specifically increases in summer precipitation.

1.4 Dissertation outline

The complex interactions between summer temperature, precipitation, phenology, thermoregulation, and forage availability hinder our ability to accurately predict how the prey species of the Arctic peregrine falcon will respond to climate change and interannual variation in conditions. The main objective of Chapter 2 was to investigate the relationship between annual variation in weather and spatiotemporal variation in the abundance of multiple avian guilds in an Arctic tundra ecosystem in central Nunavut, Canada (Figure 1.1): songbirds (Passeriformes), shorebirds (Charadriiformes), gulls, loons (Gaviidae), and geese (Anatidae). I spatially stratified the study area based on vegetation productivity, terrain ruggedness and the abundance of freshwater and conducted distance sampling to estimate strata-specific densities of each guild during the summers of 2010-2012. I also monitored temperature and rainfall each year and estimated annual lemming abundance using snap trapping.

To determine how peregrine falcons responded to variation in prey abundance, I quantified the diet fed to nestling falcons throughout the three years of this study using a combination of two methods: direct observations from motion-sensitive cameras at nest sites (Chapter 3) and stable isotope analysis (Chapter 4). Cameras at nest sites are becoming a common means for quantifying nestling diet (Reif and Tornberg 2006), but there are two main problems associated with this method: food items delivered to nestlings often cannot be identified, and quantification of error around diet estimates for individual nests is problematic. In Chapter 3, I present a novel method of incorporating unidentified food items into diet estimates and quantifying error around these estimates for individual nests. In Chapter 4, I used the diet estimates from Chapter 3 as informative prior hypotheses in Bayesian mixing models to estimate diet from stable isotope data (Parnell et al. 2010). Bayesian mixing models have become a common method to estimate diet, but results are often ambiguous with high uncertainty (Phillips et al. 2014). A commonly cited advantage of Bayesian mixing models is the ability to include informative prior hypotheses predicting diet composition based on previous knowledge, which has the potential to improve the precision and accuracy of mixing model results (Moore and Semmens 2008). However, few studies have taken advantage of informative priors, so it is unclear exactly how they will influence results from Bayesian mixing models. Using stable isotope signatures of falcon nestling plasma and prey tissue samples as inputs for Bayesian mixing models, I compared the resulting diet estimates with and without the prior hypotheses of diet composition from Chapter 3.

In Chapter 5, I combined the results from Chapters 2-4 to investigate whether peregrine falcons switched to alternative prey when their primary prey of insectivorous birds declined. Using prey density estimates from Chapter 2 and prey delivery rates to nestlings from Chapter 3, I examined the functional response of peregrine falcons to changes in prey density. If peregrine falcons were able to sustain themselves on alternative prey, total prey intake rates would be sustained despite a decline in the density of their primary prey. I also compared peregrine falcon nestling survival across all years of the study to determine if peregrine reproductive output was influenced by prey density and prey intake rates.

I conclude the dissertation in Chapter 6 by comparing the proportional availability of each prey type to its proportional contribution to peregrine falcon diets (i.e. prey selection). I interpret prey selection to distinguish whether Arctic peregrine falcons are generalists or specialists and speculate how vulnerable Arctic peregrine falcons are to climate change. Finally, I compare the results of my research with those from studies of peregrine falcons in other regions of the Arctic to examine how widespread the effects of climate change may be on this top predator.

1.5 Study area

This study was conducted in the Northern Arctic Ecozone (Marshall et al. 1996) among the Coxe Islands and the mainland at the northern tip of the Melville Peninsula, near the community of Igloolik, Nunavut, Canada (Figure 1.1: 69.5345°N, 82.5070°W). The region has short cool summers with monthly mean temperatures fluctuating from 1.6 to 7.0°C (Figure 2.2). Spring thaw begins in early June and the majority of snow cover on land is melted by early July. Sea ice persistence varies annually, but it is generally gone by mid-late July. Summer rainfall is low averaging 86 mm from June to August (Figure 2.2). The study area encompasses 2030 km^2 of ocean (57% of area), rugged coastline, and rolling tundra. Cliffs are numerous throughout the area, generally occurring along the shore of the ocean or large inland lakes that frequent the area. Cliffs provide suitable nesting habitat for raptors such as peregrine falcons and rough-legged hawks (*Buteo lagopus*), as well as common ravens (*Corvus corax*), glaucous gulls (*Larus hyperboreus*), herring gulls (*L. argentatus*), Canada geese (*Branta canadensis*), and common eiders (*Somateria mollissima*). Black guillemot colonies occur on rocky shorelines and small rocky islands. Inland rolling tundra is vegetated with lichens, mosses, graminoids (e.g., *Luzula* spp., *Carex* spp., *Alopecurus magellanicus*, and *Poa* spp.), herbs (e.g., *Saxifraga* spp., *Bistorta vivipara*, and *Pedicularis* spp.) and low shrubs (*Salix* spp., *Dryas* spp., and *Cassiope tetragona*). Small lakes and wetland areas are numerous throughout the tundra providing habitat for a diverse community of songbirds and shorebirds such as Lapland longspurs (*Calcarius lapponicus*), snow buntings (*Plectrophenax nivalis*), American golden-plovers (*Pluvialis dominica*), semipalmated plovers (*Charadrius semipalmatus*), phalaropes (*Phalaropus* spp.), and sandpipers (*Calidris* spp.). Collared and brown lemmings (*Dicrostonyx groenlandicus* and *Lemmus trimucronatus*, respectively) and Arctic ground squirrels (*Urocitellus parryii*) also occur throughout the tundra.

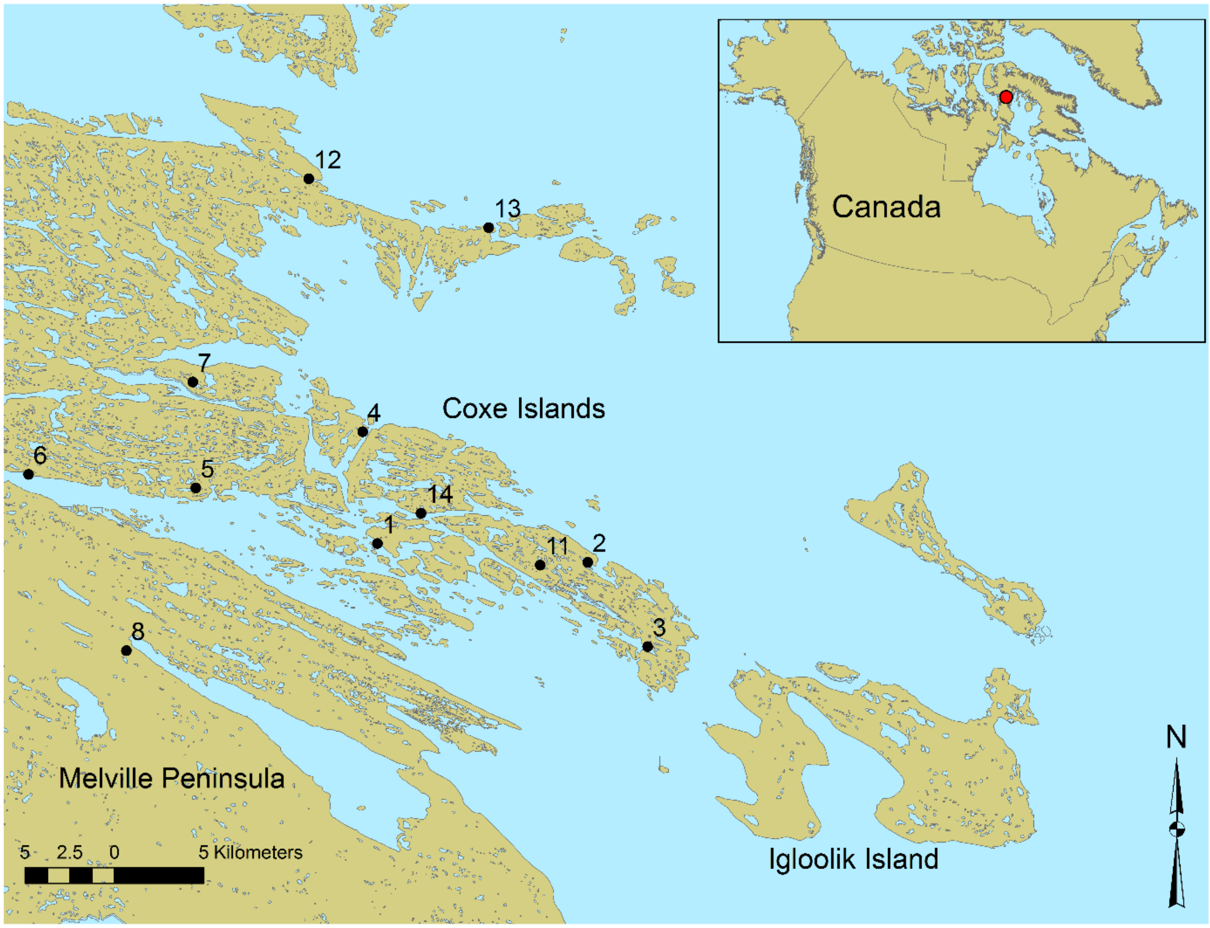

Figure 1.1. Study area location near Igloolik, Nunavut, Canada. Black dots represent Arctic peregrine falcon nests monitored from 2010-2012. Numbers are unique identities for nest sites used throughout this dissertation.

2 The influence of weather and lemmings on spatiotemporal variation in the abundance of multiple avian guilds in the Arctic

2.1 Introduction

Spatial and temporal variation in the abundance of organisms is of central importance to the study of ecology (Andrewartha and Birch 1954), particularly in the face of environmental change (Pearson and Dawson 2003). Climate change, one of the most significant environmental perturbation occurring today, can have a strong influence on the distribution and abundance of organisms by altering the trophic interactions within a community (Post and Forchhammer 2008, Van der Putten et al. 2010, Blois et al. 2013). In Arctic ecosystems, where the time available for breeding is short and the food chain is relatively simple, altered trophic interactions may be more critical than at southern latitudes (Ims and Fuglei 2005, Pearce-Higgins et al. 2005). In addition, some of the most severe changes in climate are occurring in Arctic ecosystems: temperatures are rising at almost twice the rate of the rest of the planet and summer rainfall has increased significantly over the last century (Kattsov et al. 2005, Trenberth et al. 2007). Particular attention should, therefore, be paid to the influence of climate on trophic interactions within Arctic communities.

In experimental and natural systems, the negative effects of a warming climate are exacerbated in species at higher trophic levels (Petchey et al. 1999, Pounds et al. 1999) because these species adjust their phenology with climate change more slowly than species at lower trophic levels (Hoye et al. 2007, Møller et al. 2008, Both et al. 2009, Thackeray et al. 2010). Asynchrony in phenological change can create a mismatch between the needs of a predator and the availability of their prey (Cushing 1969). Herbivorous and insectivorous Arctic-breeding birds feeding at low trophic levels may be most susceptible to phenological mismatch because their food responds quickly to changing weather patterns. Climate warming has been associated with an advance in the annual summer pulse in arthropod abundance, making it asynchronous with the hatching of insectivorous shorebird chicks, which experienced reduced growth rates (Tulp and Schekkerman 2008, McKinnon et al. 2012). A mismatch between the timing of vegetation green-up and the hatching of herbivorous snow geese (*Chen caerulescens*) resulted in lower gosling body condition and first-year survival (Dickey et al. 2008, Aubry et al. 2013). Gauthier et al. (2013) found a similar mismatch between the phenology of snow geese and tundra vegetation, but they did not find any evidence for reduced productivity or abundance of geese.

Climate change in the Arctic can alter trophic interactions between birds and their prey even if their respective phenologies are unaffected. Declines in the persistence of summer sea ice reduced Arctic cod (*Boreogadus saida*) abundance causing several marine bird species to switch to alternative prey (Gaston et al. 2012b, Moody et al. 2012, Provencher et al. 2012). In addition to warming temperatures, summer rain storms in the Arctic are predicted to become more frequent and severe under most climate models (Kattsov et al. 2005), which may reduce foraging opportunities for insectivorous shorebirds (Schekkerman et al. 2003, Kendall et al. 2011).

Warming temperatures in the Arctic can also lead to benefits for birds, potentially countering negative effects caused by altered trophic interactions. Up to half of the energy metabolized by shorebird chicks is used for feeding and thermoregulation (Schekkerman et al. 2001), so Arctic-breeding shorebirds could benefit from warming temperatures associated with climate change. McKinnon et al. (2013b) found that even when food availability was below average, dunlin (*Calidris alpina*) chicks in the sub-Arctic were able to maintain above average growth rates with increasing summer temperatures. Snow geese spent less time brooding their young as temperatures increased, allowing more time and energy to be allocated to foraging

(Fortin et al. 2000). Warmer Arctic temperatures are also reducing spring snow cover (Brown and Robinson 2011), increasing nest density, nest success and overall productivity for a variety of goose species in different circumpolar regions (Madsen et al. 2007, Dickey et al. 2008, Jensen et al. 2014). In geese and other Arctic-breeding birds, earlier spring snow melt results in earlier nest initiation (Skinner et al. 1998, Smith et al. 2010, Grabowski et al. 2013), which is correlated with increases in clutch size, and nestling growth and survival (Lindholm et al. 1994, Meltofte et al. 2007)

Trophic interactions independent of weather, such as predation, can also influence the abundance of Arctic-breeding birds. Arctic foxes (*Vulpes lagopus*) prey primarily on collared lemming (*Lemmus trimucronatus*) and brown lemming (*Dicrostonyx groenlandicus*) when lemmings are abundant, but switch to their alternate prey of bird eggs when lemming abundance declines (Bêty et al. 2002). Lemming populations cycle throughout the Arctic peaking every 3-5 years, so Arctic fox predation rates on bird eggs also fluctuate (Underhill et al. 1993). In the Canadian and Russian Arctic, population size, clutch size, egg survival and nest success of multiple species of geese and shorebirds all correlated positively with lemming abundance, declining when lemming populations crashed and Arctic foxes began consuming bird eggs (Bêty et al. 2001, Blomqvist et al. 2002, Perkins et al. 2007, McKinnon et al. 2013a, Nolet et al. 2013). Predictions made under various climate change scenarios indicate the amplitude and frequency of peaks in the lemming cycle are likely to decrease (Gilg et al. 2009), which may increase predation pressure on Arctic-breeding birds. The complex interactions between summer temperature, rain, spring snow cover, phenology, thermoregulation, and food availability, coupled with fluctuations in predation pressure, hinder our ability to accurately predict how Arctic-breeding birds will respond to climate change.

The main objective of this study was to investigate the relationship between annual variation in weather and lemming abundance, and spatiotemporal variation in the abundance of multiple avian guilds in an Arctic tundra ecosystem in central Nunavut, Canada: songbirds (Passeriformes), shorebirds (Scolopacidae and Charadriidae), gulls (Laridae, Sternidae and Stercorariidae), loons (Gaviiformes), and geese (Anatidae). Species within each guild occupy similar ecological niches in terms of diet and foraging habitat (see Table 2.1 for references), so I expected similar responses to landscape and weather variables within each guild. I hypothesized that spatial variation in the abundance of all guilds was correlated with some combination of vegetative productivity, topography, and the abundance of freshwater (Table 2.1). I also hypothesized that abundance of all guilds was positively correlated with mean summer temperature and negatively correlated with summer rainfall. Although a general warming climate may result in phenological mismatch across trophic levels over a longer temporal scale (e.g., decades), I predicted the short-term influence of warm weather and low rainfall would result in higher bird abundance, potentially due to increased feeding opportunities, reduced costs of thermoregulation, and decreased spring snow cover. Finally, I hypothesized that the abundance of all guilds was positively correlated with lemming abundance. Understanding the relationship between weather, the lemming cycle, and avian abundance will provide additional insight into the sensitivity of Arctic-breeding birds to climate change.

2.2 Methods

2.2.1 Spatiotemporal stratification

I used three landscape metrics for spatial stratification. First, as a measure of tundra productivity and the amount of vegetative cover versus bare rock, I used the Normalized Difference Vegetation Index (NDVI), which estimates the amount of photosynthetic activity occurring within a pixel based on the reflectance values of red and near infrared wavelengths (Pettorelli et al. 2011b). NDVI is a good predictor of above ground estimates of vegetative productivity such as biomass, ecosystem respiration, and gross ecosystem productivity in various Arctic tundra ecosystems (Boelman et al. 2003, Huemmrich et al. 2010). I calculated NDVI using a 30 m resolution Landsat Thematic Mapper image taken on 18 July 2010 (United States Geological Survey http://earthexplorer.usgs.gov), which corresponds to the timing of vegetation green up and is consistent with the period used in a remote sensing study of shorebird breeding habitat in the same region (Morrison 1997). Using a Geographic Information System (GIS; ArcMap 9.3.1, ESRI, Redlands, CA, USA) NDVI calculations were applied to pixels occurring on land only using land and water layers (Natural Resources Canada, http://www.geobase.ca). I then calculated the mean NDVI value within a 15 × 15 pixel roving window (450 × 450 m) and classified pixels with a binomial variable: either high (0.1 – 1) or low vegetative productivity (-0.13 – 0.1) (*N*: 0 = low, 1 = high). Pixels in the low productivity range were surrounded mostly by bare ground and exposed rock while those in the high range were surrounded by tundra vegetation (B.R. personal observation), which is consistent with studies using NDVI (Carlson and Ripley 1997).

As a second landscape metric, I used a terrain ruggedness index derived from a 30 m resolution digital elevation map (Natural Resources Canada, http://www.geobase.ca). The index was calculated for each pixel as the standard deviation in elevation (m) of surrounding pixels in a 33 × 33 pixel roving window (990 × 990 m). Pixels were binomially classified as low (0 – 10 m) or high (>10 – 89 m) ruggedness (*R*: 0 = low, 1 = high).

The final landscape metric was the proportion of pixels classified as standing freshwater (i.e., excluding rivers or streams), which was based on the land and water GIS layers (30 m resolution) and a 33 × 33 pixel roving window. I binomially classified pixels as being surrounded by low (0 – 0.08) or high (>0.08 – 1.0) amounts of freshwater (*W*: 0 = low, 1 = high). The scale and break points for all variables were subjectively chosen so that the landscape was divided into ecologically distinct habitat types. I combined the above binomial metrics to create 8 strata from each unique combination of metric categories and applied this stratification to terrestrial areas (Table 2.2, Figure 2.1).

Data on bird abundance was collected each summer from 2010-2012, allowing me to temporally stratify the data. Each summer I deployed a remote weather station (PortLog, Rainwise Inc., Bar Harbor, ME, USA) to collect daily mean temperatures and total rainfall. The summers of 2010 and 2011 were warmer and dryer than the mean for Igloolik from 1980-2000 (Figure 2.2). Conversely, summer 2012 had temperatures more similar to the 20-year mean, but received significantly more rainfall in June (Figure 2.2). To estimate spring snow cover throughout the study area, I used Moderate Resolution Imaging Spectroradiometer (MODIS) data (National Snow and Ice Data Center: http://www.nsidc.org), which classifies 250 m resolution pixels as snow or bare ground using the Normalized Difference Snow Index (Hall et al. 2006). Using MODIS data from 18 June 2010, 17 June 2011, and 17-18 June 2012 (days with sufficiently cloud-free skies), I estimated the proportion of pixels within the study area classified as snow relative to bare ground; the majority of migratory birds breeding in the study area generally arrive by these dates (Forbes et al. 1992). Spring snow cover was 99% in 2010 and 2011, and 77% in 2012. I temporally stratified the abundance data (see below) based on daily mean temperatures, total summer rainfall, and spring snow cover, considering 2010 and 2011 to be warm and dry with high spring snow cover ($T = 0$), and 2012 to be cool and wet with moderate spring snow cover ($T = 1$).

I estimated annual lemming abundance for the study area with snap traps (Museum Special, Forestry Suppliers Inc., Jackson, MS, USA). Following a protocol similar to Gruyer et al. (2008), I set snap traps along 4 transects greater than 100 m apart: 2 in a wet meadow habitat dominated by sedges (*Carex* spp.) and 2 in a dry mesic habitat dominated by *Dryas* spp. Each transect consisted of 20 stations 15 m apart with 3 snap traps within 2 m of each station (60 traps per transect). Traps were baited with peanut butter, set in the morning, and checked every 24 hours for 3 consecutive days (720 trap nights/year). Each morning all traps that had been triggered (either by misfire or catching an animal) were re-baited and re-set. Annual lemming abundance for the study area was expressed as the total number of lemmings caught along all transects per 100 trap nights; this metric of lemming abundance had a positive, logarithmic relationship with lemming density in another study in Nunavut (Gauthier et al. 2013). During 2011, there was a peak in lemming abundance (3.24 lemmings/100 trap nights), which was preceded by low lemming abundance in 2010 (0.29 lemmings/100 trap nights) and followed by a decline in 2012 (0.10 lemmings/100 trap nights). I also temporally stratified the bird abundance data by lemming abundance, considering 2010 and 2012 to be low ($L = 0$) and 2011 to be high ($L = 1$).

2.2.2 Distance sampling design

To estimate the density of each guild, I used distance sampling to estimate a detection function, which predicts the probability of an individual being detected as a function of its perpendicular distance from the transect (Buckland et al. 2001). Each summer 30 new random start locations were generated >1 km apart within each stratum using GIS. One km transects were walked using a map, compass, and GPS unit to navigate from each start location, ensuring that the observer remained within a single stratum. Transects were straight lines when possible, but curved as needed to remain in a stratum and avoid water bodies (Buckland et al. 2001). Each year, I attempted to survey a minimum of ten transects per stratum from 12 July to 30 August (Table 2.2), which roughly encapsulated the time between hatching and southern migration for birds breeding in the study area (Forbes et al. 1992). No transect was surveyed more than once in a year. Transects were surveyed primarily on fair weather days with good visibility, low wind, and no precipitation. Each transect took between 15 and 45 minutes to survey depending on the number of birds observed. Surveys occurred from 06:00 to 21:00 and time of survey was tested as an explanatory variable in detection functions to account for potential variation in activity. During the breeding season, Arctic birds can be active for up to 12 hours per day and this activity can occur any time throughout the 24 hours of daylight (Tulp et al. 2009, Ashley et al. 2012, Steiger et al. 2013), so timing of surveys is less critical than at more southern latitudes. Along each transect every bird observed was recorded along with its distance (laser range finder, Bushnell, Overland Park, KS, USA) and compass bearing relative to the observer's GPS location, which was used to estimate perpendicular distance to the transect using a GIS as required for distance sampling. All individuals were classified as songbird, shorebird, gull, loon, or goose and identified to species when possible (see Appendix A Table A1 for a list of species observed). If multiple birds within the same guild occurred in a cluster at the same location, they were considered a single observation and cluster size was recorded.

Treating guilds separately and combining data across strata, I used Distance 6.0 release 2 software (Thomas et al. 2010) and Akaike Information Criteria corrected for small sample size (AIC_c) (Burnham and Anderson 2002) to determine the most appropriate detection function and to parameterize the top models. I first estimated the detection functions with all observations and then truncated the data at the distance that predicted the probability of detection to be 0.15

(Buckland et al. 2001). I used the multiple covariate distance sampling engine in Distance, which allows for additional covariates in the detection function (Marques and Buckland 2003). I tested whether the covariates time of day (0 = morning/evening, 06:00-09:59 and 17:00-21:00; 1 = midday, 10:00-16:59), date (before 7 August, 7 August – 18 August, after 18 August; represented with two dummy variables with after 18 August as the base category), or year (2010, 2011, or 2012; represented with two dummy variables with 2012 as the base category) the survey was conducted, or terrain ruggedness (0 = low, 1 = high) in which the transect was located, significantly improved the detection function fit. Thirty candidate models were compared for the detection functions (Table A2).

2.2.3 Statistical analysis of spatiotemporal variation

My goal was to determine whether the stratification variables significantly explained variation in the number of individuals observed within each guild (a measure of abundance). Because there is uncertainty and error associated with the density estimates produced by Distance, these density estimates cannot be used directly in statistical analyses. Therefore, I used a method for analysing designed experiments with distance sampling data, where treatment effects on abundances are of interest (Buckland et al. 2009). Using this approach, data from stratified distance sampling can be summarized as counts of animal clusters and mean cluster size within each stratum, along with each cluster's detection probability. Counts of clusters can then be modelled as a function of the strata variables in a generalized linear model with a Poisson error distribution. Using a log link function, variation in survey effort and detection probability across strata can be accounted for with an offset term in the Poisson model:

$$E\left(n_k\right) = \exp\left(\sum_{j=1}^{p} x_{jk}\beta_j - \ln\left(\frac{H_k}{2l_k}\right)\right)$$

where n_k is the count of clusters in strata k, x_{jk} are the p different variables used to describe each strata k, β_j are their associated coefficients, H_k is the product of the mean cluster size for strata k and the total probability of a cluster being detected along a transect in strata k (estimated from the detection function), and l_k is the total length of all transects surveyed in strata k; $-\ln(H_k/2l_k)$ is the offset (Buckland et al. 2009).

Treating each guild separately, I used the original count data and $\mathrm{AIC_c}$ model selection to choose between competing *a priori* candidate models with the above form, each with different combinations of tundra productivity (N), terrain ruggedness (R), proportion of freshwater (W), weather (T), lemming abundance (L), and interactions as the x_j's. Because only 3 transects were surveyed in strata with high vegetation productivity ($N = 1$) in 2010 (Table 2.2), I did not include both T and L in any one candidate model for guilds I believed would be influenced by vegetation productivity (Table 2.3: shorebirds, songbirds and geese). By including only one of T or L in a model, data from 2010 was combined with data from either 2011 or 2012, respectively, which adequately increased the sample size of transects surveyed in strata with high vegetation productivity (Table 2.2). I used the 'glm' function in the statistical package R (R Core Team 2014) to parameterize each candidate model. Because there is uncertainty in the estimation of the detection function, and hence the offset, the standard errors, confidence intervals and P-values for each parameter in the top models may be unreliable (Buckland et al. 2009). To account for uncertainty in the offset, I calculated bootstrap standard errors and 95% and 99% percentile confidence intervals for all parameters based on 999 nonparametric bootstrap resamples of transects within strata. I used Distance and R to analyse each bootstrap resample with the same method used for the original count data (for details see Buckland et al. 2009). For each guild, I re-stratified transects using only the significant variables (based on bootstrap standard errors and the 95% percentile confidence intervals) in the top Poisson model. I then estimated bird density within these new strata using Distance with the appropriate detection function for each guild (Table 2.3).

2.3 Results

2.3.1 Detection functions

For all guilds except songbirds, the half normal detection function model was chosen as the most parsimonious using AIC_c; the hazard rate model was most parsimonious for songbirds (Table 2.3). Details of the AIC_c analysis and graphs of each detection function are presented in Appendix A (Table A2, Figure A1). The detection functions for each guild fit the data well (Table 2.3, Figure A1). The detection function for songbirds included date as a covariate, which predicted the probability of detecting a bird beyond 10 m from the transect was higher at the beginning of the post-hatching period and declined as the season progressed (Figure A1). The detection function for geese included year as a covariate, which predicted the probability of detection increased from 2010 to 2011 and then decreased in 2012 (Figure A1). Detection functions for the other guilds did not have any covariates (Table 2.3).

2.3.2 Spatiotemporal variation

For some guilds there was not overwhelming support for one top model, so I made inferences based on all models with ΔAIC_c values <2 (Table 2.4). There was strong evidence that songbirds were less abundant during the cool, wet summer with moderate spring snow cover ($T = 1$; see negative coefficients significantly different than 0 for the T term in Table 2.4; Figure 2.3A). Although the weather variable (T) was included in the top models for geese, the coefficient was not significantly different than 0. Abundance of shorebirds and gulls both increased significantly during the lemming peak (Table 2.4, Figure 2.3B and 2.3D).

Averaged across all summers, songbirds were more abundant in strata with high amounts of freshwater ($W = 1$) and low vegetative productivity ($N = 0$) (Figure 2.3A). The significant $T \times N$ interaction term in both top models for songbirds, however, indicated that songbird abundance declined during the cool, wet summer with moderate snow cover ($T = 1$), but only in strata with low vegetation productivity ($N = 0$) (Table 2.4, Figure 2.3A). Regardless of lemming abundance, shorebirds were more abundant in flat strata ($R = 0$); shorebirds also had a positive association with vegetation productivity, but only during the peak lemming year (significant $L \times N$ interaction term; Table 2.4), which is consistent with the densities estimates produced in Distance (Figure 2.3B). Averaged across all summers, loons were more abundant in flat areas ($R = 0$) with high amounts of freshwater ($W = 1$). The significant $R \times W$ interaction term indicated that loon abundance increased with the amount of freshwater only in flat areas (Table 2.4, Figure 2.3E). Geese were more abundant in strata with high vegetative productivity (Table 2.4), which is consistent with density estimates (Figure 2.3C). For geese, the significant interaction between the weather variable and water ($T \times W$) indicated they were more abundant in strata with high amounts of water during the warm, dry summers with high spring snow cover, but less abundant in these strata during the cool, wet summer with moderate spring snow cover (Table 2.4, Figure 2.3C). Finally, the significant $R \times W$ interaction term in the top model for gulls indicated that gulls were most abundant in flat areas with high amounts of water (Table 2.4, Figure 2.3D).

2.4 Discussion

The landscape metrics I considered explained significant variation in the abundance of multiple guilds of Arctic-breeding birds. By focusing only on landscape metrics that were important for each guild, I estimated guild-specific spatiotemporal variation in density. My density estimates fell within the range of those reported in other Arctic studies (Forbes et al.

1992, Trefry et al. 2010, Liebezeit et al. 2011, Andres et al. 2012). Breeding bird densities vary considerably across the Arctic, which has been attributed to variation in primary productivity correlated with mean annual temperature and latitude (Bliss et al. 1973, Freedman and Svoboda 1982). My study area in the Northern Arctic Ecozone had an intermediate density of birds with higher densities than the Arctic Cordillera to the north (e.g., Ellesmere Island, Nunavut; (Freedman and Svoboda 1982)) and lower densities than the sub-Arctic to the south (e.g., Cape Churchill, Manitoba; (Sammler et al. 2008)).

The spatial variation in abundance I observed generally supported my hypotheses (Table 2.1) and matched what would be expected based on ecological knowledge of each guild. For example, loons that require large lakes for breeding and foraging (Earnst et al. 2006) were most abundant in flat areas with high amounts of freshwater; gulls, which often breed on marshy hummocks, raised beaches, and inland tundra around large ponds (Gaston et al. 2012a, Weiser and Gilchrist 2012), were most abundant in the same habitats as loons. Shorebirds were most abundant in flat areas with high vegetative productivity, as predicted based on habitat preference (Liebezeit et al. 2011). The amount of freshwater present may not have influenced overall shorebird abundance because some species prefer well drained, sparsely vegetated tundra (e.g., American golden-plovers), while others prefer wet, marshy habitats (e.g., sandpipers and phalaropes) (Latour et al. 2005).

By explicitly controlling for spatial variations in bird abundance, I was also able to determine how annual changes in weather, spring snow cover, and lemming abundance created more complex spatiotemporal patterns. During the warm, dry summers with high spring snow cover, songbirds were most abundant in rocky habitats with low vegetative productivity and high amounts of freshwater, which matches the preferred nesting habitat of Arctic songbirds

(Freedman and Svoboda 1982). During the cool, wet summer songbird abundance declined, but this response was less pronounced in strata with high vegetation productivity, where foraging opportunities for insectivores and granivores is greatest (Hussell and Montgomerie 2002). In Alaska and Scandinavia, cold conditions during precipitation events decreased daily arthropod activity, reducing foraging opportunities for insectivorous birds and resulting in negative demographic consequences (Schekkerman et al. 2003, Kendall et al. 2011). Cold temperatures, high wind and precipitation can reduce arthropod activity and abundance across the Canadian Arctic (Bolduc et al. 2013). The bulk of Arctic-breeding songbirds' diet consists of arthropods (Custer and Pitelka 1978, Montgomerie and Lyon 2011), so declining arthropod availability associated with cool, wet weather may have driven the spatiotemporal variation in songbird abundance observed in my study.

Regardless of weather conditions and spring snow cover, herbivorous geese were most abundant in areas with high vegetative productivity, which likely afforded the best foraging opportunities. Overall, goose abundance was not significantly influenced by weather and snow cover, but there was a correlation between weather conditions and the spatial distribution of geese relative to the amount of freshwater. Geese redistributed themselves from dryer areas in the cool, wet summer to wetter areas in the warm, dry summers, which may have been an antipredator strategy; Lecomte et al. (2009) found incubating geese that were required to travel far distances to access water had a higher chance of losing their eggs to predation than those breeding in close proximity to water. Predation pressure may explain why lower spring snow cover and high amounts of rainfall, which generally benefit Arctic-breeding geese (Madsen et al. 2007, Dickey et al. 2008, Jensen et al. 2014), did not result in an increase in goose abundance. The cool, wet summer with moderate snow cover coincided with a sharp decline in lemming abundance. Arctic fox predation on goose eggs increases dramatically when lemmings decline after a peak year (Bêty et al. 2001, Bêty et al. 2002), which may have offset any increase in nest success associated with favourable spring conditions.

Although goose eggs are preferred alternate prey for Arctic foxes, shorebird eggs are consumed incidentally, making predation risk on shorebird nests highest where geese are most abundant, particularly when lemmings are scarce (McKinnon et al. 2013a). Shorebird abundance declined with lemming abundance throughout the study area, but this pattern was most pronounced in habitats with high vegetation productivity, where geese were most abundant. Incidental predation of shorebird eggs by Arctic fox may have been the mechanism that drove reductions in shorebird abundance during crashes in the lemming cycle observed in this and other studies (Blomqvist et al. 2002, Perkins et al. 2007).

Gulls also fluctuated in concert with lemming abundance. Similar to shorebirds, the eggs of Sabine's gulls (*Xema sabini*) are preyed on by Arctic foxes (Stenhouse et al. 2001), which may have contributed to the decline in gull abundance while lemmings were scarce. Glaucous gulls and, in particular, long-tailed jaegers (*Stercorarius longicaudus*) consume large numbers of lemmings during peaks years (Wiley and Lee 1998, Weiser and Powell 2011), which may have resulted in a positive numerical response for these species (Therrien et al. 2014).

This study demonstrated that low lemming abundance and cool, wet weather were correlated with declines in multiple avian guilds. Because both of these unfavourable conditions were present during the summer of 2012, songbirds and shorebirds likely experienced high predation risk and low forage availability as poor weather reduced arthropod activity and abundance. Although lemming abundance was also low in 2010, weather was warm and dry and predator abundance was likely lower than 2012, which followed a lemming peak. Predators exhibit a positive numeric response during lemming peaks (Gilg et al. 2006, Therrien et al. 2014), so predation risk toward birds is highest during the lemming declines that follow, when predators are abundant and their primary prey are unavailable (Bêty et al. 2001, Bêty et al. 2002, Nolet et al. 2013). The amount of summer rainfall in the eastern Canadian Arctic has increased over the last 30 years (Anctil et al. 2013) and the amplitude and frequency of lemming peaks is declining in other circumpolar regions (Gilg et al. 2009). Both of these patterns are predicted to intensify under various climate change scenarios (Kattsov et al. 2005, Gilg et al. 2009), which may have negative impacts on the productivity of songbirds, shorebird, gulls and possibly geese.

Given the results of this and other studies, predicting how climate change will impact the diversity and abundance of birds in the Arctic remains challenging (Krebs and Berteaux 2006). Temperature increases will likely lead to longer growing seasons along with increases in primary production and arthropod abundance (Callaghan et al. 2005, Bolduc et al. 2013, Gauthier et al. 2013). Warmer ecosystem may, therefore, support a higher density of shorebirds, songbirds, and geese, particularly as species disperse further north (Brommer et al. 2012, Sokolov et al. 2012). However, increases in summer rainfall (Kattsov et al. 2005), which reduces foraging opportunities for insectivores, may negate advantages gained by warmer weather. Heavy summer rainfall can directly cause nestling mortality of Arctic-breeding raptors (Pokrovsky et al. 2012, Anctil et al. 2013), but the potential indirect effect of heavy rainfall on raptors through reductions in their avian prey should also be considered. Warmer temperatures and increased rainfall also advance spring snow melt, creating benefits for geese (Dickey et al. 2008), but potentially leading to phenological mismatch between peaks in arthropod abundance and hatching of insectivores (Tulp and Schekkerman 2008). Shifts in winter weather and snow conditions associated with climate change are affecting the lemming cycle (Kausrud et al. 2008), which is clearly linked to the productivity of Arctic-breeding birds. Although the short-term nature of this study and lack of replication across multiple cool, wet summers limits my ability to make long-term predictions, I provide an example of a relatively simple way to monitor the correlation between weather, spring snow cover, lemming abundance, and spatiotemporal variations in a diversity of Arctic-breeding birds.

Table 2.1. *A priori* hypotheses predicting the relationship between the abundance of different avian guilds and three landscape metrics.

	Hypotheses			
Guild	**Vegetation**	**Topography**	**Standing freshwater**	**References**
Songbirds	abundance positively correlated with productivity	more abundant in flat vs. rugged habitats	neutral	(Hussell and Montgomerie 2002, Montgomerie and Lyon 2011, Hendricks and Verbeek 2012)
Shorebirds	abundance positively correlated with productivity	more abundant in flat vs. rugged habitats	abundance positively correlated with amount of standing water	(Parmelee 1992, Nol and Blanken 1999, Tracy et al. 2002, Johnson and Connors 2010)
Gulls	neutral	neutral	abundance positively correlated with amount of standing water	(Pierotti and Good 1994, Wiley and Lee 1998, Hatch 2002, Weiser and Gilchrist 2012)
Geese	abundance positively correlated with productivity	neutral	abundance positively correlated with amount of standing water	(Hughes et al. 1994, Mowbray et al. 2000, Mowbray et al. 2002)
Loons	neutral	neutral	abundance positively correlated with amount of standing water	(Barr et al. 2000, Russell 2002, Earnst et al. 2006)

Table 2.2. Values of the landscape metrics for each of the 8 strata used to stratify the 2030 km^2 study area at the northern tip of the Melville Peninsula, Nunavut, Canada.

Strata	**Tundra productivity (*N*)**	**Terrain ruggedness (*R*)**	**Freshwater (*W*)**	**Total area (km^2)**	**Transects sampled**		
					2010	**2011**	**2012**
1	low	high	low	148	12	18	12
2	high	high	low	24	0	17	12
3	low	high	high	79	9	14	11
4	high	high	high	11	0	6	8
5	low	low	high	76	17	16	12
6	low	low	low	182	14	11	10
7	high	low	high	98	7	27	19
8	high	low	low	123	2	11	7

Table 2.3. Detection function model forms determined to be most parsimonious (AIC$_c$[b]) for each avian guild.

	Truncation (m)						
Guild	**Left**	**Right**	**Model form**	**Series expansion**	**# adjustment terms**	**Covariates**	***P*-value[a]**
Songbirds	0	50	hazard rate	n/a	0	Julian day	0.87
Shorebirds	0	40	half normal	cosine	1	n/a	0.57
Gulls	20	245	half normal	n/a	0	n/a	>0.99
Geese	0	375	half normal	n/a	0	year	0.90
Loons	50	260	half normal	n/a	0	n/a	0.72

[a] *P*-values were obtained from a Kolmogorov–Smirnov test of the fit of the observation data to the detection function.

[b] See Appendix A, Table A2 for details of the AIC$_c$ analysis.

Table 2.4. Top log-linear Poisson models predicting the counts of bird clusters observed along transects within 16 different strata.

	ΔAIC$_c$/Akaike weight			**Coefficient ± SE**[a]	
Guild	**Model 1**	**Model 2**	**Term**	**Model 1**	**Model 2**
Songbirds	0.00/0.64	1.78/0.26	*T*	-0.80 ± 0.22**	-0.62 ± 0.29*
			W	0.39 ± 0.17**	0.47 ± 0.21**
			N	-0.45 ± 0.22*	-0.46 ± 0.21*
			T×*N*	0.65 ± 0.35*	0.67 ± 0.35*
			T×*W*	-	-0.31 ± 0.33
			int.	-9.60 ± 0.17**	-9.64 ± 0.19**
Shorebirds	0.00/0.79	-	*L*	0.96 ± 0.45*	-
			R	-3.00 ± 0.80**	-
			N	-0.12 ± 0.51	-
			L×*N*	1.31 ± 0.70*	-
			int.	-10.18 ± 0.35**	-
Loons	0.00/0.38	0.83/0.25	*L*	0.32 ± 0.30	-
			R	-1.17 ± 0.36**	-1.12 ± 0.36**
			W	1.24 ± 0.30**	1.27 ± 0.30**
			R×*W*	-1.15 ± 0.59*	-1.18 ± 0.60*
			int.	-12.16 ± 0.26**	-12.03 ± 0.21**
Geese	0.00/0.72	-	*T*	0.52 ± 0.56	-
			W	1.05 ± 0.46*	-
			N	3.25 ± 0.41**	-
			T×*W*	-1.59 ± 0.75*	-
			int.	-12.65 ± 0.45**	-
Gulls	0.00/0.21	0.38/0.17	*L*	0.71 ± 0.23**	0.78 ± 0.24**
			R	-0.13 ± 0.31	-0.57 ± 0.24**
			W	0.43 ± 0.28	-
			N	-	-0.30 ± 0.23
			R×*W*	-0.87 ± 0.49*	-
			int.	-12.69 ± 0.27**	-12.33 ± 0.24**

Table 2.4 notes

All terms used, except the intercept (int.), were categorical (0 = low, 1 = high) and include summer weather (T), lemming abundance (L), terrain ruggedness (R), amount of freshwater (W), and vegetation productivity (N). Only models with $\Delta \mathrm{AIC}_c$ values <2 are shown.

aBootstrap standard errors

*Coefficient estimate significantly different from 0 ($\alpha = 0.05$) based on bootstrap percentile confidence intervals.

**Coefficient estimate significantly different from 0 ($\alpha = 0.01$) based on bootstrap percentile confidence intervals.

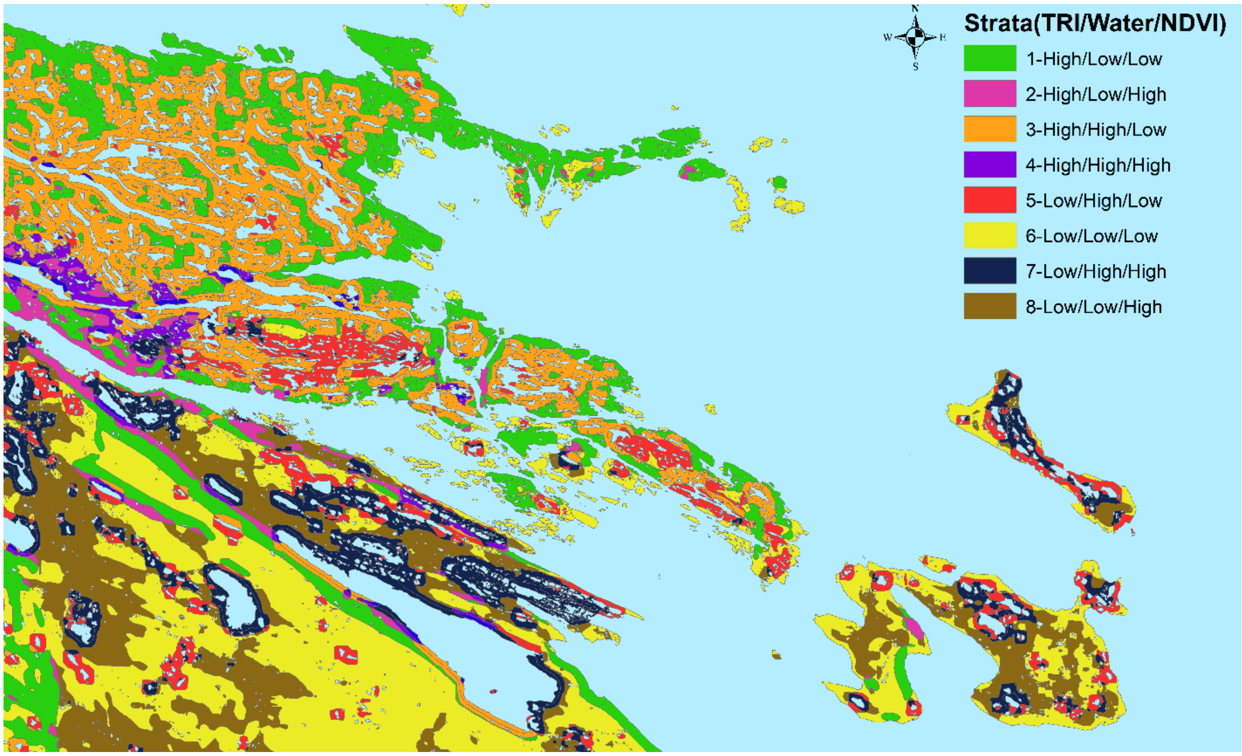

Figure 2.1. Spatial distribution of the strata used to estimate the density of various avian guilds using distance sampling. Strata were based on a Terrain Ruggedness Index (TRI), the amount of standing fresh water, and the Normalized Difference Vegetation Index (NDVI).

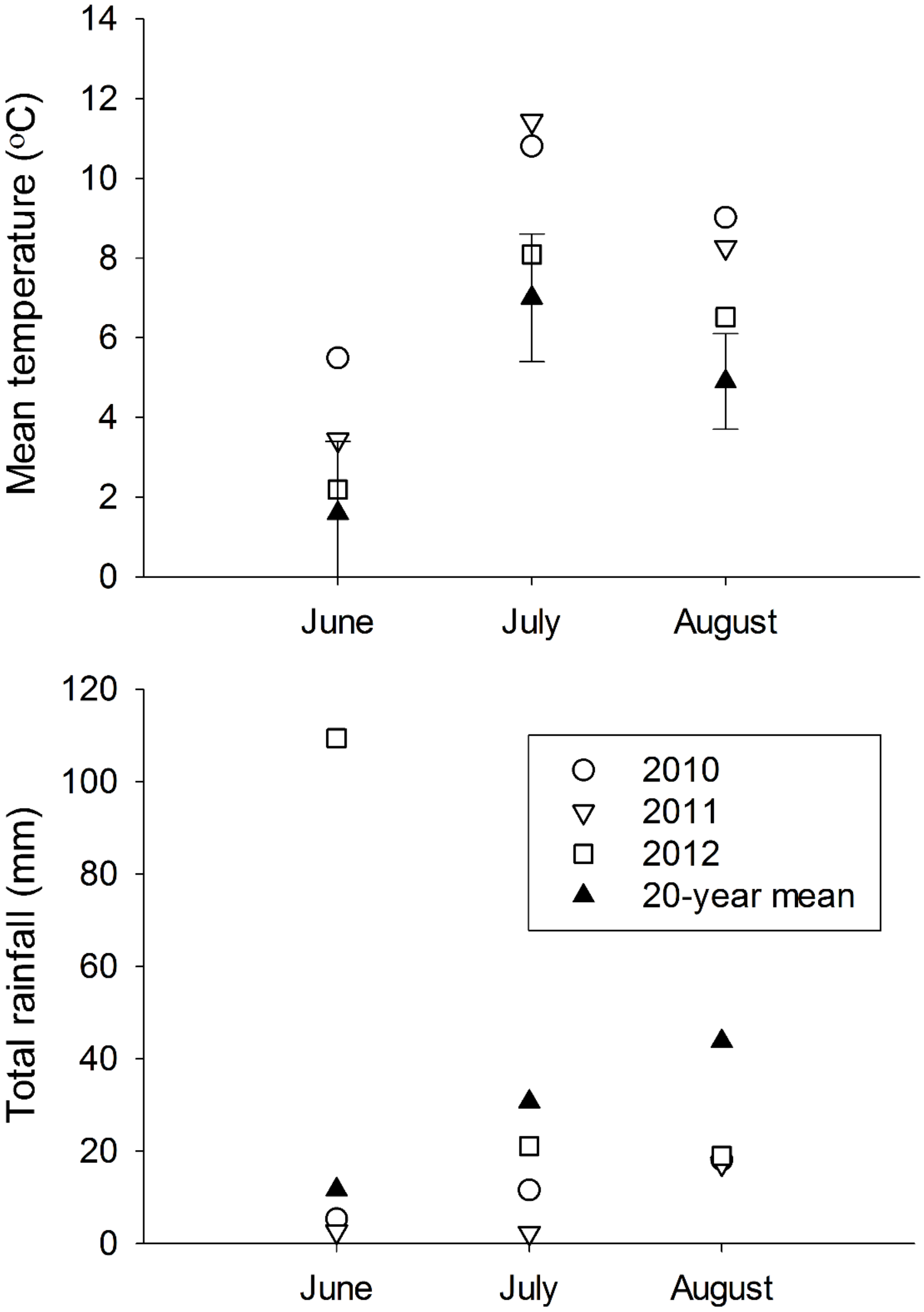

Figure 2.2. Mean monthly temperature and total monthly rainfall in the Igloolik study area. Data from 2010-2012 were collected during this study using a remote weather station located on the Coxe Islands. The 20-year mean is based on data from 1980-2000 collected by Environment Canada at the Igloolik airport (http://www.weather.gc.ca).

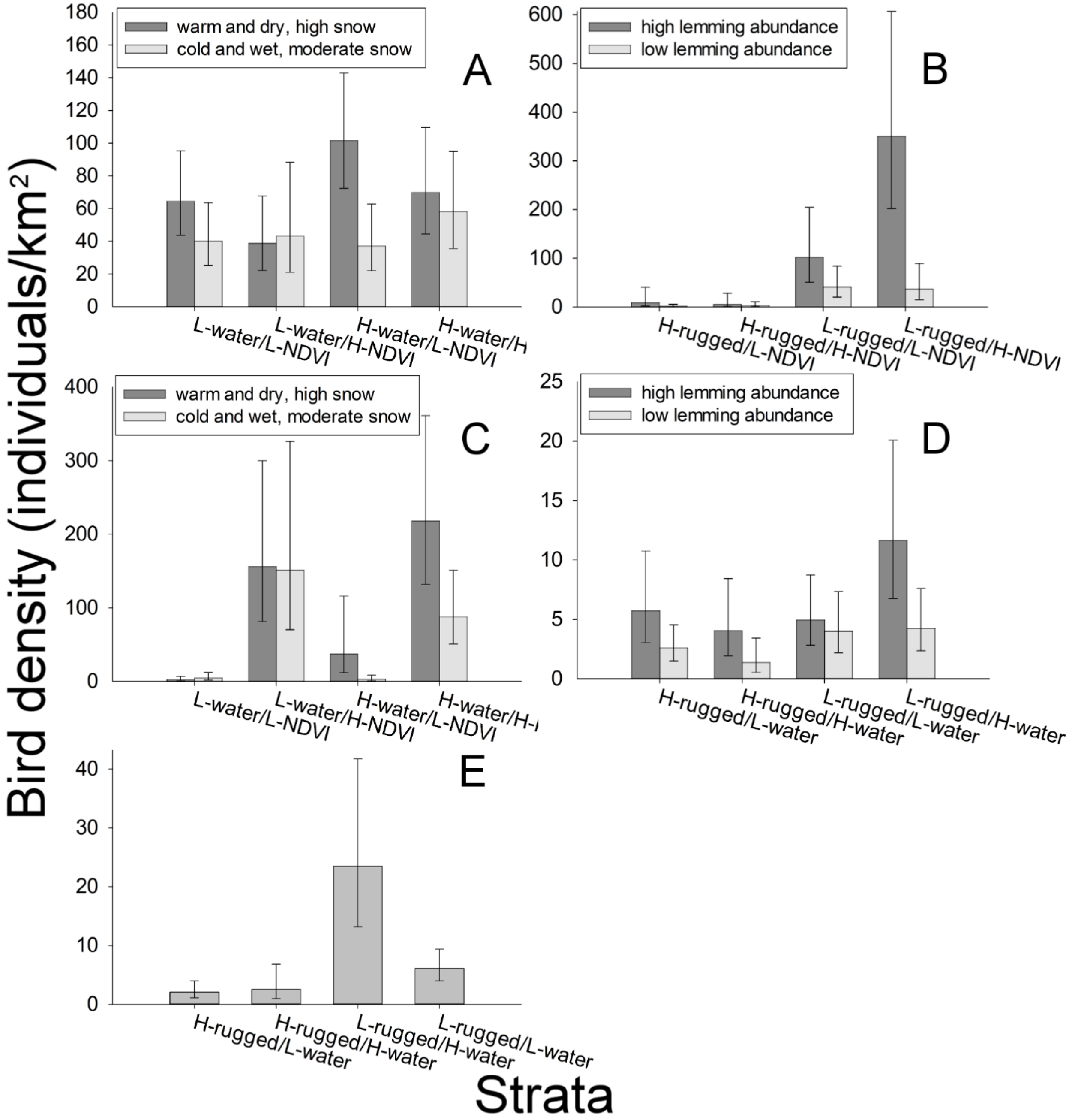

Figure 2.3. Guild-specific density estimates in relation to summer weather and landscape metrics. For each guild (A – songbirds, B – shorebirds, C – geese, D – gulls, E – loons) only landscape metrics found to significantly influence the number of individuals observed along transects were used (Table 2.4). The binomial landscape metrics (low (L) or high (H)) include the proportion of area made up of standing freshwater (water), terrain ruggedness (rugged) and vegetation productivity (NDVI). Note the scale on the density axis is different for each guild. Error bars show the 95% confidence interval around each density estimate.

3 Estimating nestling diet with cameras: quantifying uncertainty from unidentified food items

3.1 Introduction

Quantification of diet is an important aspect of avian ecology, particularly during the breeding season when demand for food is greatest. The quantity and composition of nestling diet influences growth rate, immunological development and, ultimately, survival and fitness (Birkhead et al. 1999, Naef-Daenzer and Keller 1999, Schwagmeyer and Mock 2008, Navarro-López et al. 2014, Resano-Mayor et al. 2014). There are many methods for determining nestling diet including stable isotope analysis (Moreno et al. 2010, Pokrovsky 2012), direct observation (Schwagmeyer and Mock 1997), faecal analysis (Michalski et al. 2011, Orlowski et al. 2014) and, for birds of prey, prey remains and pellet analysis (Simmons et al. 1991, Symondson 2002).

One of the most cost effective and accurate methods of determining diet with minimal disturbance to the study organism is the use of cameras at nest sites (Wille and Kampp 1983, Franzreb and Hanula 1995, Margalida et al. 2005, Tornberg and Reif 2007, Zarybnicka et al. 2011). This technique first emerged in the early 1980s and has become widely adopted as cameras have become smaller, cheaper, and more advanced. A wide variety of surveillance techniques have been utilized including motion-sensitive and preprogramed cameras, time-lapse photography, and video cameras (see Reif and Tornberg 2006 for a review of methods). Nest cameras can document food deliveries to nestlings while simultaneously collecting a host of other important data (e.g., phenology, behaviour and causes of mortality). One common problem in most diet studies employing nest cameras is the inability to identify all food items to fine-scale taxonomic levels or other categories. Unidentified or broadly classified food items often constitute upwards of 20-40% of all observed deliveries (e.g., Rogers et al. 2006, Takagi and Akatani 2011, Schroeder et al. 2013).

As the proportion of unidentified food items increases, so too does the uncertainty around estimates of diet composition. Unidentified food items are particularly problematic if the proportional contribution of each food source to the total biomass consumed is required. Techniques have been developed to assign biomass estimates to unidentified food items (e.g., Miller et al. 2014), but attempts to quantify the amount of uncertainty around estimates of diet composition are lacking. Variance around diet estimates can be reported for the population (e.g., standard deviation or error), but this does not account for the uncertainty related to unidentified food items, nor does it allow for measures of uncertainty for individual nests.

In this chapter I demonstrate a method of incorporating unidentified food items into estimates of diet composition for individual broods, while also quantifying uncertainty around these estimates. This method allows for the proportional contribution of each food source to overall diet to be estimated in both frequency of deliveries and biomass. I demonstrate my method using data collected with motion-sensitive cameras monitoring Arctic peregrine falcon (*Falco peregrinus tundrius*) nests in Nunavut, Canada.

3.2 Methods

3.2.1 Nest monitoring

I monitored between 4 and 7 peregrine falcon nests per year from 2010 to 2012 (Figure 1.1), accumulating data for 21 nest-years (Appendix B, Table B1). Once peregrines laid eggs and began incubating (13-20 June), I secured a motion-sensitive camera (PC85 Rapidfire or PC8000 Hyperfire, Reconyx Inc., Holmen, Wisconsin, USA) to a large rock 1-1.8 m from each nest. The Infrared motion detector and lens of each camera was aimed ~ 0.15 m above the scrape (nest cup) using a laser pointer. Cameras were programmed to take an image every time motion was detected at a maximum rate of 1 image/2 seconds (e.g., Appendix C, Figure. C1-3). Cameras had infrared illuminators allowing images to be taken in low light conditions. Each camera was in place until all nestlings had fledged from the nest (20-25 August). Nests were visited once per week to replenish the cameras' memory cards and batteries. Because I was interested in nestling diet, I only analyzed prey deliveries while nestlings were 1-14 days old. Once nestlings were > 14 days old, they started moving around the nest cliff, so some prey deliveries occurred outside of the camera's field of view.

3.2.2 Estimating diet along with uncertainty

Prey items delivered to nests were identified to the finest taxonomic level possible and then assigned to one of five ecologically meaningful prey categories: insectivorous birds (songbirds and shorebirds; Passeriformes, Scolopacidae, and Charadriidae), gulls (Laridae, Sternidae and Stercorariidae), ducks (Anatidae), black guillemots (*Cepphus grille*), or lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) (e.g., Appendix C, Figure C1-3). Prey items that could not be identified due to low lighting, poor camera focus, or a blocked field of view were assigned to one of two possible categories: unidentified or unidentified avian (Table 3.1 provides example datasets from 4 separate nests).

I then determined all of the possible ways in which unidentified prey items could be allocated among the different categories. Because I had multiple, nested, categories, which is common in studies quantifying diet with nest cameras, I first allocated prey items from the broadest unidentified category. In my example, a prey item in the unidentified category could have been either a lemming or one of the avian prey categories. I therefore determined all of the possible ways in which the unidentified prey items could be allocated to the lemming and the unidentified avian categories (possible outcomes; e.g., Table 3.2) using the ‘compositions’ function in the ‘partitions’ package (Hankin 2006) for the R Statistical Environment (R Core Team 2014).

Next, I calculated the probability of each possible outcome *j* (Po_j) occurring by using probability theory:

$$Po_j = \frac{\prod\left(P_i^{N_{ij}}\right)\left(\sum N_{ij}\right)!}{\prod\left(N_{ij}!\right)}$$

where P_i is the probability of an unidentified prey item being the *i*th category, and N_{ij} is the number of unidentified prey items assigned to category *i* in outcome *j*. The P_i values can be determined based on knowledge of the specific system being studied. For example, unidentified prey items could be considered to have an equal probability of being in each prey category, or probabilities could be based on the relative availability of prey from each category within the study system (e.g., prey surveys). The latter strategy assumes the consumer being studied is a generalist that consumes each prey type in proportion it its availability. Alternatively, P_i’s could be based on the total number of identified prey items in each category. In my system, for example, deliveries of avian prey were more frequent than lemmings (Table 3.1), so I assumed unidentified deliveries had a higher probability of being avian. I therefore assumed P_i was equal to the proportion of all identified prey items that were assigned to category *i* across all nests in a given year (Table 3.3). P_i could also be calculated for each nest individually, but for nests with a high proportion of unidentified prey (e.g., Table 3.1, site 8), these proportions may not accurately represent true probabilities.

Using the above equation and the N_{ij} and P_i values from Tables 3.2 and 3.3, respectively, I estimated the probability of each possible outcome, which produces a probability space (Table 3.2). Although the first possible outcome is the most probable, the possibility of the other outcomes occurring can be accounted for and used to estimate uncertainty around diet estimates. I simulated 100 samples from the probability space using the 'sim' function from the 'partitions' package (Hankin 2006) in R. I then added the number of prey assigned to the unidentified avian and lemming categories in each of the 100 simulated samples to the number of identified prey deliveries in each of these categories (Table 3.4). If I was concerned only with the proportion of avian versus lemming prey within the diet of peregrine nestlings, I could stop here and calculate these proportions for each of the simulated samples and calculate measures of central tendency (e.g., mode) and dispersion (e.g., 95% confidence intervals) across the 100 simulated samples. But, because I was interested in estimates of diet composition with a finer taxonomic resolution, I repeated this process again.

In the second iteration, I determined all of the possible outcomes of allocating the updated unidentified avian prey items from each of the 100 simulated samples among the four avian categories. The additional prey categories resulted in a larger number of possible outcomes, particularly if there were a large number of unidentified avian prey. For example, sample 1 in Table 3.4 had 364 possible outcomes for which the 11 unidentified avian prey could be allocated to the four avian categories. As before, I used the above equation to calculate the probability of each possible outcome to produce a probability space, assuming P_i was equal to the relative proportion of each identified avian prey item for a given year (Table 3.3). I then simulated another 100 samples from each of the 100 probability spaces, resulting in 10,000 samples.

For each sample, the proportional contribution of each prey category can be calculated either in frequency of deliveries or total biomass of deliveries. I expressed diets in terms of biomass; for each of the 10,000 samples, the proportional contribution of prey type i to the diet of nestlings was expressed as $n_i w_i / \Sigma(n_i w_i)$, where n_i is the number of deliveries of prey type i during the observation period (after allocating unidentified prey deliveries) and w_i is the estimated mass of prey type i. Prey masses were estimated based on the literature and the size of prey items relative to the size of nestlings in camera images (Table 4.1; Appendix B, Table B2).

Treating each prey category separately, I then used kernel density estimation across the distribution of 10,000 proportions to determine the most probable proportion (mode). I estimated 50, 75 and 95% confidence intervals around the most probable proportion by calculating the highest density regions within the probability distribution created from the kernel density estimation (Hyndman 1996). I used the ‘hdr’ function within the ‘hdrcde’ package (Hyndman 2013) for R to conduct the kernel density estimation and calculate the highest density regions. Because I used kernel density estimation separately for each prey category, the modes of the proportions did not necessarily sum to one. If proportions that sum to one are required, they can be calculated based on the most probable allocation of unidentified prey items (possible outcomes), and the 10,000 samples can be used only for calculating confidence intervals.

3.3 Results

Peregrine falcon diet varied across nests and years. Diets were dominated by insectivorous birds with a small component of ducks and marine birds in some nests (center columns of Figures 4.2a, 4.3a, and 4.3b). In 2011, the lemming component of diets increased, but there was still a substantial contribution of insectivorous birds (center columns Figures 4.2b, 4.2c, 4.3c, and 4.3d). The width of the 95% confidence intervals around estimates of the proportional contribution of each prey category to the diet increased with the number of unidentified prey deliveries (Table 3.1, Figure 4.2: center column).

3.4 Discussion

The method presented offers a means of incorporating unidentified food items into diet estimates, while quantifying uncertainty around these estimates. A convenient aspect of this method is that it allows for nested unidentified categories at multiple taxonomic levels, which is common among studies of nestling diet using nest cameras (e.g., Behney et al. 2010, Miller et al. 2014). When a high proportion of food deliveries are unidentified, diet estimates become uncertain and it is difficult to estimate the relative contribution of each food source to the overall biomass of food consumed. I overcome this limitation by considering every possible way in which unidentified food items can be allocated to each food category and assigning a probability to each possible outcome.

Another advantage of my method is that the probabilities of possible outcomes can be based on previous knowledge of the system being studied, such as data on prey availability, diet estimated from other methods, or the identified food items documented. In my example, I assumed there was a higher probability of an unidentified prey item being an insectivorous bird than any other prey type, because insectivorous birds were more common among the known deliveries. As a result, the probabilities were skewed toward those possible outcomes with many insectivorous birds, so there was a small range of possible outcomes drawn from the probability spaces leading to narrow 95% confidence intervals around my diet estimates. Had I assumed there was an equal probability of an unidentified item being within each prey category, confidence intervals would have been wider because there would be a greater range of possible outcomes drawn from the probability spaces. I recommend that users of this method have adequate justification before assigning unequal probabilities across food categories because doing so will inevitably reduce the error around diet estimates.

This method provides a novel means of estimating error around diet estimates for individual nests, rather than just the population. Estimating error around individual nests is particularly useful if diet estimates are to be used in further statistical analysis. For example, the use of Bayesian mixing models to estimate diets based on stable isotopes is becoming common (Phillips et al. 2014), and a major advantage of the Bayesian statistical framework is that informative prior hypotheses about the diet can be incorporated into the analysis (Moore and Semmens 2008). These priors are entered as estimates of the mean proportional contribution of each food source to the diet, but a measure of standard error around the mean of one food source is also required (Parnell et al. 2010). Nest cameras provide a way to estimate prior hypotheses for Bayesian mixing models, and my method demonstrates a way of quantifying standard error around these priors.

Although studies estimating nestling diets with nest cameras are somewhat biased toward large-bodied birds, such as raptors, the method has been used on species as small as blue tits and (*Parus caeruleus*) (Tremblay et al. 2005) and ladder-backed woodpeckers (*Picoides scalaris*) (Schroeder et al. 2013). As the technology improves and cameras become smaller and higher in resolution, studies using nest cameras to estimate nestling diet will likely proliferate. My method provides a way to quantify the uncertainty associated with unidentified food deliveries, which are inevitable in any study using nest cameras.

Table 3.1. Data from four nest cameras monitoring peregrine falcon nestlings in Nunavut, Canada, showing the frequency of prey items within each category delivered to nestlings during the observation period.

Nest site	**Year**	**Unid.**	**Unid. avian**	**Insect. bird**	**Duck**	**Gull**	**Black guillemot**	**Lemming**
1	2010	2	3	55	0	0	0	1
2	2010	7	4	68	5	0	1	1
8	2011	45	3	72	0	0	0	12
14	2011	16	1	19	1	2	0	24

Table 3.2. All of the possible outcomes (*j*) of allocating the 7 unidentified prey items from nest site 2 in 2010 (Table 3.1) to either the unidentified avian or lemming categories, along with the probability of each outcome occurring (Po_j).

Outcome *j*	**Unid. avian**	**Lemming**	**Po_j**
1	7	0	0.906
2	6	1	0.090
3	5	2	0.004
4	4	3	<0.001
5	3	4	<0.001
6	2	5	<0.001
7	1	6	<0.001
8	0	7	<0.001

Table 3.3. The probability of an unidentified prey item being within each prey category for each year. Probabilities are based on the proportion of identified prey items within each prey category across all nests for a given year.

	Unidentified		**Unidentified avian**			
Year	**Lemming**	**Unid. avian**	**Insect. bird**	**Duck**	**Gull**	**Black guillemot**
2010	0.014	0.986	0.953	0.039	0.000	0.008
2011	0.269	0.731	0.968	0.010	0.021	0.000

Table 3.4. An example of 10 samples of possible outcomes simulated from the probability space shown in Table 3.2, demonstrating how the frequency of identified prey items in each prey category (site 2, 2010, in Table 3.1) were modified by allocating the unidentified.

	Unidentified		**Unidentified allocated to other categories**					
Sample #	**Unid. avian**	**Lemming**	**Unid. avian**	**Insec. bird**	**Duck**	**Gull**	**Black guillemot**	**Lemming**
1	7	0	4+7 = 11	68	5	0	1	1+0=0
2	6	1	4+6 = 10	68	5	0	1	1+1=2
3	7	0	4+7 = 11	68	5	0	1	1+0=0
4	7	0	4+7 = 11	68	5	0	1	1+0=0
5	7	0	4+7 = 11	68	5	0	1	1+0=0
6	7	0	4+7 = 11	68	5	0	1	1+0=0
7	7	0	4+7 = 11	68	5	0	1	1+0=0
8	7	0	4+7 = 11	68	5	0	1	1+0=0
9	6	1	4+6 = 10	68	5	0	1	1+1=2
10	7	0	4+7 = 11	68	5	0	1	1+0=0

4 Estimating the diet of predators with stable isotopes: using priors in Bayesian mixing models to reduce uncertainty

4.1 Introduction

Understanding the diet of predators is an important aspect of ecology. Predation can shape community structure directly by reducing prey populations or indirectly by influencing various aspects of prey behaviour (Sih et al. 1985, Creel and Christianson 2008, Zanette et al. 2011). Both the direct and indirect effects of predation can lead to trophic cascades, where changes in prey demographics or behaviour affect the organisms on which prey are consuming, often creating conservation or management concerns (Pace et al. 1999, Baum and Worm 2009, Beschta and Ripple 2009). Understanding the degree to which predation pressure shapes community structure can be difficult, particularly in multi-prey systems where the factors influencing a predator's prey preferences are unclear (Sih and Christensen 2001). As a first step, quantifying the proportional contribution of each prey type to a predator's diet (hereafter referred to as dietary proportions) is paramount when managing or conserving any system involving predator-prey dynamics, whether it be terrestrial or marine, or contains large- or small-bodied predators (e.g., Smith et al. 2004, Sutherland et al. 2011, Maxwell and Morgan 2013).

Stable isotope analysis using mixing models has become one of the most common tools for investigating the diet of animals (del Rio et al. 2009, Phillips et al. 2014). The isotopic signature (e.g., $\delta^{13}C$ and $\delta^{15}N$) of prey tissues vary across taxa and trophic levels and these signatures are maintained as prey tissues are incorporated into predator tissues after consumption (Gannes et al. 1997, Phillips et al. 2014). Mixing models use the isotopic values of prey and predator tissues and mass balancing equations to estimate the proportional contribution of various prey types (sources) to a predator’s diet (mixtures) (Phillips and Gregg 2003, Phillips 2012).

Stable isotope mixing models contain multiple sources of uncertainty which are often extensive and, until recently, were unaccounted for (Moore and Semmens 2008). Bayesian statistical techniques to quantify this uncertainty have been developed (Moore and Semmens 2008) and adopted since the release of several software packages (Jackson et al. 2009, Semmens et al. 2009a, Parnell et al. 2010, Hopkins and Ferguson 2012, Stock and Semmens 2013, Fernandes et al. 2014). To date, one of the most commonly used Bayesian mixing models is implemented with the SIAR package (Parnell et al. 2010) developed for the R Statistical Environment (R Core Team 2014). As with the other Bayesian mixing models, output from SIAR contains a posterior distribution of possible solutions to the mixing model, which can be used to obtain 95% credible intervals for the proportional contribution of different prey types to the diet of a consumer. Proponents of stable isotope mixing models explicitly caution users about making inferences based on a single summary statistic from the posterior distribution (e.g., the mode) (Phillips and Gregg 2003, Parnell et al. 2010, Phillips et al. 2014); however, published studies often use the mode, mean or median estimates of dietary proportions in further statistical analysis and disregard the often large 95% credible intervals around these estimates (e.g., L'Herault et al. 2013, Ramirez et al. 2014, Resano-Mayor et al. 2014). Bond and Diamond (2010) note the potential dangers of using inaccurate estimates of diet for conservation and management efforts, which highlights the need to quantify the uncertainty around estimates of dietary proportions and come up with solutions to reduce it.

A major benefit of Bayesian mixing models, which has the potential to improve the accuracy and precision of estimates of dietary proportions, is the ability to incorporate informative priors into the models (Moore and Semmens 2008, Parnell et al. 2010). In the SIAR package, priors are entered as mean estimates of the proportional contribution of each food source to the diet, along with the standard deviation for one food source. Priors can be based on professional knowledge, past literature, or more traditional methods such as scat analysis (Moore and Semmens 2008, Parnell et al. 2010). The published literature indicates that users of the SIAR package seldom take advantage of informative priors, possibly because few studies have examined specifically how priors affect the results of Bayesian mixing models. Franco-Trecu et al. (2013) used scat analysis to develop informative priors to estimate the diets of South American fur seals (*Arctocephalus australis*) and South American sea lions (*Otaria flavescens*). They found that informed mixing models with priors generally resulted in intermediate estimates between those obtained from uninformed models and scat analysis used in isolation, but 95% credible intervals around estimates were still wide. Chiaradia et al. (2014) tested whether the use of informative priors based on DNA analysis of scat improved the mixing model estimates of dietary proportions of little penguins (*Eudyptula minor*) fed a known diet in captivity. Using informative priors improved the accuracy of estimated dietary proportions, but the authors did not report the precision of these estimates. From these few studies, is it unclear how effective informative priors are at improving the precision and accuracy of the results from Bayesian mixing models. Factors such as the number of sources used in the mixing model and the amount of variation and correlation among source isotopic values can affect the amount of influence informative priors have on the results of Bayesian mixing models (Moore and Semmens 2008, Jackson et al. 2009, Parnell et al. 2010).

The goal of this study was to compare the results of Bayesian mixing models with and without informative priors to determine how priors, and the amount of error around them, influence the resulting estimates of dietary proportions. I studied a top predator, the Arctic peregrine falcon (*Falco peregrinus tundrius*), feeding on a diversity of marine and terrestrial prey. The diverse diet of the peregrine falcon (i.e. large number of potential sources) creates many potential solutions to the mixing models, which generally leads to large credible intervals around estimates of dietary proportions (Phillips and Gregg 2003, Parnell et al. 2010, L'Herault et al. 2013). Because peregrine falcons are central place foragers, bringing prey items back to the nest to feed nestlings, I was able to develop reliable informative priors for the Bayesian mixing models by installing motion-sensitive cameras at nest sites. Using camera images, I quantified the relative proportion of all prey types brought back to each nest (by mass) and incorporated these proportions as priors into Bayesian mixing models using the SIAR package. The diversity and composition of prey consumed by peregrines was variable across individuals with varying contributions of terrestrial and marine prey, which allowed me to assess the efficacy of informative priors at improving the accuracy and precision of estimates of dietary proportions under different scenarios. By investigating the manner in which informative priors influence results from the SIAR package, I was able to make recommendations on procedures to develop priors and when they would be most beneficial to dietary studies in the context of conservation and management.

4.2 Methods

4.2.1 Peregrine falcon monitoring

Peregrine falcon nests were monitored with motion-sensitive cameras as described in Chapter 3.2.1.

I used the isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of blood plasma from nestlings to infer the diet of peregrine falcons (see details below). I collected blood samples from nestlings within 3 to 7 peregrine falcon nests (Figure 1.1) per year from 2010 to 2012, accumulating samples from 17 nest-years (Appendix B, Table B1). Once nestlings were 10 days old, I extracted up to 1 mL of blood from all nestlings during weekly nest visits. Blood samples were taken from the ulnar vein with a 3 mL syringe and 25 gauge needle and immediately transferred to sterile vacuum blood collection tubes coated with sodium heparin (green top Vacutainer, BD). Each blood sample was stored in a cooler on ice for a maximum of 8 hours before being spun in a centrifuge (IEC Spinnete, Damon/IEC Division) at 3400 rpms for 10 minutes to separate red blood cells from plasma. Plasma from each sample was transferred to a 2 mL screw-cap microcentrifuge tube (VWR International, Radnor, Pennsylvania, USA) with a pipette and kept in a cooler on ice for a maximum of 4 days before being frozen at -20 ˚C until it was processed for stable isotope analysis.

4.2.2 Prey tissue collection

I determined the potential prey species consumed by Arctic peregrine falcons from the literature (Court et al. 1988, L'Herault et al. 2013), prey remains observed at nest sites, and images from the motion-sensitive cameras. Peregrines consumed a diversity of prey types including songbirds (Passeriformes), shorebirds (Scolopacidae and Charadriidae), gulls (Laridae, Sternidae and Stercorariidae), ducks (Anatidae), black guillemots (*Cepphus grille*), and lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*). Throughout the 3 years of this study, I opportunistically collected remains from individual prey items found at nest sites or elsewhere in the study area. I collected avian prey by shotgun only when necessary to obtain a sufficient number of samples for a prey type. I obtained lemming tissue samples from animals destructively sampled by snap trap, which was being carried out for another concurrent study (Robinson et al. 2014; Chapter 2). I dissected a ~0.5 cm^3 sample of muscle tissue from each prey item (breast for birds and thigh for mammals) and stored samples at -20 ˚C for a maximum of 3 months until they were processed for stable isotope analysis (see below). I collected a total of 79 samples from at least 15 different species (Appendix B, Table B3).

4.2.3 Stable isotope analysis

Both plasma and prey tissue samples were freeze-dried and ground to a fine powder using a mortar and pestle. I then extracted lipids from all prey tissues samples, following the methods described by Logan et al. (2008), because variable lipid content across study organisms can introduce bias into stable isotope analysis using $\delta^{13}C$ (Post et al. 2007). I weighed 700 µg of each powdered prey tissue and peregrine plasma sample into tin capsules for stable isotope analysis. Samples were analyzed by the Biogeochemical Analytical Service Laboratory at the University of Alberta (Edmonton, Alberta, Canada) for $\delta^{13}C$ and $\delta^{15}N$ using a EuroVector EuroEA3028-HT elemental analyzer coupled to a GV Instruments IsoPrime continuous-flow isotope ratio mass spectrometer. Isotopes were expressed in parts per thousand deviations from a standard (‰), with Pee Dee Belemite and air as the standards for $\delta^{13}C$ and $\delta^{15}N$, respectively. The laboratory also used NIST 8415 whole egg powder SRM as an in-house $\delta^{15}N$ and $\delta^{13}C$ QA/QC check throughout analyses with standard deviations of 0.2‰ and 0.1‰, respectively.

For mixing models, the sources (prey items) need to be grouped into isotopically distinct categories, which should be biologically meaningful (e.g., taxon, trophic guild; Phillips et al. 2005). I developed *a priori* categories for each prey type and used a K-nearest neighbour randomization test (Rosing et al. 1998) to determine if each category was significantly different in bivariate isotope space ($\delta^{13}C$ and $\delta^{15}N$). Initially, I grouped prey taxonomically (songbirds, shorebirds, gulls, ducks, guillemots, and lemmings), but the isotopic values of songbirds and shorebirds were not significantly different ($p = 0.544$), nor were those of gulls and guillemots (p

= 0.159). I then combined songbirds and shorebirds into insectivorous birds, and gulls and guillemots into marine birds, which resulted in all categories being isotopically distinct (*P* <0.001; Figure 4.1),

4.2.4 Developing informative priors

Informative priors were developed from images captured with motion-sensitive cameras as described in Chapter 3.2.2. I used only those images captured while at least one nestling was 1-14 days old (the observation period) to estimate the proportional contribution of each prey type (biomass) to the diet of nestlings (informative priors). Blood samples were collected either toward the end of or after the observation period (Appendix B, Table B1). Prey deliveries made during the observation period likely provided a good representation of the diets inferred from plasma samples because the isotopic values of plasma represents integration of prey tissues consumed during the previous week (Hobson and Clark 1993).

The SIAR package requires that informative priors sum to one, so I used the most probable allocation of unidentified prey from the 10,000 samples, rather than the modes (see Chapter 3.2.2 for details). The SIAR package allows the standard deviation of only one source to be entered into the informative priors (Parnell et al. 2010). I used the standard deviation for insectivorous birds because this was the only prey type consumed by all nests; standard deviations were similar across prey types (center columns of Fig. 4.2 and 4.3), so the choice of which standard deviation to include did not have a significant impact on the mixing model results.

4.2.5 Implementing mixing models in the SIAR package

Before implementing any mixing models, I used the method developed by Smith et al. (2013) to test the assumptions associated with stable isotope analysis and determine if my proposed mixing model (i.e. 2 isotopes and the 4 specific prey sources I considered) could reasonably establish mass balance for all peregrine falcon plasma samples. This method estimates a mixing region within isotopic space bound by the mean isotopic values of each prey source considered, while accounting for the error around these means (Figure 4.1). Any falcon plasma sample that fell outside of the mixing region (i.e. with <5% probability of being explained by the mixing model) was excluded from the analysis.

Initially, I used an uninformed mixing model with a vague prior distribution (equal probability of each prey type contributing to the diet; Parnell et al. 2010) to estimate dietary proportions for each nest. Input for the mixing models included the isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of falcon plasma (the mixture), the mean and standard deviation of the isotopic values and C and N concentrations for each prey type (Figure 4.1, Table 4.1), and the mean and standard deviation of the trophic enrichment factors for each isotope ($\Delta^{13}C$ and $\Delta^{15}N$).

I obtained trophic enrichment factors for whole blood from a study that fed captive adult peregrine falcons a fixed diet of Japanese quail (*Coturnix japonica*): 0.2 ± 0.01‰ for $\Delta^{13}C$ and 3.3 ± 0.4‰ for $\Delta^{15}N$ (Hobson and Clark 1992). Trophic enrichment for ^{15}N was potentially lower for nestlings from my study than those reported for adults because rapidly growing animals tend to experience more N depletion than non-growing individuals (Sears et al. 2009). However, the $\Delta^{15}N$ values reported by Hobson and Clark (1992) were for whole blood, which consistently has lower $\Delta^{15}N$ values than plasma across a diversity of taxa (e.g. Federer et al. 2010, Kurle et al. 2013, Chiaradia et al. 2014). Although no trophic enrichment factors estimates are available for juvenile peregrine falcons, Kurle et al. (2013) reported $\Delta^{15}N$ values of 3.3 ± 0.7‰ for the plasma of juvenile California condors (*Gymnogyps californianus*). I conducted a sensitivity analysis and found that $\Delta^{15}N$ did influence diet estimates from the uninformed mixing models, but only significantly when $\Delta^{15}N$ were unrealistically low (<1.5; Appendix B, Figure B2). I, therefore, used the trophic enrichment factors reported by Hobson and Clark (1992) in my mixing models.

The mixture for each mixing model was represented by the isotopic values of plasma samples collected from all nestlings within a nest on one or two occasions at least 1 week apart (Appendix B, Table B1). Repeated samples from the same nestling can be considered independent because of the weekly turnover rate of stable isotopes in plasma (Hobson and Clark 1993), which likely occurs even faster in rapidly growing nestlings (Reich et al. 2008)

I then used informed mixing models to estimate the dietary proportions by using the same inputs as the uninformed models ($\Delta^{15}N$ generally had no influence on the results of the informed models; Appendix B, Figure B3), but also included informative prior hypotheses for the dietary proportions estimated with images from the motion-sensitive cameras (see Chapter 3.2.2) (Moore and Semmens 2008, Parnell et al. 2010). All informed and uninformed mixing models were run with 1,000,000 iterations and a burn in of 100,000.

4.3 Results

Of the 102 plasma samples collected, only two fell outside the mixing region ($P < 0.03$; Figure 4.1). These two samples were from two separate nests, each with additional plasma samples that were within the mixing region ($P > 0.05$). I therefore had no reason to believe the assumptions associated with my mixing models were violated and simply excluded these two plasma samples from the analysis (Smith et al. 2013).

The posterior distributions of dietary proportions estimated with the uninformed mixing models were generally diffuse with 95% credible intervals often as wide as 0.5; credible intervals around the proportion of insectivorous birds were consistently wider than those around other prey types (Figure 4.2 and 4.3, Appendix B, Figure B1). The uninformed models indicated that for most nests, lemmings were the greatest contributor to diets (Figure 4.2, Appendix B and Figure B1). Other nests were predicted to have diets dominated by ducks (e.g., Figure 4.3b), or a relatively equal contribution of each prey type (e.g., Figure 4.3a).

In contrast, the distributions of dietary proportions estimated with motion-sensitive cameras (informative priors) were generally constrained with narrow 95% credible intervals (Figure 4.2 and 4.3; Appendix B, Figure B1). However, there were two nests with relatively large amounts of uncertainty around their informative priors (Figure 4.2c and 4.2d). For all but one nest (Figure 4.3d), the informative priors predicted that insectivorous birds made up at least 50% of each diet, with many nests having a diet consisting of 80 to 100% insectivorous birds (e.g., Figure 4.2a and Figure 4.3a). Priors also predicted that for almost all nests (except Figure 4.3d), the proportional contribution of lemmings to peregrine diets was <20%. As a result, the dietary proportions for lemmings and insectivorous birds estimated for the priors were often outside of the 95% credible intervals estimated with the uninformed models (Figure 4.2a-c, Figure 4.3a-c). The credible intervals from the uninformed models contained the prior estimates for lemmings and insectivorous birds only when the proportional contributions of all prey types to the diet were similar (Figure 4.3d).

If the error around informative priors was low, the posterior distribution of dietary proportions from the informed mixing models reflected the priors closely for measures of both central tendency and dispersion (Figure 4.2 and 4.3). Relatively larger amounts of error around the priors led to more uncertainty around results from the informed mixing models; however, the informed results were still more reflective of the priors than the uninformed results (e.g., Figure 4.2c). In one nest, the credible intervals around the priors were wider than those around results from the uninformed model; for this nest, the results from the informed model were more similar to those from the uninformed model than the priors (Figure 4.3d).

4.4 Discussion

The uninformed Bayesian mixing models consistently provided diffuse results with large credible intervals around estimates of dietary proportions. The error was so large that the results were often uninformative, providing no specific information about the diet of peregrine falcons. The only general conclusion that could be drawn was that lemmings were the most commonly consumed prey type, which contradicted the results from the informed mixing models.

The diffuse posterior distribution of solutions to the uninformed mixing models was a result of the geometry of the mixing space: across prey types, there was a positive correlation between δ^{13}C and δ^{15}N values producing a narrow mixing region (Figure 4.1). When the mixing region is narrow, there are a large number of potential solutions to the mixing model, especially if the isotopic values of the consumers (mixtures) are in the center of the mixing region (Phillips and Gregg 2001, Phillips and Gregg 2003, Moore and Semmens 2008). Mixing models are, therefore, particularly uninformative for predators such as Arctic peregrine falcons, that feed on both terrestrial and marine prey because δ^{13}C and δ^{15}N within prey tissues both generally increase from terrestrial to marine habitats (e.g., Harding and Stevens 2001, Semmens et al. 2009b, L'Herault et al. 2013).

Another problem with the results from the uninformed models was the consistent over-estimation of lemmings and under-estimation of insectivorous birds in peregrine falcon diets (relative to the priors), which was also driven by the geometry of the mixing space. The isotopic value of insectivorous birds is roughly on a line between lemmings and marine birds and a line between lemmings and ducks (a product of source isotopic values being positively correlated;

Figure 4.1). The isotopic value of many falcon plasma samples were close to that of insectivorous birds and also fell on one of these lines; a mixture with this position in the mixing region could be a result of consuming a large amount of insectivorous birds relative to all other prey types, or a combination of lemmings and marine birds, or lemmings and ducks. Although there were solutions within the posterior distribution that estimated a high contribution of insectivorous birds (upward of ~50%; Figure 4.2 and 4.3), the latter two scenarios were more common within the distribution, resulting in inaccurate diet estimates. These well-known limitations of mixing models associated with mixing space geometry (Phillips and Gregg 2003, Moore and Semmens 2008, Phillips et al. 2014) often preclude the use of stable isotopes to obtain accurate and precise estimates of the diet of many predators.

My results clearly demonstrate that the use of informative priors with small amounts of error can alleviate some of the problems associated with mixing space geometry. Motion-sensitive cameras indicated that insectivorous birds contributed the majority of peregrine diets in most nests, and that the marine contribution was very minimal and possibly zero. Based on observations of foraging peregrines, and prey remains found at peregrine nests during this and other studies (Burnham and Mattox 1984, Court et al. 1988, Rosenfield et al. 1995), I have high confidence that insectivorous birds were the dominant prey consumed. Using informed priors based on the camera images constrained the solutions of the mixing models to include mostly insectivorous birds, resulting in more accurate results from the informed models.

The posterior distributions of the informed models were more reflective of the priors than the uninformed models (Figure 4.2 and 4.3) because there was a high correlation between the isotopic values across prey types in this study and a low amount of error around my priors. When the isotopic data alone produces a very diffuse posterior distribution of solutions from an uninformed mixing model, the priors will be more influential on the results than the data (Moore and Semmens 2008, Jackson et al. 2009, Parnell et al. 2010, Chiaradia et al. 2014). I also observed that as the error around priors increased, results from the informed mixing models became more influenced by the isotope data, and subsequently more similar to the uninformed models. Developers of other mixing models have reported that priors had little influence on their results, which is likely a result of having a larger sample size within their mixture and more ideal mixing space geometry in their system compare to ours (Ward et al. 2010, Hopkins and Ferguson 2012).

Based on the results presented here, if ecologists need accurate and precise estimates of a predator's diet for conservation or management, I recommend the use of informative priors within Bayesian mixing models, particularly if the mixing space geometry is problematic (e.g. correlation between sources isotopic values, narrow mixing polygon; Phillips and Gregg 2003). In addition, if a predator has the potential to consume a variety of different prey types, but it is suspected that some individuals (or groups of individuals) have a diet composed of mostly one prey type, mixing models with informative priors can improve the accuracy of results. Individual variation in prey preferences among predators is an emerging problem in ecology (Semmens et al. 2009b, Pettorelli et al. 2011a), which could be confounded by results from stable isotope analysis because mixing models assume that all sources consumed are included in the mixing model (Phillips et al. 2014). I recommend that ecologists develop novel ways of estimating informed priors, ideally separately for each predator (or group of predators), that provide reliable estimates of diet with low error. If the study organism is a central place forager, like the peregrine falcon, motion-sensitive cameras provide an effective way of estimating priors, and unidentified prey items can be used to estimate error (Chapter 3). Informative priors based on methods such as stomach content or scat analysis, which are biased by variable digestion rates across prey types (Klare et al. 2011), may provide misguided influence to Bayesian mixing models (e.g., Franco-Trecu et al. 2013).

It could be argued that reliable priors estimating diet with limited bias may allow ecologists to forgo stable isotope analysis all together. However, managers and conservation practitioners often require a high level of confidence in their estimates of diet to make management decisions. For example, the composition of a predator's diet must be known accurately to determine if predator management is necessary to increase the abundance of a declining prey species (e.g., Thirgood et al. 2000, Elbroch and Wittmer 2013, Latham et al. 2013). In these cases, acquiring as much evidence as possible to support potential management actions is desirable. Indeed, the fact that peregrine falcon diets estimated with motion-sensitive cameras provided feasible solutions to the mixing models, based on the isotopic values of plasma and prey tissues, gave me more confidence in my results.

As the Bayesian model framework for analysing stable isotope data rapidly progresses, other methods of dealing with poor mixing space geometry, increasing the reliability of results, are being developed. Yeakel et al. (2011) developed a method that incorporates prey availability data into mixing models to help distinguish between prey sources with similar isotopic values. This method provides an alternative to using informative priors based on estimates of dietary proportions, but previous knowledge of how prey availability influences prey use by predators is still necessary. Whether it is easier to obtain prior information about prey availability or prey use by predators is likely system-dependent. Semmens et al. (2009b) developed a method to account for variation in isotopic values among individual consumers by assigning individuals to hierarchical levels of population structure (e.g., sub populations, social group and individual).

This method also allows for the use of informative priors, which would likely increase its efficacy for systems with poor mixing space geometry; however this remains to be tested.

The conservation and management of many systems requires knowledge of the influence predators have on prey. As a result, methods to accurately estimate the composition of predator diets are in high demand. Applying Bayesian mixing models to stable isotope data is a powerful tool for estimating diet that is continually developing (Phillips et al. 2014). However, Bayesian mixing models often produce ambiguous results because of problematic mixing space geometry (Phillips and Gregg 2003). I demonstrated that even if the mixing space geometry is flawed, incorporating informative priors into Bayesian mixing models can produce precise (and likely accurate) estimates of diet composition. More studies examining results from informed Bayesian mixing models for predators consuming a known diet (e.g., Chiaradia et al. 2014) and for systems with a diversity of mixing space geometries would provide managers and conservation practitioners with even more confidence in this method.

Table 4.1. The taxonomic classification of each prey type, along with the mean and standard deviation of the carbon and nitrogen concentrations within their tissues, and the mass assumed for individual prey deliveries of each type.

Prey type	**Taxonomy**[a]	**Estimated mass**[b] **(g)**	**C conc. (%)**		**N conc. (%)**	
			Mean	**SD**	**Mean**	**SD**
Lemming	Cricetidae	40	44.0	3.1	14.0	1.0
Insectivorous bird	Passeriformes, Scolopacidae, Charadriidae	30	45.5	1.2	14.4	0.3
Duck	Anatidae	50	44.8	0.7	14.6	0.3
Marine bird	Laridae, Sternidae,	150	46.3	5.2	14.6	1.9
	Alcidae	300				

[a] Appendix B, Table B3 provides a complete list of all species collected along with sample size.

[b] Appendix B, Table B2 describes how these masses were estimated with references.

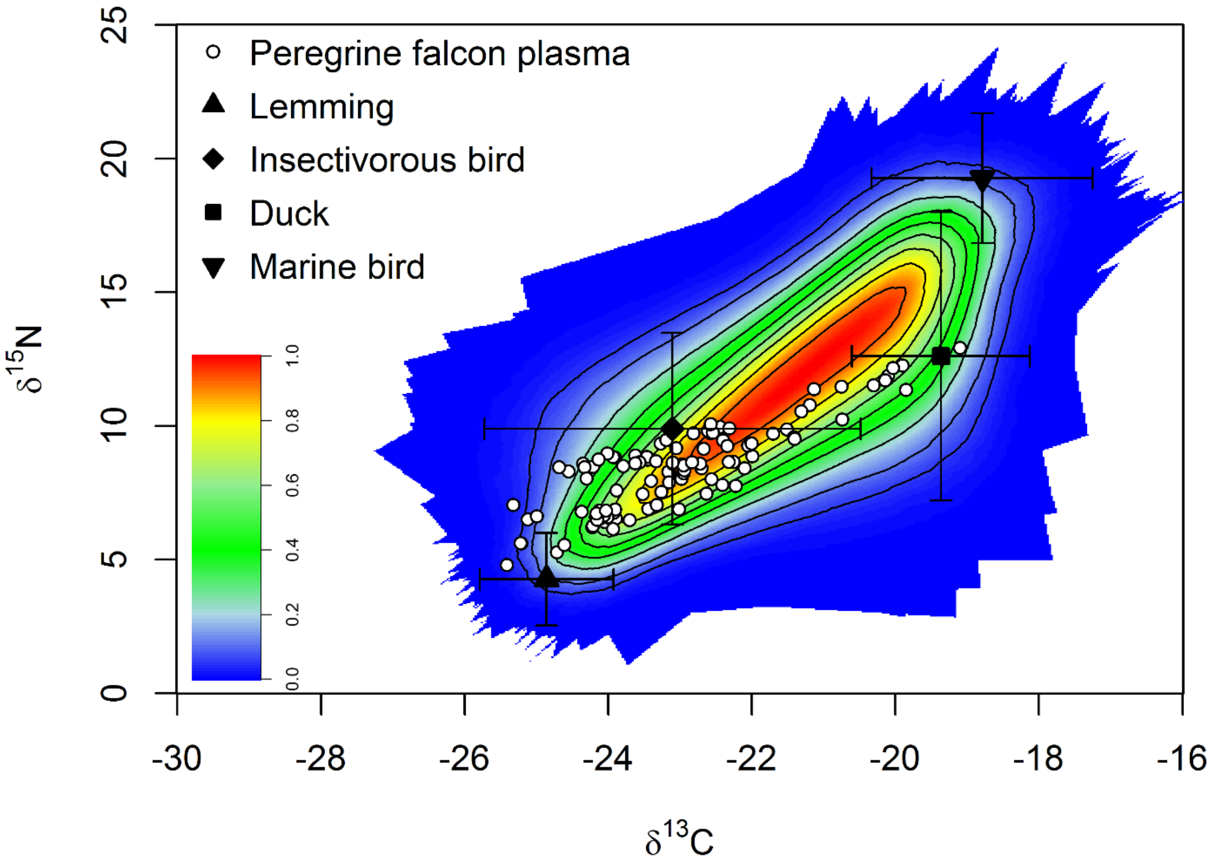

Figure 4.1. The mixing space geometry for the Bayesian mixing models used to estimate peregrine falcon diet. Shown are the mean and standard deviations of the isotopic values for each prey type (corrected for diet-blood fractionation) relative to the isotopic values of each nestling peregrine plasma sample. Contour lines and colour ramp show how variation in the isotopic value of peregrine falcon plasma (mixture) would influence the probability that a mixing model using the prey types (sources) shown could be reasonably solved (Smith et al. 2013). Peregrine plasma samples outside the outer 5% probability contour were not used in my mixing models.

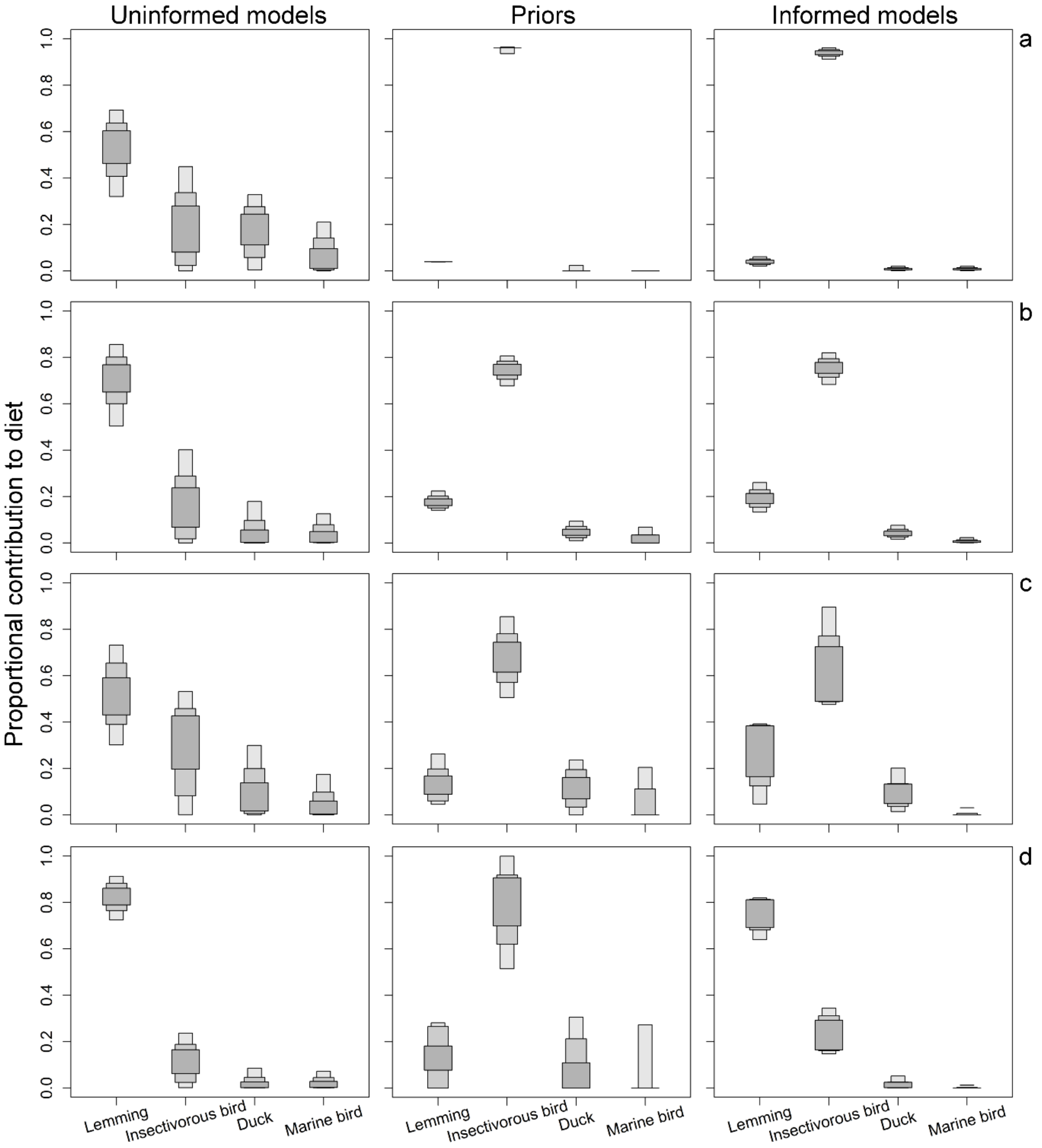

Figure 4.2. A comparison of the posterior distribution of dietary proportions for each prey type consumed by peregrine falcons estimated with uninformed mixing models (left column), motion-sensitive cameras (center column; priors), and informed mixing models (right column), which incorporated priors into the uninformed models. Each row of graphs represents a single nest. The influence of priors on the informed model changes as the error around priors increases from a-d. Nest-years shown are site 5, 2010 (a); site 8, 2011 (b); site 13, 2011 (c); and site 5, 2011 (d); see Figure 1.1 for geographic location of sites.

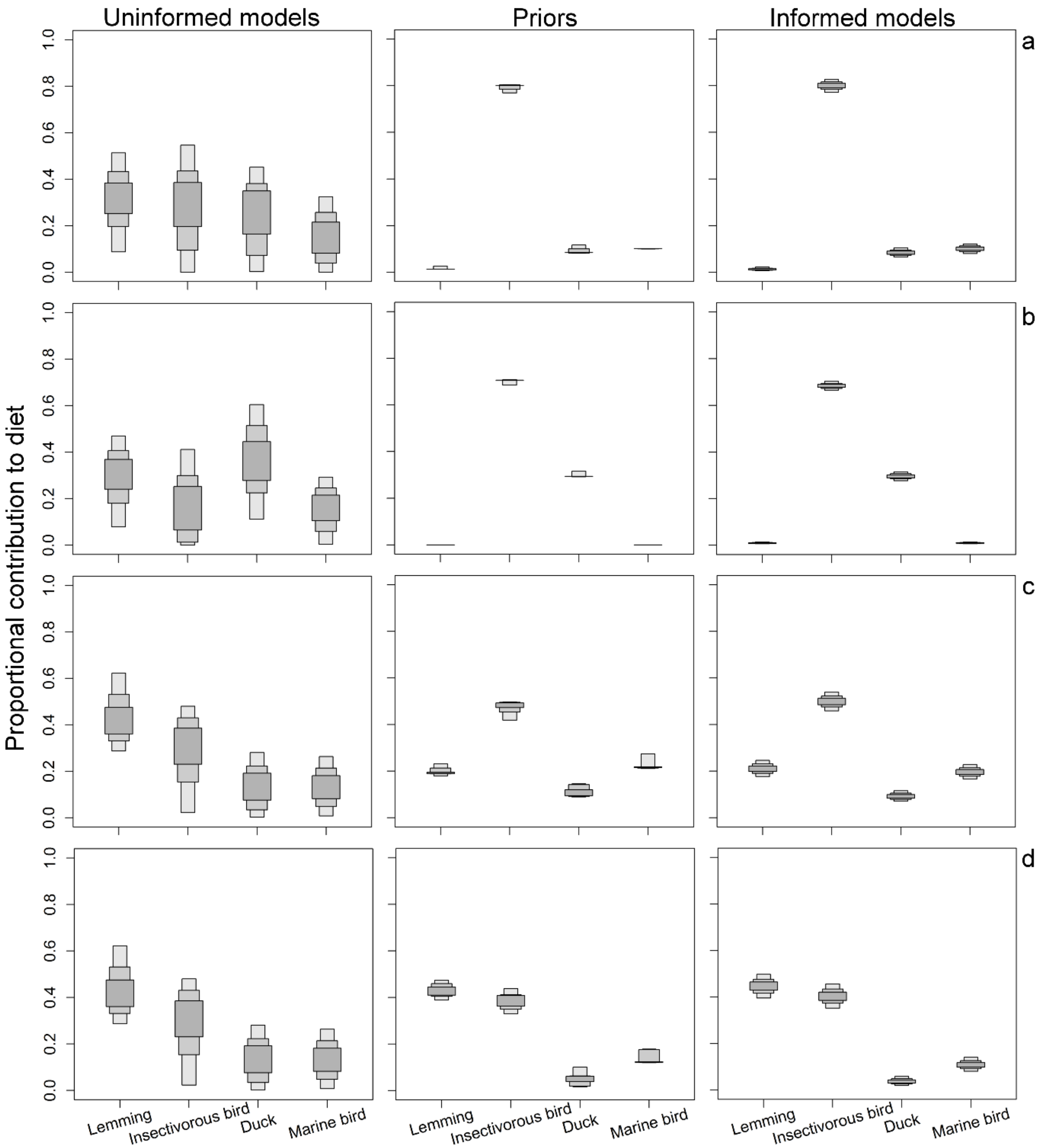

Figure 4.3. A comparison of the posterior distribution of dietary proportions for each prey type consumed by peregrine falcons estimated with uninformed mixing models (left column), motion-sensitive cameras (center column; priors), and informed mixing models (right column), which incorporated priors into the uninformed models. Each row of graphs represents a single nest. The influence of priors on the informed model changes as the distribution of prey types within the diet becomes more even from a-d. Nest-years shown are site 2, 2010 (a); site 13, 2010 (b); site 2, 2011 (c); and site 14, 2011 (d); see Figure 1.1 for geographic location of sites.

5 Weather-mediated prey depletion causes a functional response for a top predator

5.1 Introduction

To understand the potential ecological implications of global climate change, the mechanisms by which weather influences predator-prey interactions must be investigated (Post et al. 2009, Legagneux et al. 2012). Weather variables (e.g., temperature, precipitation) can affect predators and prey directly by influencing physiology (e.g., McKinnon et al. 2013b), behaviour (e.g., Sharma et al. 2009), phenology (Thackeray et al. 2010), or demography (e.g., Sillett et al. 2000). The complexity of ecological change increases when the direct effects of weather on one trophic level cascade up or down the food chain, creating indirect effects, which can be more consequential than direct effects (Barton et al. 2009, Bêty et al. 2014, Ockendon et al. 2014).

A potential mechanism behind the indirect effects of weather on predator-prey interactions are functional and numerical responses (Bowler et al. 2014): changing weather patterns lead to fluctuations in prey density, which alters the intake rate of a predator (functional response), resulting a change in predator density (numerical response) (Holling 1959a). The combined functional and numerical response, or total response, then dictates the predation pressure on prey populations. In multi-prey systems where predators switch between alternative prey, predator intake rate can be a function of the relative density of all prey types (Smout et al. 2010, Hellström et al. 2014). The interaction of weather with functional and numerical responses could, therefore, be complex, particularly if weather influences each prey population differently.

In Arctic ecosystems, the climate is changing more dramatically than elsewhere (Kattsov et al. 2005, Trenberth et al. 2007) and food chains are relatively simple with limited alternative prey (Krebs et al. 2003, Ims and Fuglei 2005, Gilg et al. 2006, Legagneux et al. 2012), so the influence of weather on trophic interactions could be strong (Gilg et al. 2009, Ernakovich et al. 2014). For example, cold weather during precipitation events in the Arctic reduces arthropod activity and abundance, which decreases growth rate and survival of juvenile shorebirds (Scolopacidae) (Schekkerman et al. 2003, Kendall et al. 2011), likely through a functional response. Arctic-breeding songbirds (Passeriformes) are also primarily insectivores (Custer and Pitelka 1978, Montgomerie and Lyon 2011), so they too could experience functional and numerical responses related to weather (Robinson et al. 2014). Cold temperatures, wind and precipitation influence the availability of arthropods to insectivores at broad spatial and temporal scales across the Canadian Arctic (Tulp and Schekkerman 2008, Bolduc et al. 2013) and the frequency and severity of summer rainstorms are predicted to increase in the future (Kattsov et al. 2005, Collins et al. 2013, Bintanja and Selten 2014), so the indirect effects of weather on predator-prey interactions could be widespread.

The interaction between weather and the functional and numerical responses of insectivores also has the potential to cascade up to top predators. Arctic peregrine falcons (*Falco peregrinus tundrius*) rely on insectivorous birds as their primary prey (Reid et al. 1997, Jaffré et al. 2015), particularly the flux of naive fledglings that become active when falcon nestlings are growing and demand for food is high (Court et al. 1988, Rosenfield et al. 1995). Decreases in insectivorous bird abundance associated with cold, wet weather could lead to decreases in peregrine falcon encounter rates with these prey, resulting in lower consumption rates (i.e. a functional response). However, peregrine falcons consume a diversity of alternative prey, ranging from lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) to ducks (Anatidae), gulls (Laridae, Sternidae and Stercorariidae), and black guillemots (*Cepphus grille*), which could supplement their diet when insectivorous birds are scarce. There is some evidence that Arctic peregrine falcons respond functionally and numerically to lemming density (Court et al. 1988), but this response varies across the Arctic (Reid et al. 1997). The lemming cycle, which peaks every 3-4 years, affects shorebird population demographics because avian and mammalian predators consume shorebird eggs and juveniles when lemmings are scarce (Blomqvist et al. 2002, McKinnon et al. 2013a, Robinson et al. 2014). There is evidence for spatial and temporal variation in the density of all prey groups consumed by Arctic peregrines (Chapter 2; Robinson et al. 2014), but it is unclear whether this translates into a functional response. Reductions in prey consumption rates associated with prey depletion could also result in reduced nestling survival, so examining the functional response of Arctic peregrine falcons is important.

In this study, I investigated the interaction between weather and the functional response of Arctic peregrine falcons by examining peregrine diet, prey delivery rates, reproductive output, summer rainfall, temperature, and spatiotemporal variation in prey density. Over 3 years, I observed a reduction in the density of insectivorous birds and gulls during a cool, wet summer, relative to the previous two summers, which were dry and warm (Chapter 2; Robinson et al. 2014); there was also a corresponding reduction in the production and survival of peregrine falcon nestlings. I predicted that low prey density during the cool, wet summer reduced prey delivery rates to peregrine falcon nestlings, driving the reduction in the number of nestlings surviving per nest. If my prediction was true, I expected that peregrine falcons would exhibit a functional response and that prey delivery rates in relation to prey density during the cool, wet summer would fall on the decreasing portion of the response curve. I also predicted that the number of peregrine falcon nestlings surviving to fledging age per nest would be significantly lower during the cool, wet summer.

5.2 Methods

5.2.1 Spatiotemporal variation in prey density

Details of the methods used to estimate spatiotemporal variations in avian prey throughout the inland portion of the study area (songbirds, shorebirds, and gulls) are described in Chapter 2.2. In summary, spatial variation in densities were estimated separately for various strata, which were classified by the amount of standing fresh water, tundra vegetation productivity (Normalized Difference Vegetation Index), and terrain ruggedness (standard deviation in elevation) (Figure 2.1). Annual variation in songbird density was correlated summer temperature, precipitation and spring snow cover, while shorebird and gull densities were correlated with lemming abundance. The summers of 2010 and 2011 were warm and dry with high amounts of spring snow cover while 2012 was cool and wet with low spring snow cover; I therefore pooled data across 2010 and 2011 to produce estimates of songbird density. Similarly, shorebird and gull data were each pooled across 2010 and 2012, which had low lemming abundance compared to the lemming peak in 2011, to produce density estimates. Density estimates used for each strata are presented in Figure 2.3.

I also employed distance sampling (Buckland et al. 2001) to estimate the density of ducks, gulls, and black guillemots throughout the marine habitats. Each year, 90-120 km of transects were surveyed by boat along all coast lines throughout the study area. Boat speed was <20 km/hour and surveys were conducted only on fair-weather days with good visibility, low wind, no precipitation and calm waters. All other survey techniques replicated those in Chapter 2.2.2. Density estimates were produced separately for each year using Distance 6.0 release 2 software (Thomas et al. 2010). Detection functions were chosen separately for each prey group using Akaike Information Criteria corrected for small sample size (AIC_c) with data pooled across years. I first estimated the detection functions with all observations and then truncated the data at the distance that predicted the probability of detection to be 0.15 (Buckland et al. 2001). Annual density estimates were then applied to the marine areas (Figure 2.1). The study area contained two small islands (0.029 and 0.079 km^2) with dense black guillemot colonies where peregrine falcons hunted regularly. I assigned densities to these islands using breeding density estimates for black guillemot colonies from the literature (1430 individuals/km^2; Evans 1984, Ewins and Tasker 1985).

Annual variation in lemming abundance was first estimated using snap trapping (details in Chapter 2.2.1). I then followed Gauthier et al. (2013) to estimate lemming density (D = individuals/ha) as a function of abundance (I = lemmings/100 trap nights): $\log(D) = 1.33\log(I) + 0.55$. These density estimates applied to strata 8 only, where snap trapping occurred. To extrapolate these estimates to other strata, I counted the number of lemming burrows observed within 1 m of the terrestrial distance sampling transects and assumed variation in lemming density across strata was proportional to the variation in mean burrow density (Table 5.4).

5.2.2 Estimating prey available to foraging peregrine falcons

To estimate peregrine home-ranges I equipped 10 adult female peregrine falcons with 22 g solar powered Platform Transmitting Terminals (PTTs; Microwave Telemetry, Inc., Columbia Minnesota, USA.) using standard backpack-style attachment with Teflon ribbon (Meyburg and Fuller 2007); PTTs were programmed to acquire GPS locations (± 18 m accuracy) every 2 hours. Although male peregrines are the primary forager, their small body size and mass precluded me from equipping them with 22 g PTTs; the habitat utilized by the females over the course of the breeding season likely represents the territory defended by the pair, where male foraging took place (Newton 1979). Peregrines were captured at the nest while nestlings were 5-10 days old with a noose carpet placed over a pigeon or quail carcass directly on the nest platform (Bloom et al. 2007); nestlings were protected in a small cage secured to the nest cliff before the captures.

I estimated utilization distributions (UDs) separately for each peregrine using relocation data from the time of PTT deployment to the time of fledging (~1 – 31 August) and fixed-kernel analysis (Worton 1989) with the plug-in method for determining the smoothing factor (Gitzen et al. 2006). Smoothing factors and UDs were estimated using the Hpi and kde functions, respectively, within the ks package (Duong 2014) developed for the R statistical environment (R Core Team 2014). I assumed the prey available to foraging peregrines were within the minimum convex polygon (MCP) encompassing the 95% isopleth of each UD. I used MCPs because 95% isopleths often included multiple, disconnected polygons (Figure 5.1) and I assumed prey within the area between polygons were available for consumption. For some nests, MCPs encompassed neighbouring nest sites (Figure 5.1); I assumed prey surrounding neighbouring nest sites were not available because of territoriality, so the polygon of the 95% isopleth surrounding each neighbouring nest site was excluded from each MCP. The female from most monitored nests was equipped with a PTT for only one year of the study (Appendix B, Table B1); I assumed the territory used around each nest was consistent across all years when estimating prey availability. Although there is no published data to support this assumption, unpublished data from a female Arctic peregrine falcon breeding on Baffin Island, Nunavut, demonstrates that breeding season habitat use is extremely similar across years (http://www.frg.org/track_pefa12.htm). There were 2 monitored nests for which females were not equipped with PTTs in any year (sites 5 and 6; Figure 1.1). For these nests I used the MCPs from neighbouring nests and topography to estimate the boundaries defining the area available for foraging (Figure 5.1).

5.2.3 Prey delivery rates and nestling survival

Prey delivery rates for each nest were estimated based on images from motion-sensitive cameras as described in Chapter 3.2.2, except that rates were expressed as g of prey/nestling/day, rather than proportions. Observation periods over which delivery rates were estimated were ≤3.5 days, to minimize variation associated with nestling age.

Motion-sensitive cameras (see Chapter 3.2.1) were also used to determine nest-specific reproductive output (fledglings/occupied nest) and causes of nestling mortality. Nestlings that survived to 25 days of age were assumed to have fledged (Anctil et al. 2013); after 25 days nestlings can no longer be monitored reliably because they begin moving around the nest cliff.

5.2.4 Functional response

To account for variation in prey delivery rates associated with nestling age, I first binned delivery rate data into 3 categories based on the age of the oldest nestling of each brood half-way through the observation period over which delivery rate was estimated: 0-4, 5-9, and 10-14 days. Treating each age class and prey type separately, I compared 3 functional response model forms (Type I, II, and III *sensu* Holling 1959b) estimating prey delivery rates as a function of prey density along with a null model (Table 5.1). I also combined all prey types to determine if there was a functional response to the total amount of prey available. All prey delivery rates and prey density estimates were expressed in terms of prey mass (g/nestling/day and g/km^2, respectively) using the masses shown in Table 4.1. Functional response model forms for each prey type and age class were compared using AIC$_c$. All models were parameterized using the nls function in the R Statistical Environment (R Core Team 2014).

Based on the analysis in Chapter 2, I knew there was a decrease in overall prey density in 2012, relative to 2010 and 2011. To determine if there was also a decline in total prey delivery rates (all prey combined) across the peregrine population in 2012, I used linear regression to model prey delivery rate (g/nestling/day) as a function of year, nestling age class and an interaction between these variables; 2012 and the 10-14 day age class were used as reference categories. To determine if there was a fitness consequence to declines in prey abundance in 2012, I used Poisson regression to determine if the number of fledglings produced per nest was significantly different across years.

5.3 Results

5.3.1 Spatiotemporal variation in prey density

Details of the distance sampling results and prey density estimates from terrestrial avian prey are presented in Chapter 2.3.2. For the marine prey, the half-normal detection function with no series expansion, adjustments terms or covariates were best for all prey types (Table 5.2). Densities of all marine birds varied across years, but not significantly (Table 5.3).

Lemming abundance varied across years: 0.31, 3.24, and 0.10 lemmings/100 trap nights for 2010, 2011, and 2012, respectively; abundance indices translated into density estimates of 75, 1694, and 17 individuals/km^2, respectively. Table 5.4 presents strata-specific density estimates, assuming variation in lemming density across strata was proportional to variation in burrow density.

5.3.2 Functional response

For most nestling age classes and prey types, the null model relating prey delivery rates to prey density was most parsimonious, indicating that peregrines did not exhibit a functional response (Table 5.5). The type II model form for lemmings was most parsimonious for the 5-9 day age class, and the type I model was most parsimonious for the 10-14 day age class (Figure 5.2; Table 5.5). For ducks, there was a type I functional response for the 10-14 day age class

(Figure 5.2; Table 5.5). There was equal support for the type II and III model forms for total prey for the 10-14 day age class (Figure 5.2; Table 5.5).

Prey delivery rates across all age classes were significantly higher in 2010 and 2011 relative to 2012 (significant 'Year' parameters: Table 5.6). In 2010 and 2011, prey delivery rates were significantly higher for the oldest nestling age class, but significantly lower in 2012 (Figure 5.2; significant interaction terms: Table 5.6). The number of nestlings surviving to fledging age per nest was also significantly lower in 2012 (mean ± SE = 0.67 ± 0.31) than 2010 (2.17 ± 0.39; $P < 0.01$) and 2011 (2.83 ± 0.42; $P < 0.01$). Annual percent nestling mortality across the population ranged from 13% (4/30) in 2010, to 0% (0/31) in 2011, and 50% (8/16) in 2012. The cause of all mortalities in 2010 and 2011 could not be determined. In 2012, 8 nestling mortalities were observed: 3 nestlings from 1 nest were killed by short-tailed weasel (*Mustela erminea*) predation; 2 nestlings from 1 nest starved after the parents stopped delivering prey for 3 consecutive days; 2 nestlings from 2 nests, both the youngest of the brood, could not compete with other nestlings for food and starved; and the cause of 1 nestling mortality could not be determined.

5.4 Discussion

Arctic peregrine falcons exhibited a functional response to spatiotemporal variations in prey densities, but only to certain prey types and while nestlings were > 4 days old. Lemmings and ducks were the only individual prey types for which delivery rates increased with density. The functional response to lemming density was a result of an increase in lemming consumption during the lemming peak in 2011 (Chapter 4), which is consistent with observations of peregrine falcons in Rankin Inlet, Nunavut (Court et al. 1988). In regions of the Arctic where lemmings are non-cyclic, peregrine falcons have not exhibited a functional response to changes in lemming densities (Reid et al. 1997). Peregrine falcons may not have responded functionally to fluctuations in marine bird density because these prey were used only opportunistically. Nests surrounded by more marine habitat (sites 2, 12, and 13; Figure 1.1) had higher marine and duck components in their diet (Figure 4.3b and 4.3c; Appendix B, Figure B1f), which is also consistent with peregrine falcons breeding in Rankin Inlet, Nunavut (L'Herault et al. 2013). However, increases in the use of marine prey were not consistent enough to translate into a functional response (Figure 5.2).

Peregrines did response functionally to changes in duck density while nestlings were 10-14 days old. Studies of peregrine falcons breeding in Yukon Territory and Alaska showed that ducks were selected for relative to availability and made up the majority of nestling diets by biomass (Palmer et al. 2004, Dawson et al. 2011). Both studies examined prey use over the entire brood-rearing period, whereas I quantified diet only while nestlings were ≤14 days old. Larger-bodied prey, such as ducks, were likely consumed more frequently toward the end of the brood-rearing period when the larger female peregrine (relative to the male) begins to hunt (Court et al. 1988), which may explain why I observed a lower contribution of ducks to peregrine diets than other studies.

Although insectivorous birds are considered the primary prey of Arctic peregrine falcons (Court et al. 1988, Rosenfield et al. 1995, Reid et al. 1997, Jaffré et al. 2015), there was no evidence of peregrines responding functionally to fluctuations in insectivorous bird densities. In Chapter 4, I showed that peregrine diets were dominated by insectivorous birds in all years. However, the contribution of insectivorous birds to peregrine diets decreased with a corresponding increase in the contribution of lemmings during the lemming peak in 2011. Indeed, delivery rates of insectivorous birds to some nests in 2011 were low considering the high density of insectivorous birds available (Figure 5.2), which was likely a result of high lemming abundance. Similarly, nests that opportunistically fed on marine birds and ducks also showed a decrease in insectivorous birds in their diet (Figure 4.3). The use of insectivorous birds is, therefore, likely a function of the relative densities of alternative prey. Insectivorous birds may dominate the diet of peregrines because they are abundant or easy to capture, but switch to alternative prey when the proportional abundance of alternative prey increases. Prey switching (Murdoch 1969, Oaten and Murdoch 1975), which is often termed multi-species functional response (Asseburg 2006), has been observed in a variety of generalist raptors and other predators consuming a diversity of prey (e.g., Messier 1995, Smout et al. 2010, Smout et al. 2013, Hellström et al. 2014).

Variation in prey delivery rates could have been driven by factors other than prey density, such as predator density or predator:prey ratios (Abrams and Ginzburg 2000). Predator- or ratio-dependent functional responses are generally caused by competition among predators for prey (Arditi and Ginzburg 1989). Because peregrines are territorial and density of breeding pairs is generally low, intraspecific competition for prey is unlikely to influence prey delivery rates. The same rational for a strictly prey-dependent functional response was used by Moleón et al. (2012) in their study of Bonelli's eagles (*Aquila fasciata*) preying on rabbits and partridge.

The clearest functional response exhibited by peregrine falcons was to variations in total prey density while nestlings were 10-14 days old. My prediction, that reduced prey abundance during the cool, wet summer of 2012 resulted in decreased prey delivery rates, was supported because data from 2012 fell on the decreasing portion of the functional response curve for total prey (Figure 5.2). This prediction was further supported because prey delivery rates across the population were significantly lower in 2012, particularly for the 10-14 day age class (Figure 5.3).

When nestlings were young, it appears provisioning parents were able to provide an adequate supply of food, even when prey densities were depleted in 2012. The increasing demand for food from nestlings as they grew (Steen et al. 2012) was satisfied with an increase in prey delivery rates in 2010 and 2011, but not in 2012. In 2012 there was a decline in insectivorous bird, lemming, and gull densities (Chapter 2); as a result, it seems total prey density in 2012 was not high enough to allow parents to meet the demands of their growing nestlings. In 2012, there was also a corresponding decline in the number of nestlings surviving to 25 days, indicating there was likely a fitness consequence to decreases in prey delivery rates, which has been observed in peregrine falcons breeding in Australia (Olsen et al. 1998).

Studies of functional and numerical responses in other territorial birds claim that a change in reproductive output in relation to changes in prey density translates to a numerical response (Gilg et al. 2006, Moleón et al. 2012). Although peregrine reproduction decreased in 2012 when prey densities were low, it is unlikely that they experienced a true numerical response. Many other factors over broad temporal and spatial scales likely contribute to the overall population size (e.g., conditions on the wintering grounds and along migration routes, immigration/emigration, and age of first breeding). As with other raptors, it would be hard to detect a numerical response in peregrines falcons because overall population size can be strongly influenced by the density of floaters (non-breeding adults) in the population (Ratcliffe 1993). Even if population size fluctuates, breeding density could remain relatively constant. In my study, fluctuations in breeding density (1 pair/107.6km^2, 1 pair/121.2km^2, and 1 pair/116.6km^2 in 2010, 2011, and 2012, respectively) did not correspond to the sharp decline in reproductive output that occurred during the cool and wet summer when prey density declined.

In addition to depleting prey, cool, wet weather associated with severe rainstorms can directly reduce Arctic peregrine nestling survival while nestlings are small and unable to thermoregulate (Bradley et al. 1997, Anctil et al. 2013). In my study, the majority of rain during 2012 fell in June before peregrine eggs hatched, and all post-hatch mortality occurred after nestlings were >14 days old. In addition, based on images from motion-sensitive cameras, there was no evidence of any nestling mortality being caused directly by rain (based on the definitions provided in Anctil et al. 2013). Half of nestling mortalities in 2012 were caused by starvation, supporting my prediction that low prey density during the cool, wet summer reduced prey delivery rates to peregrine falcon nestlings, leading to reduced nestling survival.

My data suggest that the heavy rain in June of 2012 reduced the breeding success of many avian prey species, preventing the pulse in fledglings that peregrines regularly rely on to feed their nestlings. As a result, the cool, wet weather associated with heavy rain indirectly caused a decline in Arctic peregrine falcon reproductive output. Heavy rainstorms are predicted to become more severe and frequent in many regions of the Arctic (Kattsov et al. 2005, Collins et al. 2013, Bintanja and Selten 2014), and the direct and indirect effects of these changes in weather on the reproduction of peregrines and other predators could be additive. Studies of climate change influences on ecosystems often focus on changing temperature as the mechanism driving changes in trophic interactions (e.g., Visser et al. 2004, Both et al. 2006, Møller et al. 2008). However, evidence is accumulating that changes in precipitation also could have major implications for a variety of avian species (e.g., Glenn et al. 2011, Pokrovsky et al. 2012, Hansen et al. 2013, Wellicome et al. 2014, Öberg et al. 2015).

Studies investigating the influence of climate on Arctic tundra food webs often focus on determining whether the ecosystem is more limited by top-down or bottom-up forces (e.g., Gauthier et al. 2011, Legagneux et al. 2012). Whether tundra food webs are limited by primary production or predation pressure is an important issue, but results from this study demonstrate the need to consider the indirect effects of climate change on predators through changes in their prey. Others have shown the indirect effects of climate change on trophic interactions appear to be more severe and widespread than the direct effects (Barton et al. 2009, Ockendon et al. 2014). It is important that studies investing the indirect effects of climate change focus on both mesopredators and top predators: changing weather patterns affect the interactions between arthropods and insectivorous (Schekkerman et al. 2003, Bolduc et al. 2013), which subsequently affect the interaction between insectivores and their predators. Understanding the influence of weather on interactions across >3 trophic levels is required to appreciate the impacts of climate change on Arctic ecosystems. My study demonstrates how variation in weather can affect trophic interactions and can be used to guide the objectives of long-term studies addressing climate change over broader temporal scales.

Table 5.1. Functional response model forms relating prey delivery rates (D g/nestling/day) to prey density (P g/km^2); *a* and *b* are parameters. The performance of model forms was compared separately for each prey type and nestling age class using AIC$_c$.

Model name	**Model form**
Null	$D = a$
Type I	$D = aP$
Type II	$D = \frac{aP}{1 + abP}$
Type III	$D = \frac{aP^2}{1 + abP^2}$

Table 5.2. Detection function model forms determined to be most parsimonious (AIC_c) for each marine guild.

	Truncation (m)						
Guild	**Left**	**Right**	**Model form**	**Series expansion**	**# adjustment terms**	**Covariates**	***P*-value**
Gulls	0	400	half normal	n/a	0	n/a	0.93[a]
Duck	0	190	half normal	n/a	0	n/a	0.39[b]
Black guillemots	0	270	half normal	n/a	0	n/a	0.83[b]

[a] *P*-value obtained from a χ^2 goodness of fit test

[b] *P*-value obtained from a Kolmogorov-Smirnov test

Table 5.3. Marine prey density estimates and 95% confidence intervals for each year. Estimates were produced from distance sampling data.

	2010		**2011**		**2012**	
Prey type	**ind/km^2**	**95% CI**	**ind/km^2**	**95% CI**	**ind/km^2**	**95% CI**
Gull	0.35	0.08-1.55	5.76	2.56-12.96	3.13	1.44-6.78
Duck	12.75	3.54-45.89	4.04	1.33-12.25	5.69	2.41-13.44
Black guillemot	0.49	0.13-1.78	1.57	0.25-9.90	1.99	0.33-11.86

Table 5.4. Mean density of lemming burrows observed along distance sampling transects and strata-specific estimates of lemming density for each year. Abundance estimates from snap trapping on strata 8 each year were transformed into density estimates assuming variation in lemming density was proportional to variation in burrow density.

Strata	**Burrow density (#/km^2)**	**2010**		**2011**		**2012**	
		ind/km^2	**g/km^2**	**ind/km^2**	**g/ km^2**	**ind/km^2**	**g/km^2**
1	7688	54	2124	1210	47904	12	470
2	14119	99	3901	2221	87970	22	862
3	16655	116	4602	2621	103772	26	1016
4	16012	112	4425	2520	99770	25	977
5	8275	58	2287	1302	51559	13	505
6	9577	67	2646	1507	59671	15	584
7	19587	137	5412	3082	122043	30	1195
8	10769	75	2976	1694	67100	17	657

Table 5.5. Results from AIC$_c$ analysis comparing various functional response model forms (Table 5.1) relating peregrine falcon prey delivery rates to prey density, treating each peregrine nestling age class and prey type separately. Bolded models were assumed to represent the functional response. Model forms not shown for a given age class and prey type did not converge during parameterization.

Age class	**Prey type**	**Model form**	**K**	**AIC$_c$**	**ΔAIC$_c$**	**Akaike weight**
0-4	Insect	**Null**	**2**	**165.05**	**0.00**	**>0.999**
		Type I	2	188.77	23.72	<0.001
	Lemming	**Null**	**2**	**91.02**	**0.00**	**0.983**
		Type II	3	100.24	9.22	0.010
		Type III	3	101.82	10.80	0.004
		Type I	2	102.61	11.59	0.003
	Duck	**Null**	**2**	78.06	0.000	0.981
		Type I	2	86.87	8.81	0.012
		Type III	3	88.04	9.98	0.007
	Total	**Null**	**2**	**164.81**	**0.00**	**>0.999**
		Type I	2	198.71	33.91	<0.001
5-9	Insect	**Null**	**2**	**229.62**	**0.00**	**>0.999**
		Type I	2	249.62	20.00	<0.001
		Type II	3	267.10	37.48	<0.001
		Type III	3	268.08	38.45	<0.001
	Lemming	**Type II**	**3**	**141.92**	**0.00**	**0.746**
		Type I	2	144.57	2.65	0.198
		Type III	3	147.27	5.35	0.051
		Null	2	152.22	10.30	0.004
	Marine	**Null**	**2**	150.47	0.00	0.977
		Type I	2	158.00	7.53	0.023
	Duck	**Null**	**2**	**116.47**	**0.00**	**0.983**
		Type I	2	125.47	9.01	0.011

Table 5.5. cont.

Age class	**Prey type**	**Model form**	**K**	**AIC$_c$**	**ΔAIC$_c$**	**Akaike weight**
5-9	Duck	Type II	3	128.05	11.59	0.003
		Type III	3	128.16	11.69	<0.001
	Total	**Null**	**2**	**229.76**	**0.00**	**>0.999**
		Type I	2	264.15	34.39	<0.001
10-14	Insect	**Null**	**2**	**271.02**	**0.00**	**0.990**
		Type II	3	280.21	9.19	0.010
		Type III	3	290.74	19.71	<0.001
		Type I	2	294.81	23.79	<0.001
	Lemming	**Type I**	**2**	**178.86**	**0.00**	**>0.999**
		Null	2	213.51	34.65	<0.001
		Type III	3	214.92	36.05	<0.001
	Marine	**Null**	**2**	**200.97**	**0.00**	**0.940**
		Type I	2	207.95	6.98	0.029
		Type III	3	208.93	7.96	0.018
		Type II	3	209.41	8.44	0.014
	Duck	**Type I**	**2**	**214.56**	**0.00**	**0.577**
		Type II	3	216.17	1.60	0.259
		Type III	3	218.00	3.44	0.103
		Null	2	219.04	4.48	0.061
	Total	**Type III**	**3**	**274.77**	**0.00**	**0.455**
		Type II	**3**	**274.98**	**0.21**	**0.410**
		Null	2	277.21	2.44	0.135
		Type I	2	308.33	33.56	<0.001

Table 5.6. Estimates, standard errors (SE) and *P*-values for the parameters of a linear regression model predicting total prey delivery rates to peregrine falcon nestlings (g/nestling/day) as a function of year, nestling age class and an interaction between these variables. Year 2012 and age class 10-14 days were used as reference categories.

Parameter	**Estimate**	**SE**	***P***
Intercept	96.84	20.32	<0.001
Year 2010	110.83	27.83	<0.001
Year 2011	59.16	26.50	0.03
Age class 0-4	9.82	28.74	0.73
Age class 5-9	34.76	28.74	0.23
(2010)×(0-4)	-99.70	40.86	0.02
(2011)×(0-4)	-103.47	45.59	0.03
(2010)×(5-9)	-102.55	39.35	0.01
(2011)×(5-9)	-92.04	39.96	0.03

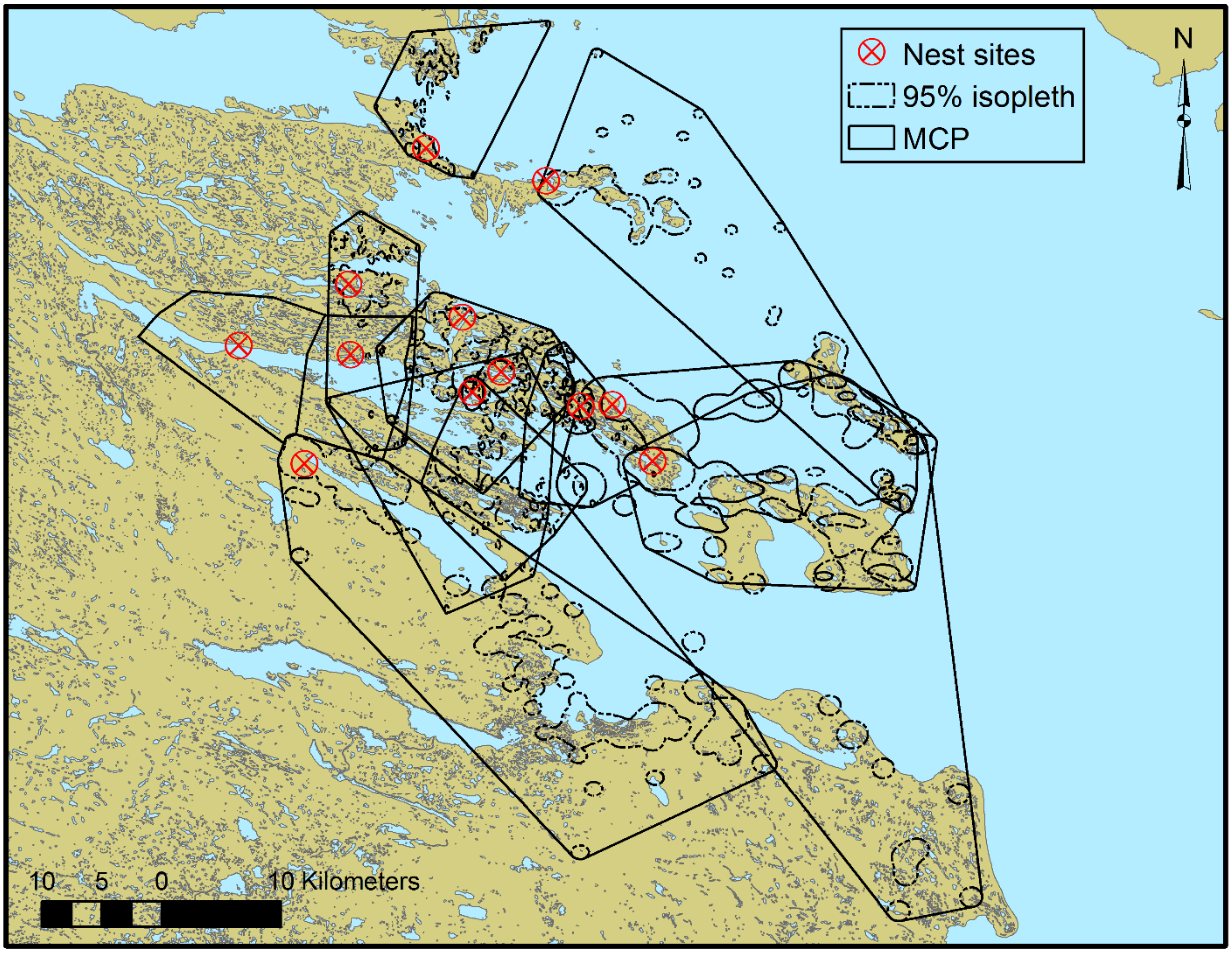

Figure 5.1. Home-ranges of adult female peregrine falcons represented by the 95% isopleth of utilization distirbutions (dashed line). The solid lines represent the minimum convex polygon around each 95% isopleth, which is the area assumed to be available to foraging peregrine falcons.

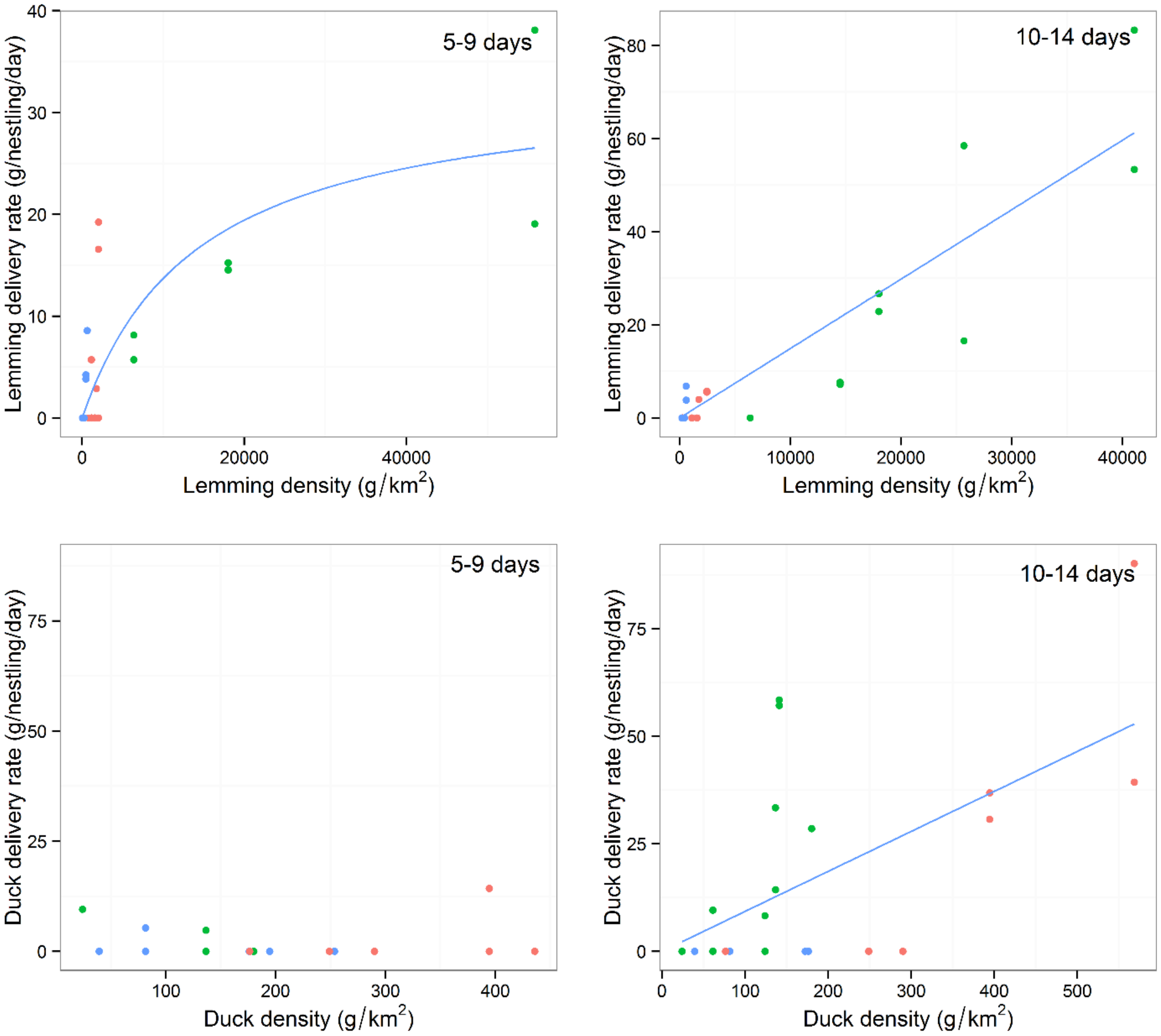

Figure 5.2. Functional responses for different prey types and falcon nestling age classes (indicated in upper right corner of each graph) showing the relationship between prey density within peregrine falcon home-ranges and prey delivery rates to falcon nestlings (red = 2010, green = 2011, blue = 2012). Blue curves represent the models found to best represent each functional response using AIC$_c$ analysis (Table 5.5). Graphs with no curve indicate the null model was best.

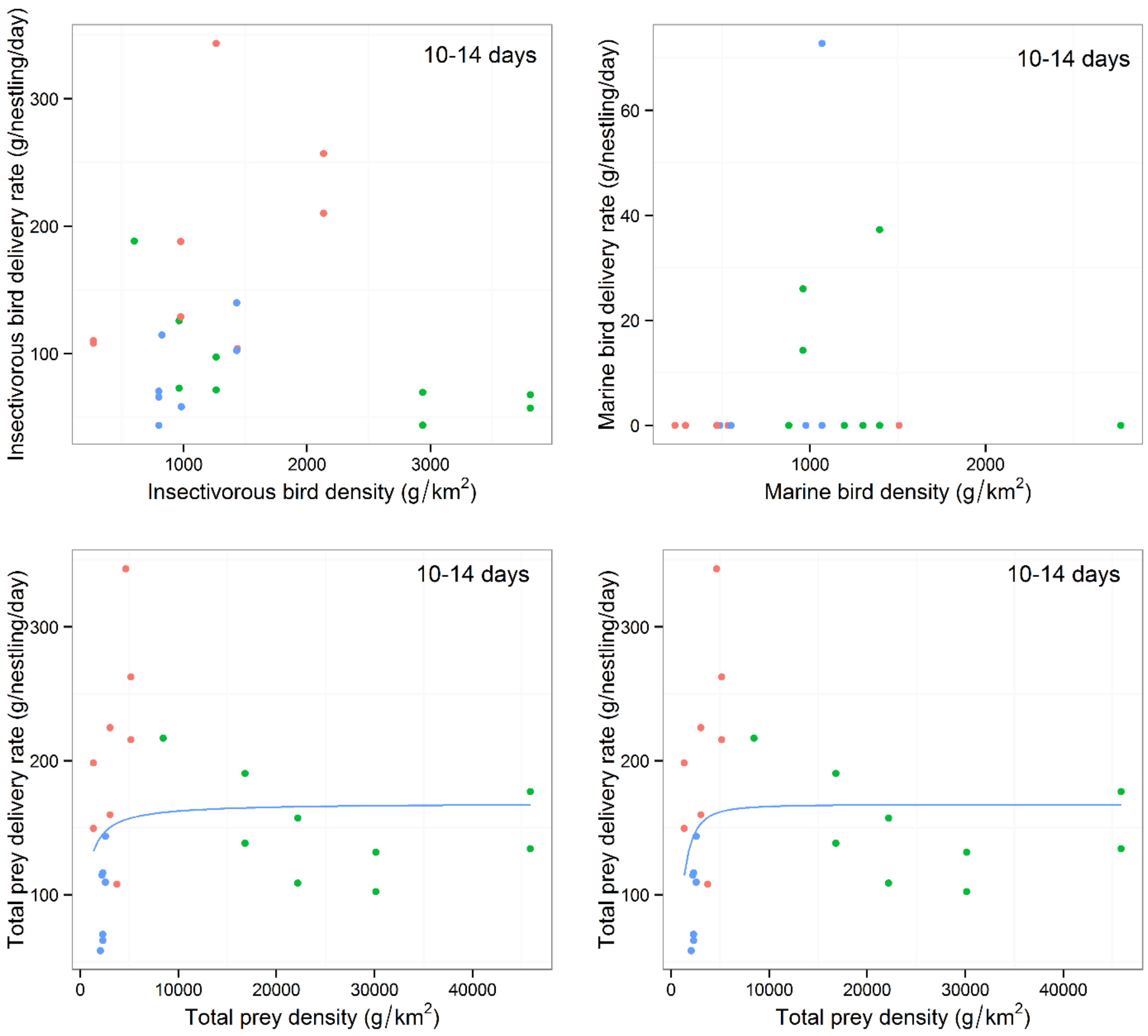

Figure 5.2. cont.

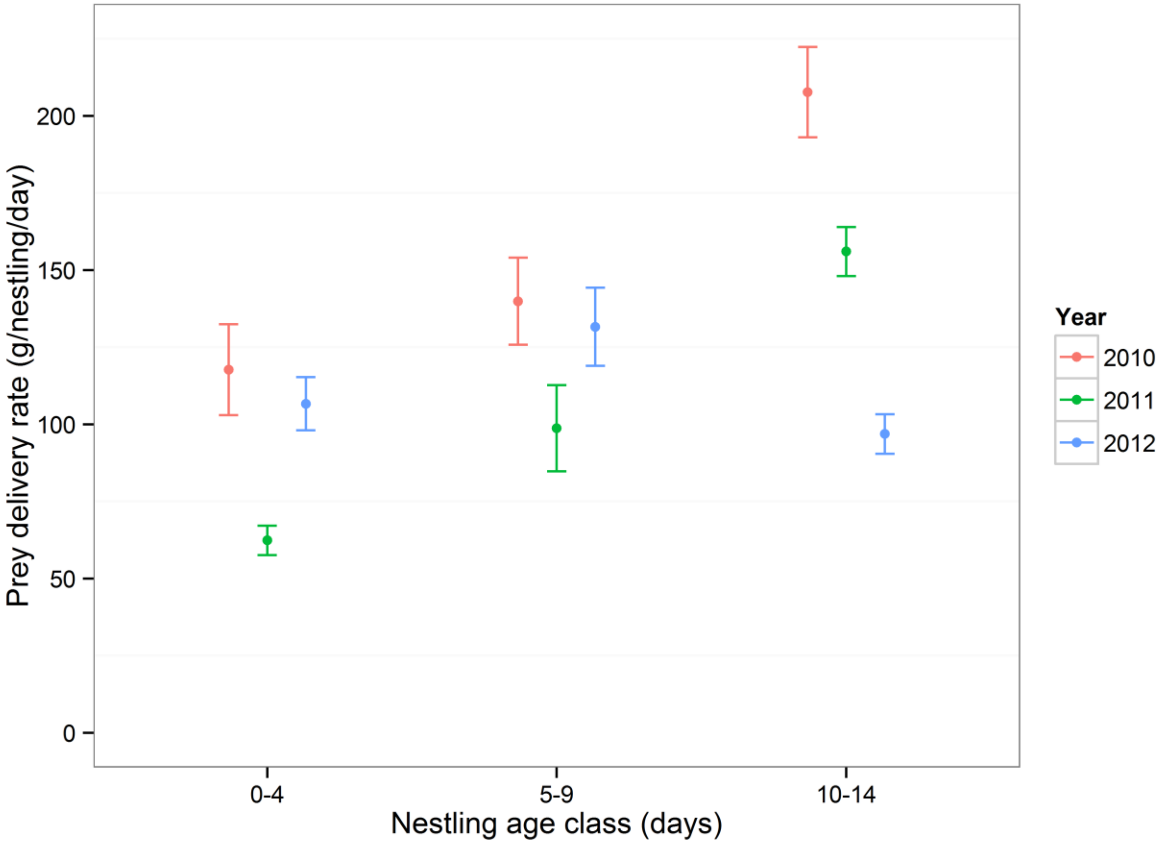

Figure 5.3. Mean (± standard error) prey delivery rates (total prey biomass) to different age classes of peregrine falcon nestlings during each year of this study.

6 Conclusion

6.1 Diet preferences of the Arctic peregrine falcon

As with other predators (Kassen 2002), it has been suggested that peregrine falcons (*Falco peregrinus*) living in extreme environments have a more generalized diet than those living in temperate regions with more consistent prey availability (Jenkins and Avery 1999, Jenkins and Hockey 2001). If this were true, I would expect Arctic peregrine falcons (*F. p. tundrius*), which breed in one of the most extreme habitats on the planet, to show little selection for any single prey type, instead consuming prey in proportion to their availability. I would also expect that Arctic peregrine falcons could buffer the effects of depletions in one prey type by switching to alternative prey (Murdoch 1969).

Results from my dissertation contradict this hypothesis and suggest that Arctic peregrine falcons generally specialize on insectivorous birds. By examining the relationship between the proportional contribution of each prey type to falcon diets (Chapter 4) and the proportional availability of each prey type within falcon home-ranges (Chapters 2 and 5), it is clear that insectivorous birds were strongly selected for; it is also apparent that peregrines did not switch to alternative prey when the abundance of insectivorous birds declined (Figure 6.1). If prey switching occurs, the relationship between proportional use and proportional availability of the primary prey should be sigmoidal: use of the primary prey will be disproportionately low when that prey type is relatively rare, and disproportionally high when it is relatively abundant (Murdoch 1969, van Baalen et al. 2001, van Leeuwen et al. 2013). Instead, use of insectivorous birds was disproportionately high, regardless of abundance (Figure 6.1). Selection ratios can also be used to test for non-random prey selection, where values of 1 indicate prey are being used in proportion to availability, and values > or < 1 indicate selection or avoidance, respectively

(Manly et al. 2002). Using diet estimates from Chapter 4 and prey availability estimates from Chapters 2 and 5, selection ratios for insectivorous birds were significantly greater than 1 in 2010 and 2011 (Figure 6.2). Selection ratios and the consistently high contribution of insectivorous birds to peregrine diets, regardless of insectivorous bird density (Figure 6.1), rejects the notion that Arctic peregrine falcons are generalists as predicted by Jenkins and Hockey (2001)

Inconsistent availability of any one prey type is the mechanism by which stochastic environments drive selection for a generalist diet (Kassen 2002). Having a diverse diet allows a predator to maintain adequate consumption rates as long as at least one potential prey type is available. Although the Arctic can be considered an extreme environment, the availability of prey, insectivorous birds in particular, may be consistently high over time, which could drive peregrine falcons breeding there to become specialists. Jenkins and Hockey (2001) conducted a meta-analysis of peregrine falcons breeding throughout the globe and found that reproductive output increased with latitude, and that Arctic peregrine populations were the most productive in the world. They suggested high reproductive output of Arctic peregrines was related to an increase in the synchronicity and productivity of bird breeding seasons with latitude (Ricklefs 1980, Wyndham 1986). Highly synchronized and productive breeding seasons would result in a reliable pulse of naïve fledgling prey for peregrines while their nestlings are growing and demand for food is highest. I did not distinguish between adult and fledgling prey in this study, but observations of other populations of Arctic peregrines suggest that the majority of insectivorous prey fed to peregrine nestlings were fledglings of the prey species (Court et al. 1988, Rosenfield et al. 1995). Low variation in the abundance of insectivorous birds in Arctic tundra ecosystems is likely the mechanism that causes Arctic peregrines to specialize on this prey type.

Lemmings (Cricetidae) are another group of prey reliably abundant in Arctic tundra ecosystems, cycling regularly with dramatic peaks in density occurring every 3-4 years (Kausrud et al. 2008), yet peregrines consistently underutilized lemmings relative to their availability (Figure 6.1). Use of lemmings increased during the lemming peak in 2011, but not as dramatically as the increase in abundance. As a result, the proportional contribution of lemmings to peregrine diets was always low relative to their proportional availability (Figure 6.1). Selection ratios for lemmings were also significantly < 1 in all three years of this study, even during the lemming peak (Figure 6.2). The lack of selection for lemmings suggests that peregrine falcons are specialized avian predators, only consuming mammals to supplement their diet when mammals are extremely abundant. Many predators specializing in small mammals inhabit Arctic, subarctic and alpine ecosystems including rough-legged hawks (*Buteo lagopus*), snowy owls (*Bubo scandiacus*), long-tailed skuas (*Stercorarius longicaudus*), Arctic foxes (*Vulpes lagopus*), and short-tailed weasels (*Mustela erminea*), all of which exhibit a different response than peregrines to fluctuations in small mammal abundance (lemmings: *Dicrostonyx groenlandicus*, *Lemmus trimucronatus*, and *L. lemmus*; voles: *Myodes rufocanus*, and *Microtus agrestis*). Although some of these predators can take advantage of alternative prey when small mammals are scarce, most still consume a disproportionally high amount of small mammals and all exhibit strong functional and numerical responses to variation in small mammal density (Gilg et al. 2006, Hellström et al. 2014, Therrien et al. 2014). Peregrine falcons in my study did exhibit a functional response to variation in lemming density and some evidence suggests that Arctic peregrine falcons respond numerically to lemmings (Court et al. 1988, Bradley and Oliphant 1991). However, given their degree of specialization for avian prey throughout their global distribution (White et al. 2002), it is unlikely that Arctic peregrines could be sustained by cyclic small mammal populations alone.

Ducks (*Clangula hyemalis* and *Somateria mollissima*), gulls (*Larus hyperboreus* and *L. argentatus*), and black guillemots (*Cepphus grylle*) contributed up to 50% of nestling diets, but the use of these prey was variable across peregrine nests and there was only a functional response to variation in duck density (Figure 5.2 and 6.1). Black guillemot adults were fed to peregrine nestling when the parents had black guillemot colonies in their territory, but diets were still dominated by insectivorous birds (e.g. Figure 4.4a and c). In 2010 and 2012, selection ratios for marine prey and ducks was significantly < 1; in 2011, some breeding pairs selected strongly for ducks, but selection ratios across the population did not differ significantly from 1 (Figure 6.2). Other studies have shown Arctic peregrine falcons use a limited amount of marine prey (Burnham and Mattox 1984, Court et al. 1988, Rosenfield et al. 1995, L'Herault et al. 2013). Because of their large size, only the downy young of ducks and gulls are available as prey to peregrines until the larger female peregrine begins hunting toward the end of the brood-rearing period (Court et al. 1988). I quantified peregrine diets only while nestlings were ≤ 14 days old, so all observations of duck and gull prey deliveries were downy young. Toward the end of the brood-rearing period when nestlings were >14 days old, some female peregrines travelled up to 30km from their nests (Figure 5.2), indicating they were likely hunting and contributing to nestling provisioning. From my research, it is unclear how important ducks and marine prey were during the later stages of the chick-rearing period. Given their larger size relative to insectivorous birds, marine prey could contribute substantial amounts of biomass to nestling diets and may be an important supplemental prey type, particularly at the end of the brood-rearing period (Dawson et al. 2011).

6.2 Influence of diet on Arctic peregrine falcon reproductive output

The functional response by Arctic peregrine falcons to declines in total prey density during the cool, wet summer shown in Chapter 5, along with the decrease in reproductive output, demonstrates that prey availability can limit nestling survival in Arctic peregrines. In Rankin Inlet, Nunavut, the number of young fledged by peregrine falcons from successful nests increased with the ratio of terrestrial to marine habitat surrounding nests (L'Herault et al. 2013). Because the diet of Arctic peregrine falcons is generally dominated by terrestrial prey, it was suggested that there was a fitness cost to nesting in coastal areas because foraging peregrines had to travel further inland to access their preferred prey. To test the prediction that there is a fitness cost associated with less access to terrestrial prey, I used Poisson regression (glm command in R with the Poisson family and log link function) to estimate the number of fledglings produced in a nest as a function of the density of each prey type available within falcon home-ranges. Using AIC_c analysis I determine the density of insectivorous birds within home-ranges best explained variation in the number of fledglings produced (Table 6.1). As predicted, the number of fledglings produced increased significantly with insectivorous birds density ($P = 0.051$ for the insectivorous bird parameter; Figure 6.3).

In contrast, a study of *F. p. anatum* breeding in the subarctic boreal region of Yukon Territory, Canada, found that prey abundance surrounding nest sites did not influence the number of young fledged (Dawson et al. 2011); instead, it appeared the composition of prey surrounding nests may have been more influential on reproductive output. Dawson et al. (2011) found that pairs with a higher component of ducks, geese and grebes in their diet, which were selected for relative to availability, fledged more young. Further, they reported that peregrines also selected for shorebirds, but avoided small passerines, and that an increase in the number of sparrows (Emberizidae) in the diet was related to a decrease in the number of fledglings produced (Dawson et al. 2011).

Although peregrine falcons are avian specialists, the specific type of prey preferred by each subspecies in each habitat is highly variable (Jenkins and Hockey 2001). Regardless of which prey type is preferred, breeding density and reproductive output of peregrine falcons may be higher when the preferred prey for that habitat is more abundant. When the preferred prey type declines, forcing peregrines to diversify their diet by switching to alternative prey, reproductive output is likely reduced (Olsen et al. 2008, Dawson et al. 2011).

6.3 The sensitivity of Arctic peregrine falcons to severe weather and the potential implications of climate change

Summer rainstorms have increased in frequency and severity in the Arctic over the last 3 decades, which has reduced the reproductive output of Arctic peregrine falcons breeding in Rankin Inlet, Nunavut (Bradley et al. 1997, Franke et al. 2010, Anctil et al. 2013). When severe rainstorms occur during the brood-rearing period, mortality can be high. Bradley et al. (1997) defined ≥ 3 days of consecutive rain as a heavy rainstorm and found that nestling mortality was positively correlated with the amount of rain that fell during these storms. Anctil et al. (2013) monitored nestling mortality at a finer temporal scale using motion-sensitive cameras at nest sites and found that nestling mortality could occur within 2 hours when nestlings were exposed directly to rain. They defined 8 mm of rain as the minimum amount of daily rainfall that caused nestling mortality and found a significantly negative correlation between the proportion of nestlings surviving and the number of days in July and August that received ≥ 8 mm of rain. In addition, they found the number of days with ≥ 8 mm of rain in Rankin Inlet significantly increased from 1980-2010 with an additional 2 days of heavy rain on average in the later period (Anctil et al. 2013). A continued increase in the frequency and severity of summer rainstorms is likely to have a negative effect on Arctic peregrine falcon reproductive output by directly reducing nestling survival.

My research provides the first evidence that high amounts of summer rainfall can also indirectly reduce peregrine falcon nestling survival by depleting the density of insectivorous birds, the Arctic peregrine falcon's primary prey. Unlike the studies in Rankin Inlet, I found no evidence of nestling mortality cause directly by rain. During the cool, wet year of my study (2012), most rain fell in June, with 3 days receiving > 8 mm, one of which received 35 mm. Only 1 day received ≥ 8 mm of rain throughout July and August of 2012, and total rainfall for these months was less than the 20-year mean for Igloolik and similar to the previous two warm and dry summers (Figure 2.2).

Although the rain in June occurred before nestlings hatched, it did appear to have an effect on the density of insectivorous songbirds and shorebirds. Shorebirds are income breeders, obtaining almost all energy for egg formation after they arrive on their Arctic breeding grounds in mid-June (Klaassen et al. 2001). Demand for food during the pre-laying period is among the highest of the year, so shorebirds can spend 75-95% of their time foraging (Morrison and Hobson 2004, Meltofte et al. 2007). Cold weather associated with heavy rainfall reduces the availability of arthropods to insectivorous birds (Schekkerman et al. 2003, Tulp and Schekkerman 2008, Bolduc et al. 2013), so the substantial amount of rain in June 2012 in Igloolik may have prevented many insectivorous birds from acquiring the necessary resources for egg formation. Flooding caused by heavy rain can also lead to nest loss for ground-nesting birds during the incubation period (Meltofte et al. 2007). Mass nest-failure for insectivorous birds during the laying and incubation period may have been the mechanism driving the decline in insectivorous birds observed in July and August in the Igloolik study area. Without the regular pulse in fledgling prey there was not a sufficient supply of food to meet the demands of the growing falcon nestlings, potentially contributing to the increase in falcon nestling mortality.

Because there are both direct and indirect effects of heavy summer rain on nestling survival, continued increases in rainfall associated with global climate change could have widespread consequences for Arctic peregrine falcons. Observations over the twentieth century demonstrate that increases in Arctic precipitation falling as rain have exceeded the global average, which has been largely attributed to anthropogenic greenhouse gas emissions (Kattsov and Walsh 2000, McBean et al. 2005, Min et al. 2008). According to almost all climate models, precipitation in the Arctic will continue to increase and potentially accelerate during the twenty-first century; high latitude projections of precipitation change are considered to be one of the most robust and well-understood results from climate change models (Kattsov et al. 2005, Collins et al. 2013, Bintanja and Selten 2014). Although the most drastic changes in precipitation are predicted to occur in autumn and winter, extreme summer rainfall events are expected to become more frequent, resulting in significant changes during the summer months (Kattsov et al. 2005). Results from Rankin Inlet demonstrate rainstorms must be frequent and severe to directly cause mortality of peregrine falcon nestlings (Bradley et al. 1997, Anctil et al. 2013). Results from my dissertation show that even if rainstorms are relatively less frequent and occur earlier in the breeding season, prey depletion may reduce nestling survival. With only three years of data from Igloolik, it is impossible to compare the severity of the direct effects of rain observed at Rankin Inlet to the indirect effects observed at Igloolik. The degree with which continued climate change influences the demographics of Arctic peregrine falcon populations will be largely dependent on spatiotemporal variations in changing weather patterns and prey abundance. At a broad spatial scale across the circumpolar Arctic, avian prey densities decrease with latitude (Bliss et al. 1973, Freedman and Svoboda 1982), while projected changes in precipitation increase (Kattsov et al. 2005, Collins et al. 2013, Bintanja and Selten 2014), so the influence of climate change on Arctic peregrine falcon populations may be more severe in more northern populations. Continued long-term monitoring of Arctic peregrine falcon population biology and foraging ecology at multiple study areas with different latitudes, prey densities and weather patterns, is necessary to fully understand how climate change will affect this top predator.

6.4 Future directions: indirect effects of climate change and the importance of monitoring multiple trophic levels

Climate change can either affect populations directly through abiotic mechanisms or indirectly by altering species interactions. In a meta-analysis, Ockendon et al. (2014) demonstrated that the indirect effects of climate change appear to be more widespread than the effects caused by direct abiotic mechanisms. Similarly, Cahill et al. (2013) found that altered species interactions, particularly changes in food availability, was the most commonly demonstrated climate-induced cause of extinctions and population declines. Because of the many biotic interactions across species, considering only the direct effects of climate change on one species has been cautioned against by ecologists for over a decade (Harrington et al. 1999, Pearson and Dawson 2003, Mustin et al. 2007). Despite these cautions, climate envelope modelling, correlative studies predicting changes in the distribution and abundance of a species in relation to climate, are common (Heikkinen et al. 2006, Hijmans and Graham 2006). Although some studies employing the climate envelope paradigm model the distributional change of a community of species, potential changes to the interactions among species are generally not considered (e.g., Thomas et al. 2004, Huntley et al. 2007, Hole et al. 2009).

To detect the indirect effects of climate change on ecosystems, it is essential to monitor multiple trophic levels simultaneously (Harrington et al. 1999, Visser and Both 2005). Studies detecting the cascading influence of climate on multiple trophic levels are becoming more common (e.g., Post et al. 1999, Aubry et al. 2013, Bêty et al. 2014, Marquis et al. 2014), but very few have attempted to monitor all trophic levels within a community (but see Post and Forchhammer 2001). In Arctic ecosystems, where food chains are relatively short and simple, monitoring the response of all trophic levels to climate change is feasible (Callaghan et al. 2004, Legagneux et al. 2012, Gauthier et al. 2013). For my dissertation, I monitored only 2 trophic levels over 3 years; although I was able to detect meaningful ecological relationships, expanding my research to include more trophic levels over a broader time scale is recommended.

I have 4 recommendations for the expansion of future research investigating Arctic-breeding raptors and the ecosystems they inhabit. Ideally, all of the research initiatives I recommend should be conducted in addition to the continual long-term monitoring of Arctic peregrine falcons. First, a study involving the lower trophic levels of tundra ecosystems is needed. Models predict climate change will influence the availability of arthropods to Arctic insectivores (Tulp and Schekkerman 2008, Bolduc et al. 2013), which may have been the mechanism driving the reductions in insectivorous bird density observed in my research. I recommend investigating the influence of annual variation in weather patterns on arthropod abundance and their food (detritus and tundra vegetation). Second, studies of insectivorous birds should be expanded to include the foraging ecology and population demographics of multiple species within this group (e.g., Lapland longspurs, *Calcarius lapponicus*; snow buntings, *Plectrophenax nivalis*; various sandpipers, *Calidris* spp.). By linking studies of insectivorous birds with studies of weather patterns and arthropods, a mechanistic understanding of the direct and indirect effects of climate change on insectivore-arthropod interactions would be revealed. Third, studies providing a better understanding of variation in the spatial distribution in lemming abundance would be beneficial. Investigations of the mechanism(s) driving the lemming cycle are ubiquitous (for a review, see Krebs 2010), but less attention has been paid to spatial variation in lemming densities. The abundance of lemmings has indirect effects on birds breeding in the Arctic because predators switch to these alternative prey when lemmings decline after peak years (Blomqvist et al. 2002, McKinnon et al. 2013a, Nolet et al. 2013). Using remote sensing techniques to conduct a long-term stratified mark-recapture study of lemmings in combination with studies of insectivores and their prey could lead to a better understanding of climate change influences on these complex interactions. Finally, I recommend that long-term studies of peregrine falcon foraging ecology be expanded to include other cliff-nesting raptors, such as gyrfalcons (*Falco rusticolus*) and rough-legged hawks, and their prey. Rough-legged hawks specialize in small mammals, such as lemmings, voles, and Arctic ground squirrels (*Urocitellus parryii*) (Hellström et al. 2014, Pokrovsky et al. 2014). Although gyrfalcons are considered ptarmigan (*Lagopus mutus*) and hare (*Lepus arcticus*) specialists, ground squirrels can be used as an alternative food source (Poole and Boag 1988). Both raptor species cycle regularly with temporal fluctuations in their primary prey (Potapov 1997, Nielsen 1999, Sundell et al. 2004), so interactions with their prey species and peregrine falcons (competition for prey and nest sites) could be complex. By continuing the research presented in this dissertation and expanding it include gyrfalcons and rough-legged hawks, and the trophic levels below them, a more complete understanding of the impacts of climate change on Arctic tundra ecosystems would be achieved.

Table 6.1. AIC_c analysis comparing generalized linear models (Poisson) predicting the number of fledglings produced by peregrine falcon nests as a function of the density of different types of prey available within falcon home-ranges.

Model parameters	**K**	**AIC_c**	**ΔAIC_c**	**Akaike weight**
insectivorous birds	2	71.23	0.00	0.30
total prey	2	72.31	1.08	0.18
lemmings	2	72.36	1.12	0.17
lemmings + insect. + (lemming× insect.)	4	72.63	1.39	0.15
lemmings + insectivorous birds	3	73.98	2.74	0.08
Marine birds	2	74.48	3.24	0.06
ducks	2	74.54	3.31	0.06

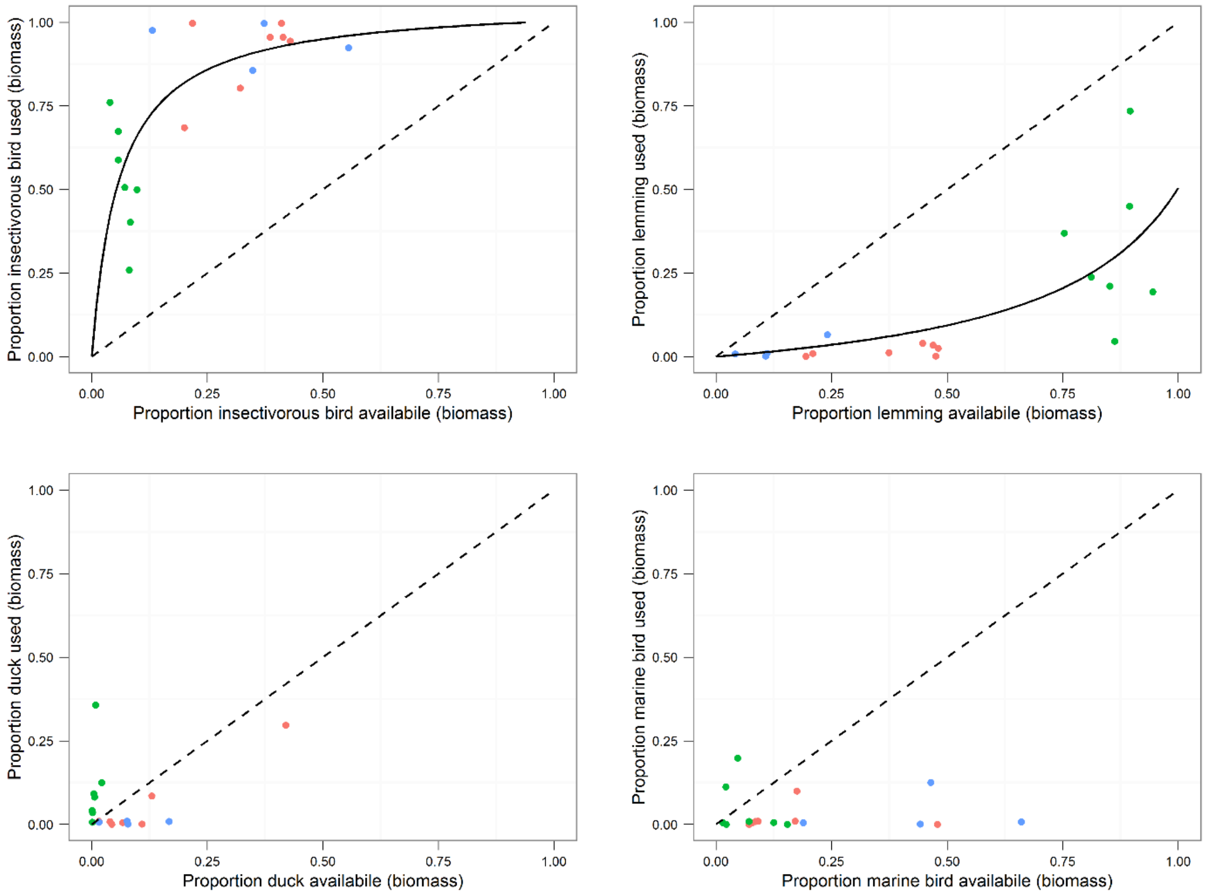

Figure 6.1. Proportional contribution of each prey type to the diet of nestling peregrine falcons in relation to proportional availability of each prey type within peregrine falcon home ranges. Dashed lines represent no selection; points above the dashed line indicate peregrines were selecting for that prey type, while points below indicate peregrines were avoiding it (red = 2010, green = 2011, blue = 2012). Solid lines for insectivorous birds and lemmings are merely to help visualize the relationship; functions represented by these lines were parameterized using non-linear regression, but no model selection techniques were applied.

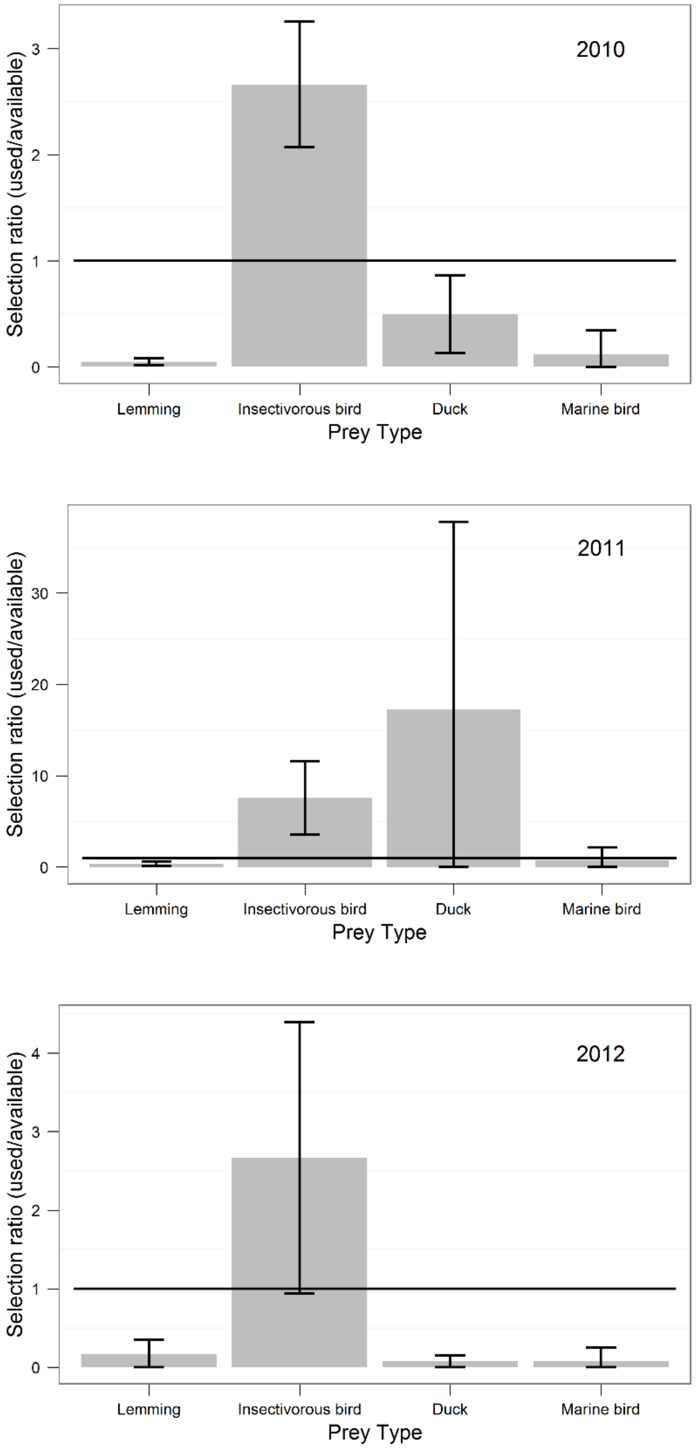

Figure 6.2. Selection ratios for each prey type estimated for the entire population of peregrine falcons (Manly et al. 2002) for each year of the study. A selection ratio of 1 indicates no selection and ratios > or < 1 indicate selection or avoidance, respectively. Error bars represent Bonferroni confidence intervals.

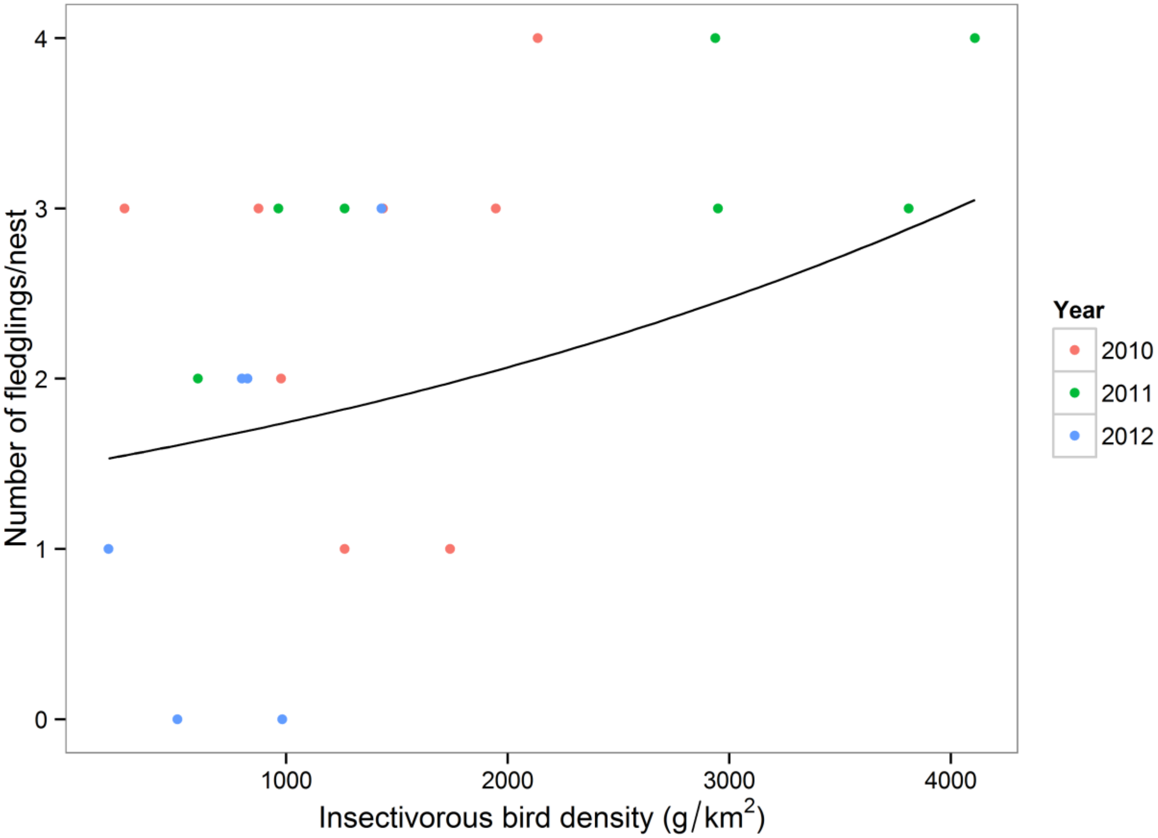

Figure 6.3. Number of fledglings within a nest surviving to 25 days old in relation to the density of insectivorous birds within the home-range surrounding the nest. The black line represents a generalized linear model parameterized with a Poisson error distribution and a log link function.

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Appendices

Appendix A

Table A1. List of avian species observed along transects. Transects were located on the Coxe Islands, Igloolik Island, and the northern tip of the Melville Peninsula, Nunavut, and surveyed from 25 July – 5 September, 2010 – 2012.

Avian Guild	Common	Scientific
Songbirds	snow bunting	*Plectrophenax nivalis*
	horned lark	*Eremophila alpestris*
	Lapland longspur	*Calcarius lapponicus*
	American pipet	*Anthus rubescens*
Shorebirds	dunlin	*Calidris alpina*
	red phalarope	*Phalaropus fulicarius*
	red-necked phalarope	*Phalaropus lobatus*
	American golden plover	*Pluvialis dominica*
	black-bellied plover	*Pluvialis squatarola*
	semipalmated plover	*Charadrius semipalmatus*
	saird's sandpiper	*Calidris bairdii*
	buff-breasted sandpiper	*Tryngites subruficollis*
	purple sandpiper	*Calidris maritima*
	stilt sandpiper	*Calidris himantopus*
	white-rumped sandpiper	*Calidris fuscicollis*
Geese	brant	*Branta bernicla*
	snow goose	*Chen caerulescens*
	Canada goose	*Branta canadensis*
	tundra swan	*Cygnus columbianus*
Gulls	glaucous gull	*Larus hyperboreus*
	herring gull	*Larus argentatus*
	Sabine's gull	*Xema sabini*
	Thayer's gull	*Larus thayeri*

Table A1. cont.

Avian Guild	**Common**	**Scientific**
	parasitic jaeger	*Stercorarius parasiticus*
	long-tailed jaeger	*Stercorarius longicaudus*
	Arctic tern	*Sterna paradisaea*
Loons	common loon	*Gavia immer*
	Pacific loon	*Gavia pacifica*
	red-throated loon	*Gavia stellata*
	yellow-billed loon	*Gavia adamsii*
Other	sandhill crane	*Grus canadensis*
	long-tailed duck	*Clangula hyemalis*
	common eider	*Somateria mollissima*
	king eider	*Somateria spectabilis*
	gyrfalcon	*Falco rusticolus*
	peregrine falcon	*Falco peregrinus*
	black guillemot	*Cepphus grylle*
	rough-legged hawk	*Buteo lagopus*
	snowy owl	*Bubo scandiacus*
	Rock ptarmigan	*Lagopus muta*
	common raven	*Corvus corax*

Table A2. Details of the AIC_c analysis used to choose the most appropriate detection function for each avian guild. Birds were surveyed on the Coxe Islands, Igloolik Island and the northern tip of the Melville Peninsula, Nunavut, from 2010-2012. The ΔAIC_c value of the model used for each guild is bolded. If multiple models had a $\Delta AIC_c < 4$, the model with the least number of parameters was chosen to satisfy the rule of parsimony. Models with no ΔAIC_c value (-) did not converge during parameter estimation.

Key function	**Series expansion**	**# Adjustment terms**	**Covariates**	**# Parameters**	**ΔAIC_c** **Songbirds**	**Shorebirds**	**Gulls**	**Geese**	**Loons**
Half Normal	-	0	-	1	9.80	15.75	**2.30**	6.39	**0.94**
Half Normal	-	0	Time	2	6.94	17.31	4.22	8.21	0.00
Half Normal	-	0	Rugged	2	9.81	16.73	0.00	6.46	1.74
Half Normal	-	0	Year	3	10.93	16.00	2.49	**0.00**	1.25
Half Normal	-	0	Julian Day	3	5.90	12.41	5.89	**3.71**	2.47
Half Normal	Cosine	1	-	2	8.66	**1.91**	4.28	7.56	2.93
Half Normal	Cosine	1	Time	3	6.04	3.55	6.21	9.41	1.95

Table A2. cont.

Key function	**Series expansion**	**# Adjustment terms**	**Covariates**	**# Parameters**	**ΔAIC$_c$**				
					Songbirds	**Shorebirds**	**Gulls**	**Geese**	**Loons**
Half Normal	Cosine	1	Rugged	3	8.71	3.09	2.00	7.76	3.71
Half Normal	Cosine	1	Year	4	9.94	2.89	4.49	1.70	7.89
Half Normal	Cosine	1	Julian Day	4	5.29	0.00	7.88	5.22	4.43
Half Normal	Hermite Poly.	1	-	2	11.71	17.66	4.29	8.35	2.94
Half Normal	Hermite Poly.	1	Time	3	-	-	-	-	-
Half Normal	Hermite Poly.	1	Rugged	3	-	-	2.00	-	-
Half Normal	Hermite Poly.	1	Year	4	-	-	-	-	-
Half Normal	Hermite Poly.	1	Julian Day	4	-	-	-	-	-
Hazard Rate	-	0	-	2	9.72	2.54	4.91	7.02	2.67

Table A2. cont.

Key function	**Series expansion**	**# Adjustment terms**	**Covariates**	**# Parameters**	**ΔAIC$_c$**				
					Songbirds	**Shorebirds**	**Gulls**	**Geese**	**Loons**
Hazard Rate	-	0	Time	3	9.74	8.00	6.64	8.85	5.37
Hazard Rate	-	0	Rugged	3	13.89	7.90	3.56	7.42	5.37
Hazard Rate	-	0	Year	4	13.01	7.58	7.17	3.86	5.56
Hazard Rate	-	0	Julian Day	4	**0.00**	7.67	8.57	5.14	7.27
Hazard Rate	Cosine	1	-	3	8.58	3.43	5.79	8.89	4.45
Hazard Rate	Cosine	1	Time	4	8.98	13.34	8.69	10.71	7.32
Hazard Rate	Cosine	1	Rugged	4	10.01	13.31	5.11	8.87	7.32
Hazard Rate	Cosine	1	Year	5	11.94	13.47	10.67	5.54	7.89
Hazard Rate	Cosine	1	Julian Day	5	-	13.27	10.69	7.56	9.19

Table A2. cont.

Key function	**Series expansion**	**# Adjustment terms**	**Covariates**	**# Parameters**	**ΔAIC$_c$**				
					Songbirds	**Shorebirds**	**Gulls**	**Geese**	**Loons**
Hazard Rate	Simply Poly.	1	-	3	11.44	2.89	6.62	9.02	4.25
Hazard Rate	Simply Poly.	1	Time	4	10.01	7.93	-	10.83	5.70
Hazard Rate	Simply Poly.	1	Rugged	4	14.82	8.10	5.16	9.32	5.77
Hazard Rate	Simply Poly.	1	Year	5	12.40	7.79	8.61	5.52	7.13
Hazard Rate	Simply Poly.	1	Julian Day	5	0.97	8.96	9.90	7.09	5.05

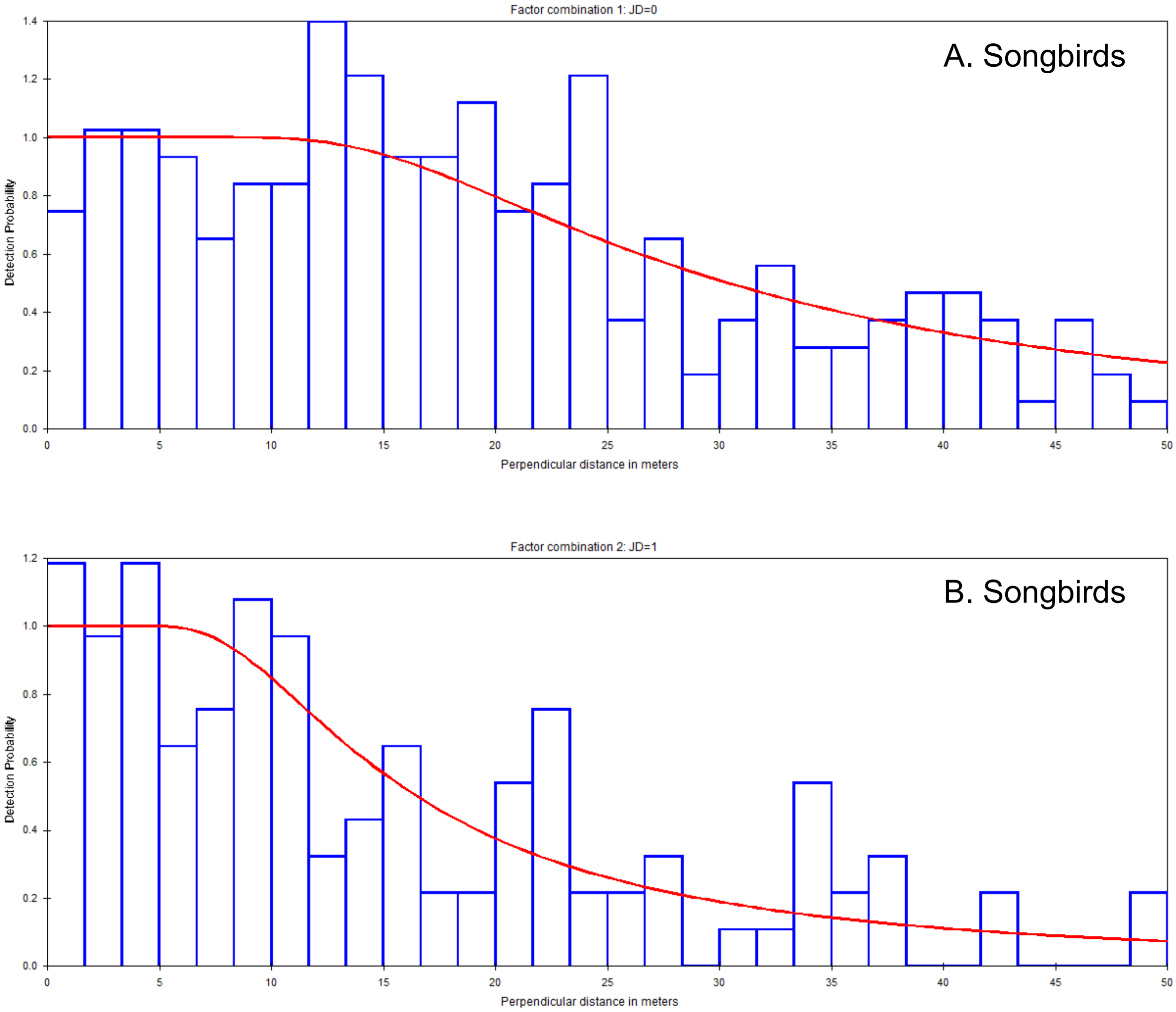


Figure A1. Estimated detection functions (red lines) and frequency histograms of the actual number of birds observed at different distances from transects (blue bars). If a covariate was included in the detection function for a guild, a different detection function is shown for each value of the covariate. Transects were located on the Coxe Islands, Igulik Island, and the northern tip of the Melville Peninsula, Nunavut, and surveyed from 25 July – 5 September, 2010 – 2012.

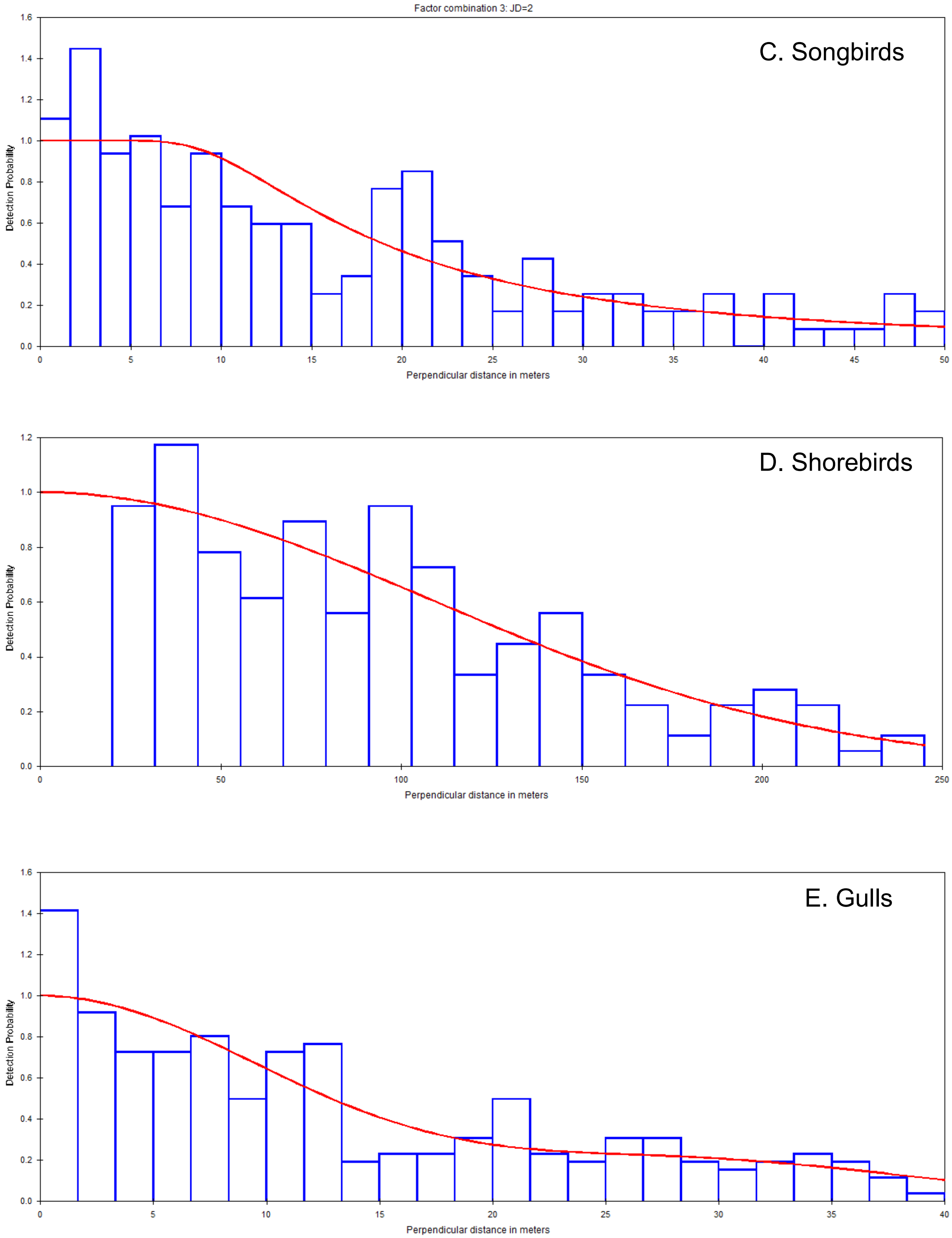


Figure A1. cont.

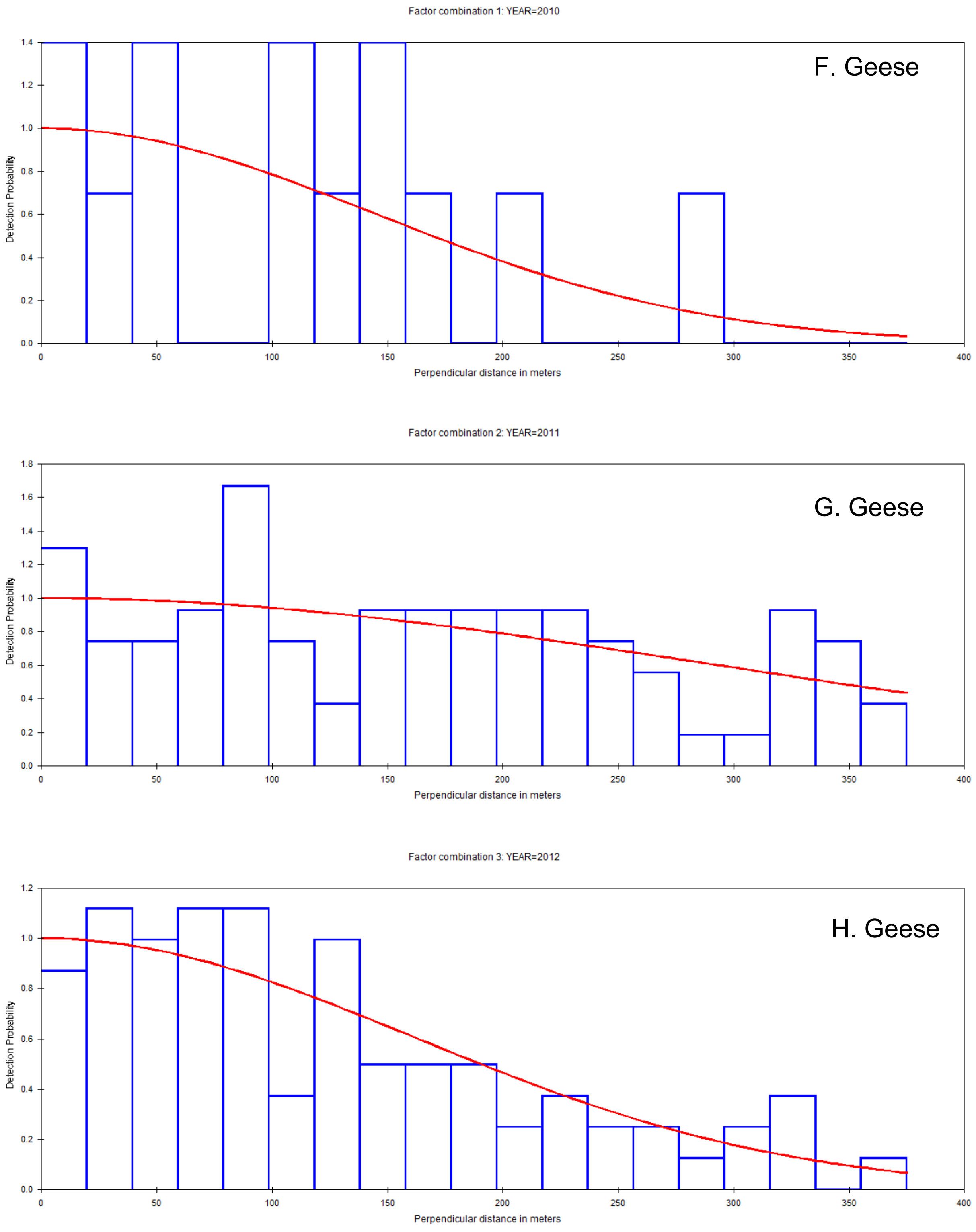


Figure A1. cont

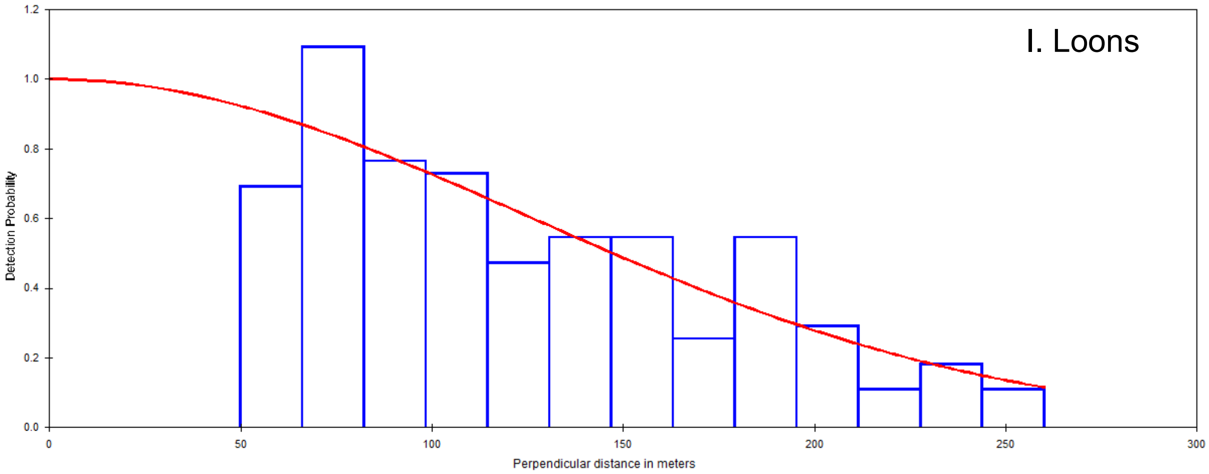


Figure A1. cont.

Appendix B

Table B1. Number of nestlings at each peregrine falcon nest along with the dates blood samples were taken and over which nestlings were monitored with motion-sensitive cameras and PTTs were deployed on adult females.

			Dates (dd-mm)		
Site	**Year**	**# nestlings**	**Blood sample**	**Camera image**	**PTT deployment**
1	2010	1	NA	23-07 to 29-07, 04-08 to 06-08	27-07
2	2010	2	03-08, 09-08	25-07 to 05-08	NA
3	2010	3	01-08, 10,08	NA	04-08
4	2010	4	01-08, 07-08	24-07 to 28-07, 01-08 to 04-08	NA
5	2010	3	06-08	27-07 to 30-07	NA
7	2010	3	09-08, 16-08	24-07 to 26-07	NA
8	2010	4	08-08, 15-08	02-08 to 08-08	02-08
11	2010	3	06-08, 13-08	30-07 to 02-08	NA
13	2010	3	07-08, 14-08	31-07 to 05-08	31-07
2	2011	4	03-08, 10-08	27-07 to 30-07, 03-08 to 04-08	03-08
4	2011	4	01-08, 07-08	NA	01-08
5	2011	4	31-07, 06-08	16-07 to 19-07	NA
7	2011	4	03-08, 11-08	NA	29-07
8	2011	3	13-08, 20-08	05-08 to 13-08	NA
11	2011	3	10-08, 14-08	22-07 to 07-08	30-07
12	2011	3	04-08, 11-08	28-07 to 04-08	28-07
13	2011	2	01-08, 07-08	18-07 to 29-07	NA
14	2011	3	02-08, 10-08	02-08 to 07-08	02-08
2	2012	3	08-08, 14-08	28-07 to 10-08	NA

Table B1. cont.

			Dates (dd-mm)		
Site	**Year**	**# nestlings**	**Blood sample**	**Camera image**	**PTT deployment**
3	2012	3	07-08, 14-08	23-07 to 26-07, 30-07 to 01-08	NA
7	2012	3	NA	18-07 to 31-07	NA
6	2012	3	01-08, 10-08	17-07 to 03-08	NA
11	2012	2	NA	22-07 to 30-07	NA
13	2012	1	NA	02-08 to 08-08	NA

Table B2. The average mass of prey deliveries for each prey type was estimated using the literature and the size of prey items relative to the peregrine adult and nestlings within motion-sensitive camera images. The table below summarizes the masses I used and provides references and rational for each prey type.

Prey Type	Species	Age	Mass from literature (g)	Mass assigned (g)	Rational	Reference
lemming	*Lemmus trimucronatus*	adult	43	40	Mean of both species	Legagneux et al. (2012)
	Dicrostonyx groenlandicus	adult	36			
Insectivorous bird	*Calidris pusilla*	adult	22.7	30	Mean of all species	Lindström et al. (2002)
	C. minutilla	adult	19.1			
	C. fuscicollis	adult	35.4			
	C. bairdii	adult	35.2			
	Calcarius lapponicus	adult	29.2			Legagneux et al. (2012)
	Plectrophenax nivalis	adult	30			Montgomerie and Lyon (2011)
Duck	*Somateria mollissima*	0	75	50	All deliveries were small ducklings likely < 5 days old, often with the heads missing and never much larger than insectivorous prey.	Starck and Ricklefs (1998)
	Clangula hyemalis	0	25			

Table B2. cont.

Prey Type	Species	Age	Mass from literature (g)	Mass assigned (g)	Rational	Reference
Marine	*Larus argentatus*	9	200	150	Deliveries I always downy nestlings roughly 10 days old, usually with the upper body and/or head missing.	Savoca et al. (2011)
	Cepphus grylle	adult	300	300	All deliveries were adults; black guillemot nestlings are protected within their nests under rocks.	Butler and Buckley (2002)

Table B3. The prey type, scientific name, common name, collection date, isotopic values (δ13C and δ15N), and C and N concentrations for each prey tissue sample.

Prey type	**Taxonomy**	**Species**	**Date collected**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**C (%)**	**N (%)**
duck	*Somateria mollissima*	common eider	11/08/2011	-20.05	11.82	44.34	14.27
			11/08/2011	-18.36	13.50	44.82	14.43
			15/08/2011	-19.78	7.50	44.78	14.80
			15/08/2011	-19.95	8.01	45.53	14.88
			15/08/2011	-19.49	7.11	43.62	14.32
			15/08/2011	-19.75	7.90	45.44	14.74
insectivorous bird	*Anthus rubescens*	American pipit	12/08/2011	-24.82	6.41	43.93	13.96
			18/08/2011	-21.70	6.42	45.61	14.29
			18/08/2011	-21.59	6.76	44.59	14.22
			29/07/2013	-23.21	6.12	44.84	14.45
			30/07/2013	-25.27	5.52	46.55	14.57
			16/08/2013	-21.43	6.82	46.42	14.73
	Calcarius lapponicus	Lapland longspur	06/08/2011	-23.23	5.91	44.05	14.22
			09/08/2011	-22.78	6.36	45.41	13.85
			09/08/2011	-23.51	6.07	43.67	13.75
			31/07/2012	-23.09	7.49	44.28	14.07
			21/08/2012	-23.81	6.29	44.87	14.26
			28/08/2012	-21.95	6.15	43.29	13.68
			12/07/2013	-24.60	5.83	46.67	14.65
			12/07/2013	-24.14	5.68	45.83	14.15

Table B3. cont.

Prey type	**Taxonomy**	**Species**	**Date collected**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**C (%)**	**N (%)**
insectivorous bird	*Calcarius lapponicus*	Lapland longspur	20/07/2013	-23.93	7.00	46.61	14.83
			05/08/2013	-24.07	5.88	46.5	14.77
			11/08/2013	-23.66	8.47	47.04	14.65
			12/08/2013	-23.47	6.81	48.04	15.04
	Calidris fuscicollis	white-rumped sandpiper	11/08/2013	-22.23	6.61	47.06	14.94
	Calidris spp.	sandpiper	09/08/2011	-22.31	7.32	45.00	13.98
			09/08/2011	-22.60	8.82	44.4	14.06
			15/08/2011	-23.15	5.36	45.54	14.27
			11/08/2013	-24.08	4.51	45.38	14.83
	Plectrophenax nivalis	snow bunting	10/08/2011	-19.06	6.92	45.13	14.32
			28/08/2012	-23.96	4.82	44.83	14.23
			15/07/2013	-25.81	12.98	44.25	14.17
			15/07/2013	-24.88	11.61	46.08	14.34
			23/07/2013	-22.78	7.07	46.22	14.83
			02/08/2013	-23.62	6.65	45.40	14.5
			07/08/2013	-21.72	6.20	46.43	14.84
			07/08/2013	-22.70	6.05	48.30	15.34
			16/08/2013	-24.01	4.61	45.48	14.48
	Pluvialis dominica	golden plover	12/08/2011	-24.17	5.05	44.92	13.92
			12/08/2011	-23.50	6.37	43.75	14.05
			21/08/2012	-24.81	3.87	44.67	14.33

Table B3. cont.

Prey type	**Taxonomy**	**Species**	**Date collected**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**C (%)**	**N (%)**
lemming	*Lemmus trimucronatus* or *Dicrostonyx groenlandicus*	lemming	30/11/2010	-24.72	1.21	44.61	14.31
			04/08/2011	-25.32	0.59	45.89	14.65
			04/08/2011	-25.26	1.12	45.33	14.47
			04/08/2011	-25.39	1.02	46.16	14.59
			05/08/2011	-25.15	-0.02	35.04	11.01
			05/08/2011	-24.18	1.03	43.76	14.51
			05/08/2011	-24.77	2.88	43.83	13.96
			05/08/2011	-24.92	0.83	44.89	14.35
			05/08/2011	-24.26	1.26	43.48	14.49
			06/08/2011	-25.38	-0.08	45.18	14.35
			06/08/2011	-25.26	0.94	46.1	14.53
			06/08/2011	-25.11	-0.02	44.88	14.25
			06/08/2011	-25.13	0.91	40.29	12.61
			12/08/2013	-25.95	1.74	46.97	14.50
marine bird	*Cepphus grylle*	black guillemot	14/08/2011	-18.58	17.19	45.11	14.33
			14/08/2011	-18.34	17.14	45.15	14.44
			14/08/2011	-18.27	18.05	45.09	14.44
			14/08/2011	-18.60	17.65	67.64	21.91
	Larus argentatus	herring gull	09/08/2011	-19.10	14.81	44.41	14.36
			09/08/2011	-20.26	14.21	46.11	12.23
			16/08/2011	-18.91	15.22	45.46	14.46

Table B3. cont.

Prey type	**Taxonomy**	**Species**	**Date collected**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**C (%)**	**N (%)**
marine bird	*Larus argentatus*	herring gull	16/08/2011	-18.76	14.67	44.57	14.40
			02/08/2013	-17.08	15.10	47.00	14.67
			08/08/2013	-19.21	16.23	46.76	14.06
			15/08/2013	-20.01	15.04	45.43	13.66
	Larus hyperboreus	glaucous gull	14/08/2011	-18.95	17.07	47.38	15.42
			14/08/2011	-18.72	17.08	43.73	14.02
	Larus spp.	gull	24/07/2013	-19.77	16.39	45.43	14.73
			31/07/2013	-20.37	14.11	42.99	12.78
			17/08/2013	-18.99	15.88	46.89	14.73
	Sterna paradisaea	Arctic tern	15/08/2011	-19.34	15.62	43.69	14.00
			15/08/2011	-19.59	16.11	44.52	13.91
			16/08/2011	-18.57	16.32	45.18	14.46
			16/08/2011	-18.38	15.47	42.82	14.13

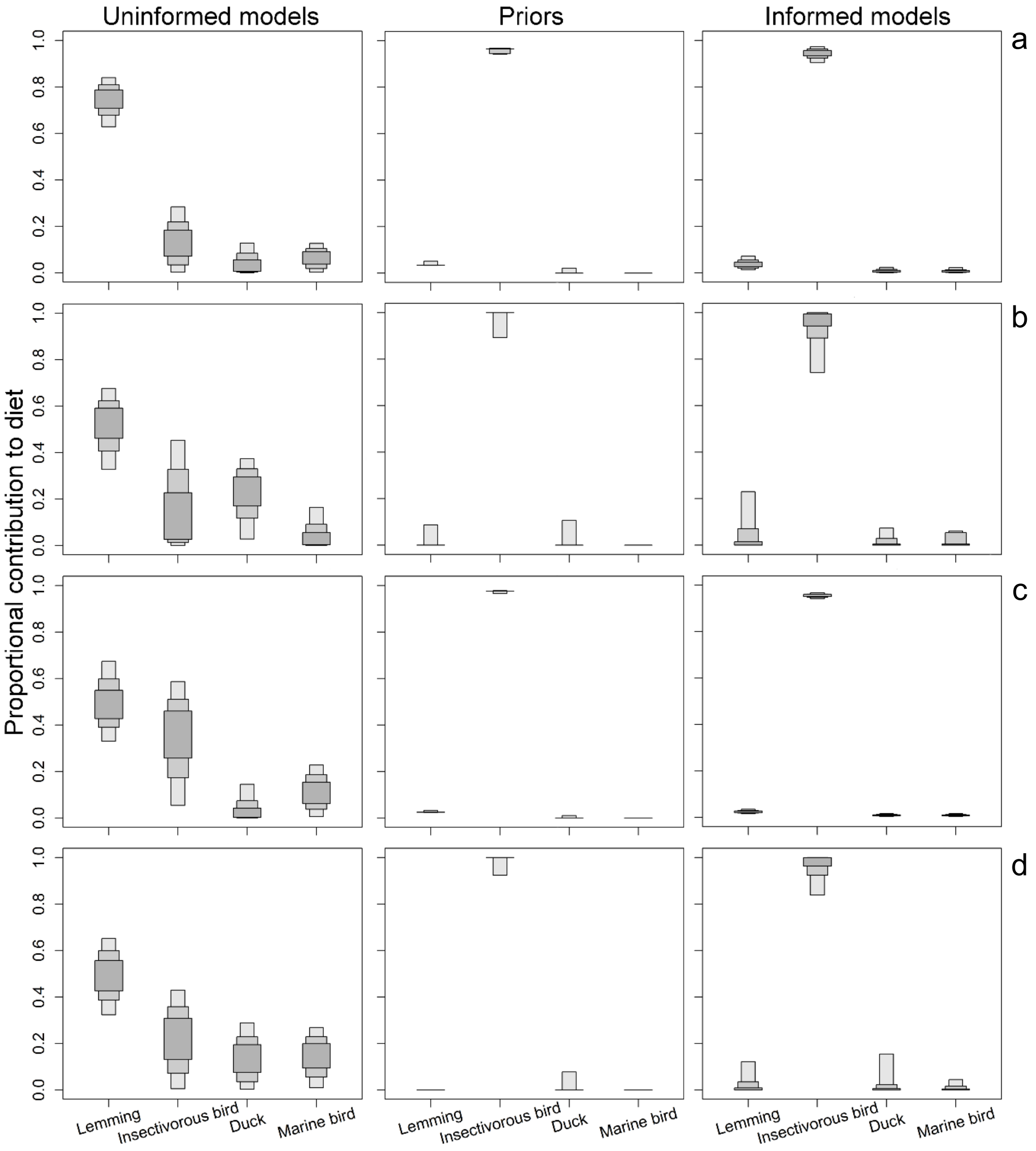


Figure. B1. A comparison of the posterior distribution of dietary proportions for each prey type consumed by peregrine falcon nestlings from four nests. Diets were estimated with uninformed mixing models, motion-sensitive cameras (priors), and informed mixing models, which incorporated priors into the uninformed models. Each row of graphs represents a single nest. Nest-years shown are site 4, 2010 (a); site 7, 2010 (b); site 8, 2010 (c); site 11, 2010 (d); site 11, 2011 (e); site 12, 2011 (f); site 2, 2012 (g); site 3, 2012 (h); and site 6, 2012 (i) ; see Figure 1.1 for geographic location of sites.

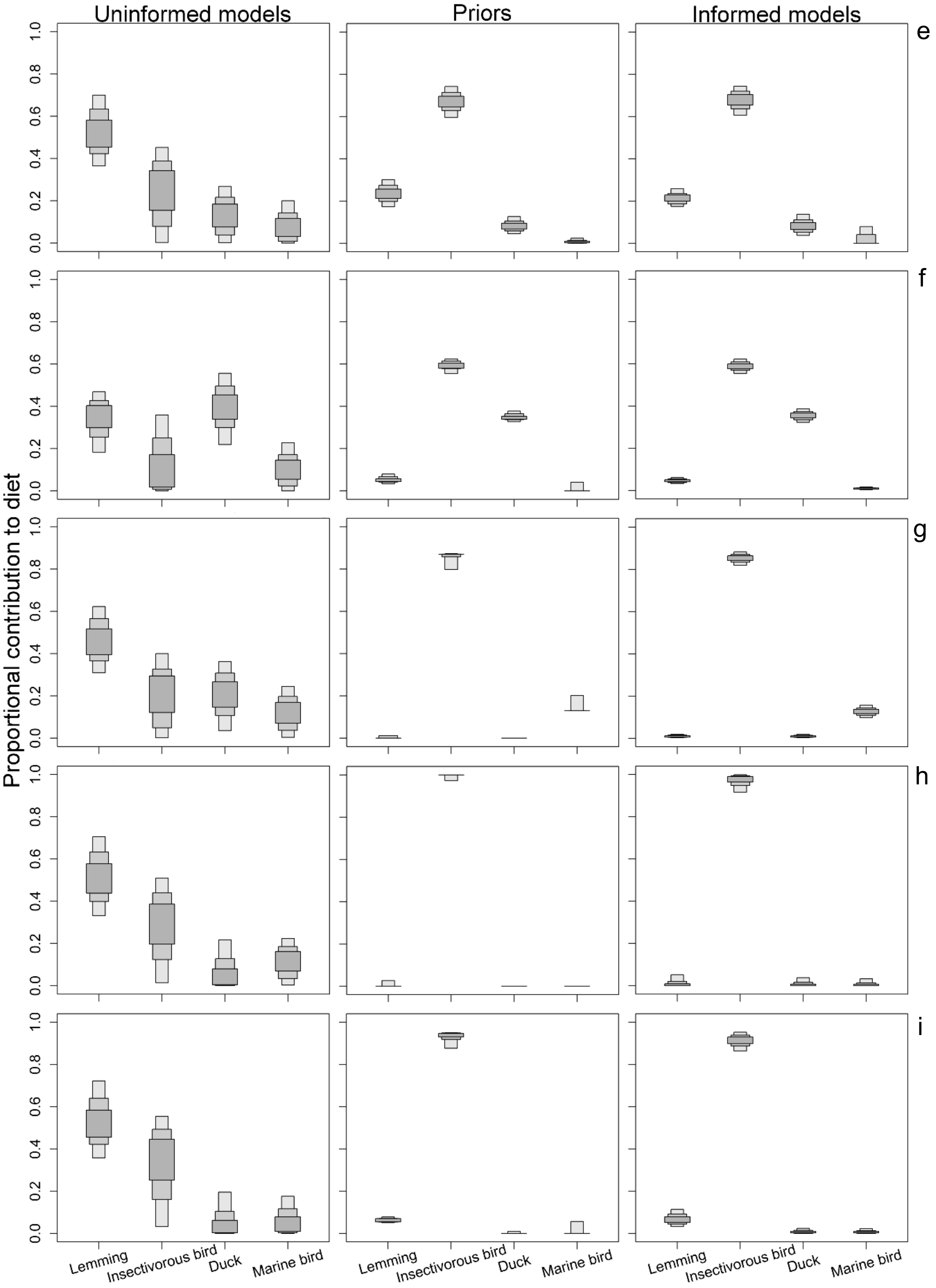


Figure B1. cont.

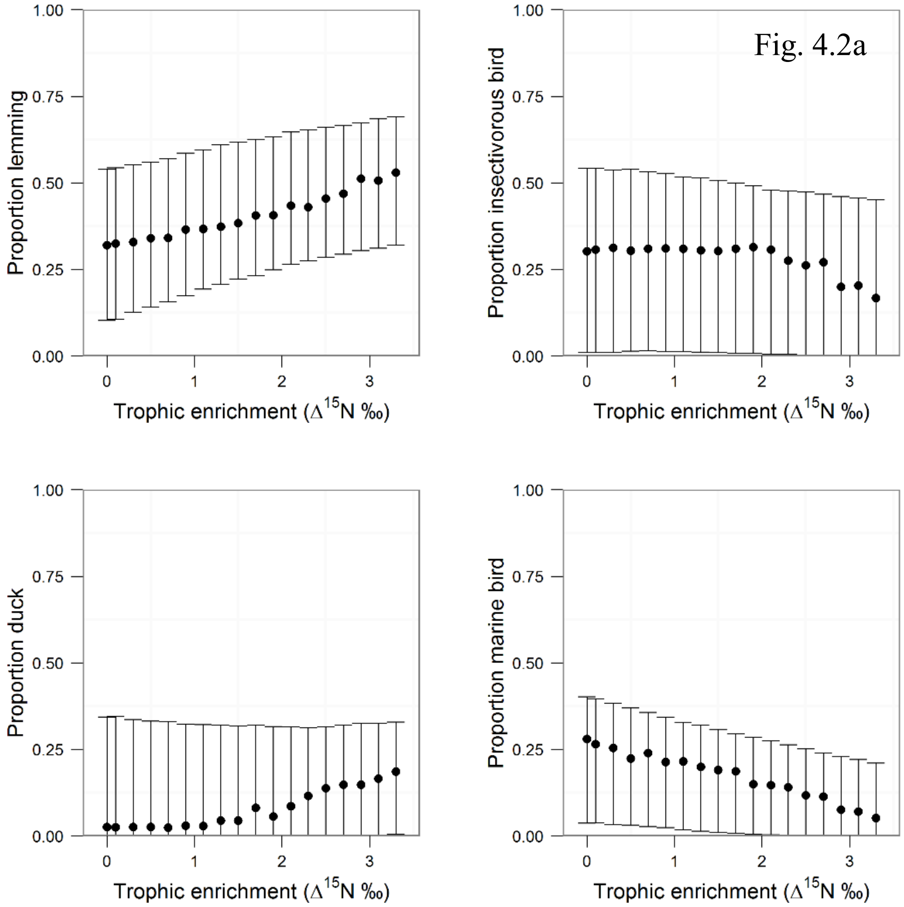


Figure B2. Influence of the trophic enrichment factor (Δ^{15}N) on estimates of the proportional contribution of each prey type to the diet of nestling peregrine falcons. Shown are the modes and 95% credible intervals of the posterior distribution of solutions to uninformed Bayesian mixing models. Each set of 4 graphs corresponds to a nest presented in Figures 4.2 and 4.3 (indicated in the upper right corner of each)

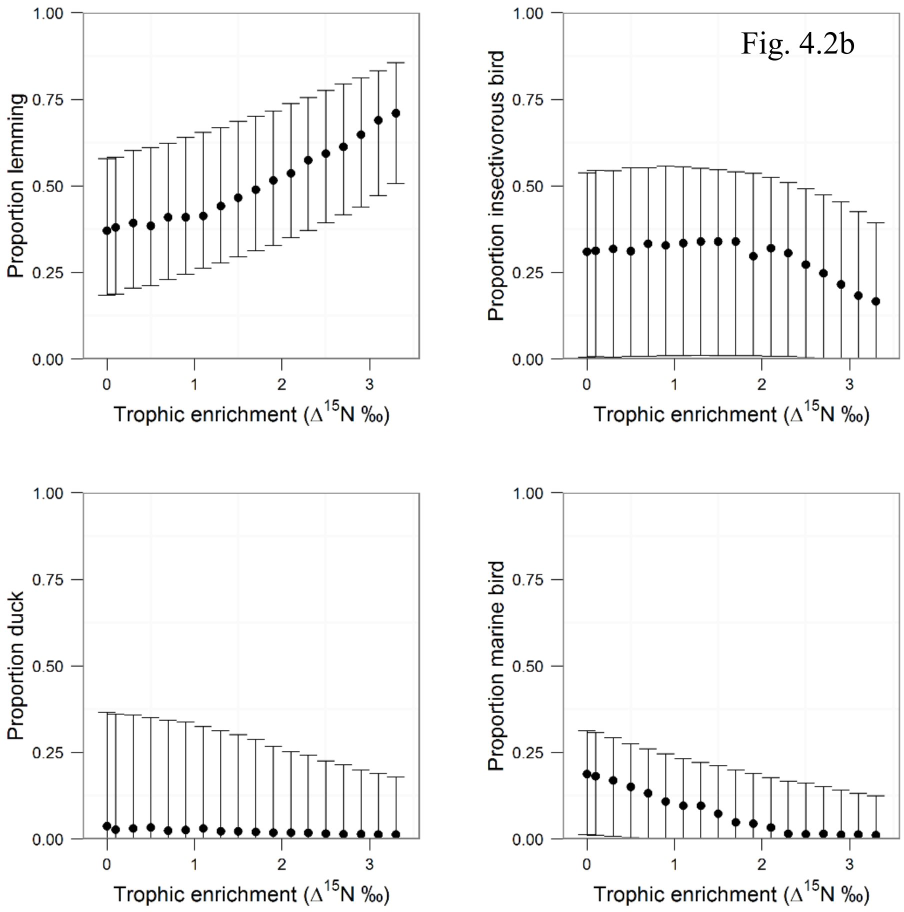
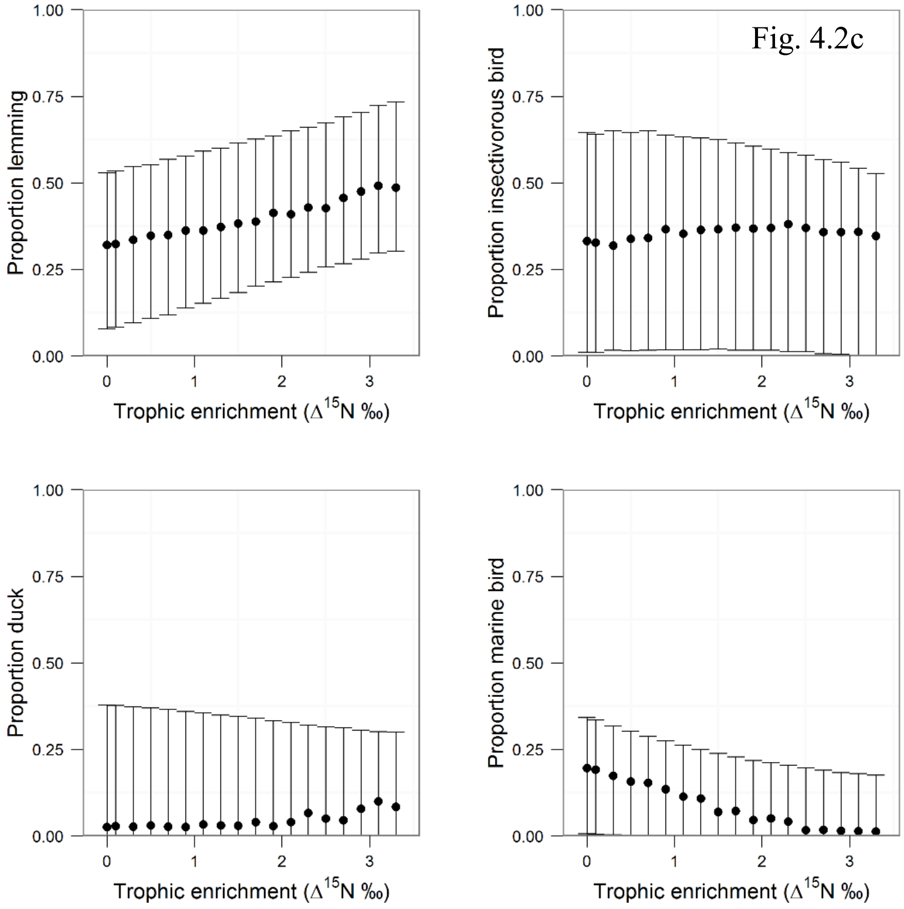


Figure B2. cont.



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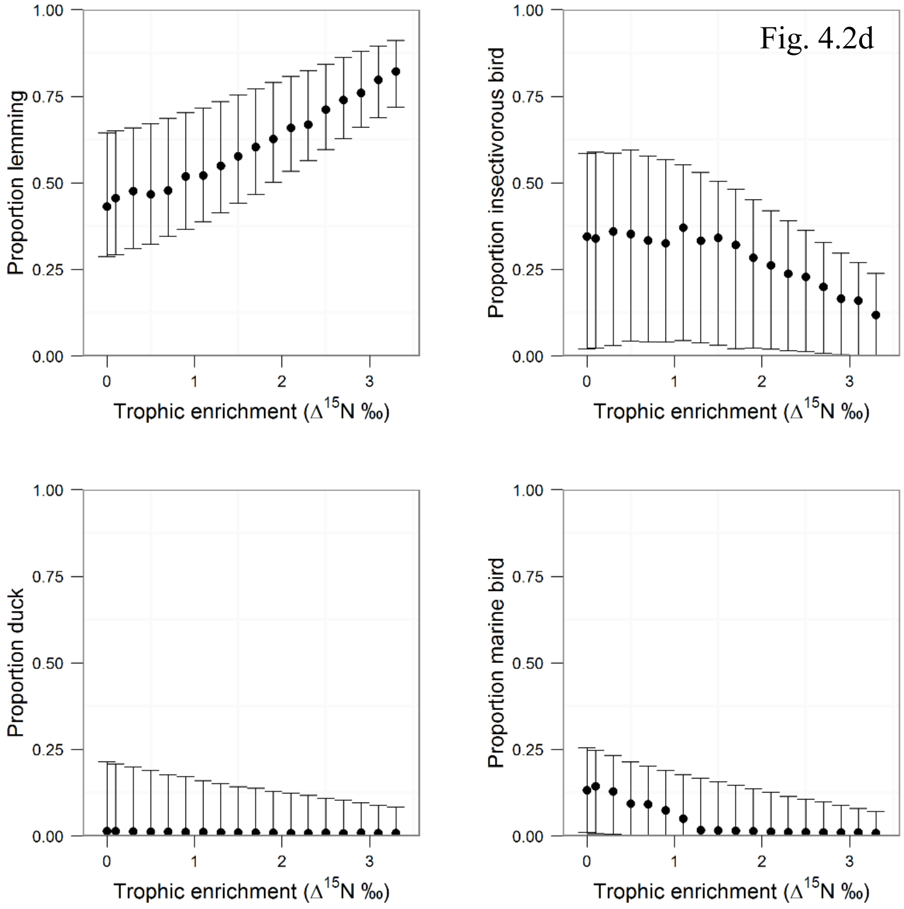


Figure. B2 cont.

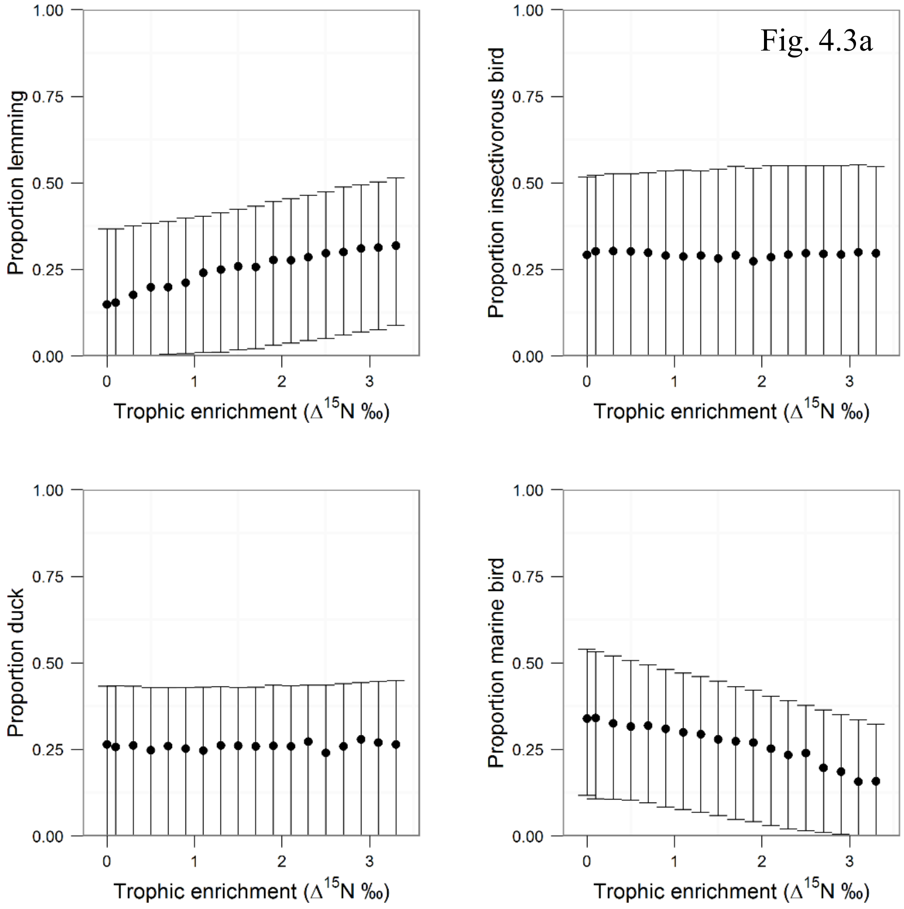
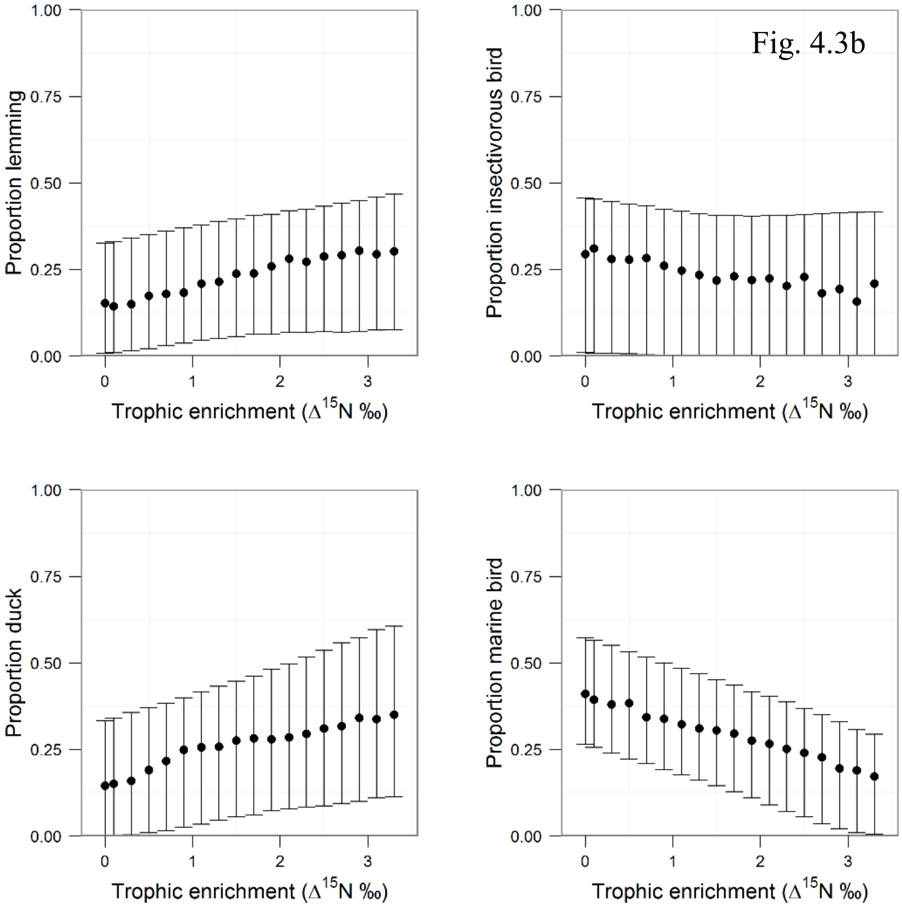


Figure B2. cont.



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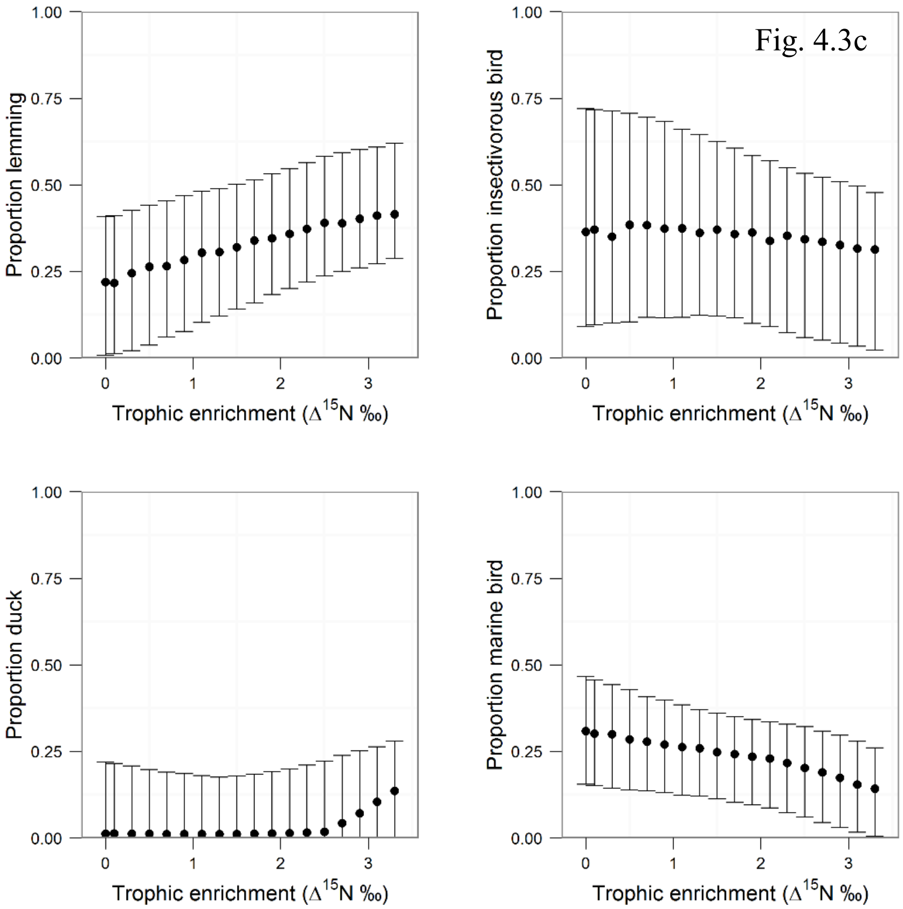

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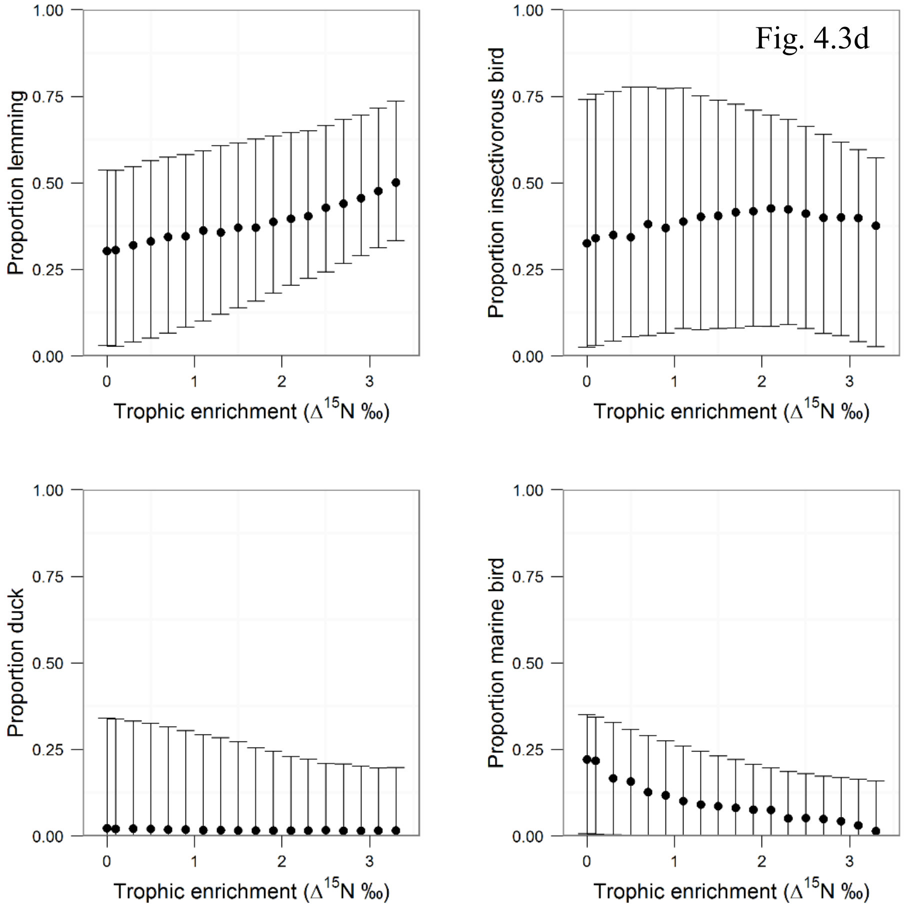


Fig. 4.3d

Figure B2. cont.

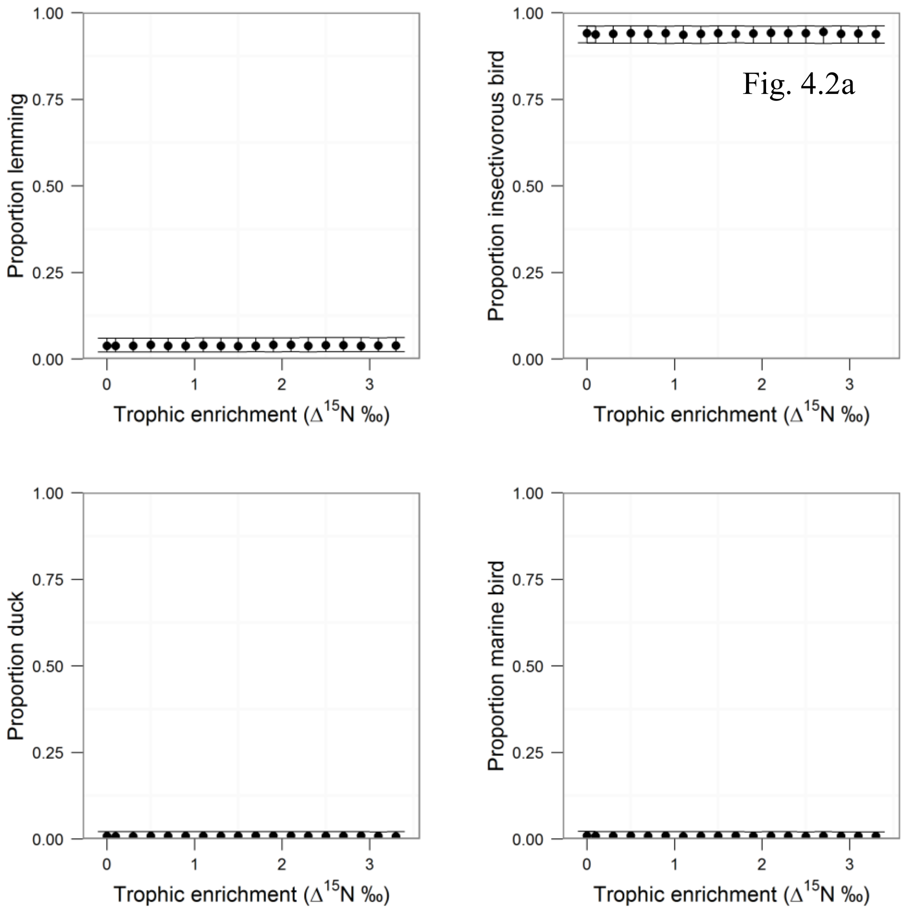


Figure. B3. Influence of the trophic enrichment factor ($\Delta^{15}N$) on estimates of the proportional contribution of each prey type to the diet of nestling peregrine falcons. Shown are the modes and 95% credible intervals of the posterior distribution of solutions to informed Bayesian mixing models. Priors for the informed models were based on data from motion-sensitive cameras monitoring nests. Each set of 4 graphs corresponds to a nest presented in Figures 4.2 and 4.3 (indicated in the upper right corner of each)

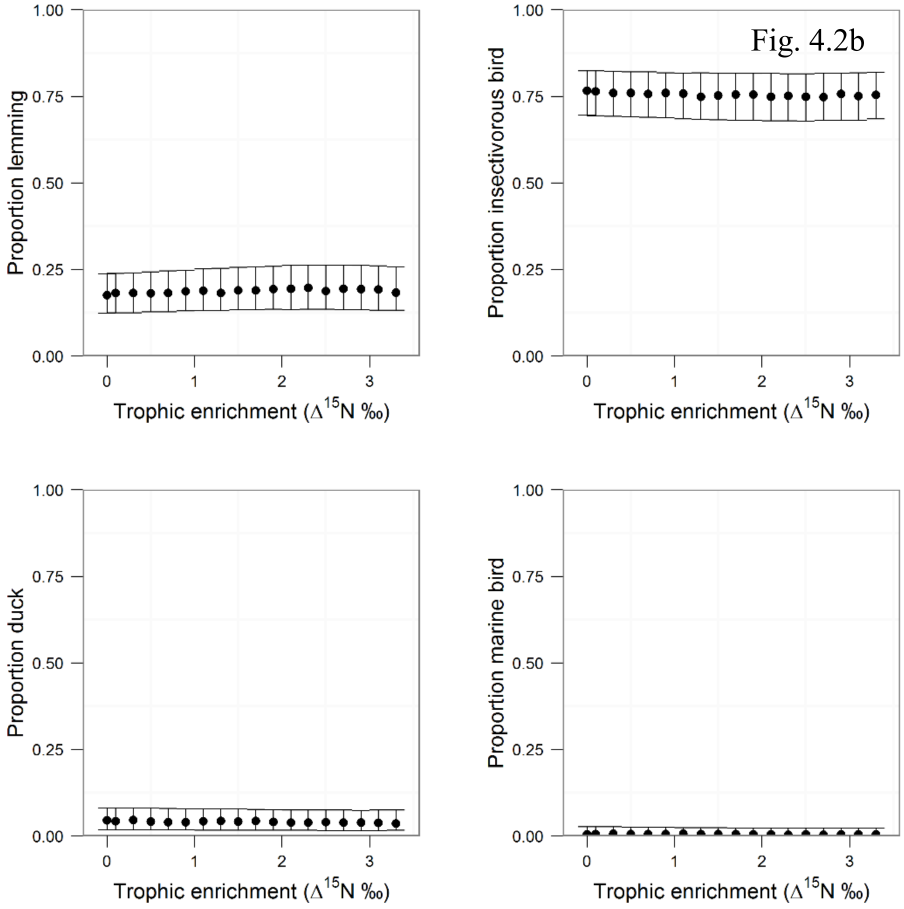


Figure. B3 cont.

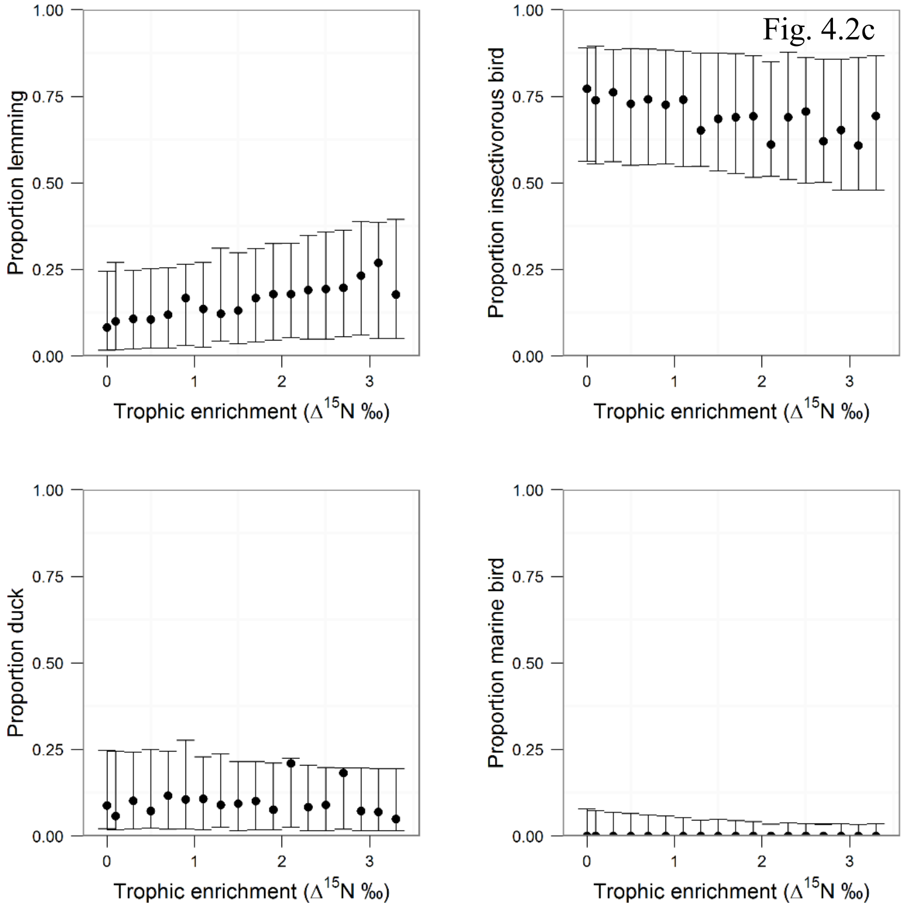


Figure. B3 cont.

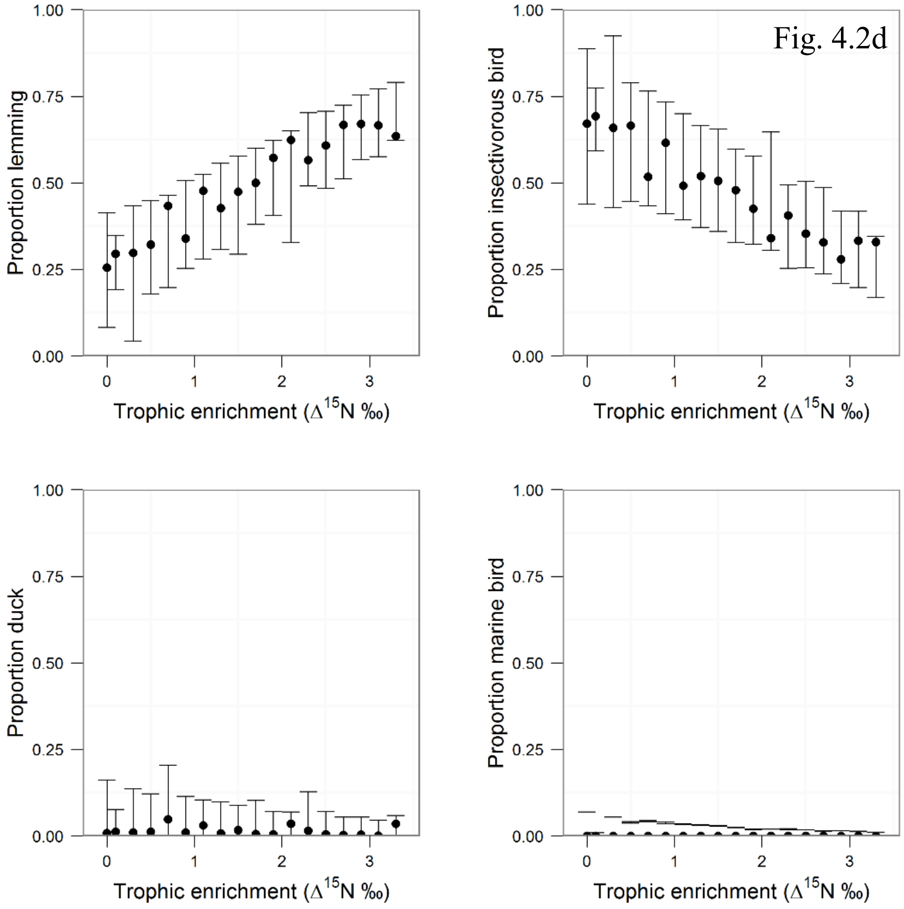


Figure. B3 cont.

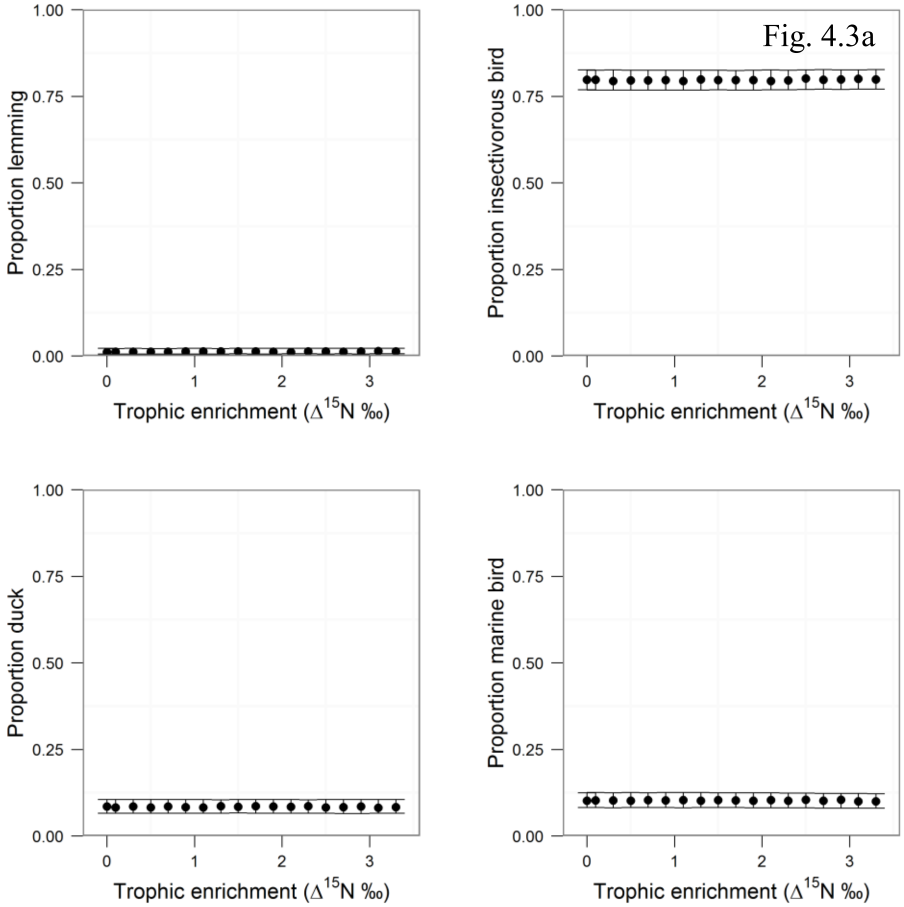
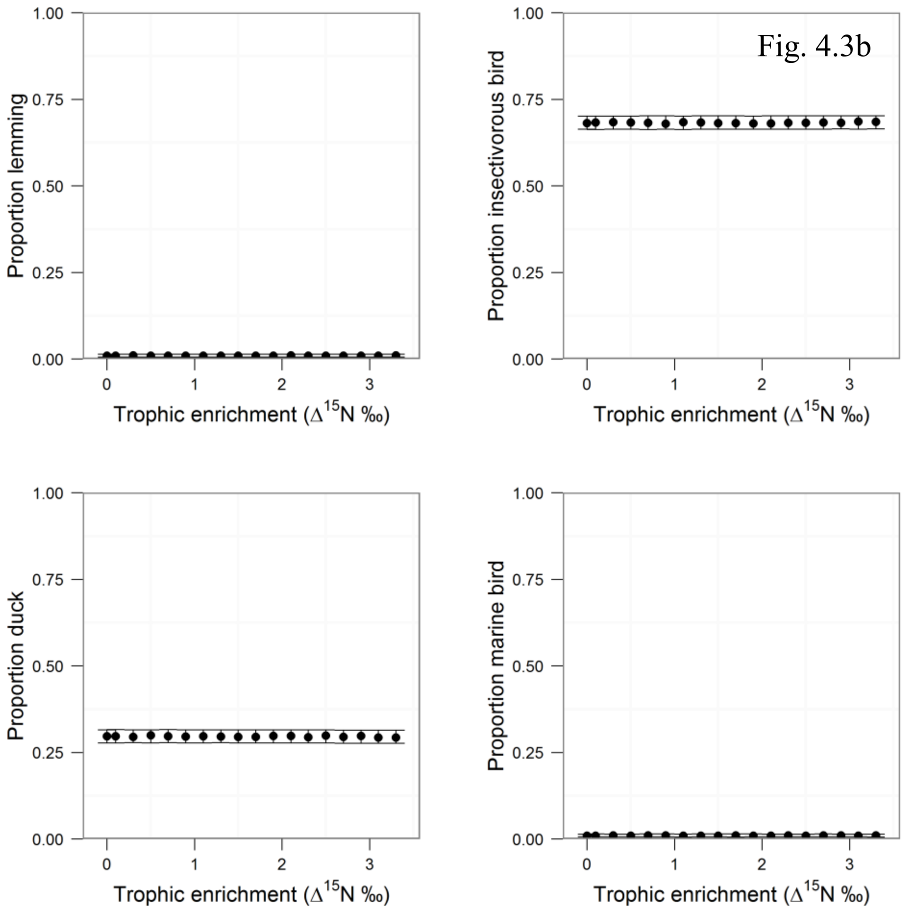


Figure. B3 cont.



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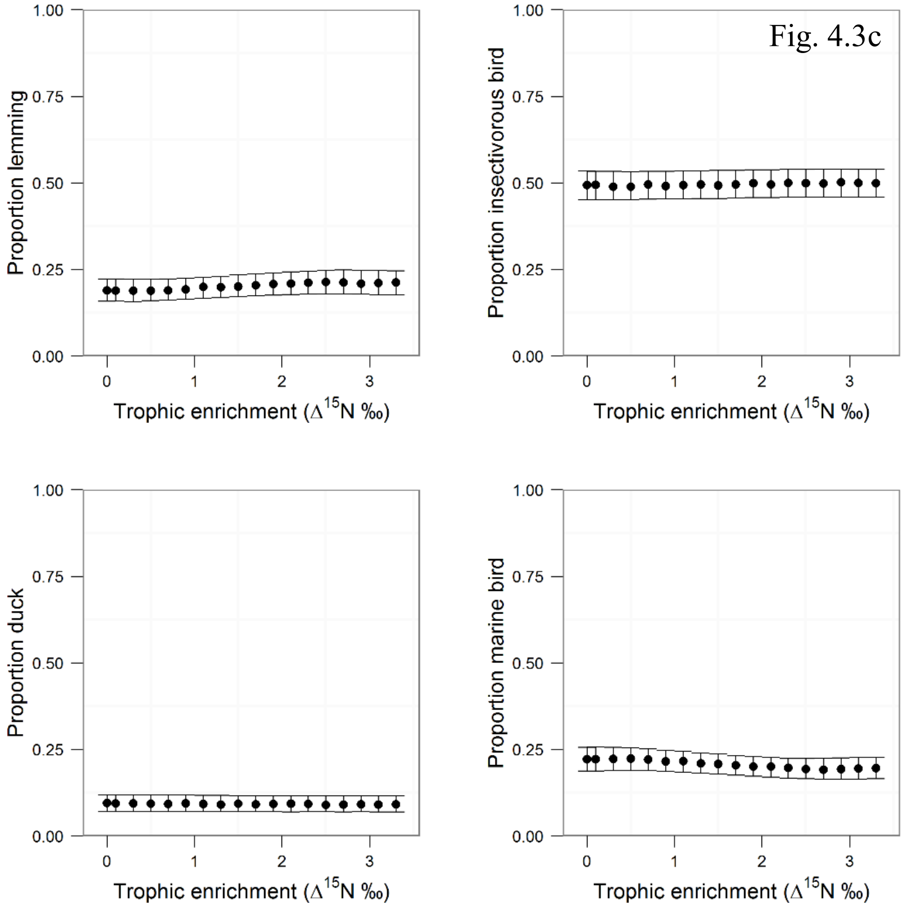

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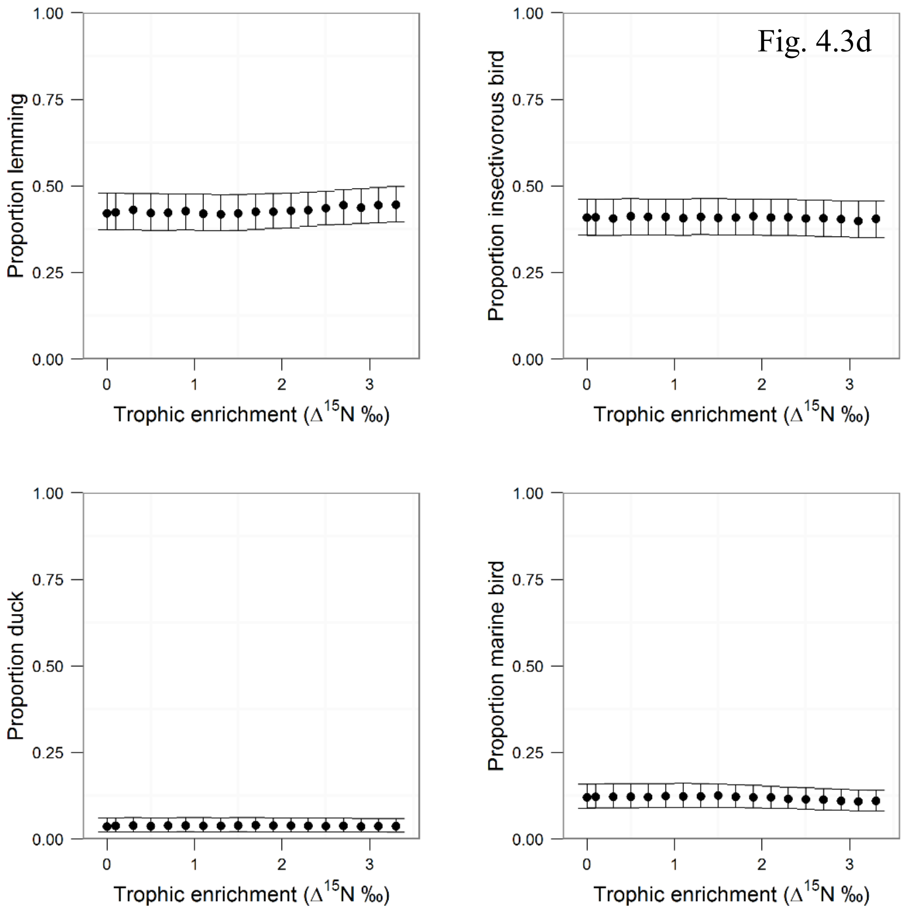
Fig. 4.3d

Figure. B3 cont.

Appendix C

Figure C1. Example of a prey delivery (semipalmated plover, *Charadrius semipalmatus*) captured by a motion-sensitive camera (PC8000 Hyperfire, Reconyx) monitoring an Arctic Peregrine Falcon nest in Nunavut, Canada.

Figure C2. Example of a prey delivery (snow bunting, *Plectrophenax nivalis*) captured by a motion-sensitive camera (PC8000 Hyperfire, Reconyx) monitoring an Arctic Peregrine Falcon nest in Nunavut, Canada.

Figure C3. Example of a prey delivery (duckling, likely a common eider, *Somateria mollissima*) captured by a motion-sensitive camera (PC8000 Hyperfire, Reconyx) monitoring an Arctic Peregrine Falcon nest in Nunavut, Canada.