

GYRFALCON DIET DURING THE BROOD REARING PERIOD ON THE SEWARD
PENINSULA, ALASKA, IN THE CONTEXT OF A CHANGING WORLD

by

Bryce W. Robinson

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DEFENSE COMMITTEE AND FINAL READING APPROVALS

of the thesis submitted by

Bryce W. Robinson

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The following individuals read and discussed the thesis submitted by student Bryce W. Robinson, and they evaluated his presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

Marc J. Bechard, Ph.D.	Chair, Supervisory Committee
David Anderson, Ph.D.	Member, Supervisory Committee
Travis L. Booms, Ph.D.	Member, Supervisory Committee
Julie Heath, Ph.D.	Member, Supervisory Committee

The final reading approval of the thesis was granted by Marc J. Bechard, Ph.D., Chair of the Supervisory Committee. The thesis was approved for the Graduate College by Jodi Chilson, M.F.A., Coordinator of Theses and Dissertations.

DEDICATION

To the increased understanding of the life of the Gyrfalcon, enabling its conservation and preservation for generations to come.

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ABSTRACT

As climate change impacts increase so does our need to understand their effects on ecosystem dynamics. I studied Gyrfalcon (*Falco rusticolus*) diet during the brood rearing period to improve our knowledge on dietary habits during nesting, and provide necessary information for understanding climate change impacts to Arctic ecosystems. I studied diet over two breeding seasons on the Seward Peninsula, Alaska, using two methods: motion-activated cameras and the collection of prey remains. I observed three important dietary shifts: the proportion of ptarmigan in the diet declined significantly throughout the season, the proportion of large prey items declined significantly throughout the season, and there was a between-season shift in predominant prey type from ptarmigan (*Lagopus lagopus and L. muta*) in 2014 to squirrel in 2015. The decrease in the proportion of ptarmigan coincided with an increase in Arctic ground squirrel (*Urocitellus parryii*) in the diet, indicating a within-season switch from ptarmigan to squirrel as the main prey item. Despite the shift in prey composition, dietary breadth did not change. These results suggest that the Gyrfalcon is a facultative specialist, an important consideration regarding the predicted impacts of climate change on species interactions in the Arctic, as facultative shifts between prey types may help offset negative impacts to population dynamics caused by changes in prey populations. I also compared dietary characterization by method to assess whether biases existed between camera and prey remains data. I then related my results to Roseneau (1972) who used prey remains collection to quantify diet of the same population 46 years previous as a

case study to assess the use of past diet studies to monitor changes in Gyrfalcon prey use. The number of total prey items and the number of squirrels was significantly greater from camera data than prey remains analysis. This result suggests that prey remains analysis under-represented the contribution of squirrel to the diet. The underrepresentation of squirrel to the diet as provided by prey remains analysis, and the differences between the contribution of squirrel in my study and Roseneau (1972), reveals the limitations of prey remains analysis for a complete characterization of diet, and also suggests the limitations of using Roseneau as a baseline study to assess dietary change in western Alaska. I further summarized 19 prior Gyrfalcon diet studies to evaluate their value as baselines by which to compare and confidently assess the impacts of climate change on Gyrfalcon diet. I conclude that historical studies of Gyrfalcon diet are of limited value for measuring the impacts of climate change due to biased methods, short duration, small samples sizes, and a lack of standardization of methods. My case study involving two diet studies on the same population illustrates the benefits of camera data to quantify diet and illustrates the clear need to develop recurring, standardized diet studies across the circumpolar Gyrfalcon range to assess dietary shifts as a measure of climate change impacts on Arctic communities.

PREFACE

This thesis is separated into three chapters, an introductory chapter and two chapters formatted to facilitate publication as individual manuscripts. Each chapter examines Gyrfalcon diet during the brood rearing period in the context of climate change, but there is some overlap in material from the introduction, study area, and field methods. The focus of Chapter One is to place the importance of Gyrfalcon diet into the context of climate change in Arctic systems. Chapter Two focuses on important factors associated with the changes in the composition of Gyrfalcon diet during the brood rearing period. Chapter Three examines the benefits of using direct methods to characterize Gyrfalcon diet, and the importance for developing baseline diet studies using these methods to measure the impacts of climate change to Arctic animal communities.

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CHAPTER ONE: INTRODUCTION TO CLIMATE CHANGE IN TUNDRA SYSTEMS

Anthropogenic induced climate change has been reported in all of Earth's biomes. The Arctic is a system that warrants increased study because it is among the most vulnerable to climate change, and because system-wide changes are occurring more rapidly and at a greater magnitude than what is currently being observed in other systems (Ims and Fuglei 2005, Post et al. 2009). This rapid change in the Arctic is due to a multiplicity of interactions that function on many levels (Screen and Simmonds 2010, Gilg et al. 2012, Screen et al. 2015). First, studies report changes in the frequency and intensity of weather events such as spring and winter precipitation, and predictions are that patterns of extreme weather will continue to intensify in the future (Rawlins et al. 2010, Bengtsson et al. 2011, Kusunoki et al. 2015). This perturbation in weather patterns is important, because it has already been shown to correlate with decreases in reproductive output in birds (Steenhof et al. 1997, Moss et al. 2001). In Arctic Canada, increases in both the frequency and intensity of spring rainfall has been correlated with a long term decline in nest success of Peregrine Falcons (*Falco peregrinus*; Anctil et al. 2014). In Greenland, an extreme precipitation event caused near complete nest abandonment and failure in an Ivory Gull (*Pagophila eburnea*) colony (Yannic et al. 2014). Both examples may represent the reality of increased selection pressures attributed to anthropogenic climate change.

Second, increases in density, height, and distribution of shrubs on the tundra landscape have already been seen in Arctic and sub-Arctic biomes, and are predicted to continue (Rupp et al. 2000, Zhang et al. 2013, Myers-Smith et al. 2015). A reconfiguration of plant assemblages may have large impacts on animal distributions and the dynamics of species interactions, where species associated with dense shrubs and taiga forest benefit from range expansion, but tundra obligate species face climate-induced habitat loss resulting in potential extirpation from particular areas (Lehikoinen et al. 2014, Tape et al. 2015, Wheeler et al. 2015). Due to the effects of vegetation structure on the distributions of both predator and prey species, changes in vegetation characteristics may have important consequences for interactions between key system members (Kauffman et al. 2007).

Third, climate change is affecting the phenology of system events that govern the yearly cycles of many species (Badeck et al. 2004, Gilg et al. 2012). Changes in phenology are predicted to continue and cause mismatch events between organisms, such as breeding birds and their invertebrate prey (Both and Visser 2005, Gilg et al. 2012, Grabowski et al. 2013). In northern latitudes, reduction in sea ice has resulted in increased humidity, which exacerbates temperature amplification and results in changes in the rate and timing of snowmelt (Hoye and Forchhammer 2008, Gilg et al. 2012, Grabowski et al. 2013). Snowmelt is a key event in Arctic phenology as it represents the start of the Arctic breeding season. Many Arctic bird species depend on the predictability in the timing of events such as snowmelt. For example, the arrival of migratory birds and the start of their breeding season correlates closely with the timing of snowmelt, as it signals the emergence of resources such as microorganisms and arthropods, dietary

components that are essential for obtaining the energy required for reproduction (Grabowski et al. 2013). Snowmelt also signals the emergence of microtines and other small mammals that are important prey for many predators. A disruption in the timing of snowmelt holds the potential to cause mismatch events at varying trophic levels in Arctic food webs (Tulp and Schekkerman 2008, Gilg et al. 2012).

Changes in weather patterns and severity, changes in system phenology such as snowmelt and ice-off, and changes to landcover all have compounding effects, enhancing the impacts of each with the potential to disrupt system dynamics, particularly life history strategies and species interactions (Hunter et al. 2010, Smith et al. 2010). Species interactions are important components of system ecology, where disruptions at any level can have major implications for system functioning (Berlow et al. 1999). Organisms at various trophic levels will likely shift phenology at different rates due to their life history strategies, where the timing of events depends on specific factors often unique to an individual species (Møller et al. 2010). These shifts can create a mismatch between species interactions, when the breeding period of a predator is no longer matched with the optimal abundance of prey needed for successful reproduction (Both and Visser 2005, Gilg et al. 2012, McKinnon et al. 2012). Mismatch and the resulting altered species interactions can have severe consequences at the ecosystem level such as a loss in biodiversity (Visser and Both 2005). Therefore, it is important to understand species interactions and the factors that influence selection pressures on the phenology of each species (Ims and Fuglei 2005, Visser and Both 2005). Understanding these selection pressures may enable a deeper understanding of how changes in phenology impact species interactions, and provide the tools necessary to predict the impacts of climate

change on system dynamics in the Arctic, and in turn enact conservation protocols when necessary and possible.

Predators play a dual role in system dynamics. They control and maintain healthy population dynamics of prey species and act as a mechanism to facilitate the evolution of life history traits (Doligez and Clobert 2003, Møller et al. 2010). Understanding predator-prey interactions enables an understanding of system balances and functioning, in turn allowing a proper perspective for assessing the impact of changes on the community. Knowing the diet of predators is important for these reasons, and because predators depend on healthy prey populations for their own health and population maintenance, they act as indicators of system balance or disruption (Barraquand et al. 2014).

The purpose of this research is to improve our understanding of system members particularly vulnerable to the impacts of predicted change on Arctic systems. Specifically, this research aims to enhance our understanding of dietary habits during the brood rearing period of the Gyrfalcon (*Falco rusticolus*), an apex avian predator of Arctic tundra. Through the use of advanced techniques this study provides a more complete assessment of diet and a description of fluctuation in prey use not only between seasons, but within-seasons. This level of description is a necessary step to predict how perturbations in prey populations may impact Gyrfalcon productivity in the future. Based on prior knowledge regarding the impacts of climate change on tundra systems, the potential disruption of species interactions and community dynamics, and the importance of predators as indicators of system change, we stand to gain great insight into the impacts of change on tundra communities through research on raptor-prey relationships.

One way to do so is through proper diet description over time as a basis for elucidating the impacts of global change on species interactions and community health in the Arctic.

The following chapters of this thesis detail the importance of understanding the dietary habits of the Gyrfalcon in the context of a changing world. In Chapter Two, “Gyrfalcon Dietary Plasticity During the Brood Rearing Period,” I describe Gyrfalcon dietary habits over the course of two breeding seasons on the Seward Peninsula in western Alaska. I found that prey use changed during the course of the breeding season, and that it differed between years of the study. I conclude that the Gyrfalcon exhibits dietary plasticity which may be important for future breeding success given the predicted impacts of climate change in tundra systems. In Chapter three, “Gyrfalcon Diet Description in the Context of a Changing World,” I compare the results of two methods used in my study, prey remains analysis and camera analysis. I also relate my results to research conducted on the same population 46 years ago. The comparison of methods used in my study, and relating the results of my study and the results of a prior study on the same population illustrates the importance of continued dietary description with standardized techniques that provide the most detailed view of prey use during the brood rearing period.

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CHAPTER TWO: GYRFALCON DIETARY PLASTICITY DURING THE BROOD
REARING PERIOD

Abstract

As climate change impacts increase so does our need to understand their effects on ecosystem dynamics. I studied Gyrfalcon (*Falco rusticolus*) diet during the brood rearing period to increase knowledge of dietary habits during nesting, and provide necessary information for understanding climate change impacts to Arctic ecosystems. I studied diet on the Seward Peninsula, Alaska, in 2014 and 2015 using motion-activated cameras in 20 nests. I observed two important dietary shifts: the proportion of ptarmigan in the diet declined significantly throughout the season, as did the proportion of large prey items. The decrease in the proportion of ptarmigan (*Lagopus lagopus* and *L. muta*) coincided with an increase in Arctic ground squirrel (*Urocyon parryii*) in the diet. Despite the shift in prey composition, dietary breadth did not change. A lack of change in diet breadth indicates that there was a within-season switch from ptarmigan to squirrel as the main prey item. The results of my study suggest that the Gyrfalcon is a facultative specialist, due to a mid-season switch in predominant prey type. This is an important result for predicting effects of climate change on species interactions in the Arctic, as facultative shifts between prey types may help offset negative impacts to predator populations caused by changes in prey availability.

Introduction

The Arctic is among the most vulnerable of biomes to the impacts of climate change as evidenced by shifts and disruptions in system processes that are occurring at a higher rate and magnitude than what is currently being observed in other ecosystems (Ims and Fuglei 2005, Post et al. 2009). Rapid change in the Arctic is due to a multiplicity of interactions that function on many levels (Screen and Simmonds 2010, Gilg et al. 2012, Screen et al. 2015). Factors involved in interactions that influence rapid change include increases in precipitation events, increases in shrub height and distribution, reduction in the distribution of sea ice, reduction in the depth and distribution of the permafrost zone, and shifts in the phenology of important events such as snowmelt and ice-off (Rupp et al. 2000, Høye and Forchhammer 2008, Post et al. 2009, Zhang et al. 2013). Changes in ecological systems have compounding effects, enhancing the impacts of each with the potential to disrupt life history strategies and species interactions (Hunter et al. 2010, Smith et al. 2010). Species interactions are important ecological components, where disruptions at any level can have major implications for ecosystem functioning (Berlow et al. 1999). Organisms at different trophic levels will likely shift phenology at different rates due to their life history strategies, where the timing of life events depends on specific variables often unique to an individual species (Møller et al. 2010).

Organisms that have narrow survival strategies are more susceptible to disruptions in their ecosystem such as those predicted by anthropogenic climate change (Hayhow et al. 2015, Kellermann and van Riper 2015). Dietary specialists are especially susceptible due to potential changes in habits, distributions, and population structure of their preferred food items, along with their inability to shift to other food sources (Ims and

Fuglei 2005, Schmidt et al. 2012). Considering this sensitivity and the predicted impacts of climate change on ecological dynamics in the Arctic, dietary specialists inhabiting tundra biomes may face increasing pressures on their vitality and breeding success.

Because of their dietary habits, predators such as raptors act as indicators of the health of their ecological system (Sergio et al. 2008, Barraquand et al. 2014, Ehrich et al. 2015). The stability of raptor populations, health of individuals, and reproductive output of pairs may indicate how an ecosystem is handling system disruption (Steenhof et al. 1997). It is important to study dietary habits of predators to understand their role as ecological system indicators, and pinpoint the cause of ecological disruptions apparent in raptor populations or individual health. Predator diets follow a continuum from generalism to specialization (Glasser 1982, Hanski et al. 1991, Malo et al. 2004). Generalist predators differ from specialists in their ability to shift to alternative prey types when primary prey are less abundant. Due to the predicted rate of change in Arctic communities, it is necessary to know the position of Arctic predators on the spectrum from specialist to generalist to fully understand their role as an indicator of the ecological consequences of climate change (Nystrom et al. 2006, Dawson et al. 2011, Pokrovsky et al. 2014).

Previous diet studies characterize the Gyrfalcon (*Falco rusticolus*) as a dietary specialist (Potapov and Sale 2005, Watson et al. 2011). In most of its range, the Gyrfalcon relies on ptarmigan (*Lagopus spp.*) as its primary prey and supplements its diet with alternative prey during fluctuations in ptarmigan populations (Potapov and Sale 2005, Watson et al. 2011). Any disruption in the cycle or abundance of ptarmigan has the potential to affect Gyrfalcon populations that depend on them to breed (Nielsen and Cade

1990, Nielsen 1999, 2003, Potapov and Sale 2005). However, Gyrfalcons have been observed to shift their diet during the breeding season in response to changes in prey availability (Nielsen and Cade 1990, Nielsen 2003). The tendency for mid-season dietary shifts challenges the notion of Gyrfalcons as specialist predators. Moreover, dietary plasticity in Gyrfalcons may have important population level consequences in the context of a changing tundra system.

I examined the mechanisms for shifts in prey use during the breeding season and their potential implications in the context of climate change to further understand Gyrfalcon dependence on ptarmigan, their characterization as a dietary specialist, and the presence of dietary plasticity. Diet during nesting on the Seward Peninsula may follow within-season shifts away from a diet consisting of mostly ptarmigan as a result of two mechanisms: system phenology and nestling development. Shifts away from ptarmigan use may be the result of system phenology such as seasonal changes in prey abundance or availability. Diet may shift away from ptarmigan in the late season when migratory birds are more abundant and available, and ptarmigan are less available due to the cessation of territory defense and displays in males, and cryptic behaviors associated with nesting and brood rearing (Nielsen and Cade 1990, Nielsen 2003). Shifts may also be a result of nestling development and changes in the energetic needs of young. As nestlings grow their energetic needs increase with their size and with feather development. The ability for adults to provide enough food may become more difficult, and may cause a shift from optimal items, such as ptarmigan, to prey types that are encountered more frequently but are perhaps less optimal due to smaller size. Prey use may also shift away from ptarmigan as the most used prey type, but prey size may remain the same due to dietary needs

related to an optimal biomass. Dietary shifts may also correlate with an increase in diet breadth because migratory birds increase in their abundance and availability across the season due to rapid reproductive rates at these high latitudes, providing abundant and vulnerable juveniles, thus rendering more available prey across the landscape. Increased energetic needs of nestlings may be met by supplementing ptarmigan with an increase in contribution of migratory birds to the overall diet and increasing diet breadth. I characterized prey use by changes in the proportion of ptarmigan, proportion of prey size classes, and diet breadth over two temporal scales, age of nestlings and Julian date. I chose to assess prey use over two temporal scales to test two hypotheses: that changes in prey use are influenced by changes in the dietary needs of growing Gyrfalcon nestlings, and that changes in prey use are influenced by ecosystem phenology. The Gyrfalcon may possess dietary plasticity relative to prey abundance, complicating their classification as a specialist but providing insight into their ability to augment fluctuations in ptarmigan populations with alternative prey, an important aspect for surviving the impacts of global change.

Methods

Study Area

The study area covered 14,150 km² of the Seward Peninsula, described by Bente (2011). Topography consisted of rolling hills interspersed with mountainous terrain, numerous rock outcroppings, and cliff-lined river systems. The vegetation was predominantly Arctic tundra dominated by low-lying vegetation in coastal and highland areas, and dense willow (*Salix* spp.) and alder (*Alnus* spp.) thickets along riparian

corridors. The study area provided abundant nesting habitat for Gyrfalcons, with an annual mean of 35 (range 31 to 39) occupied breeding territories (Bente 2011).

Nest Treatment

In 2014 and 2015, occupancy surveys for nesting Gyrfalcons were conducted to determine nest sites appropriate for camera installation. Surveys consisted of ground-based surveys and aerial surveys. Ground-based surveys, the primary method employed in 2014, consisted of hiking to historic nest locations located within 5 km of the road system. Aerial surveys were conducted from a Robinson R-44 Helicopter. Observations during aerial surveys were made primarily by a front seat observer with contributions from a secondary observer in the back seat of the aircraft. On occasion the pilot also contributed to observations. Flights consisted of frontal approaches on the observer's side when possible at a distance varying from 50-200 m depending on sensitivity of detected birds, characteristics of the nest cliff, and wind intensity. When occupancy was determined by either foot or aerial survey, we recorded information regarding number of eggs, and number and age of offspring. I then used information regarding nest phenology to prioritize the installation for nest cameras: nests with eggs received highest priority to ensure cameras were installed before hatch.

After I determined Gyrfalcon occupancy from aerial and ground-based surveys, I installed Reconyx PC800 motion-activated cameras (hereafter referred to as "nest camera") at 23 (10 in 2014, 13 in 2015) occupied Gyrfalcon nests to record prey deliveries during the brood-rearing period. Of these nests, 5 received camera treatment in both 2014 and 2015. All other nests in 2015 that received camera treatment were new sites not surveyed in 2014. I installed nest cameras prior to hatch when possible (N=15

ests) 1–2 m laterally from the nest and 1 m above the nest using a wall mount bracket attached to the cliff face. I drilled two holes into the cliff using a hammer drill, and attached the wall mount with concrete screws. I attached the nest camera to the wall mount with a swivel bracket, allowing the camera to be adjusted to the appropriate angle to capture prey deliveries. I programmed nest camera motion activation at high sensitivity to take three rapid photographs (1 frame/sec) followed by a 15 sec sleep period, and one motion independent time-lapse photograph recurring every 30 min. All nest camera photographs were automatically time-stamped with Alaska Daylight Time (AKDT), and calendar date. I removed nest cameras at the end of the brood-rearing period after all nestlings had fledged and prey deliveries to the nest had ceased (approximately 55 days post hatch).

Data Analysis

I catalogued prey items from nest camera images and identified items to lowest taxonomic level possible. I counted whole or headless prey as one item and noted individual parts delivered during a 24-hour period to avoid double counting, because they likely comprised one individual prey item. I also noted the condition of any prey removed by adults to minimize double counting because Gyrfalcons are known to cache prey (Booms and Fuller 2003). I assigned average mass values for species (Kays and Wilson 2009 for mammals, Sibley 2014 for birds) to identified items for biomass calculations. I assigned biomass for young or partially grown prey items by visually estimating their size as a proportion of adult size, and applying the proportion to the average biomass value of the species. Due to the regional variation in Arctic ground squirrel (*Urocitellus parryii*) mass, I calculated an average mass from the literature (Sheriff et al. 2013). I

visually estimated mass values for unknown items by comparing them to a known item's size (e.g., an item approximately the size of a Lapland Longspur (*Calcarius lapponicus*) received a mass assignment of 27 g) following Booms and Fuller (2003).

I used EstimateS, version 9.1.0 (Colwell 2013), to produce a rarefaction curve to assess the completeness of diet sampling, adopting the 100 sample-order randomization. Rarefaction curves represent the cumulative means of re-sampling the pooled individuals to produce the statistical expectation of adding additional individuals (Gotelli and Colwell 2001). Thus, the point at which the curve begins to level illustrates the number of samples (individual prey items for this study) required to capture all species that comprise the Gyrfalcon diet in my study area.

To evaluate the important drivers of prey type for influencing changes in prey use I organized prey items in two ways: biomass categories and ecologically meaningful prey categories. Prey items were organized into three biomass categories based on the biomass range catalogued in the diet: small (0 to 200 g), medium (201 to 400 g), and large (>400 g). Prey items were organized into seven ecologically meaningful prey categories following Robinson et al. (2015): ptarmigan, shorebird, passerine, jaeger, squirrel, microtine, and other (raptor, waterfowl, and seabird). Items that could not be identified to these groups were placed in one of two categories: unknown bird or unknown.

To investigate the two hypotheses of temporal factors associated with dietary shifts, system phenology as a determinant of prey use and nestling age as a determinant of prey use, I organized proportion of total biomass of each category by Julian date as a measure of seasonal factors, and nestling age as a measure of nestling development into 5-day periods (hereafter referred to as "week" and "age", respectively). For both "week"

and “age,” I plotted percent contribution by prey type and contribution of biomass category in a vertical bar chart to illustrate the change in prey use across time. Diet breadth was calculated using the standardized version of Levin’s Index of Diet Breadth (Hurlbert 1978):

$$B_i = \frac{1}{n-1} \left[\frac{1}{\sum_j p_{ij}^2} - 1 \right]$$

I calculated diet breadth for each nest using the seven ecologically relevant prey categories by “week” and “age” to illustrate the change in prey use across these two temporal scales.

Statistical Analysis

I created generalized linear mixed models (GLMMs) using the package “lme4” in the statistical platform R 3.2.3 (Bates et al. 2014, R Core Team 2015) with a binomial distribution and log link to test the hypotheses that date and nestling age influenced the use of particular prey categories. All models included nest as a random intercept to account for the repeated sampling of each nest, and year as a fixed effect to control for differences between years. I included “week” and “age” as predictors of prey size and the number of ptarmigan in the diet. I created linear mixed models (LMMs) using the package “lme4” with log link and nest as a random variable and year as a covariate to test the hypothesis that date and nestling age influence diet breadth. I used an information theoretic approach to evaluate models and to test parameter support against the intercept-only model (Burnham et al. 2011). I ranked and compared models using Akaike’s Information Criterion (AIC, Akaike 1974) and considered there to be evidence for a single best model if there were no other models within $\Delta AIC < 2$ of the AIC-best model (Burnham and Anderson 2002). I reported 85% confidence intervals for parameter

estimates (Arnold 2010) and considered a variable to be influential when it was included in a competitive model and the confidence interval did not overlap zero. I note that inference from this study would be no different had I used the more traditional 95% confidence intervals. I carried out all analyses in the statistical platform R 3.2.3 (R Core Team 2015).

Results

Overall Diet Composition

I recorded 2,008 prey items constituting 40 species and 15 families in two breeding seasons (Table 2.1). Cameras did not capture prey deliveries in three of 23 nest, resulting in a sample size of 20 nests. Total biomass estimated was 808.4 kg for an average 40.4 Kg in biomass per nest. After 1000 prey delivery detections, only three species were added for an additional 200 prey delivery detections. Between 1600 and 1800 prey delivery detections, only one additional species was added to the total species detected in the diet. Thus, sampling effort was adequate for a full characterization of species that comprise the Gyrfalcon diet during brood rearing (Fig. 2.1).

By overall biomass, ptarmigan was the most used prey type (52%), followed by squirrel (36%), and shorebird (5%, Table 2.1). Diet composition differed between years. In 2014, ptarmigan was the most common prey type (76%), followed by squirrel (15%), and jaeger (6%). In 2015, the most used prey type switched to squirrel (51%), followed by ptarmigan (36%), shorebird (6%), jaeger (2%), and passerine (2%) (Fig. 2.2).

Change in Prey Use Across Brood Rearing

Of the three models for comparing temporal effects on the proportion of ptarmigan in the diet, the top model contained the predictor “week,” the covariate year,

and the random intercept nest (Table 2.2). All other models were $\Delta AIC > 2$ (Age $\Delta AIC=6.66$; Table 2.2) from the top model, thus were considered uninformative. “Week” had an influence on the proportion of ptarmigan in the diet, where the proportion of ptarmigan decreased by “week” ($\beta=-0.14$, CI= -0.17, -0.11) (Fig. 2.3). The percent contribution of ptarmigan to the diet decreased by “week” over both seasons, corresponding with an increase in the contribution of squirrel (Fig. 2.4). In 2014, the shift in percent contribution was less substantial, but in 2015 the shift in percent contribution of ptarmigan reflected that squirrel was the dominant prey item throughout the season (Figs. 2.2, 2.4).

The top model predicting temporal effects on the proportion of size class “large” in the diet contained the predictor “week” and the random intercept nest (Table 2.3). All other models were $\Delta AIC > 2$ (Age $\Delta AIC=5.35$; Table 2.3) from the top model, thus were considered uninformative. “Week” also had an influence on the proportion of the size class “large”, where the proportion of large prey decreased by week ($\beta=-0.06$, CI= -0.09, -0.03 (Fig. 2.5). The percent contribution of size class “large” to the diet decreased slightly by week, but throughout the season size class large remained as the dominant size class (Fig. 2.6).

The top model predicting the effect of “week” on diet breadth was the null model, which contained only the covariate year and the random intercept nest (Table 2.4). The top model predicting the effect of “age” on diet breadth was the null model, which contained only the covariate year and the random intercept nest (Table 2.4). However, in both instances the model including “week” or “age”, respectively, received weak support, suggesting diet breadth may have been influenced slightly by time.

Discussion

Gyr Falcon diet changed during the brood rearing period and between years, supporting the presence of dietary plasticity. The proportion of ptarmigan in the diet decreased as the season progressed, whereas diet breadth did not, indicating that prey use switched from one optimal prey item to another rather than to a more generalized diet. In both years, ptarmigan was the most used prey type in the early season. As the season progressed, dietary contribution of squirrel increased to the point that it became the most used prey type, an effect that was more substantial in 2015.

The most used prey type in the diet switched between years from ptarmigan in 2014 to squirrel in 2015. This switch was likely not the result of differences in prey use between nests that received camera treatments in each year, because the effect of nest was included as a random intercept in all models and received no support. The between-years switch of prey types and the within-season switch from ptarmigan to squirrel illustrate a facultative shift maintaining a specialist diet likely focused on abundance of prey with optimal attributes rather than one optimal prey species. A facultative specialist may change a key food item when other profitable prey are available (Glasser 1982). Whether or not a particular food type is included in the optimal diet depends on its own abundance, as well as on the abundances of more preferred food types. As changes in the abundance of food types occur, the optimal diet could switch from specialization on one food type to specialization on another with or without increases in diet breadth (Pyke 1984). Changes in prey use seen in this study support this further, and revise our understanding of Gyr Falcon dietary behaviors in Alaska.

The proportion of the prey size class “large” also decreased as the season progressed. Although ptarmigan frequency decreased and diet breadth remained unchanged, squirrel frequency later in the season coincided with an increase in the contribution of both medium and small sized items. Due to the difference in biomass between ptarmigan (485 g) and squirrel (713 g), the number of items in the prey size class “large” decreased, however biomass contribution of prey size class “large” remained unchanged. The increased number of smaller prey types (e.g. items in size class “medium” and “small”) in the diet in conjunction with a decreased number of large prey items but not biomass contribution, balanced out the change to prey type, thus the contribution of additional prey types to the diet did not appreciably affect diet breadth.

This study describes a switch in diet within the nesting season that has been described in previous Gyrfalcon studies that investigate within-season prey use (Poole and Boag 1988, Nielsen and Cade 1990, Booms and Fuller 2003), but has not been described in Alaskan populations (Cade 1960, Roseneau 1972). The shift from ptarmigan to squirrel seen in this study may be a result of behavioral changes in ptarmigan throughout their reproductive cycle as well as the result of predation pressures in the early season, or it may be an increase in the abundance and availability of squirrel, or both (Nielsen and Cade 1990, Nielsen 1999). Squirrels may be both abundant and in close proximity to some or most nest sites at this time of the season and in some years in western Alaska. This dietary plasticity suggests that the Gyrfalcon will take prey other than ptarmigan or even birds. During the brood rearing period, the Gyrfalcon may be able to supplement ptarmigan with prey of similar characteristics such as biomass and behaviors so long as they are available. In other times of the year, such as the early

breeding season when Gyrfalcon require prey for egg-laying, ptarmigan is the only prey type available for birds on inland territories. Although Gyrfalcon may possess the ability to supplement ptarmigan with other prey during the brood rearing period, it is important to consider their full annual cycle to understand the connection between climate change impacts to dietary behaviors and breeding success.

Populations of specialist predators fluctuate with populations of preferred prey species, whereas generalist predators are able to switch from one prey to another with fluctuations in preferred prey populations (Korpimaki 1985, Korpimaki and Norrdahl 1989, Redpath and Thirgood 1999, Redpath et al. 2001). On the Seward Peninsula, Gyrfalcon breeding numbers showed little fluctuation over the course of a six-year study (Bente 2011), and were very similar to those provided by a previous study on the same population (Roseneau 1972). A lack of an appreciable population shift in this case either suggests a lack of population fluctuation in ptarmigan, or the Gyrfalcon's ability to supplement the diet with alternate prey when ptarmigan were less available (Korpimaki et al. 1990, Kurki et al. 1997). The dietary shift between years in this study suggests the latter, as the contribution of ptarmigan to overall diet in 2015 dropped substantially and was replaced by the use of Arctic ground squirrel. In places such as Greenland, Iceland, and Sweden, the number of occupied Gyrfalcon sites fluctuate by year in what appears to be a cyclic pattern (Nielsen 1999, Nyström et al. 2005, Burnham and Burnham 2011). In other parts of the Gyrfalcon range, such as Alaska, the number of occupied territories have relatively little fluctuation between years with no obvious regular or cyclic pattern (Mindell et al. 1987, Mindell and White 1988, Bente 2011). The confounding results in regularity of population fluctuations could be a result of the use of Arctic ground squirrel

as alternate prey during periods when ptarmigan availability declines, a relationship that is suggested for small mammalian predators (Reid et al. 1997). Another possibility for the irregularity in population fluctuations may be the presence of two species of ptarmigan on the Seward Peninsula. Rock and Willow Ptarmigan may follow different population cycles, allowing the Gyrfalcon to utilize the most abundant species at a given time, maintaining a steady ptarmigan use that is unaffected by population fluctuations of one ptarmigan species. Still, as an alternate prey item, Arctic ground squirrel has been suggested to be critical for maintaining a relatively diverse predator community in the Arctic (Reid et al. 1997, Barker and Derocher 2010), a role that seems to be supported from the results of this study.

The within-season and between-season variations in prey use seen in this study suggest that squirrels are more important to the Gyrfalcon diet during breeding in Alaska than has been previously shown, which is important considering the predicted impacts of climate change on species interactions in the Arctic. Climate change impacts such as changes in the height, density, and distribution of shrub cover in the Arctic is predicted to impact ptarmigan populations (Watson et al. 2011). Ptarmigan may occupy the same range, but become functionally less available for the Gyrfalcon due to changes in landscape cover where increases in shrub cover increase refugia, or they may experience range shifts or reductions. Climate change is also predicted to impact the distribution of Arctic ground squirrel, where increases in shrub cover would negatively impact their distribution, but increases in forbes would positively impact their distribution (Wheeler et al. 2015). A full understanding of the role of both ptarmigan and squirrel in the Gyrfalcon diet enables a better understanding of potential climate change impacts to Gyrfalcon

populations and species interactions in the Arctic system. Because Arctic ground squirrel shows strong associations to habitats that are likely to undergo climate induced changes (Barker and Derocher 2010), predictive models investigating future Gyrfalcon distribution should not only consider the area of predicted ptarmigan habitat as an important indicator, but area of Arctic ground squirrel habitat as well.

Prey use patterns described in this study support the need for further research of Gyrfalcon dietary habits during brood rearing. The between and within-season changes in prey use support the need to quantify diet over many years to assess whether such sharp fluctuations in prey use are typical and correlate with cyclical patterns common among prey populations in the Arctic. Studies should focus on determining the cause of mid-season shifts in prey use, such as changes in ptarmigan abundance or availability, or the increase in the abundance or availability of squirrels. Further focus on prey use patterns may elucidate the importance or preference between ptarmigan and squirrel in western Alaska. The preference for either is an important consideration, as climate change may impact each prey type differently. Studies should also focus on determining whether the ability of the Gyrfalcon to switch from ptarmigan to squirrel between seasons and within-seasons indicates a dietary plasticity that will help augment the predicted impacts of climate change on both ptarmigan and ground squirrel populations. Finally, it is necessary for studies to assess prey abundance on the landscape and the connection to prey use during brood rearing. Connecting abundance and availability to use will enlighten us regarding prey use trends and preference, and how other prey items may replace ptarmigan or ground squirrel. This will provide insight into how changes in prey

populations will impact Gyrfalcon prey use, breeding success, and population stability in a changing world.

Tables

Table 2.1. Summary of prey items catalogued from motion-activated cameras installed in 20 Gyrfalcon nests during the brood rearing period in 2014 and 2015 on the Seward Peninsula, Alaska. Information regarding species identified as well as items identified to lowest taxonomic level possible are given by # of items, total biomass estimated, and percent of total biomass estimated.

Species	2014			2015			All Years		
	#	Total biomass (grams)	% biomass	#	Total biomass (grams)	% biomass	#	Total biomass (grams)	% biomass
Birds									
Ptarmigan	520	250975	75.64	367	170115	35.67	887	421090	52.07
<i>Numenius spp.</i>	26	9680	2.92	29	12760	2.68	55	22440	2.77
Long-tailed jaeger	3	629	0.19	38	11400	2.39	41	12029	1.49
Unknown bird	49	6967.5	2.10	48	4208	0.88	97	11175.5	1.38
Wilson's Snipe	13	1271	0.38	79	8295	1.74	92	9566	1.18
American Robin	6	462	0.14	117	9009	1.89	123	9471	1.17
Bar-tailed Godwit	12	4080	1.23	2	680	0.14	14	4760	0.59
Whimbrel				8	2660	0.56	8	2660	0.33
<i>Pluvialis spp.</i>	15	1737	0.52	14	1750	0.37	29	3487	0.43
Lapland Longspur	35	945	0.28	28	756	0.16	63	1701	0.21
Pectoral Sandpiper	16	1168	0.35	2	147	0.03	18	1315	0.16
Red-breasted Merganser				2	1260	0.26	2	1260	0.16
Plover spp.				6	825	0.17	6	825	0.10
Northern Pintail	1	800	0.24				1	800	0.10
Cackling Goose				1	625	0.13	1	625	0.08
Surfbird				3	570	0.12	3	570	0.07

<i>Calidris spp.</i>	6	426	0.13	2	103	0.02	8	529	0.07
Bristle-thighed Curlew				1	490	0.10	1	490	0.06
Grey-cheeked Thrush	2	64	0.02	12	384	0.08	14	448	0.06
Northern Harrier				1	420	0.09	1	420	0.05
Short-eared Owl				1	350	0.07	1	350	0.04
<i>Stercorarius spp.</i>	1	300	0.09				1	300	0.04
American Golden-Plover	1	145	0.04	1	145	0.03	2	290	0.04
Crested Auklet				1	285	0.06	1	285	0.04
Red Knot	1	135	0.04	1	135	0.03	2	270	0.03
Pacific Golden-Plover				2	260	0.05	2	260	0.03
Wandering Tattler	1	110	0.03	1	110	0.02	2	220	0.03
Unknown Shorebird	1	73	0.02	1	105	0.02	2	178	0.02
Rock Sandpiper				2	140	0.03	2	140	0.02
Long-billed Dowitcher	1	115	0.03				1	115	0.01
Passerine spp.	1	27	0.01	4	157	0.03	5	184	0.02
Golden-crowned Sparrow	1	29	0.01	2	58	0.01	3	87	0.01
Snow Bunting	2	84	0.03			0.00	2	84	0.01
Spotted Sandpiper	2	80	0.02				2	80	0.01
Varied Thrush				1	78	0.02	1	78	0.01
Fox Sparrow				2	64	0.01	2	64	0.01
American Pipit	2	42	0.01	1	21	0.00	3	63	0.01
White-crowned Sparrow	2	58	0.02				2	58	0.01
<i>Zonotrichia spp.</i>	2	58	0.02				2	58	0.01
Western Sandpiper	2	52	0.02				2	52	0.01
Semipalmated Sandpiper	2	29	0.01				2	29	0.00
American Tree Sparrow				1	20	0.00	1	20	0.00
Savannah Sparrow	1	20	0.01				1	20	0.00

Common Redpoll	1	13	0.00					1	13	0.00
Redpoll spp.	1	13	0.00					1	13	0.00
Total Birds	729	280587.5	84.56	781	228385	47.89		1510	508972.5	62.93
Mammals										
Arctic ground squirrel	69	49197	14.83	343	243488	51.05		412	292685	36.19
Brown Lemming				10	875	0.18		10	875	0.11
Vole spp.				13	682.5	0.14		13	682.5	0.08
Greenland Collared				13	650	0.14		13	650	0.08
Lemming										
Tundra Vole				11	577.5	0.12		11	577.5	0.07
Lemming spp.	1	80	0.02	2	175	0.04		3	255	0.03
Red-backed Vole				3	94.5	0.02		3	94.5	0.01
<i>Microtus spp.</i>				1	52.5	0.01		1	52.5	0.01
Unknown	17	1947	0.59	15	1943.5	0.41		32	3890.5	0.48
Total Mammals	87	51224	15.44	411	248538.5	52.11		498	299762.5	37.07
Total kills	816	331811.5		1192	476923.5			2008	808735	

Table 2.2. AIC output for three competing models that explain the effect of system phenology (“week” and “age” of nestlings) on the proportion of ptarmigan in the Gyrfalcon diet during the 2014 and 2015 breeding seasons in western Alaska. “Week” showed the strongest support for influencing proportion of ptarmigan (AICWt=.97).

	K	AIC	Δ_AIC	AICWt	Cum.Wt
week	4	2318.95	0.00	0.97	0.97
age	4	2325.60	6.66	0.03	1.00
intercept-only	3	2353.55	34.60	0.00	1.00

Table 2.3. AIC output for three competing models that explain the effect of system phenology (“week” and “age” of nestlings) on proportion of size class large in the Gyrfalcon diet during the 2014 and 2015 breeding seasons in western Alaska. “Week” showed the strongest support for influencing the proportion of size class large in the diet (AICWt=.89)

	K	AIC	Δ_{AIC}	AICWt	Cum.Wt
week	4	2475.05	0.00	0.89	0.89
age	4	2480.41	5.35	0.06	0.96
intercept-only	3	2481.07	6.01	0.04	1.00

Table 2.4. AIC output for 2 competing models showing the effect of system phenology (“week”) on diet breadth during the brood rearing period during the 2014 and 2015 breeding seasons in western Alaska. The intercept-only model outcompeted the model containing the parameter “week”, indicating that the addition of the parameter “week” in the model does not influence diet breadth changes.

	K	AIC	Δ_AIC	AICWt	Cum.Wt
intercept-only	4	31.77	0.00	0.71	0.71
week	5	33.57	1.79	0.29	1.00

Table 2.5. AIC output for 2 competing models showing the effect of nestling “age” on diet breadth during the brood rearing period during two breeding seasons in western Alaska. The intercept-only model outcompeted the model containing the parameter “age”, indicating that the addition of the parameter “age” in the model does not influence diet breadth changes.

	K	AIC	Δ_AIC	AICWt	Cum.Wt
intercept-only	4	-371.64	0.0	0.66	0.66
week	5	-370.35	1.3	0.34	1.00

Figures

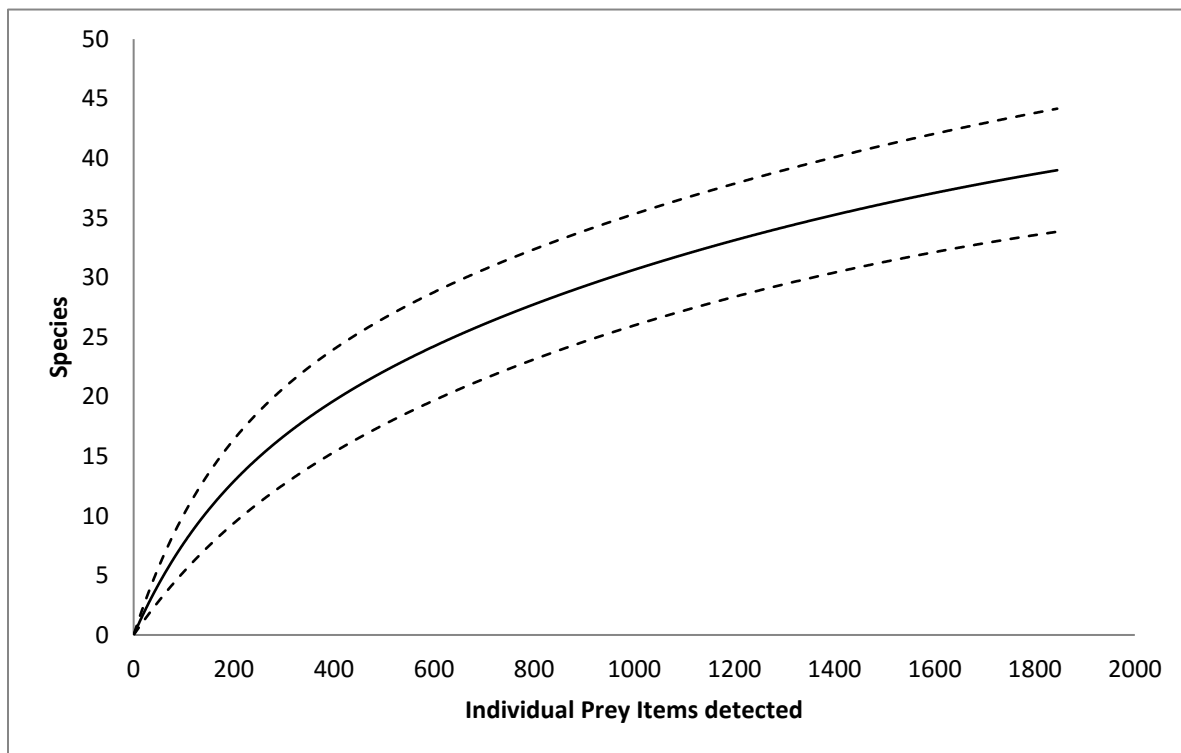


Figure 2.1. Rarefaction curve illustrating the effect of each additional prey item to the overall total of species that comprised the diet. After 1600 detections, only 1 additional species was detected in the overall diet, illustrating that sampling effort was adequate in this study for fully describing Gyrfalcon diet on the Seward Peninsula, Alaska.

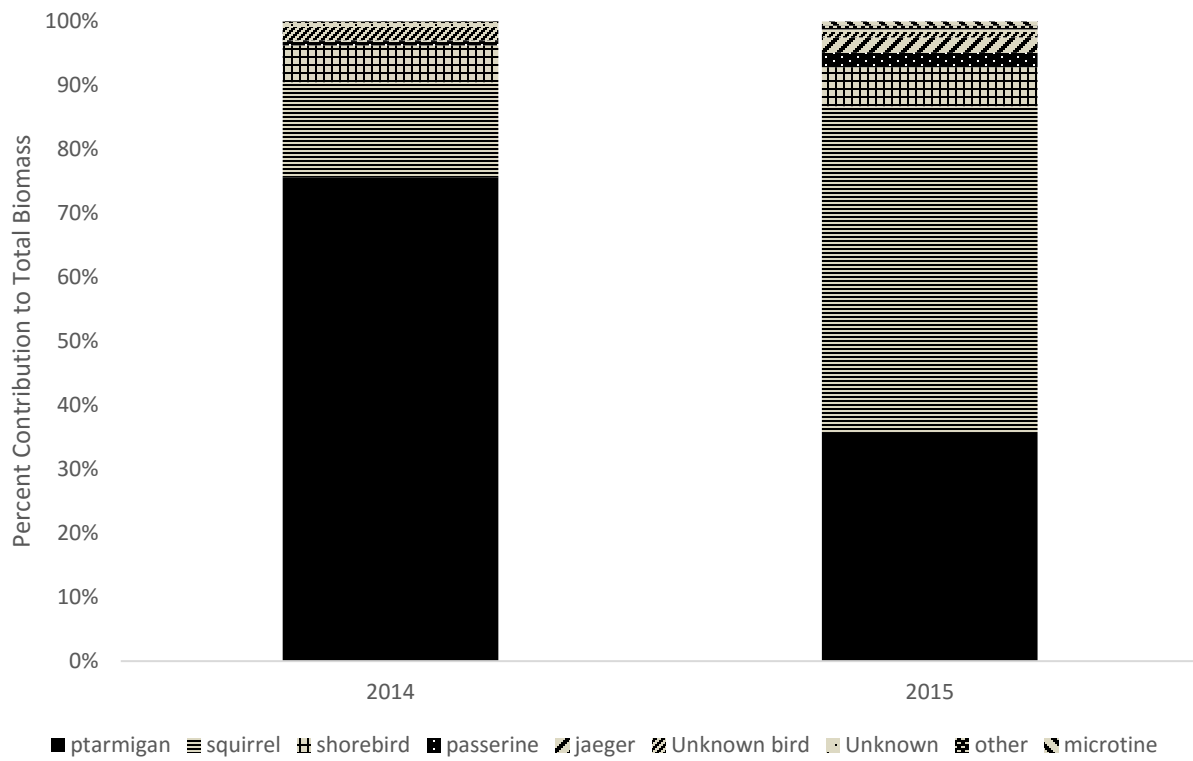


Figure 2.2. Percent Biomass contribution of prey items to Gyrfalcon diet during brood rearing on the Seward Peninsula in 2014 (n=10 nests) and 2015 (n=10 nests). In 2014, ptarmigan constituted the majority of the diet with squirrel and shorebird as other main contributors to total biomass. In 2015, squirrel constituted the majority of the diet, with ptarmigan, shorebird, jaeger, and passerine as other main contributors to total biomass.

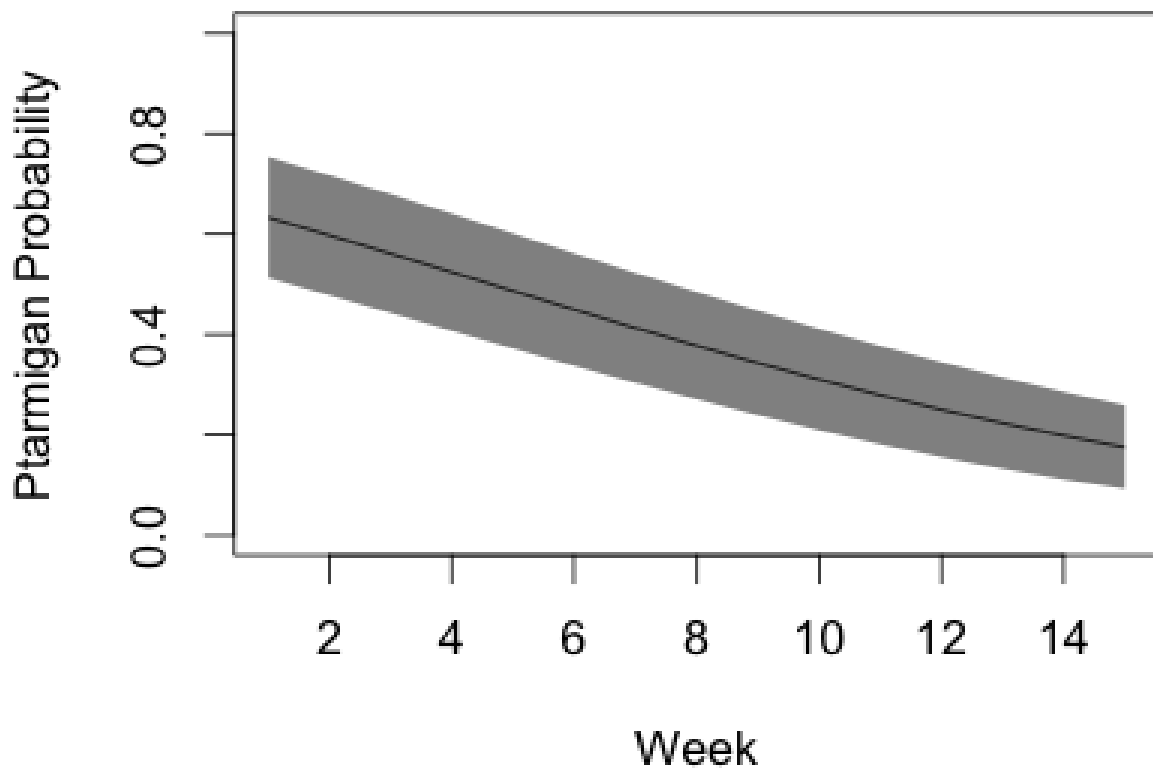
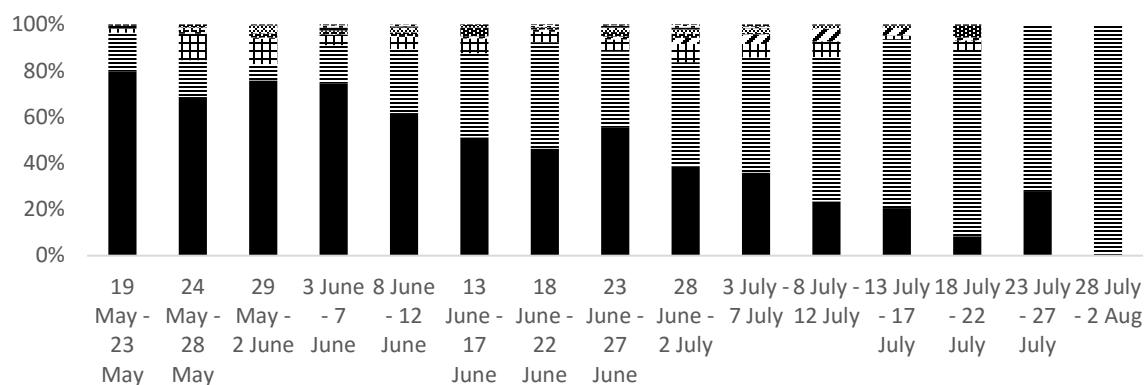
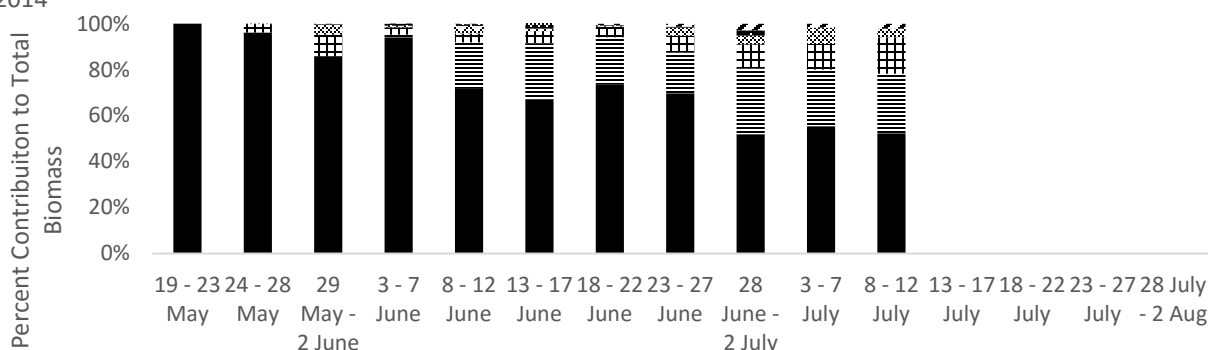


Figure 2.3. Probability that a prey delivery to Gyrfalcon nestlings is ptarmigan as a function of “week” during two breeding seasons in western Alaska. Grey shading indicates the 85% confidence interval. As “week” increases, probability of ptarmigan as a prey item decreases.

Both Years



2014



2015

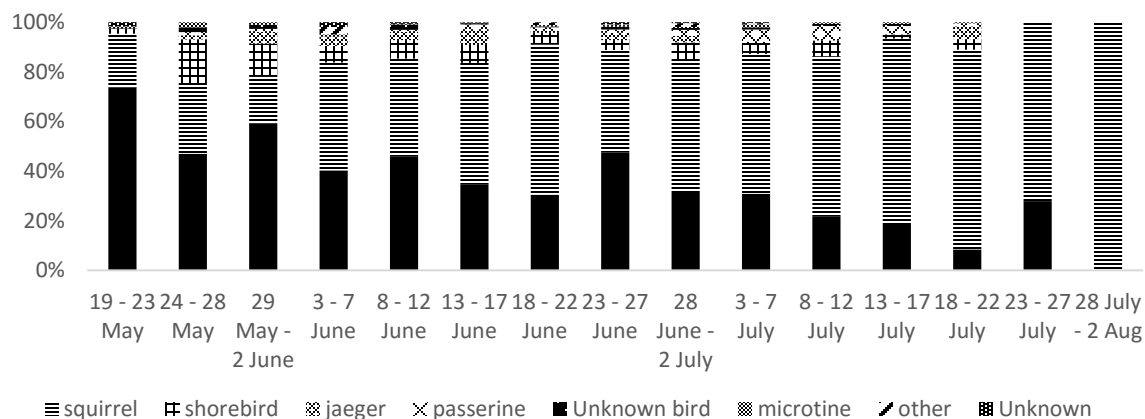


Figure 2.4. Change in percent contribution of prey items by “week” (5-day period) over the course of two breeding seasons: both years (top), 2014 (middle), and 2015 (bottom) as told by prey items catalogued by nest cameras in 20 nests (10 in 2014, 10 in 2015). Percent contribution of ptarmigan decreased by “week” in both 2014 and 2015.

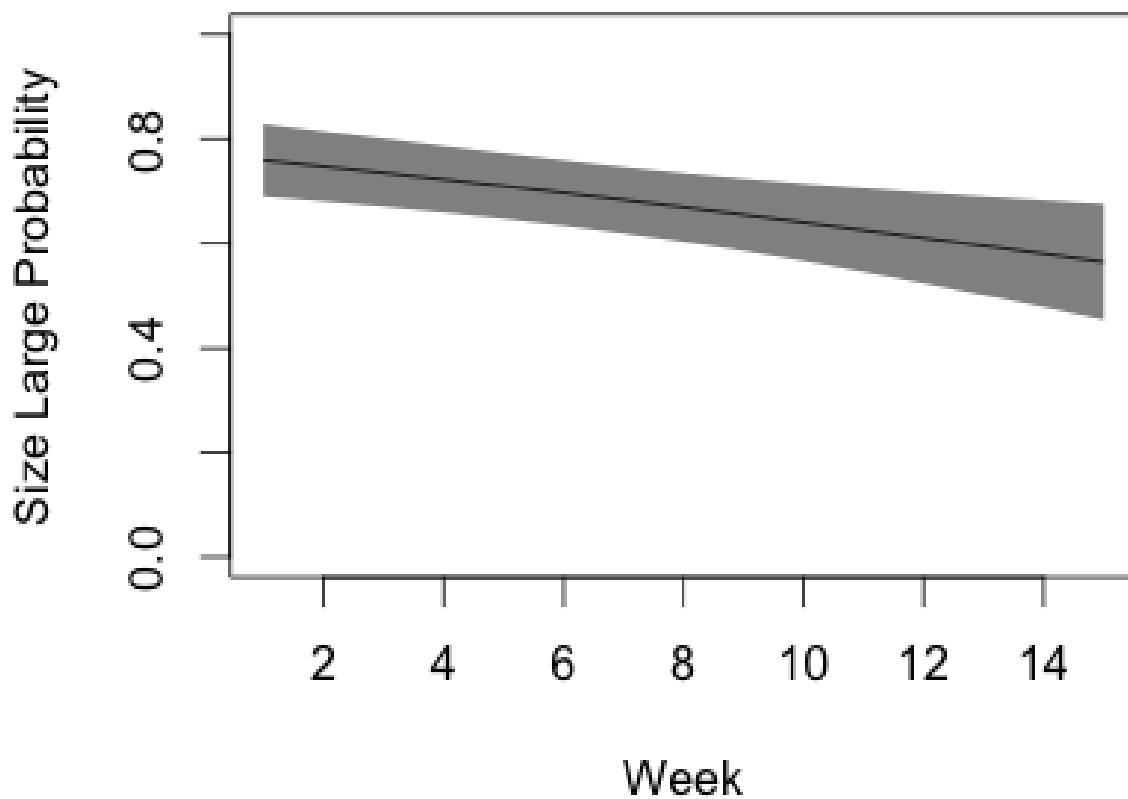


Figure 2.5. Probability that a prey delivery to Gyrfalcon nestlings is “large” as a function of “week” during two breeding seasons in western Alaska. Grey shading indicates the 85% confidence interval. Probability of the prey item being size class large decreases as “week” increases.

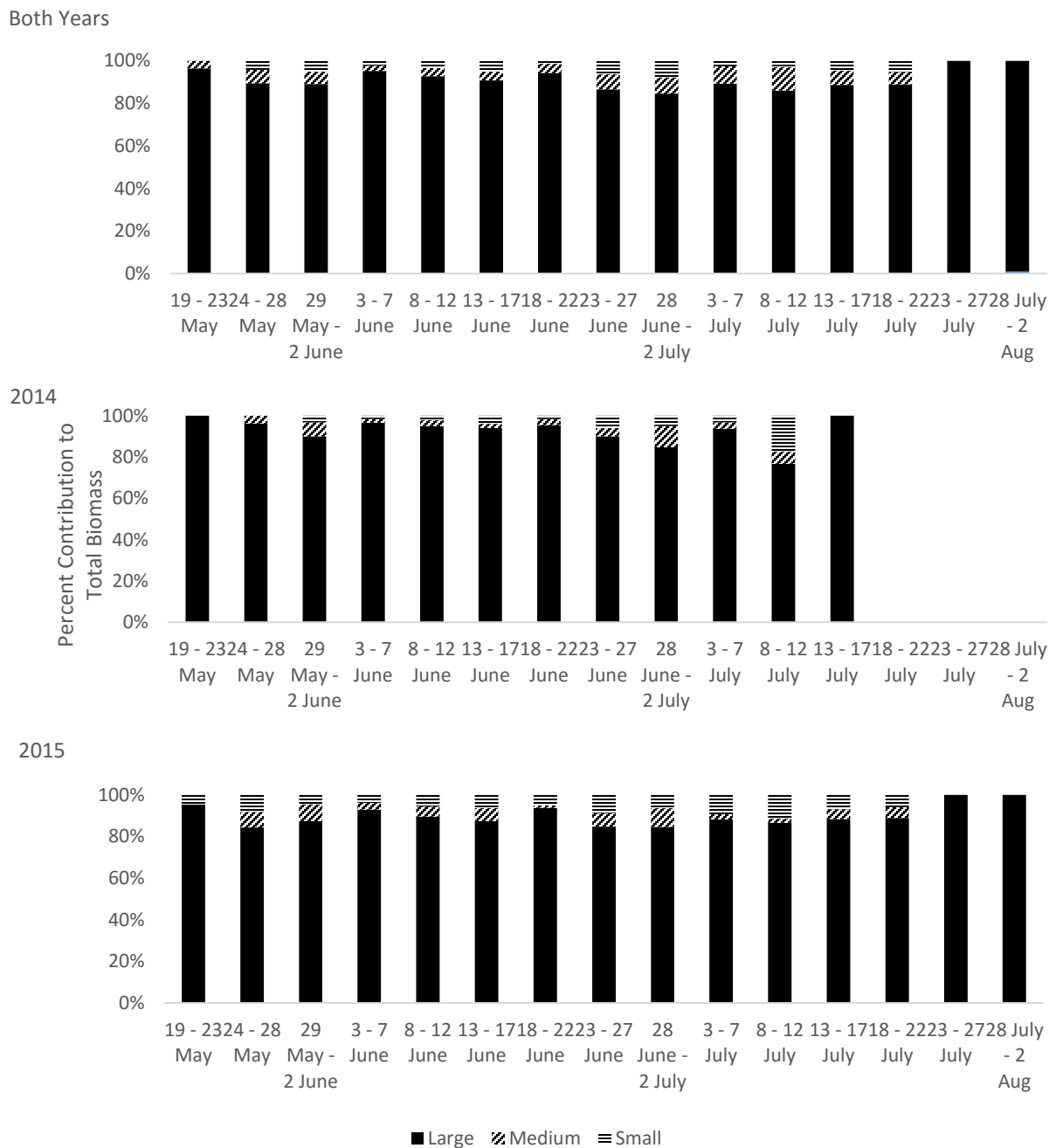


Figure 2.6. Percent contribution of biomass categories by “week” as organized by 5-day periods across the brood rearing period: both years (top), 2014 (middle), and 2015 (bottom). Generally, the same patterns appear between years where there is a shift to a larger prey type (squirrel) across time but with less substantial shift in 2014 when ptarmigan were the most used prey type in the diet.

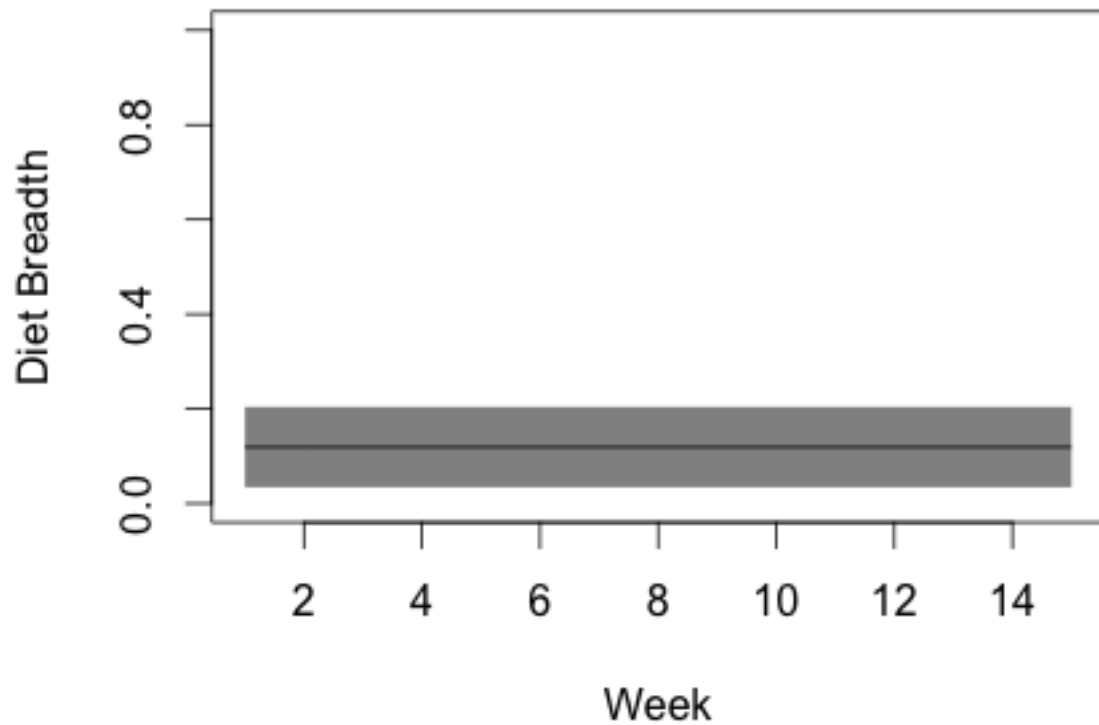


Figure 2.7. Visual representation of the null model describing diet breadth as a function of “week” during the 2014 and 2015 breeding seasons in western Alaska. Grey shading indicates the 85% confidence interval. “Week” had no influence on diet breadth.

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CHAPTER THREE: GYRFALCON DIET DESCRIPTION IN THE CONTEXT
OF A CHANGING WORLD

Abstract

The impacts of climate change are increasing, along with the need to understand their effects on ecosystem dynamics. I studied Gyrfalcon (*Falco rusticolus*) food habits during the brood rearing period to improve current knowledge regarding dietary habits during nesting, and provide necessary information for understanding climate change impacts to Arctic ecosystems. I studied dietary habits over two breeding seasons on the Seward Peninsula, Alaska, using two methods: motion-activated cameras and the collection of prey remains. I compared the results of each method to assess the improvements of camera analysis to diet description. I then related my results to one study (Roseneau 1972) that used prey remains collection to quantify diet of the same population 46 years previous as a case study to assess the use of past diet studies to monitor change to Gyrfalcon prey use. The use of nest cameras provided a greater number of prey items catalogued per nest, but did not provide a greater number of ptarmigan catalogued per nest. This suggests that prey remains analysis failed to detect the contribution of some prey types to the overall diet. Cameras catalogued a greater number of squirrel than did prey remains, suggesting that prey remains analysis under-represented the contribution of squirrel to the diet. The under-representation of the contribution of squirrel provided by prey remains analysis, and the differences between my study and Roseneau (1972), reveals the limitations of prey remains analysis for a

complete characterization of diet. The result also suggests the limitations of using Roseneau (1972) as a baseline study to assess dietary change in western Alaska. I further summarized 19 prior Gyrfalcon diet studies to evaluate their value as baselines by which to compare and confidently assess the impacts of climate change on Gyrfalcon diet. I conclude that most historical data sets of Gyrfalcon diet are of limited value for measuring the impacts of climate change due to biased methods, short duration, small samples sizes, and a lack of standardization of methods. My case study involving two diet studies on the same population illustrates the benefits of camera data to quantify diet and the clear need to develop recurring, standardized diet studies across the circumpolar Gyrfalcon range to assess dietary shifts as a measure of climate change impacts on Arctic communities.

Introduction

Arctic ecosystems are already showing the ecological effects of climate change (Ims and Fuglei 2005, Post et al. 2009). Climate change effects operate on many levels including increases in the frequency and intensity of spring rainfall, increases in shrub height and distribution, reduction in the distribution of sea ice, reduction in the permafrost zone, and shifts in the phenology of important system events such as snowmelt (Rupp et al. 2000, Hoyer and Forchhammer 2008, Post et al. 2009, Screen and Simmonds 2010, Gilg et al. 2012, Zhang et al. 2013, Myers-Smith et al. 2015, Screen et al. 2015). Ecosystem-wide changes that have compounding effects have the potential to disrupt life history strategies and species interactions (Hunter et al. 2010, Smith et al. 2010), which can have major implications for system functioning (Berlow et al. 1999, McKinnon et al. 2012, Schweiger et al. 2014). Our ability to monitor and understand the

impacts of climate change on the Arctic require recurring and standardized baseline studies on species interactions (Post et al. 2009).

Species interactions of top predators such as raptors are of particular importance because top predators serve as indicators of the health of their ecosystem (Barraquand et al. 2014, Ehrich et al. 2015, Pokrovsky et al. 2015). The stability of raptor populations, health of individuals, and reproductive output of pairs may indicate how a system is handling disruption (Newton 1979). Diet of raptors can provide insight into species interactions, especially during periods when energy demands are highest, such as during the brood rearing period (Pokrovsky et al. 2015). Therefore, regular diet description can serve as a baseline for investigating the impacts of climate change on systems and provide a foundation to test higher level hypotheses of system change (Nystrom et al. 2006, Dawson et al. 2011, Pokrovsky et al. 2014).

The Gyrfalcon (*Falco rusticolus*) is an apex avian predator of the Arctic tundra, an ecosystem with a circumpolar distribution that is already showing the impacts of climate change (Hinzman et al. 2005, Rawlins et al. 2010, Watson et al. 2011, Gilg et al. 2012). Although generally considered a dietary specialist that depends on birds in the genus *Lagopus* as its primary prey for most of the year, this characterization is incomplete because the degree of diet specialization varies among populations, and because the diet of Gyrfalcons may vary throughout the year and between years (Nielsen and Cade 1990, Booms and Fuller 2003, Potapov and Sale 2005).

Indirect analyses for describing diet of nesting raptors holds many biases (Marti et al. 2007). These biases have been discussed in many Gyrfalcon diet studies (Langvatn 1977, Huhtala et al. 1996, Nielsen 1999) and include misrepresenting the contribution of

particular prey types (e.g. overestimating the contribution of large prey items and underestimating the contribution of small prey items due to detection biases), and underestimating some prey types due to treatment of the prey item such as the removal of the item from the nest site following feeding. Additionally, studies describe biases related to combining estimations of two indirect methods, an approach that is suggested by some studies and dissuaded by others (Marti et al. 2007). Due to these biases, raptor diet studies are encouraged to standardize and report methods and results in detail to enable comparison to other studies, and collect and analyze data in an unbiased a manner as possible (Marti et al. 2007).

Considering the substantial body of literature that exists on Gyrfalcon diet, my objective was to determine the utility of published Gyrfalcon diet studies for assessing if and how species interactions (i.e., diet) have changed over time concurrent with documented climate change. I studied Gyrfalcon diet during the brood rearing period on the Seward Peninsula from 2014 to 2015. I characterized diet through camera analysis and the collection of prey remains, and compared the results to assess the strengths and limitations of each. I then related my results to a diet study on the same population that occurred 46 years earlier (Roseneau 1972) to illustrate the utility of historical diet studies as baseline data sets with which to measure the impacts of climate change on the Arctic systems. I reviewed and summarized the utility of 19 prior Gyrfalcon diet studies for use as baseline diet descriptions to measure the impacts of climate change on Gyrfalcon predator prey dynamics. For use as baseline diet description, a study should meet the following criteria to qualify as useful for comparison with present studies: direct method for cataloguing diet, appropriate study duration and sample size, and standardization of

methods including full descriptions of sampling techniques and data analysis. These criteria are important because they lessen the innate biases in study design and methodology that may misrepresent diet, provide a more correct interpretation of dietary descriptions during breeding, and provide the opportunity for study repetition that allows for assessing climate change impacts to Gyrfalcon predator prey dynamics. The comparison with Roseneau (1972) and the review of Gyrfalcon diet studies support both the importance and the need for developing baseline descriptive studies using repeatable, standardized methods and direct observation that are aimed to achieve an understanding of the impacts of climate change to Arctic communities.

Methods

Study Area

The study area consists of 14,150 km² of the Seward Peninsula, described by Bente (2011). Topography consisted of low valleys and rolling hills interspersed with mountainous terrain, numerous rock outcroppings, and cliff-lined river systems. The vegetation is predominantly Arctic tundra dominated by low-lying vegetation in coastal and highland areas, and dense willow (*Salix* spp.) and alder (*Alnus* spp.) thickets along riparian corridors. The study area provided abundant nesting habitat for Gyrfalcons, with an annual mean of 35 (range 31 to 39) occupied breeding territories between 2005 and 2010 (Bente 2011).

Nest Treatment

In 2014 and 2015, occupancy surveys for nesting Gyrfalcons were conducted to determine nest sites appropriate for camera installation. Surveys consisted of ground-based surveys and aerial surveys. Ground-based surveys, the primary method employed

in 2014, consisted of hiking to historic nest locations located within 5 km of the road system. Aerial surveys were conducted from a Robinson R-44 Helicopter as an observation platform. Observations during aerial surveys were made primarily by a front seat observer with contributions from a secondary observer in the back seat of the aircraft. On occasion the pilot also contributed to observations. Flights consisted of frontal approaches on the observer's side when possible at a distance varying from 50-200m depending on sensitivity of detected birds, characteristics of the nest cliff, and wind intensity. When occupancy was determined, we recorded information regarding number of eggs and number and age of offspring. I then used information regarding nest phenology to prioritize the installation of nest cameras. In both ground-based surveys and aerial surveys, nests with eggs received highest priority to ensure cameras were installed before hatch.

After I determined Gyrfalcon occupancy from aerial and ground-based surveys, I installed Reconyx PC800 motion-activated cameras (hereafter referred to as "nest camera") at 23 (10 in 2014, 13 in 2015) occupied Gyrfalcon nests to record prey deliveries during the brood-rearing period. Five nests received camera treatment in both 2014 and 2015. The remaining 18 nests received camera treatment in only one year. I installed nest cameras prior to hatch when possible (N=15 nests) 1–2 m laterally from the nest and 1 m above the nest using a wall mount bracket attached to the cliff face. I drilled two holes into the cliff using a hammer drill, and attached the wall mount with concrete screws. I attached the nest camera to the wall mount with a swivel bracket, allowing the camera to be adjusted to the appropriate angle to capture prey deliveries. I programmed nest camera motion activation at high sensitivity to take three rapid photographs (1

frame/sec) followed by a 15 sec sleep period, and one motion independent time-lapse photograph recurring every 30 min. All nest camera photographs were automatically time-stamped with Alaska Daylight Time (AKDT), and calendar date. I removed nest cameras at the end of the brood-rearing period after all nestlings had fledged and prey deliveries to the nest had ceased (approximately 55 days post hatch).

I collected pellets and prey remains from nests, below nests, and at accessible perch sites of occupied cliffs that received camera treatment. At camera installation, I discarded all pellets and prey remains found after an intensive search in an attempt to clean all old items from the area. Pellets and prey remains collected at subsequent visits represented the diet during the brood rearing period and were directly comparable to camera data. I collected pellets and prey remains from camera nests twice during the brood rearing period, once at nestling age 20-30 days, and then at nestling age 50-60 days after all nestlings had fledged and deliveries to the nest site had ceased. I identified the minimum number of individuals present in prey remains based on the most commonly found bone, body part, or feathers representing one individual (Nielsen 1999, Booms and Fuller 2003). To replicate the methods of Roseneau (1972, p. 8) I disregarded the contribution of pellets to the diet description for this analysis.

I catalogued prey items by sequentially reviewing all images from 20 nest cameras that were successful in capturing prey deliveries. I identified items to lowest taxonomic level possible. I counted whole or headless prey as one item, and noted individual parts delivered during a 24-hour period to avoid double counting. Because Gyrfalcons are known to cache prey, I also noted the condition of any removed prey item to minimize double counting (Booms and Fuller 2003). I assigned average mass values

for species for biomass calculations (Kays and Wilson 2009 for mammals, Sibley 2014 for birds). I assigned biomass for immature prey items by visually estimating their size as a proportion of adult size, and applying the proportion to the average biomass value of the species. Due to the regional variation in mass of Arctic ground squirrels, I calculated an average mass from across Alaskan populations (Sheriff et al. 2013). I estimated biomass of unknown items by visually estimating mass related to a known item's size (e.g., an item approximately the size of a Lapland Longspur (*Calcarius lapponicus*) received a mass assignment of 27 g) following Booms and Fuller (2003). I organized prey items into functional categories that were based on broad similarities of the prey types (Robinson et al. 2015). I designated ten functional categories including unknown items: ptarmigan, shorebird, waterfowl, passerine, jaeger, squirrel, microtine, unknown bird, unknown, and other (raptor and seabird). I catalogued percent contribution to total biomass by functional category to illustrate the importance of each prey category to overall diet.

Data Analysis

I compared the results from two different methods used to quantify Gyrfalcon diet in this study, camera analysis and prey remains analysis. I disregarded nests (5) that captured less than ten items in total from analysis because these nests failed within the first week of brood rearing and did not represent the true ability of the method to quantify prey use. I ran Shapiro Wilks Normality Test to check for the assumption of normality in the dataset. Due to non-normal data, I ran non-parametric Wilcoxon Rank Sum tests to compare number of prey items, number of ptarmigan, and number of squirrels in camera

and prey remains data. I used 0.05 as an alpha-value, where results of $p < 0.05$ were deemed significant. All analyses were performed in R 3.2.3 (R Core Team 2015).

I compared the results from my camera analysis to a study conducted on the same population 46 years prior that used prey remains analysis to characterize diet (Roseneau 1972). Roseneau (1972) assessed diet through pellet and prey remains collections from in and around nest sites over three breeding seasons: 10 nests in 1968, 14 nests in 1969, and 16 nests in 1970. Pellet analysis in his study was only used for detection of microtine prey items, thus his description of diet during breeding is based primarily on the prey remains analysis due to the low contribution of microtines to the overall diet (Fig. 3.1). Number of collection visits at nest sites ranged from one to seven, and were unequal between nest sites. Further descriptions of methodology can be found in Roseneau (1972). For comparison between studies, I adapted data from Table 6 in Roseneau (1972) to follow the functional category structure of my study.

To address the utility of past studies as baseline diet descriptions, I determined four parameters and noted past studies that did not meet bias-limiting criteria in the following categories: methods employed, sample size, study duration, and standardization of methods. For the criteria of methods employed, I recorded whether Gyrfalcon diet was described from direct observation (e.g., cameras or by viewing the nest), or indirect methods (e.g., prey remains and pellets). For sample size, I defined inadequate sample size as studies that described diet from fewer than 10 nests, because sampling diet from less than ten nests could fail to capture enough prey items to properly characterize the diet. For study duration, I defined inadequate duration as those studies that sampled diet in three breeding seasons or less because studies of less than three breeding seasons could

fail to capture natural inter-annual variation in the predominate prey types in the Gyrfalcon diet. I determined three seasons as the threshold because it is the least duration of known population cycle patterns in Tetraonidae, and thus is reasonable for the study duration criterion. (Moss and Watson 2001). Finally, I noted studies that did not follow standardized methods, i.e., irregular visits, unequal visits per nest, unequal data collection between or within-seasons, did not fully describe sampling techniques, or did not describe data analysis.

Results

Characterization of diet differed by method (Fig. 3.2). Camera analysis captured a substantial shift in prey use between years in my study, where predominate prey type switched from ptarmigan in 2014 to squirrel in 2015. However, this substantial switch in prey use was not reflected in prey remains analysis (Fig. 3.2). Number of prey items per nest differed between methods (Fig. 3.3). Significantly more prey items were recorded per nest by camera analysis than by prey remains analysis (Table 3.2). However, number of ptarmigan recorded per nest did not differ between methods (Table 3.2, Fig. 3.4). Number of squirrel per nest differed between methods (Fig. 3.5). Significantly more squirrel were recorded by camera analysis than by prey remains (Table 3.2).

Roseneau (1972) recorded 1333 prey items of 37 species and 11 families from 40 nests over three breeding seasons. Total biomass estimated was 653.2 Kg for an average of 16.3 Kg per nest. By comparison, from camera data I recorded 2,008 prey items constituting 40 species and 15 families from 20 nests in two breeding seasons. Total biomass obtained was 808.7 Kg for an average 40.4 Kg per nest, a difference from Roseneau (1972) of 155.5 Kg (24%) total biomass and 24.1 Kg (148%) biomass per nest.

I reviewed 26 Gyrfalcon studies that catalogued diet during nesting (Table 3.3). Of these studies, the majority used indirect methods to describe diet, including pellets and prey remains analyses. Few studies used direct observation, and only one study used camera analysis to quantify diet. Twenty of the studies were published in English, thus allowing a more detailed comparison of methods. The majority of historical studies lacked standardized methodology, and many had small sample sizes and were of short duration (Table 3.3).

Discussion

My comparisons of diet description methods within and between studies demonstrates further considerations and limitations of indirect analyses, and the low utility of historical data sets as baseline diet descriptions for understanding changes in Gyrfalcon prey use.

The apparent contradiction that per nest, total prey numbers increased while number of the principle prey, ptarmigan, did not is the key to interpreting my results and the limitations of historical data sets as baselines for assessing change. My results provide further consideration for the use and limitations of indirect methods for Gyrfalcon diet description. Cameras recorded a significantly greater average number of prey items delivered per nest than was recorded by prey remains analysis in my study. However, the average number of ptarmigan delivered per nest did not differ between camera and prey remains data.

The observation that number of total prey detections differed between methods while ptarmigan detections did not suggest that ptarmigan detection was not biased between the two methods, and that another prey type was responsible for the differences I

observed. The substantial switch in prey use between years not reflected in prey remains analysis suggests the inability of this method to properly describe the contribution of squirrel to the Gyrfalcon diet and may not capture changes in predominate prey type in the diet over time. Camera data revealed that adult Gyrfalcons often removed squirrel carcasses from nests after feeding, which may partially explain the misrepresentation of squirrel in the diet between years.

The inability of prey remains analysis to detect the true contribution of squirrel in my study suggests a new limitation of the use of prey remains to quantify diet: that the varying treatment of prey types such as the removal of squirrel remains from the nest following feeding may decrease detection of important prey types and their true contribution to Gyrfalcon diet. A misrepresented contribution of particular prey types to the Gyrfalcon diet is important, but more important is the inconsistency in this misrepresentation seen between years in this study. Although prey remains analysis captured the increase in the contribution of squirrel in the diet in 2015, the method failed to capture the degree of this increase, where squirrel became the most used prey type in 2015. This switch in predominate prey type is especially important in this case, considering the predicted impacts of climate change on both ptarmigan and Arctic ground squirrel populations (Wheeler et al. 2015). The failure to detect the switch in predominate prey type through the use of prey remains analysis represents a new limitation and consideration for the use of indirect methods for diet description: the inconsistency of biases. Biased representations of reality are common in research as in the case with indices (Johnson 2008). When known and stated biases are consistent, the data can still be useful. It is the inconsistency of biases that confuse our perceptions of reality.

Previous Gyrfalcon diet studies implicitly assumed that the biases present in the results of indirect methods were consistent and therefore useful as an index to diet. However, my results suggest that this implicit assumption is not always correct, and prey remains analysis may in some species be inconsistently biased. This is an important consideration when assessing the utility of past diet descriptions, and for drawing inferences from differences in diet of a population over time.

Differences in the dietary descriptions between my study and Roseneau (1972) further illustrate the limitations of prey remains analysis to quantify diet and why the results of camera analysis in my study should not be compared to the results of Roseneau to assess changes in Gyrfalcon prey use on the Seward Peninsula, Alaska. Apart from the differences in total biomass obtained, the larger contribution of squirrel to the diet provided by camera analysis is one of the major differences between my findings and those of Roseneau (1972), but the reasons for this difference cannot be determined due to differences in methods between the two studies. The comparison of methods in my study suggests that the use of prey remains is the likely explanation for the lower contribution of squirrel in Roseneau (1972), and that squirrel in his study may have a similar contribution to my study. The inability to utilize Roseneau (1972) as a measure of change due to the lack of confidence in dietary description of prey remains analysis shown by my study further supports the need to develop standardized baseline diet studies as a measure of climate change in western Alaska, and the inability to utilize historical studies for measuring change in other Gyrfalcon populations.

I collected information from past Gyrfalcon diet studies to support the need to develop baseline Gyrfalcon diet studies as a measure of climate change in the Arctic. In

19 studies, I found four major issues that limit their use as baseline data for measuring change in Gyrfalcon diet over time:

1. Reliance on indirect methods. Ninety-five percent of published diet studies on Gyrfalcons that I examined relied on prey remains and pellets to quantify diet during the nesting period. Only a single diet study used camera analysis to quantify prey use during the nesting period (Booms and Fuller 2003). Historical data sets derived from indirect methods are a poor baseline for studying the effects of climate change on Gyrfalcon diet, due to the innate biases resulting from these methods (Nielsen 2003, Koskimies 2005, Tornberg and Reif 2007, Pokrovsky et al. 2014), that are perhaps inconsistent in their biases as documented in this study. The comparison between methods in my study further supports the issues related to diet estimation using prey remains analysis, and suggests that studies aimed at developing baseline diet description as a measure of the impacts of climate change need to either match standardized methods employed by past studies while concurrently testing the presumed assumption of bias consistency, or begin new long term data sets with camera analysis as the primary method to describe diet.

2. Small sample size. Twelve (63%) studies sampled diet in fewer than 10 nests for the entire study period, and thus were considered of small sample sizes that limited the accuracy of diet description and the inferences drawn from the data. In at least three instances, diet description was reported from only one nest location (Summers and Green 1974, Pulliainen 1975, Muir and Bird 1984). No study that I reviewed addressed whether their sampling was sufficient to provide an adequate description of Gyrfalcon diet, therefore there is a lack in confidence for the completeness of sampling.

3. Short study duration. Forty-two percent of studies sampled diet in three breeding seasons or less and were considered of short duration. Studies of short duration may fail to capture inter-annual differences in diet that are derived from natural variation or cycles that may be present in Gyrfalcon prey, such as ptarmigan (Moss and Watson 2001). Further, studies based on a single year could provide misleading results if the diet for that particular year was not typical of the diet of that population as a whole.

4. No standardization of methods. In 47% of the studies reviewed, the investigators failed to standardize methods. For example, Roseneau (1972) made an irregular number of nest visits to collect pellets and prey remains that varied by nest and year. In some instances, an unequal number of collection visits were conducted per nest, biasing data collection between or within-seasons. Studies that used pellets and prey remains to quantify Gyrfalcon diet also differed both in their protocols and the period of the breeding cycle in which collections were made. Some studies reported frequency of prey items only, and did not adjust prey frequency to biomass for their description of percent contribution of particular items, which may be misleading given differing prey sizes and thus misrepresenting the importance of particular prey types (Langvatn 1977, Woodin 1980, Koskimies and Sulkava 2011). A lack of standardization between studies not only limits the ability to repeat studies in the future as a measure of change, but biases the description of prey use as well. Without standardized collection methods, true representation of the contribution of particular prey items to the Gyrfalcon diet is lost.

Due to the lack of standardization in Roseneau (1972) it is inappropriate to compare the results of his prey remains analysis the the results of my prey remains analysis. An inability to compare studies is unfortunate, as understanding similarities in

the contribution of Arctic ground squirrel to the Gyrfalcon diet between prey remains analyses of each study could enlighten our understanding of similar inconsistencies in squirrel detection in Roseneau (1972).

It is important to note that my objective is not to criticize or discount the value of past studies. Techniques, sample size, and duration of past studies all result from the situations and methods available at the time. Each study detailing Gyrfalcon diet is a valuable contribution to the understanding of Gyrfalcon natural history. My purpose for collecting information from past studies is to promote forward thinking on study design and methodology, and the development of dietary studies across the circumpolar Gyrfalcon range aimed at assessing future changes to Gyrfalcon prey use as a measure of the impacts of climate change to tundra systems. Studies included in this review were designed to accomplish varying objectives, none of which were aimed towards repeatability as a measure of the impacts of climate change to tundra systems.

The compounding effects of rapid change in the Arctic has the potential to disrupt system dynamics, particularly life history strategies and species interactions (Hunter et al. 2010, Smith et al. 2010). Because disruptions in species interactions can have major implications for system functioning (Berlow et al. 1999), key species interactions in a system need to be understood to assess the impacts of climate change on system health (Berlow et al. 1999, Ims and Fuglei 2005, Wirta et al. 2015). It is especially important to understand species interactions involving top predators because such interactions can serve as indicators of system health or perturbation (Barraquand et al. 2014, Ehrich et al. 2015). Recurring and standardized baseline studies that are descriptive in nature are an essential foundation for testing higher level hypotheses of

ecosystem level changes. Given the large number of published studies on Gyrfalcon diet, one could assume that published diet descriptions provide the baseline data needed to evaluate change over time. However, this assumption is tenuous due to issues related to biases of sampling techniques, sample sizes, study duration, lack of standardization within and between studies, and a new consideration identified in this study: the inconsistency in the description of contribution of prey items over time. Inconsistencies in the true contribution of Arctic ground squirrel in this study suggest that past Gyrfalcon diet studies may possess the same issue in their representation of some prey items in the diet, further limiting their utility as a measure of dietary change over time.

There is a clear need to continue diet description using camera analysis as a baseline to assess the impacts of climate change on Gyrfalcon prey use and species interactions on the Seward Peninsula, Alaska. Gyrfalcon dietary habits vary by region (compare Cade 1960, Booms and Fuller 2003, Nielsen 2003). Regional diet variation limits the ability to compare dietary descriptions from different locations across the circumpolar Gyrfalcon distribution. Because past studies and studies between regions should not be directly compared to assess change, there is a need to establish long term or recurring descriptive studies on Gyrfalcon dietary habits in each region of its circumpolar distribution in order to achieve a global understanding of the impacts of climate change to Arctic communities at the local level.

Tables

Table 3.1. Details of this study and Roseneau (1972), that catalogued Gyrfalcon diet on the Seward Peninsula, Alaska, 42 years apart using differing primary methodologies to characterize diet, camera analysis and prey remains analysis, respectively.

Study	No. years	No. nests	No. species	No. families	No. items	Total Biomass (Kg)	Biomass per nest
Robinson (camera)	2	20	40	15	2009	808.4	40.42
Roseneau (prey remains)	3	40	37	11	1333	653.2	16.33

Table 3.2. Differences in Gyrfalcon diet as described by cameras and prey remains on the Seward Peninsula, Alaska, in 2014-2015 via a Wilcoxon Rank Sum Test.

	Mean	Standard Error	Z	P-value
# of Prey Items				
Cameras	117	13.5	3.37	0.0007557*
Prey Remains	44.5	7		
# of Ptarmigan				
Cameras	51.6	8.3	1.6481	0.09932
Prey Remains	31.7	6.8		
# of Squirrel				
Cameras	23.8	6.9	2.8155	0.00487*
Prey Remains	2.8	1.1		

Table 3.3. Description of historic Gyrfalcon diet studies, including number of studies by location, methods, and bias-limiting criteria indicating their limited utility for assessing the impacts of climate change on prey use and species interactions in the Arctic.

Region	Methods							
	# of studies	# Indirect Methods		# Direct Methods			# with Inadequate sample size	# with Inadequate study duration
		Pellets	Prey Remains	Direct Observation	Cameras	# with Lack of standardization		
Alaska	5	4	5			2	1	1
Canada	2	2	2	2		2	2	2
Greenland	2	2	2		1	1	2	2
Iceland	6	5	6			1	2	2
Norway	3	3	3			2	3	1
Finland	3					1		
Russia	5	4	5	1			2	
Percent of studies		77	88	12	4	95*	47*	63*

*Excludes studies published in languages other than English, where methodology is unclear other than that written in the English abstract.

Figures

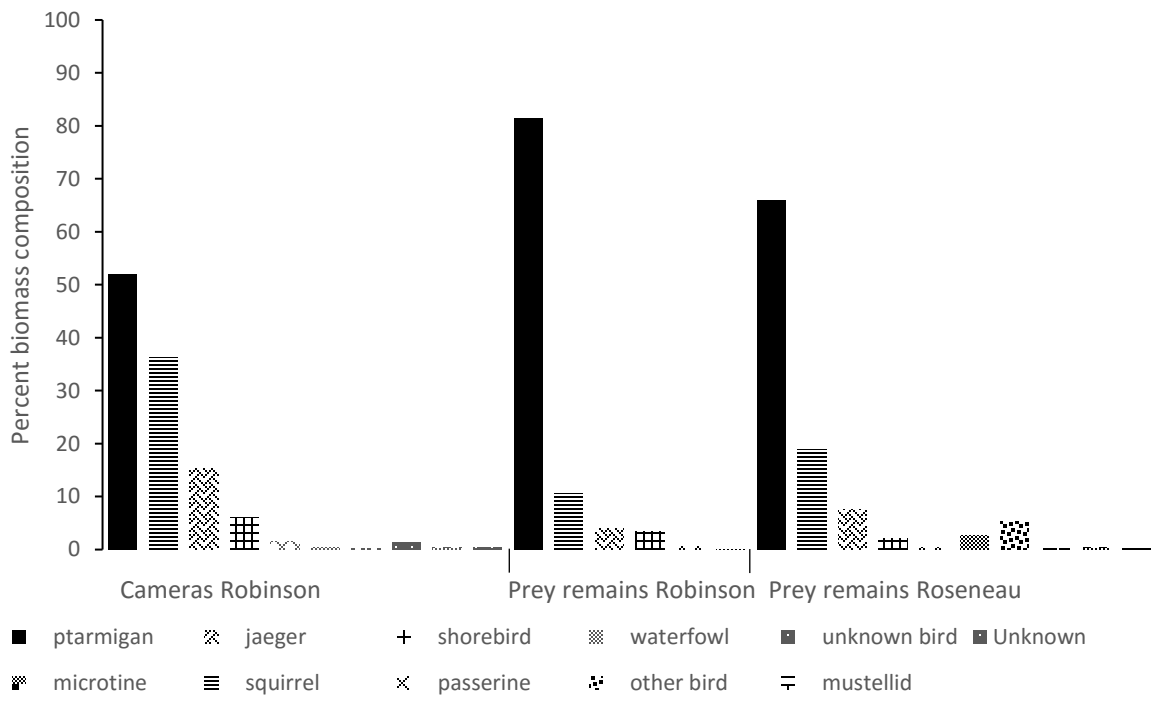


Figure 3.1. Gyr Falcon diet described by percent contribution of prey type on the Seward Peninsula, Alaska, in two studies conducted 42 years apart using differing methodology. This study catalogued diet using camera analysis and prey remains analysis in 20 nests over two breeding seasons, and Roseneau (1972) catalogued diet using prey remains analysis in 40 nests over three seasons.

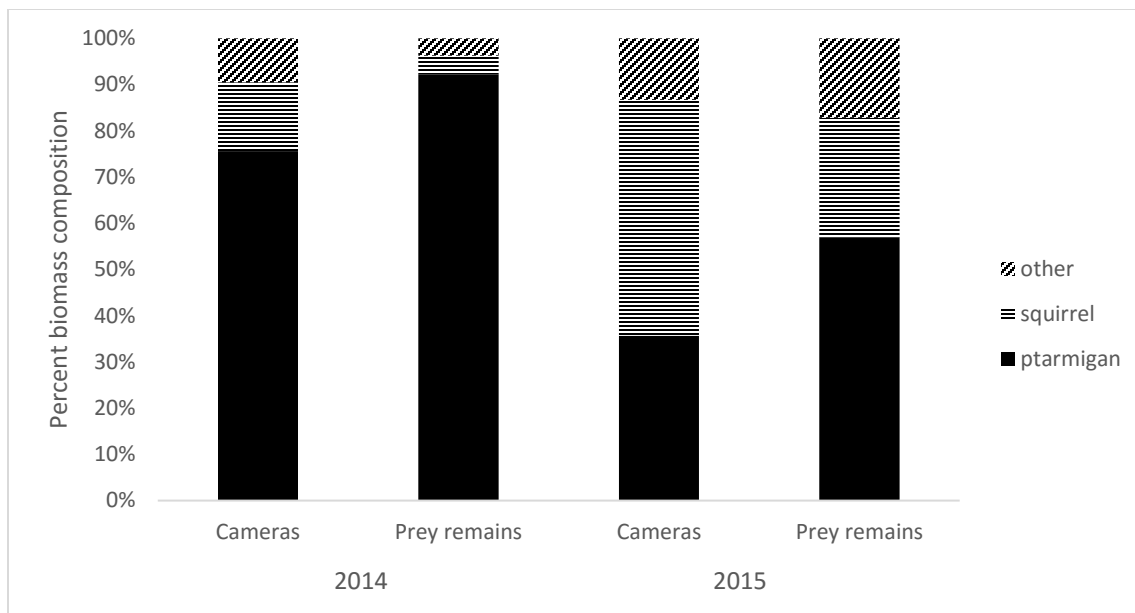


Figure 3.2. Percent contribution of prey type in Gyr Falcon diet described by two methods, Camera analysis and prey remains analysis, over two breeding seasons on the Seward Peninsula, Alaska.

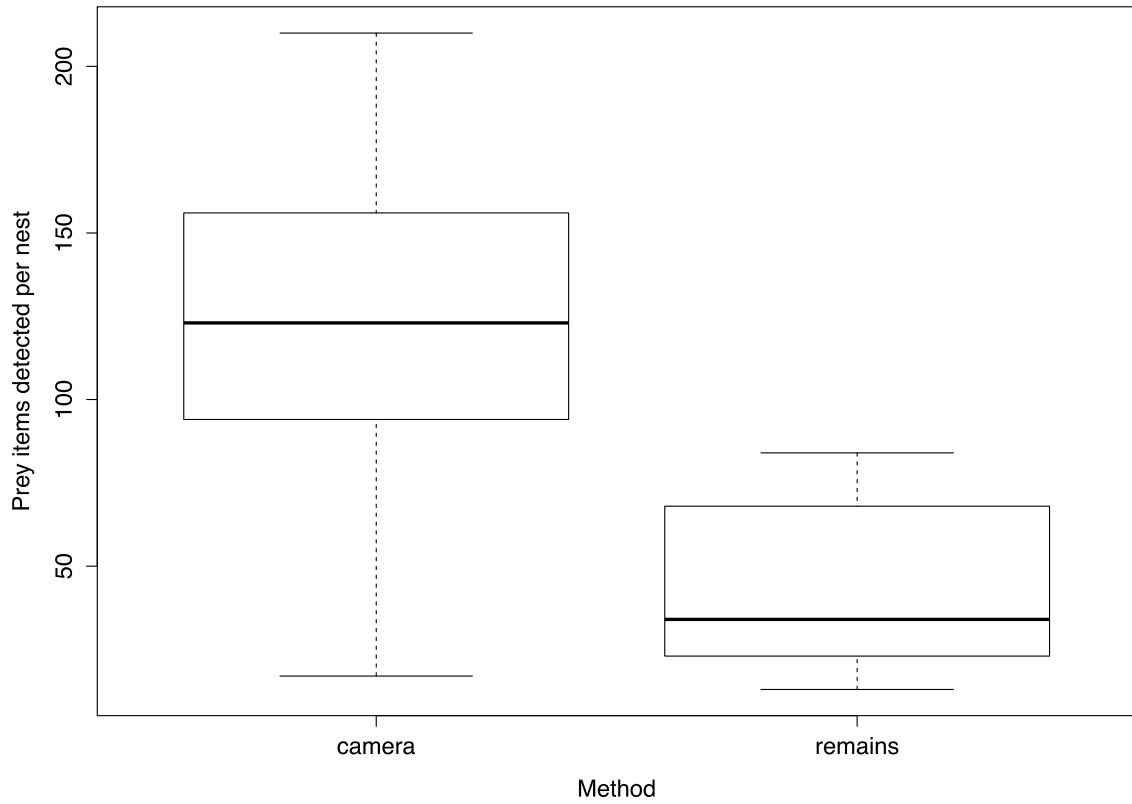


Figure 3.3. Number of prey items catalogued in the Gyrfalcon diet per nest during the brood rearing period over two seasons (2014 and 2015) by two methods, camera analysis and prey remains analysis. Significantly more prey items were catalogued by camera analysis than from prey remains analysis.

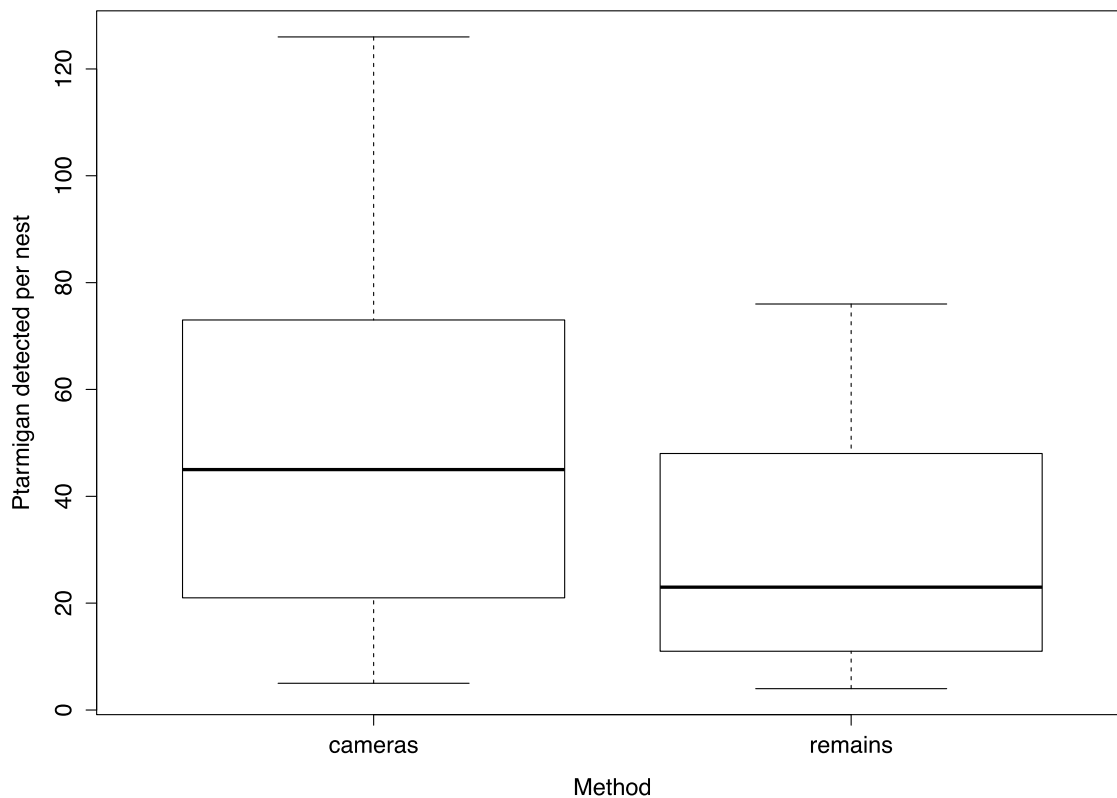


Figure 3.4. Number of ptarmigan catalogued in the Gyrfalcon diet per nest during the brood rearing period over two seasons (2014 and 2015) by two methods, camera analysis and prey remains analysis. The number of ptarmigan catalogued from camera analysis and prey remains analysis did not differ.

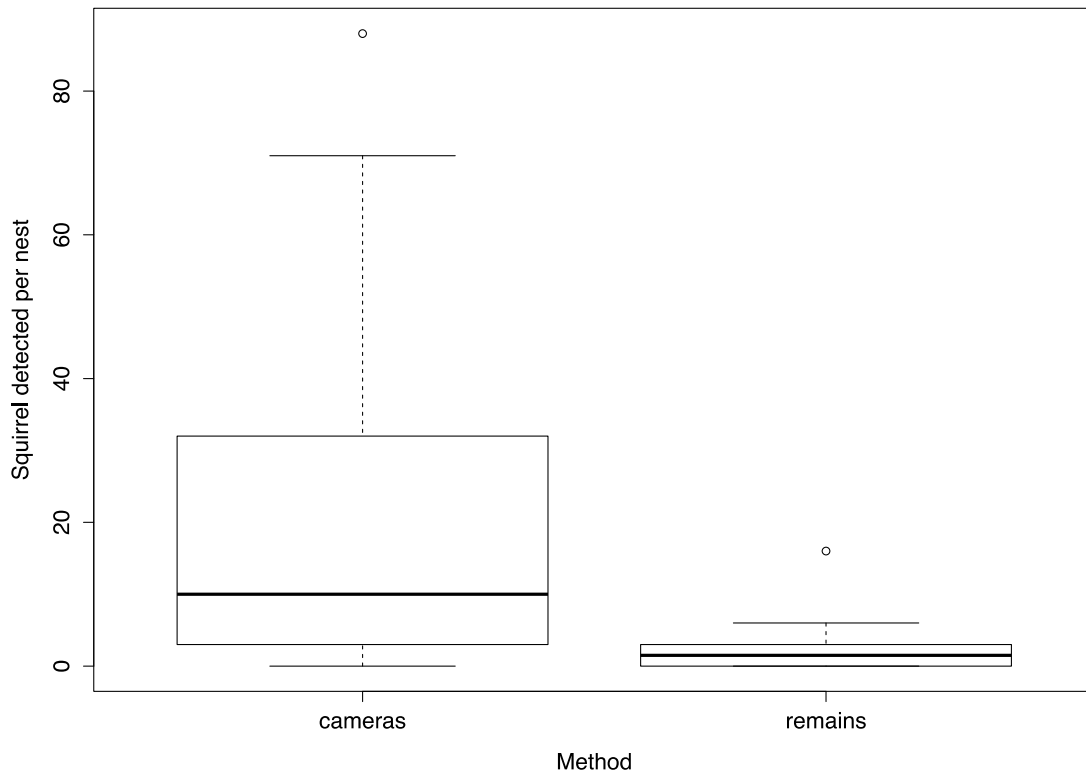


Figure 3.5. Number of squirrel catalogued in the Gyrfalcon diet per nest during the brood rearing period over two seasons (2014 and 2015) by two methods, camera analysis and prey remains analysis. The number of squirrel catalogued from camera analysis and prey remains analysis differed significantly.

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APPENDIX A**Supplementary Summary of Biomass Assignments by Prey Type, Diet by Prey
Type, Nest Output, and Nest Success**

Table A.1. Biomass assignments for each prey type identified by motion-activated cameras installed in Gyrfalcon nests over the 2014 and 2015 breeding seasons on the Seward Peninsula, Alaska.

Common Name	Scientific Name	Biomass Assignment
Redpoll spp.	<i>Acanthis spp.</i>	13
Arctic ground squirrel	<i>Urocitellus parryii</i>	713
American Golden-Plover	<i>Pluvialis dominica</i>	145
American Pipit	<i>Anthus rubescens</i>	21
American Robin	<i>Turdus migratorius</i>	77
American Tree Sparrow	<i>Spizelloides arborea</i>	20
North American brown Lemming	<i>Lemmus trimucronatus</i>	87.5
Bristle-thighed Curlew	<i>Numenius tahitiensis</i>	490
Bar-tailed Godwit	<i>Limosa lapponica</i>	340
Crested Auklet	<i>Aethia cristatella</i>	285
Fox Sparrow	<i>Passerella iliaca</i>	32
Northern collared lemming	<i>Dicrostonyx groenlandicus</i>	50
Golden-crowned Sparrow	<i>Zonotrichia atricapilla</i>	29
Grey-cheeked Thrush	<i>Catharus minimus</i>	32
Long-tailed Jaeger	<i>Stercorarius longicaudus</i>	300
Lapland Longspur	<i>Calcarius lapponica</i>	27
Long-billed Dowitcher	<i>Limnodromus scolopaceus</i>	115
Northern Harrier	<i>Circus cyaneus</i>	420
Northern Pintail	<i>Anus acuta</i>	800
Pacific Golden-Plover	<i>Pluvialis fulva</i>	130
Pectoral Sandpiper	<i>Calidris melanotos</i>	74
Ptarmigan	<i>Lagopus spp.</i>	485
Red-breasted Merganser	<i>Mergus serrator</i>	1060
Northern red-backed vole	<i>Myodes rutilus</i>	31.5
Red Knot	<i>Calidris canutus</i>	135
Rock Sandpiper	<i>Calidris ptilocnemis</i>	70
Savannah Sparrow	<i>Passerculus sandwichensis</i>	20
Short-eared Owl	<i>Asio flammea</i>	350
Semipalmated Sandpiper	<i>Calidris pusilla</i>	25
Snow Bunting	<i>Plectrophenax nialis</i>	42
Spotted Sandpiper	<i>Actitis hypoleucos</i>	40
Surfbird	<i>Calidris virgata</i>	190
Tundra Vole	<i>Microtus oeconomus</i>	52.5
Varied Thrush	<i>Ixoreus naevius</i>	78
Wandering Tattler	<i>Tringa incana</i>	110

White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	29
Western Sandpiper	<i>Calidris mauri</i>	26
Whimbrel	<i>Numenius phaeopus</i>	440
Wilson's Snipe	<i>Gallinago delicata</i>	105

Table A.2. Summary of prey use of 23 Gyrfalcon nests on the Seward Peninsula, Alaska, in the 2014 and 2015 breeding seasons described by number of prey items per type, biomass total per type, and percent biomass contribution.

Prey Type	Year								
	2014			2015			Both Years		
	#	Biomass total	% Biomass	#	Biomass total	% Biomass	#	Biomass total	% Biomass
Birds									
ptarmigan	520	250975	75.6	367	170115	35.7	887	421090	52.1
jaeger	4	929	0.3	38	11400	2.4	42	12329	1.5
shorebird	99	19101	5.8	154	29175	6.1	253	48276	6.0
passerine	55	1788	0.6	169	10624	2.2	224	12412	1.5
waterfowl	1	800	0.2	3	1885	0.4	4	2685	0.3
raptor	0	0	0.0	1	420	0.1	1	420	0.1
seabird	0	0	0.0	1	285	0.1	1	285	0.0
unknown bird	50	6994.5	2.1	48	4208	0.9	98	11202.5	1.4
Subtotal birds	729	280587.5	84.6	781	228112	47.9	1510	508699.5	62.9
Mammals									
squirrel	69	49197	14.8	343	243488	51.1	412	292685	36.2
microtine	1	80	0.0	53	3107	0.7	54	3187	0.4
Subtotal mammals	70	49277	14.9	396	246595	51.7	466	295872	36.6
Unknown	17	1947	0.6	15	1866.5	0.4	32	3813.5	0.5
Total	816	331811.5		1192	476573.5		2008	808385	

Table A.3. Summary of nest initiation dates, hatch dates, nest success, and nest output and fate of 23 Gyrfalcon nests on the Seward Peninsula, Alaska, in the 2014 and 2015 breeding season.

Year	Nest ID	Nest initiation date	Hatch date	Nest output	Nest Fate
2014	1401	14-Apr	19-May	4	S
	1407	17-Apr	22-May	3	S
	1403	18-Apr	23-May	0	F(N)
	1406	19-Apr	24-May	4	S
	1408	20-Apr	25-May	4	S
	1404	23-Apr	28-May	2	S
	1402	25-Apr	30-May	0*	F(D)*
	1405	26-Apr	31-May	1*	S**
	1409	3-May	7-Jun	0*	F(N)
	1411	24-May	28-Jun	0	F(N)
	2015	1502	4-Apr	19-May	3
1507		4-Apr	19-May	3	S
1501		6-Apr	21-May	3	S
1512		10-Apr	25-May	2	S
1505		15-Apr	30-May	0	F(N)
1504		16-Apr	31-May	4*	S
1508		18-Apr	2-Jun	0	F(N)
1511		19-Apr	3-Jun	2	S
1509		22-Apr	6-Jun	2	S
1510		24-Apr	8-Jun	2	S
1503		26-Apr	10-Jun	3	S
1506		30-Apr	14-Jun	2	S
1513		11-May	25-Jun	1	S

Table Key: F(N): Nest failure due to natural events, F(D): Nest failure due to disturbance from research, S: Nest success, NA: Not applicable or data not gathered due to nest failure. Comments: * Partial nest failure at nestling period 2 days, one nestling moved to new location. Camera relocated at nestling period 10 days, causing nest abandonment. **Partial nest failure due to activities at camera installation.

APPENDIX B**Supplementary Summary of Prior Gyrfalcon Diet Studies During Nesting**

Table B.1. Summary of prior Gyrfalcon diet studies conducted during nesting including location of study, predominant item in the diet of each study, and the methods employed to characterize diet. Of the studies, 23 (88.4%) reported a diet composed primarily of ptarmigan. Four (15.4%) studies employed the use of direct methods, and only one study used cameras to characterize diet during nesting.

Study	Location	Predominant item	Method
Bengtson 1970	Iceland	Ptarmigan	Indirect
Booms and Fuller 2003*	Greenland	Ptarmigan and Hare*	Direct & Indirect
Cade 1960	Alaska	Ptarmigan	Indirect
Cade et al. 1998	Alaska	Ptarmigan	Indirect
Dementiev and Gortchakovskaya 1945	Norway	Ptarmigan	Indirect
Ganusevich 2005***	Russia	Ruff	Indirect
Hagen 1952	Norway	Ptarmigan	Indirect
Huhtala et al. 1996	Finland	Ptarmigan	Indirect
Kalyakin and Vinogradov 1981	Russia	Ptarmigan	Indirect
Kishinskiy 1958	Russia	Ptarmigan	Indirect
Koskimies 2011	Finland	Ptarmigan	Indirect
Labutin 2006	Russia	Waterfowl	Indirect
Langvatn 1977	Norway	Ptarmigan	Indirect
Muir and Bird 1984	Canada	Hare	Direct** & Indirect
Nielsen and Cade 1990	Iceland	Ptarmigan	Indirect
Nielsen 1999	Iceland	Ptarmigan	Indirect

Nielsen 2003	Iceland	Ptarmigan	Indirect
Nystrom et al. 2005	Sweden	Ptarmigan	Indirect
Poole and Boag 1988	Canada	Ptarmigan	Direct** & Indirect
Roseneau 1972	Alaska	Ptarmigan	Indirect
Suetens and Groenendael 1976	Iceland	Ptarmigan	Indirect
Summers and Green 1974	Greenland	Hare	Indirect
Voronin 1987	Russia	Ptarmigan	Direct** & Indirect
White and Springer 1965	Alaska	Ptarmigan	Prey Remains
White and Cade 1971	Alaska	Ptarmigan	Indirect
Woodin 1980	Iceland	Ptarmigan	Prey Remains

*Only study to use cameras to quantify gyrfalcon Diet. Showed ptarmigan as main prey, until later in nesting season when there was a substantial switch to hare, much like the switch to squirrel seen in this study.

**These studies used direct methods of personal observation at nest sites to catalogue prey deliveries

Table B.2. Summary of the limitations of prior Gyrfalcon diet studies for use as a baselines for comparing the effects of system change on Gyrfalcon prey use. The majority of studies (95%) employed biased methods to characterize diet.

Study	Methods biased	Lack of standardization	Small sample size	Short duration	Methods not described
Alaska					
Cade 1960	X				
White and Springer 1965	X	X	X	X	
Roseneau 1972	X	X			
Canada					
Poole and Boag	X	X	X	X	
Muir and Bird 1984	X	X	X	X	
Greenland					
Summers and Green 1974	X	X	X	X	
Booms and Fuller 2003			X	X	
Iceland					
Bengtson 1970	X	X	X		
Woodin 1980	X		X	X	
Nielsen and Cade 1990	X			X	
Nielsen 1999	X				
Nielsen 2003	X				
Finland					
Huhtala et al. 1996	X	X			
Koskimies 2011	X				
Sweden					
Nystrom et al. 2005	X				
Norway					
Dementiev and Gortchakovskaya 1945	X	X	X	X	
Hagen 1952	X	X	X		

Langvatn 1977	X		X	
Russia				
Kalyakin and Vinogradov 1981	X		X	
Voronin 1987	X		X	
Proportion of Studies	0.95	0.47	0.63	0.42

Table B.3. Gyrfalcon diet catalogued in 20 nests on the Seward Peninsula, Alaska, over the 2014 and 2015 breeding and 40 nests on over 3 breeding seasons from 1968-70 (Roseneau 1972). Diet in 2014 and 2015 was quantified using both camera analysis and prey remains analysis, while diet in 1968-70 was quantified using prey remains analysis. Functional prey categories are ranked by percent contribution to total biomass per year and for both years combined.

Prey Type	% Contribution to Total Biomass					
	2014		2015		Both Years	
Robinson	Cameras	Prey remains	Cameras	Prey remains	Cameras	Prey remains
Birds						
ptarmigan	75.64	92.15	35.67	56.93	52.1	81.54
jaeger	0.28	0.63	2.39	11.62	1.5	3.94
shorebird	5.76	2.61	6.12	5.08	6.0	3.35
passerine	0.55	0.52	2.23	0.42	1.5	0.49
waterfowl	0.24	0	0.4	0	0.3	0
other bird	0	0	0.22	0	0.13	0
unknown bird	2.1	0	0.88	0	1.4	0
Subtotal birds	84.57	95.9	47.9	74.05	62.9	89.32
Mammals						
squirrel	14.83	4.1	51.05	25.88	36.2	10.66
microtine	0.02	0	0.65	0.06	0.4	0.02
Subtotal mammals	14.85	4.1	51.7	25.95	36.6	10.68
Unknown	0.59	0	0.4	0	0.5	0
Roseneau	1968		1969		1970	All Years
Birds						
ptarmigan		70.4		49.8	68.7	65.2
jaeger		6.7		3.4	9.6	7.4
waterfowl		1.8		5.6	2.0	2.7
shorebird		2.2		2.0	2.1	2.1

passerine	0.1	0.8	0.3	0.4
other bird	2.7	6.1	1.7	3.0
unknown bird	0.1	0.0	0.2	0.1
Subtotal birds	84.0	67.7	84.6	80.8
Mammals				
squirrel	15.2	32.2	14.7	18.6
microtine	0.5	0.1	0.5	0.4
mustellid	0.4	0.0	0.3	0.3
Subtotal mammals	16.0	32.3	15.4	19.2

APPENDIX C

Supplementary Information of Gyrfalcon Dietary Shifts During Brood Rearing

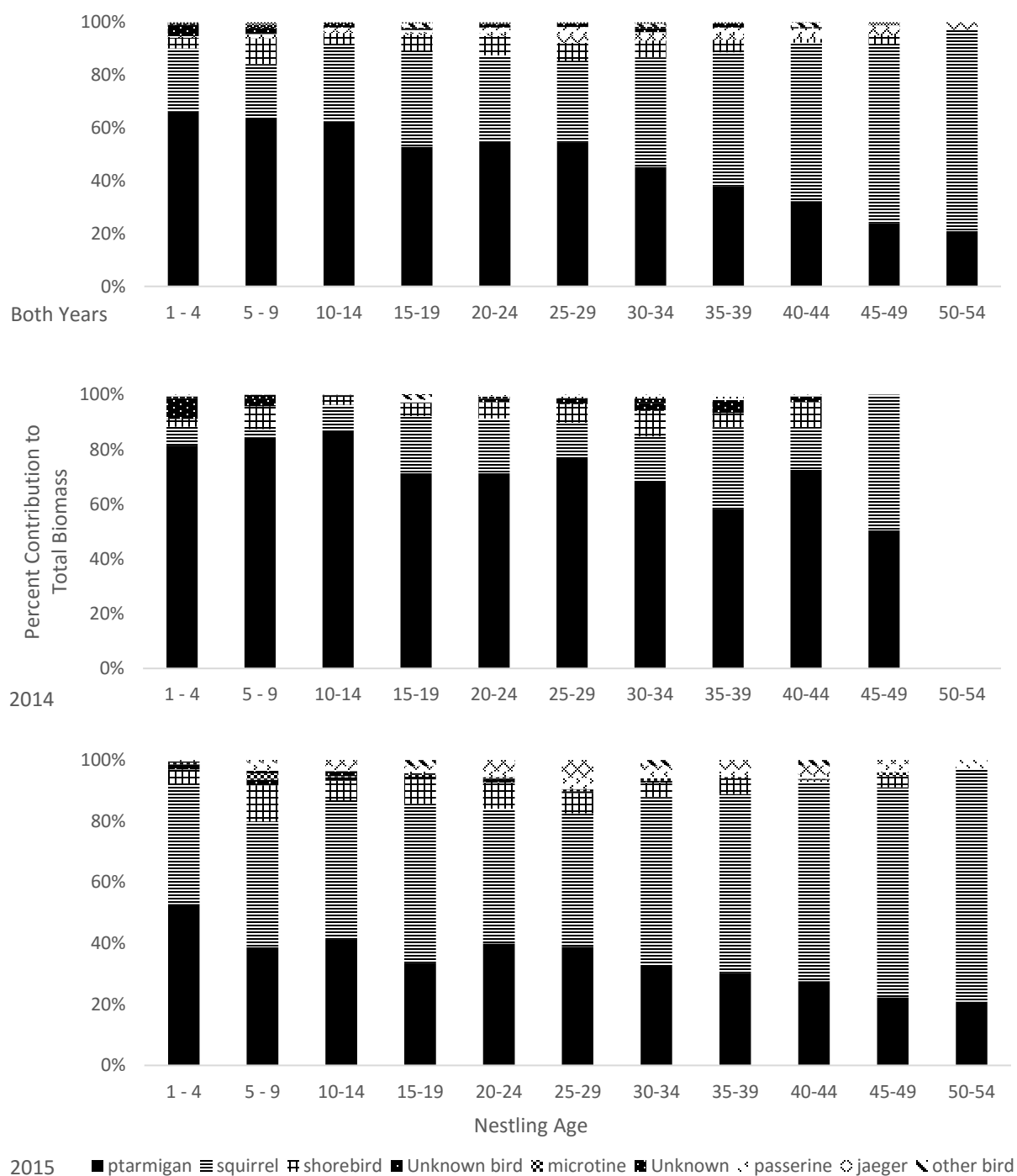


Figure C.1. Change in percent contribution of prey items by nestling age over the course of two breeding seasons (both years, 2014 and 2015 respectively) as told by prey items catalogued by nest cameras in 20 nests (10 in 2014, 10 in 2015). Percent contribution of ptarmigan decreased as nestlings aged in all years.

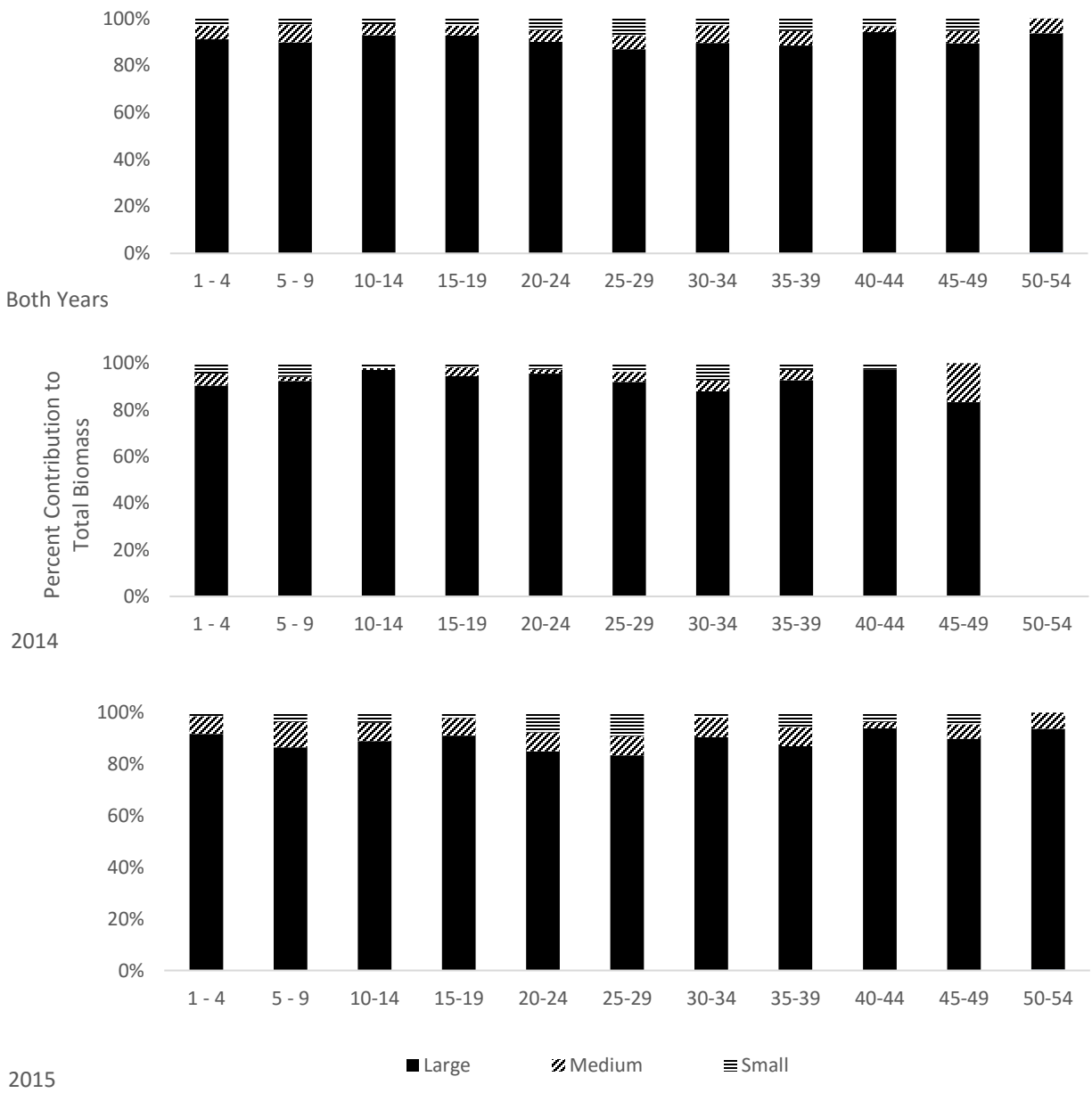


Figure C.2. Percent contribution of biomass categories by date as organized by 5-day periods across the brood rearing period. A is 2014 and 2015 combined. B is 2014. C is 2015. Generally, same pattern between years, across time there is a shift to a larger prey type (squirrel) but with less substantial shift in 2014 when ptarmigan was the dominant prey item.

APPENDIX D

Institutional Animal Care and Use Committee (IACUC) Approval



Office of Research Compliance
 Institutional Animal Care and Use Committee
 AnimalCare@boisestate.edu | 208.426.5404

DATE: February 5, 2014

TO: David Anderson, Ph.D.; Marc Bechard, Ph.D.

FROM: Institutional Animal Care and Use Committee (IACUC)
 c/o Office of Research Compliance

SUBJECT: IACUC Notification of Approval
 Project Title: *Gyr Falcon diet during the nestling period on the Seward Peninsula, Alaska*

This letter is to officially notify you of the approval of your protocol application by the Boise State University (BSU) Institutional Animal Care and Use Committee (IACUC).

Approval Number: 006-AC14-004
Annual Expiration Date: February 4, 2015

Your approved protocol is effective for 12 months. If your research is not finished within the allotted year, the protocol must be renewed by the annual expiration date indicated above. Under BSU regulations, each protocol has a three-year life cycle and is allowed two annual renewals. If your research is not complete by **February 4, 2017**, a new protocol application must be submitted.

About 30 days prior to the annual expiration date of the approved protocol, the Office of Research Compliance will send a renewal reminder notice. The principal investigator has the primary responsibility to ensure the Annual Review/Renewal form is submitted in a timely manner. If a request for renewal has not been received by the annual expiration date, the protocol will be considered closed. To continue the research after it has closed, a new protocol application must be submitted for IACUC review and approval.

All additions or changes to your approved protocol must also be brought to the attention of the IACUC for review and approval before they occur. Complete and submit a MODIFICATION/AMENDMENT FORM indicating any changes to your project.

When your research is complete or discontinued, please submit a FINAL REPORT FORM. An executive summary or other documents with the results of the research may be included.

All relevant forms are available online. If you have any questions or concerns, please contact the Office of Research Compliance, 208-426-5404 or AnimalCare@boisestate.edu.

Thank you and good luck with your research.

A handwritten signature in black ink that reads 'Kenneth M. Cornell'.

Dr. Ken Cornell
 Chairperson
 Boise State University IACUC



Date: January 28, 2015
To: Marc Bechard
From: Institutional Animal Care & Use Committee (IACUC)
 c/o Office of Research Compliance (ORC)
Subject: IACUC Notification of Approval - Renewal - 006-AC14-004
Gyr Falcon diet during the nestling period on the Seward Peninsula, Alaska

The Boise State University Institutional Animal Care & Use Committee has approved your protocol submission.

Protocol Number: 006-AC14-004 Received: 1/7/2015
Expires: 2/4/2016 Approved: 1/28/2015

Your approved protocol is effective until 2/4/2016. To remain open, your protocol must be renewed on an annual basis and cannot be renewed beyond 2/4/2017. For the activities to continue beyond 2/4/2017, a new protocol application must be submitted.

ORC will notify you of the protocol's upcoming expiration roughly 30 days prior to 2/4/2016. You, as the PI, have the primary responsibility to ensure any forms are submitted in a timely manner for the approved activities to continue. If the protocol is not renewed before 2/4/2016, the protocol will be closed. If you wish to continue the activities after the protocol is closed, you must submit a new protocol application for IACUC review and approval.

You must notify the IACUC of any additions or changes to your approved protocol using a Modification Form. The IACUC must review and approve the modifications before they can begin. When your activities are complete or discontinued, please submit a Final Report. An executive summary or other documents with the results of the research may be included.

All forms are available on the ORC website at <http://goo.gl/UB1CIF>

Please direct any questions or concerns to ORC at 426-5401 or animalcare@boisestate.edu.

Thank you and good luck with your research.

Dr. Ken Cornell
 Chair
 Boise State University Institutional Animal Care & Use Committee