

Toward a Foundation for Determining the Ecological Effects of Climate Change on
Arctic Ecosystems: Dietary Composition of and Overlap Between Two Avian Apex
Predators on the Seward Peninsula, Alaska

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ABSTRACT

Temporospatial patterns of temperature and precipitation are changing rapidly in arctic ecosystems, but the long-term effects of these changes on species interactions and energy flow are poorly understood. I sought to provide baseline data for understanding the effects of climate change by evaluating the diets of two avian apex predators in Alaska, the Golden Eagle (*Aquila chrysaetos*) and Gyrfalcon (*Falco rusticolus*). Specifically, I focused on (1) identifying the primary prey species and dietary breadth of Golden Eagles, (2) comparing the diets of Golden Eagles at successful and unsuccessful nest sites, and (3) comparing the diet of sympatric Golden Eagles and Gyrfalcons on the Seward Peninsula. I hypothesized that diets would vary between successful and unsuccessful nests of Golden Eagles due to energy requirements of young. Additionally, I predicted that while diets of Golden Eagles and Gyrfalcons would overlap, significant partitioning would occur among prey taxa that were common in both diets, consistent with niche theory and specialization. I estimated composition of Golden Eagle diet by analysis of regurgitated pellets and prey remains collected at 32 occupied nest sites (11 successful) in July 2014, and Gyrfalcon diet was estimated by direct observation at 10 successful nest sites May-July 2014. I found that the diets of both raptors consisted primarily of arctic ground squirrel (*Urocitellus parryii*) and ptarmigan (*Lagopus spp.*), but the relative proportions of these prey were reversed, with Golden Eagles preying more on squirrel (57% vs. 15% for Gyrfalcons), and Gyrfalcons preying more on ptarmigan (78% vs. 15% for Golden Eagles). The diets of Golden Eagles occupying successful and unsuccessful nests may vary but overlapped in composition by 99%. The breadth of Golden Eagle diet was significantly greater than that of Gyrfalcons, yet their diets overlapped in composition by 45% and was significantly different. These results help illuminate the

shared niche space of and competition for prey between Golden Eagles and Gyrfalcons and, potentially, variation between these predators' abilities to adapt to the effects of climate change, as changes in ptarmigan distribution and abundance are expected in Alaska. Additionally, these data help provide a baseline for future study of the effects of climate change on inter- and intratrophic interactions in arctic ecosystems.

INTRODUCTION

Many of Earth's ecosystems are expected to respond to climate change heterogeneously through time and space (Walther et al. 2002). Arctic ecosystems are complex and sensitive and currently are responding uniquely to altered temporospatial patterns of temperature and precipitation (Hinzman et al. 2005, Serreze et al. 2000). Attributable to environmental feedbacks, the Arctic's responses are predicted to be amplified, lead to system-wide changes, and be detected earlier than in ecosystems at lower latitudes (Hinzman et al. 2005, Serreze et al. 2000).

The broadest impacts to be seen in the Arctic are expected to be the result of changes in permafrost (Hinzman et al. 2005), following warming trends and changes in snow cover (Osterkamp 2007). The Arctic landscape currently is experiencing alterations in hydrologic processes, such as talik formation, plant communities, such as shrub invasion and treeline advance, and active layer processes (Hinzman et al. 2005, Serreze et al. 2000, Sturm et al. 2001, Osterkamp 2007). Thermokarsting, the process of ice-rich permafrost melting, is drastically altering the boreal forest ecosystem in interior Alaska by destroying its physical foundation (i.e. permafrost) and allowing moisture-dominated ecosystems (e.g., bog, fen, pond, etc.) to develop in its place (Osterkamp et al. 2000, Jorgenson et al. 2001). Thermokarsting and similar effects are being observed in tundra

ecosystems on the North Slope and Seward Peninsula of Alaska (Hinzman et al. 2005, Yoshikawa and Hinzman 2003).

The unique, arctic ecosystems rely on strong seasonal fluctuations in temperature and weather patterns to sustain functioning (Hinzman et al. 2005). Changes occurring to ice and snowpack are causing a positive feedback due to shifting of the annual radiation balance, hastening warming and climatic change at high latitudes (Hinzman et al. 2005, Serreze et al. 2000). Such changes will have cascading effects on ecosystems (Ernakovich et al. 2014, Ims and Fuglei 2005). For example, permafrost degradation and changes in nutrient cycling will alter spatial and temporal vegetation patterns and plant community structure (Ernakovich et al. 2014, Hinzman et al. 2005, Osterkamp et al. 2000, Jorgenson et al. 2001), having bottom-up effects on energy flow to herbivores and, indirectly, predators (Ims and Fuglei 2005). Similarly, changes in weather patterns could effect populations of top predators, which would disrupt top-down ecosystem controls. For example, a long-term decline in a population of Peregrine Falcons (*Falco peregrinus*) in Greenland could be attributed to an increasing frequency of heavy rainfall during the breeding season (Anctil et al. 2014). Large-amplitude, multiannual population cycles, such as that of the snowshoe hare (*Lepus americanus*), which are generally controlled by an interaction between predation and food (Krebs et al. 2001), will be altered if the delicate balance of spatiotemporal patterns in climate is disrupted (Ims and Fuglei 2005).

Considering that arctic ecosystems are composed of relatively simple food webs (Ims and Fuglei 2005), the impending effects of climate change become of greater concern. Nonlinear models show that complexly structured food webs with many weak or intermediate strength trophic interactions should exhibit dampened oscillatory

behavior, keeping species' populations further from extirpation, while simpler food webs with stronger interactions promote large-amplitude oscillations, allowing populations to approach closer to extirpation (McCann et al. 1998). Examples of such large-amplitude oscillations might include cyclic snowshoe hare and lemming (*Lemmus spp.*) populations persisting in the Arctic. While the cycles of such herbivore populations might be the most obvious and well-documented examples, there is evidence indicating that populations throughout characteristic food webs oscillate, often synchronously (Boutin et al. 1995, Ims and Fuglei 2005, Krebs et al. 2001, McIntyre and Adams 1999). Thus, disruption of one or multiple of these large-amplitude population cycles could have cascading trophic effects, particularly in the Arctic, where simple food webs and ecosystem functioning persist in delicate balance with the climate.

As discussed above, recent and ongoing research, such as that conducted at the Alaska Climate Science Center (University of Alaska Fairbanks), underscore the effects that climate change is having on Arctic systems (Walsh et al. 2011). However, while previous studies have established a general framework for understanding effects of climate change on arctic ecosystems, more research is needed to divulge exactly how. Understanding trophic interactions within Arctic ecosystems would help the development of management strategies aimed at mitigating the impending impacts of climate change; however, few data exist on the topic. Therefore, it is imperative to focus research on trophic interactions in the Arctic. Because responses to climate change at high latitudes will likely be detected prior to those at lower latitudes (Hinzman et al. 2005, Serreze et al. 2000), mitigation strategies for the Arctic could be used as baselines for ecosystems in temperate regions. To help understand trophic interactions we can study the ecological

niches of top predators, as multiple dimensions of their niche space determine the distribution and abundance of species (Brown 1984).

Inhabiting space with limited resources can force competitive interactions among sympatric species, including top predators (Pianka 1981), and as climate change has the potential to alter the spatiotemporal distribution and abundance of resources, especially in the Arctic (Hinzman et al. 2005), such interactions could be modified as well.

Foundational to understanding these interactions is the theory behind the ecological niche. Hutchinson (1957) described the ecological niche as a two-level hypervolume, or multidimensional space, occupied by a species or individual. The first level, deemed the fundamental niche, is the maximum space in which environmental variables (i.e. abiotic) allow the species or individual to occupy. The second operates on the fact that species and individuals exist in competition (i.e. inter- and intraspecific) with one another, thereby reducing the inhabitable hypervolume by a function of biotic factors. This reduced space is called the realized niche. While studying the fundamental niche spaces of both predators and prey can yield interesting and relevant findings (see Booms et al. 2011), because species and individuals can only persist in their realized niche spaces, focusing research on realized niches can help elucidate ecological patterns. Although often difficult to study due to their multidimensionality and reliance on other species, addressing key dimensions of realized niche spaces, such as food habits, of species with ecological roles important to the functioning of ecosystems, namely top predators, are critical steps in revealing such patterns.

Raptors are top predators in the Arctic, functioning as top-down ecosystem controls to help maintain healthy systems (Ims and Fuglei 2005). Without such controls,

Arctic ecosystems could be at risk to trophic cascade, especially considering the delicate inter-annual and interrelated population cycles of some prey species (Ims and Fuglei 2005, Krebs et al. 2001). Studying the food habits of raptors is fundamental in understanding their realized niche spaces (i.e. in the dimension of diet) and can elucidate inter- and intraspecific interactions as well as other aspects of community ecology (Marti et al. 2007). Despite raptors being imperative to the functioning of arctic ecosystems, there is a scarcity of data on the niches of raptors in arctic ecosystems. I sought to address this gap by collecting baseline data on the diets of two avian apex predators, thereby providing a requisite foundation for longer-term investigations of the ecological effects of climate change on arctic ecosystems.

The Golden Eagle (*Aquila chrysaetos*) and Gyrfalcon (*Falco rusticolus*) breed sympatrically throughout much of Alaska. While Golden Eagles breed in Alaska, adults and juveniles generally winter at lower latitudes unless prey is enough in abundance to support them through the Alaskan winter (Kochert et al. 2002, Kessel 1989). Adult Gyrfalcons breeding in Alaska are likely sedentary or make only short-distance seasonal movements (Booms et al. 2008; T. Booms, unpubl. data), while young-of-the-year exhibit more-sporadic movements in the fall and winter (McIntyre et al. 2009; Booms et al 2008; T. Booms, unpubl. data). While Golden Eagles and Gyrfalcons both require similar nesting habitat (i.e. cliffs, rock outcroppings, riparian banks, or manmade structures) in Alaska (Kochert et al. 2002, Booms et al. 2008), Golden Eagles are generalist predators, preying or scavenging on small to large avian and mammalian taxa in addition to, although less common, fish and reptiles (Kochert et al. 2002), and Gyrfalcons are more specialized, particularly toward ptarmigan (*Lagopus spp.*; Booms et al. 2008).

In Alaska, the diet of Golden Eagles is understudied, especially in the western region of the state. Although a relatively extensive dataset exists for Denali National Park and Preserve (Kochert et al. 2002; C. McIntyre, unpubl. data), only three documents providing information about the diet of Golden Eagles exist in the published literature, none of which resulted from studies focused on quantifying diet nor report data collected within the last 30 years (Mindell 1983, Ritchie and Curatolo 1982, Petersen et al. 1991). Consequently, the niche space of Alaska's migratory population of Golden Eagles is poorly understood.

The primary goal of this research was to evaluate the diet of Golden Eagles breeding on the Seward Peninsula in an attempt to understand a dimension of their niche space and how that space was related to breeding success and the niche of sympatric Gyrfalcons. This study is the first with a focus of quantifying the diet of Golden Eagles in Alaska and provides baseline data to aid in understanding the ecological effects of climate change on Arctic ecosystems. I hypothesized that, given the few data available for Alaska and data from the contiguous United States, their diet would consist primarily of arctic ground squirrel (*Urocitellus parryii*) and snowshoe hare but be quite diverse overall. I also sought to determine if any dietary differences existed between Golden Eagles at successful and unsuccessful nests (i.e. nests with and without young present when visited). While total biomass consumed would be expected to vary between Golden Eagles at successful and unsuccessful nests (Watson 2010), variation in diet between has yet to be investigated. Diet composition and prey size seem to vary with nest success in other raptor species (Barrows 1987), so I predicted that I would find a similar pattern for Golden Eagles due to the need for pairs at successful nests to provision

young, which would correspond to slight variation in the realized niche spaces of successful and unsuccessful pairs. Lastly, in an attempt to understand how the niche spaces of two sympatric top predators might be related and to further comprehend how climate change might affect arctic ecosystems, I compared the diets of Golden Eagles and Gyrfalcons breeding sympatrically on the Seward Peninsula, AK. Due to the available prey taxa on the Seward Peninsula, I hypothesized that their diets would overlap; however, considering the findings of similar studies (see Reynolds and Meslow 1984) as well as niche and competition theory, I also predicted that there would be significant partitioning among prey taxa common in the diets of both species.

In addition to providing much-needed data on the basic ecology of Golden Eagles in Alaska and investigating the questions regarding niche spaces above, the results reported herein provide baseline data to aid in understanding the effects of climate change on arctic ecosystems.

METHODS

Study Area

My study area was located on the Seward Peninsula, AK in an approximately 160-km radius of Nome, AK (Figure 1). The Seward Peninsula ranges from 64-67° N latitude and extends 320 km into the interface between the Pacific and Arctic Oceans, with the Bering Sea (Pacific Ocean) to the south and the Chukchi Sea (Arctic Ocean) to the north. It lies largely north of the arctic timberline within the tundra region with scattered areas of spruce (*Picea spp.*) and small cottonwood (*Populus tacamahacca*) stands. Dwarf shrubs, sedges, grasses, mosses, and other herbaceous plants dominate the tundra, but willow (*Salix spp.*) and alder (*Alnus spp.*) can be found along watercourses

and well-drained slopes, respectively (Hopkins and Sigafos 1950). Cliffs, rock outcroppings, large riparian banks, and mountain ranges, such as the Kigluaik, are distributed throughout the Seward Peninsula, providing suitable nesting habitat for Golden Eagles and Gyrfalcons (Figure 2). Such components constitute a relatively diverse matrix of habitats distributed across the landscape of the area. A history of mining on the Seward Peninsula has left the area littered with manmade structures (e.g., dredges and cabins), which also provide nesting habitat for Golden Eagles and Gyrfalcons (Figure 3). Ptarmigan (*Lagopus spp.*), tundra hare (*Lepus othus*), snowshoe hare, arctic ground squirrel, and several species of migratory birds inhabit the Seward Peninsula during the summer, which serve as potential prey species for breeding Golden Eagles.

Golden Eagle Diet

I visited 32 occupied Golden Eagle nest sites on the Seward Peninsula in July 2014, either on foot from the nearest road or by helicopter. I attempted to collect all regurgitated pellets (i.e. whole and partial; hereafter pellets) and uneaten prey remains (hereafter prey remains) present in/on, around, and under all accessible nests and apparent perches at each site. I visited each site once and searched for pellets and prey remains for 0.5-1 hrs, depending on the rate at which I was finding samples. If prey remains were large or appeared as though they could still be used as a source of food, I did not collect them but did document them to include in the data. I identified partial pellets as those that I could not confidently conclude had not broken into multiple pieces. Whole pellets were those that had obviously not been broken into multiple pieces. Additionally, if I found multiple partial pellets in the same area that could easily

be pieced together to comprise a whole pellet and I was confident that such pieces came from a single whole pellet, I documented and analyzed them as a single whole pellet.

I dissected pellets and analyzed prey remains in the lab and identified the minimum number of prey items by evaluating characteristic body parts (e.g., feet, mandibles, teeth, etc.) and bones (e.g., sterna, femurs, etc.). Because I was only able to visit each nest site once during the field season, it was sometimes difficult to confidently identify pellets and prey remains that were (1) from a Golden Eagle and (2) from the 2014 breeding season. To minimize the possibility of analyzing misrepresentative samples, I assigned each pellet a value of 1-5, where a value of 1 represented the least confidence in the accuracy of my identifications, and a value of 5 represented the most confidence. I determined pellet assignments by evaluating the size, composition, and state of weathering of each pellet. I only used data resulting from pellets assigned values 4 and 5 for analyses. Similarly, I only included prey remains that were collected at sites where Golden Eagles were the only raptor detected (i.e. via Alaska Department of Fish & Game surveys and/or presence of molted feathers) and that were not significantly weathered in the dataset. I identified each prey item to at least the taxonomic rank of avian order or mammalian family, which were the prey categories used for analyses. I only counted multiple individuals if I identified replicate body parts and/or bones. Note: feathers were used for taxa identification but not to positively identify the presence of multiple prey items. I identified most prey items macroscopically, but in many cases, feathers required microscopic analysis. I followed Dove and Koch (2010) for feather microscopy. To identify prey items macroscopically, I used the samples collected in the field, the U.S. Fish & Wildlife Service Forensics Laboratory's Feather Atlas, and Jones

and Manning (1992) as references. If I was unable to identify a prey item, I consulted Drs. Brian D. Linkhart and/or Liesl P. Erb (Department of Organismal Biology and Ecology, Colorado College), Dr. Travis L. Booms (Alaska Department of Fish & Game, Wildlife Diversity Program), Bryce W. Robinson (Raptor Research Center, Boise State University), and/or Michelle Cason (Institute of Arctic Biology, University of Alaska Fairbanks).

I estimated prey biomass for each prey category by multiplying the minimum number of prey items in each by body mass estimates (Marti et al. 2007). I obtained body mass estimates from the scientific literature, when available, to generate body mass estimates representative of each prey category. For prey items that I identified to a taxonomic level more specific than the prey categories, I used body mass estimates that most closely represented each taxon. I took the sum of prey biomass estimates across taxa within each prey category to obtain the final prey biomass estimate for each prey category. I calculated relative prey biomass by dividing the prey biomass for each prey category by the total prey biomass. To avoid biases, I did not include large prey taxa that were most likely scavenged (i.e. Cervidae and Canidae) in prey biomass calculations.

Gyr Falcon Diet

I obtained raw data that was collected using direct observation via motion-triggered camera traps from Bryce W. Robinson and Dr. David L. Anderson (The Peregrine Fund). The cameras were deployed at 10 occupied Gyr Falcon nest sites (all successful) on the Seward Peninsula in May 2014 to capture prey deliveries throughout the breeding cycle. The cameras were mounted directly to the face of the nest cliff and oriented to capture the adults entering the nest. A total of 816 prey deliveries were

recorded, with 749 prey items identifiable to avian order or mammalian family and 799 to class (i.e. avian or mammalian). I calculated prey biomass and relative prey biomass using the same method that I used for Golden Eagles.

Data Analyses

Quantifying the diet of raptors by analysis of pellets and prey remains has been shown to be biased towards mammalian and avian prey, respectively, and each method can yield results that vary by greater than 20% of what can be found with direct observation, which is considered the least biased method of quantifying raptor diet (Simmons et al. 1991, Lewis et al. 2004). Consequently, I pooled the pellets and prey remains data to minimize bias in my quantification of Golden Eagle diet. Such a procedure allows results obtained by indirect methods of quantifying raptor diet (e.g., analysis of pellets and prey remains) to approach results obtained by direct methods (e.g., direct observation; Simmons et al. 1991, Collopy 1983). As I collected three types of samples (i.e. whole pellets, partial pellets, and prey remains) to quantify the diet of Golden Eagles, I assumed each to be independent and any inherent biases resulting from the combination of such into a single dataset to be negligent. Based on observations made in the field and methods used by Lewis et al. (2004), I believed this to be a fair assumption.

To evaluate my first hypothesis, I examined the relative contribution of each prey category by prey biomass to the diet of Golden Eagles across all nest sites. Additionally, I calculated Simpson's diversity index (D) with the equation:

$$D = \sum_{i=1}^n p_i^2,$$

where

p = the relative proportion of the minimum number of individual prey items in the i th prey category,

and Shannon's diversity index (H) with the equation:

$$H = - \sum_{i=1}^n p_i \ln p_i ,$$

where

p = the relative proportion of the minimum number of individual prey items in the i th prey category,

across all nest sites to help evaluate dietary breadth (Simpson 1949, Shannon 1948). I report both indices so as to gain a more complete understanding of dietary diversity.

While both incorporate richness and evenness to represent diversity, Simpson's index places more weight on evenness and Shannon's more weight on richness (DeJong 1975, Marti et al. 2007).

To compare the diets of Golden Eagles at successful and unsuccessful nest sites, I first grouped the data by the two qualifiers. I then compared the dietary compositions of each group by performing Fisher's exact tests with Monte Carlo-simulated P -values (1×10^6 replicates; i.e. when contingency table was larger than 2×2) on the minimum number of individuals for each prey category using R version 2.15.3 (R Core Team 2013). To compare dietary breadth, I calculated Simpson's and Shannon's diversity indices for each group and conducted a modified two-sample t -test between groups for each index (Simpson 1949, Hutcheson 1970). To understand overlap in dietary composition, I calculated Pianka's index (O) with the equation:

$$O_{jk} = O_{kj} = \frac{\sum_i^n P_{ij}P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}},$$

where

p = the relative proportion of the minimum number of individual prey items in the i th prey category for species j and k (Pianka 1973).

To compare diet along the prey size axis, I first calculated mean prey mass for successful and unsuccessful nests by taking the mean of the body mass estimates applied to each prey item (Marti et al. 2007, May and MacArthur 1972, Steenhof and Kochert 1985). I then compared the mean prey mass for successful and unsuccessful nests with a two-sample t -test in R, which does not assume equal variances and applies Welch's approximation. Because the masses of prey items were not normally distributed, I performed the two-sample t -test after transforming the data by taking the natural logarithm of the mass of each prey item. Lastly, using the transformed data, I calculated the d/w ratio for the mean prey mass of successful and unsuccessful nests, where d is the difference between the mean of the transformed prey masses for each group and w is the average of the standard deviations (May and MacArthur 1972, Jaksic and Braker 1983, Steenhof and Kochert 1985), which provided the number of standard deviations between the mean prey mass of each group.

To compare the diets of Golden Eagles and Gyrfalcons, I evaluated variation in and overlap of dietary composition, dietary breadth, and mean prey mass, as described above for the intraspecific comparisons. Because all of the Gyrfalcon nest sites were successful, I compared the diet of Gyrfalcons and the diet of Golden Eagles at successful

nests. When necessary, I adjusted prey body mass estimates used to estimate prey biomass so that they matched for both Gyrfalcons and Golden Eagles. Note that I compared data resulting from the analysis of pellets and prey remains to data resulting from direct observation; however, as justified above, I assumed this to be a fair comparison.

All means are presented \pm one standard deviation, and statistical significance was evaluated at $P < 0.05$.

RESULTS

I visited a total of 32 Golden Eagle nest sites, 11 of which were successful, on the Seward Peninsula, AK in July 2014. I collected a total of 266 pellets (i.e. whole and partial; $\mu = 8.3 \pm 10.25$ per site) and identified a minimum of 388 individual prey items ($\mu = 12.1 \pm 13.63$ per site), which spanned 14 prey categories ($\mu = 3.1 \pm 1.40$ per site). 65.8% of the total number of pellets sampled and 69.6% of the individual prey items identified came from successful nest sites.

Golden Eagle Diet

Arctic ground squirrel and ptarmigan were the primary prey of Golden Eagles on the Seward Peninsula, representing approximately 57% and 15% of diet by prey biomass, respectively (Table 1, Figure 4). However, the diet of Golden Eagles was quite diverse overall, comprised of seven avian orders and seven mammalian families (Table 1). Simpson's and Shannon's diversity indices were 0.38 (D) and 1.39 (H), exhibiting 2.63 ($1/D$) and 4.01 (e^H) effective prey categories, respectively (Jost 2006).

Diets at Successful and Unsuccessful Golden Eagle Nests

Diets of Golden Eagles at successful and unsuccessful nests on the Seward Peninsula appeared to vary little. A Fisher's exact test comparing the minimum number of individual prey items across all 14 prey categories between the two groups yielded a nearly significant difference ($P = 0.052$). However, post hoc tests including only the prey categories with a minimum of five individual prey items and the two primary prey categories did not divulge any variation between the two groups ($P = 0.11$ and $P = 0.48$, respectively; Figure 5). Similarly, a third post hoc test with the data grouped as mammalian and avian prey did not result in a significant difference ($P = 1$). Relative proportions of the minimum number of individual prey items and prey biomass across prey categories were comparable between the two groups; however, the nature of the prey biomass data inhibited conducting similar quantitative comparisons. Additionally, dietary diversity did not vary between successful and unsuccessful nests ($P > 0.05$; Table 2). Although mean prey mass appeared to be greater at unsuccessful nests, being only 0.16 standard deviations from the mean prey mass at successful nests, it did not vary significantly between the two groups ($P = 0.17$; Table 3). 99% compositional overlap further supports that the diets of eagles at successful and unsuccessful nests were quite similar (Table 3).

Diets of Golden Eagles and Gyrfalcons

Diets of sympatrically nesting Golden Eagles and Gyrfalcons on the Seward Peninsula varied across all dimensions of diet measured. Gyrfalcon diet spanned only two mammalian families and four avian orders while Golden Eagle diet was composed of seven mammalian families and seven avian orders. A Fisher's exact

test comparing the minimum number of individual prey items across all 14 prey categories between the two groups yielded a significant difference ($P < 0.001$). Post hoc tests including only the prey categories with a minimum of five individual prey items and the two primary prey categories elucidated the source of variation between the Golden Eagles and Gyrfalcons ($P < 0.001$ and $P < 0.001$, respectively), which appeared to be the nearly reversed proportions of arctic ground squirrel and ptarmigan in their diets (Figure 6). Similarly, a third post hoc test with the data grouped as mammalian and avian prey resulted in a significant difference ($P < 0.001$), and again, the proportions were nearly reversed for the diets of the two species (Figure 7). Although quantitative analyses were carried out only on the frequency data due to statistical limitations, the above patterns were consistent with the relative prey biomass data. Additionally, dietary diversity and mean prey mass were greater in Golden Eagles than in Gyrfalcons ($P < 0.05$ and $P < 0.001$, respectively; Table 2, 3). While mean prey mass was significantly greater for Golden Eagles, it was only 0.57 standard deviations above the mean prey mass of Gyrfalcons (Table 3). This overlap along the prey size axis coupled with a compositional overlap of 45% (Table 3), indicate the existence of shared niche space between these two sympatric breeding populations of Golden Eagles and Gyrfalcons.

DISCUSSION

Golden Eagle Diet on the Seward Peninsula

I determined the primary prey of Golden Eagles breeding on the Seward Peninsula, AK to be arctic ground squirrel and ptarmigan (Table 1, Figure 4). This

finding is inconsistent with data from elsewhere in Alaska (C. McIntyre, unpubl. data; Mindell 1983; Ritchie and Curatolo 1982; Petersen et al. 1991). Although an extensive dataset from Denali National Park and Preserve (hereafter Denali) does show that arctic ground squirrel is a primary prey species of Golden Eagles, the second most common prey recorded there was snowshoe hare (C. McIntyre, unpubl. data). Additionally, McIntyre and Adams (1999) showed that Golden Eagle productivity was correlated with the abundances of Willow Ptarmigan and snowshoe hare in Denali, which indicates that these prey species are important to Golden Eagles in Alaska. Interestingly, I did not document any snowshoe hare in the diet of Golden Eagles (Table 1), which may indicate geographic variation in Golden Eagle dietary preferences in Alaska or be a result of low abundances of snowshoe hare on the Seward Peninsula in 2014. Snowshoe hare abundance data does not exist for the Seward Peninsula, so I cannot confidently draw a conclusion. However, observations made in the field, the data reported herein, and data from elsewhere in Alaska (see Merizon 2013) lead me to believe that snowshoe hare were at a lower point in their population cycle. Evidence that Golden Eagles depend on prey species that exhibit large amplitude, multiannual cycles should generate conservation concern, as Ims and Fuglei (2005) predicted that such cycles will be, and may already have been, disrupted by climate change.

The diet of Golden Eagles on the Seward Peninsula was quite diverse, spanning seven mammalian families and seven avian orders. Taking into account dietary richness and evenness, Simpson's (D) and Shannon's (H) diversity indices showed that this population of Golden Eagles utilized between 2.63 ($1/D$) and 4.01 (e^H) effective prey categories. While Steenhof and Kochert (1988) reported a dietary breadth (equivalent to

I/D) of 3.81 for Golden Eagles in Idaho, they categorized prey into “species” and “genus,” which would inflate their dietary breadth calculations in relation to mine. As my prey categories were broader (i.e. family or order) and data spanned 14 prey categories, the diet of Golden Eagles breeding on the Seward Peninsula was likely more diverse than those breeding in Idaho. Additionally, Steenhof and Kochert (1988) showed that the dietary breadth of Golden Eagles in Idaho was inversely correlated with the abundance of their preferred prey (i.e. black-tailed jackrabbit *Lepus californicus*). Although abundance data does not exist for arctic ground squirrel, ptarmigan, or hare on the Seward Peninsula, as stated above, I believe that at least snowshoe hare were at a lower point in their population cycle. Coupled with the fact that snowshoe hare have been shown to be a primary prey species of Golden Eagles elsewhere in Alaska (C. McIntyre, unpubl. Data, Mindell 1983, Ritchie and Curatolo 1982, Petersen et al. 1991), the high diversity in Golden Eagle diet that I found might be, in part, due to relatively low abundances of prey or potential prey species on the Seward Peninsula. However, I cannot confidently draw conclusions about prey selectivity or preference without prey abundance data. The dietary breadth of Golden Eagles on the Seward Peninsula was likely significantly reduced early in the breeding season. Prior to the arrival of migrants and emergence of arctic ground squirrels, snowshoe hare and ptarmigan are essentially the only prey available to Golden Eagles. McIntyre and Adams (1999) suspected this to be the case in interior Alaska. Although Golden Eagles exhibit a relatively high degree of dietary plasticity (Steenhof and Kochert 1988), the reduction of available prey during a critical phonological period could leave Alaska’s breeding population of Golden Eagles vulnerable to the potential bottom-up effects of climate change.

While total biomass consumed would be expected to vary between Golden Eagles at successful and unsuccessful nests (Watson 2010), this is the first time that variation in diet between has been investigated. Diet composition and prey size seems to vary with nest success in other raptor species (Barrows 1987), so I predicted that there would be variation between the diets of Golden Eagles at successful and unsuccessful nests. However, I did not find support for this hypothesis. Despite a near significant P -value for the prey category-wide comparison (i.e. 0.052), more-specific post hoc tests divulged that this result was not due to differences in prey categories that represented the majority of diet, both in frequency and prey biomass. Lending further support to the conclusion that the diets, and thus realized niche spaces in the dimension of diet, of Golden Eagles at successful and unsuccessful nests did not vary, dietary breadth and prey size did not prove to be significantly different between the two groups (Table 2, 3). Additionally, there was considerable overlap along the prey size axis as well as near complete overlap in dietary composition (Table 3). My hypothesis was based on dietary differences arising from differential selection of prey species by individuals provisioning for only themselves and those provisioning for young. I suspected that the requirement of Golden Eagles with young to carry prey from its location of capture to the nest would cause their diet to diverge from the diet of Golden Eagles at unsuccessful nests due to energy tradeoffs. Given the near significant P -value of the prey category-wide comparison, more data over multiple years might elucidate a pattern; however, it is also possible that Golden Eagles without young simply consume the majority of their prey at the location of capture and only rarely leave evidence of it at their nest sites. Regardless, the results of estimating the diet of Golden Eagles at unsuccessful nests would inherently vary with the

date of nest failure and/or abandonment due to changes in relative abundances of prey species throughout the breeding season.

Diets of Sympatric Golden Eagles and Gyrfalcons

Diets of Golden Eagles and Gyrfalcons breeding on the Seward Peninsula varied significantly along all dimensions of diet measured. While the comparison including the relative minimum counts, which followed the same pattern as relative prey biomass, of all 14 prey categories was statistically significant, more-specific post hoc tests showed that the main source of variation was the nearly reversed proportions of arctic ground squirrel and ptarmigan in the diets of Golden Eagles and Gyrfalcons (Figure 6). Additionally, the relative proportions of mammalian and avian prey in dietary composition followed a similar trend (Figure 7). This is consistent with niche and competition theory (Pianka 1981) and Reynolds and Meslow (1984), who found that prey taxa varied with the body size of sympatric *Accipiter*. My finding that the diets of sympatric Golden Eagles and Gyrfalcons vary in the dietary dimension of taxonomic composition serves as evidence of niche segregation between the two species. Additionally, my findings that the diets of these two raptors vary significantly both in breadth and along the prey size axis provide two more examples of dietary dimensions in which segregation was apparent (Table 2, 3). Dietary breadth being greater in Golden Eagles might indicate that their dietary plasticity is greater than Gyrfalcons on the Seward Peninsula. Being a generalist predator, Golden Eagles should be able to shift preferences for prey taxa as relative prey abundances change. Steenhof and Kochert (1988) showed this to be the case for Golden Eagles in Idaho. Gyrfalcons, however, being a more-

specialized predator, might not have such ability. Thus, this interspecific variation in dietary breadth could indicate differential abilities of these two raptors to respond to changing relative abundances of prey, which, as discussed above, might be expected as climate change progresses. For further discussion, I will refer to the dietary dimension of the ecological niche as the “trophic niche” and dietary composition, dietary breadth, and prey size as dimensions of it.

Seemingly contrary to the niche segregation discussed above, though consistent with my hypothesis, the diets, and thus trophic niches, of Golden Eagles and Gyrfalcons overlapped considerably. I found compositional overlap to be approximately 45% and prey size to overlap by 0.57 standard deviations (Table 3). May and MacArthur (1972), incorporating small-scale environmental stochasticity and assuming a one-dimensional Gaussian niche, predicted that niche spaces of two sympatric species should be separated by 1-2 standard deviations (i.e. $d/w = 1-2$). Considering this as well as the compositional overlap, Golden Eagles and Gyrfalcons might have been in competition for prey; however, Abrams (1975) emphasized that resources are often partitioned along multiple dimensions and, therefore, $d/w = 1-2$ is not always a critical value for niche separation. Such multidimensionality might explain my results. First, it is important to note that spatial segregation did not seem to occur for Golden Eagles and Gyrfalcons on the Seward Peninsula, as their nest sites were fairly interspersed with some pairs nesting very close to others (Figure 1). While I did find considerable overlap in their trophic niches, the statistically significant differences between Golden Eagles and Gyrfalcons in all of the trophic niche dimensions investigated might indicate that these two species

have partitioned prey taxa sufficiently to avoid substantial competition. Additionally, regardless of the amount of trophic niche overlap among species, competition does not exist unless (1) resources are in limited supply (Lack 1944) and (2) the supply is limited through a significant portion of the species' life histories (Wiens 1977, Reynolds and Meslow 1984). Unfortunately, because prey abundance data is not available for the Seward Peninsula, I cannot confidently draw any conclusions about competition between sympatric Golden Eagles and Gyrfalcons, except that the potential for such does exist. This potential lies largely in that I found arctic ground squirrel and ptarmigan to be the primary prey of both Golden Eagles and Gyrfalcons on the Seward Peninsula. The reduced breadth of prey taxa available early in the breeding season could force competition for prey between Golden Eagles and Gyrfalcons during this critical period. Despite overall dietary breadth, such a limiting factor could indicate the vulnerability of these top predators to changes in the distribution and abundance of even a single prey taxon (i.e. ptarmigan, when hare abundances are low), which are predicted due to climate change (Booms et al. 2011).

Implications: Climate Change and Future Direction

Understanding the realized niche spaces of Golden Eagles and Gyrfalcons in Alaska is critical to forecasting their responses to climate change, as changes in the Arctic are already occurring. Even relatively simple investigations of the trophic niches of these avian predators, such as those reported herein, can yield significant findings.

The difference in trophic niche breadth that I found between Golden Eagles and Gyrfalcons might be indicative of variation in their abilities to respond to climate change. Booms et al. (2011) predicted that the distributions, and their overlap, of Gyrfalcons and ptarmigan in Alaska will change dramatically over the next 100 years. Additionally, Ims and Fuglei (2005) predicted that population cycles of species, such as snowshoe hare and ptarmigan, will be, and may already have been, disrupted by climate change because they lie in delicate balance with the climate. As I found ptarmigan to be primary prey of both Golden Eagles and Gyrfalcons on the Seward Peninsula, one would expect changes in both of their populations as well. Golden Eagles, being generalist predators and having the ability to shift preferences for prey species as discussed above, might be able to successfully respond to changes in distributions and relative abundances of prey species resulting from climate change. Contrarily, Gyrfalcons, being specialized towards preying on ptarmigan, might not have such ability.

Although this potential differential population robustness to climate change is superficially apparent, Boutin et al. (1995) showed that the abundances of many species, including arctic ground squirrel and ptarmigan, across multiple trophic levels in a food web are correlated with the population cycle of snowshoe hare. Additionally, McIntyre and Adams (1999) found that snowshoe hare and ptarmigan can cycle synchronously. Thus, the climate-related disruption of the population cycle of one species could have ecosystem-wide effects. It is important to recall, also, that prior to the emergence of arctic ground squirrels and arrival of migrants, snowshoe hare and ptarmigan are essentially the only prey species available to both

Golden Eagles and Gyrfalcons early in the breeding season (McIntyre and Adams 1999). This effectively reduces the trophic niche breadth of both species significantly during a critical phonological period, possibly leaving them equally vulnerable to future, climate-related changes in snowshoe hare and ptarmigan distributions and abundances.

Although I cannot draw many significant conclusions from my findings, the results I reported help provide a baseline for future study of the niche spaces of these avian apex predators in the Arctic. Such research would aid in divulging the impacts of climate change on arctic ecosystems, from which mitigation and management strategies could be developed. Additionally, as we are already seeing some of the early effects of climate change, this would provide a unique opportunity to investigate theoretical questions surrounding topics including trophic dysfunctioning and cascade, the ecological niche, and competitive exclusion.

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FIGURES AND TABLES

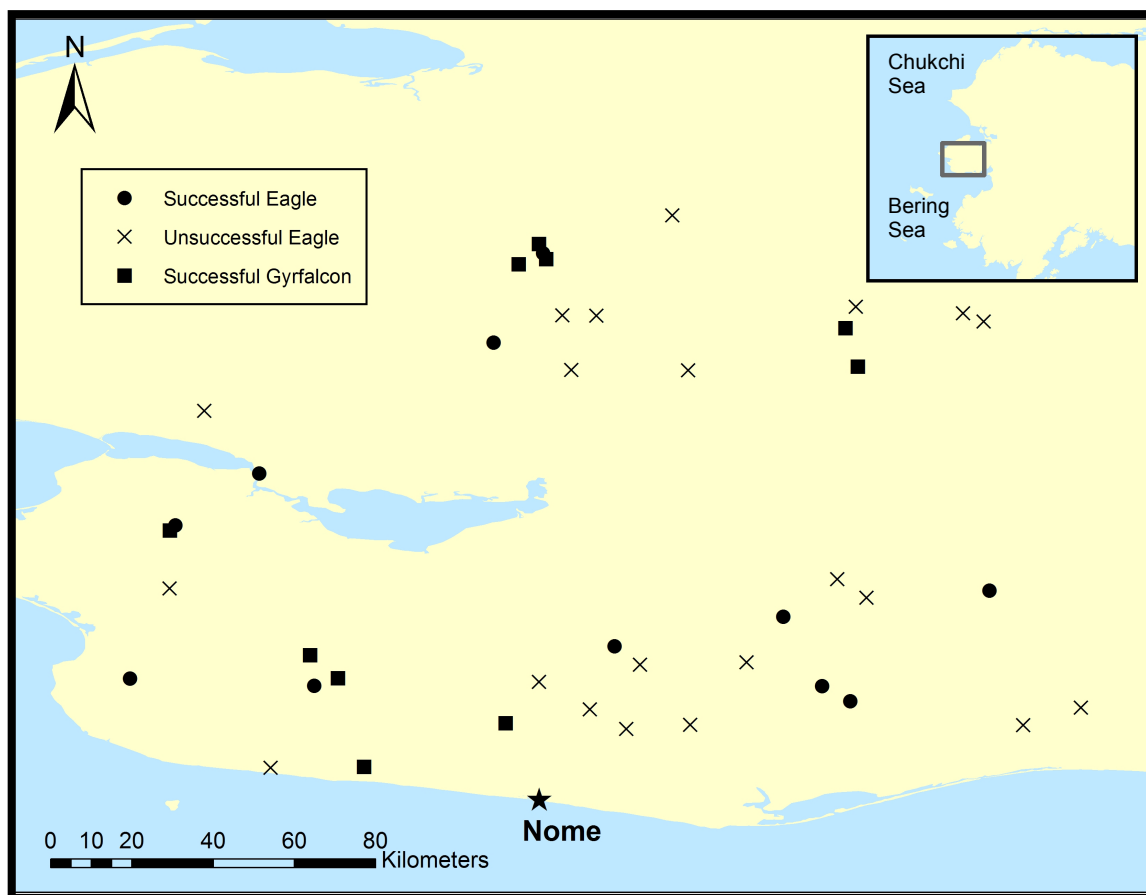


Figure 1. Map of study area, displaying nest sites of sympatrically breeding Golden Eagles and Gyrfalcons on the Seward Peninsula, AK, 2014.



Figure 2. Photograph of characteristic habitat surrounding Golden Eagle and Gyrfalcon nest sites on the Seward Peninsula, AK.



Figure 3. Photograph of manmade structure on the Seward Peninsula, AK, which could serve as a nest site for Golden Eagles or Gyrfalcons.

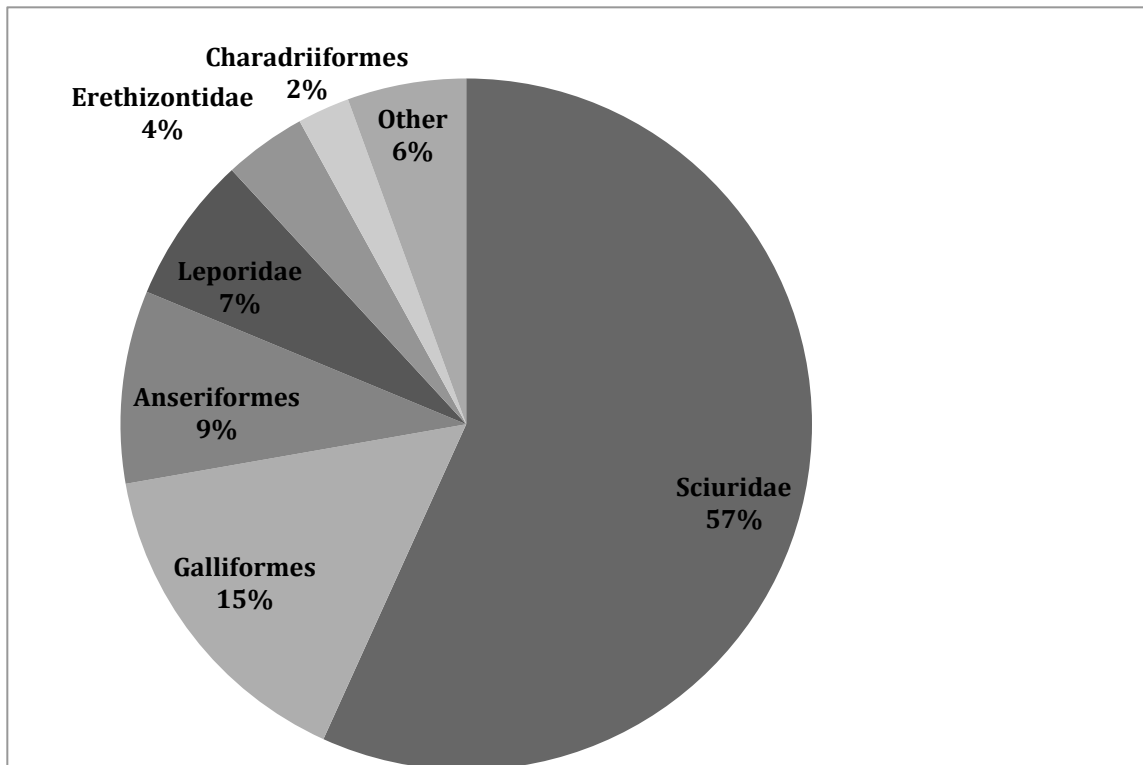


Figure 4. Dietary composition by prey biomass of Golden Eagles on the Seward Peninsula, AK, 2014. "Other" category composed of Accipitriformes (1.5%), Gruiformes (1.3%), Passeriformes (1.3%), Gaviiformes (1.3%), Cricetidae (0.2%), and Mustelidae (0.04%).

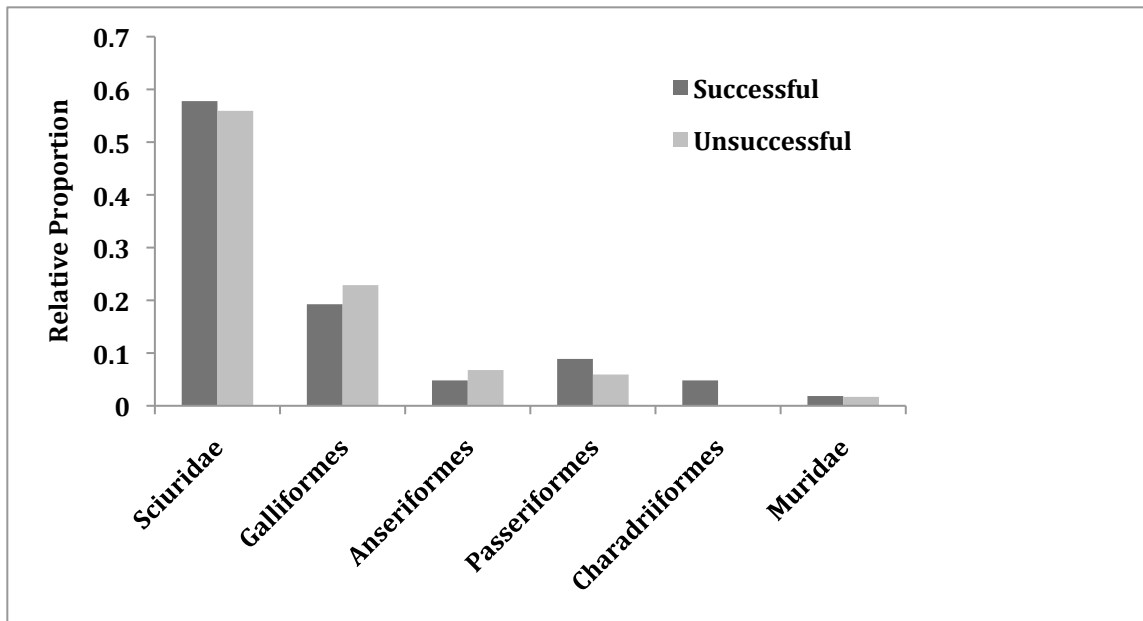


Figure 5. Bar graph of the relative proportions of the minimum number of prey items found in the prey categories with >5 prey items for the diets of Golden Eagles at successful and unsuccessful nest sites on the Seward Peninsula, AK, 2014. $P = 0.11$. Monte Carlo-simulated P -value (1×10^6 replicates) is the result of a Fisher's exact test.

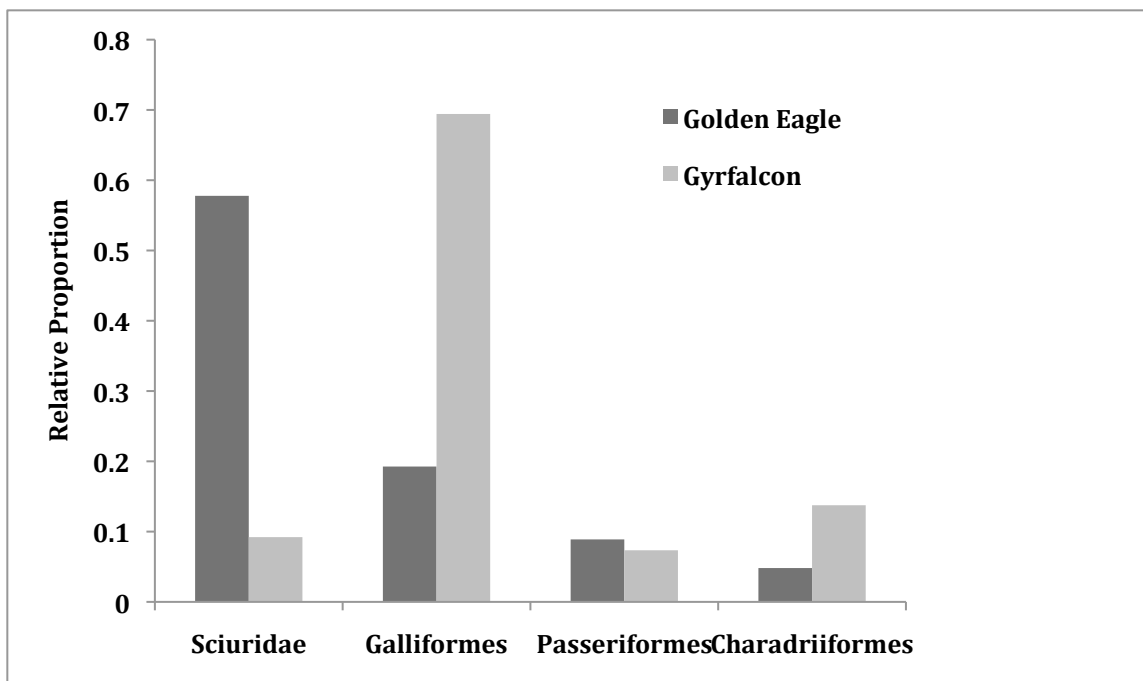


Figure 6. Bar graph of the relative proportions of the minimum number of prey items found in the prey categories with >5 prey items for the diets of Golden Eagles and Gyrfalcons on the Seward Peninsula, AK, 2014. $P < 0.001$. Monte Carlo-simulated P -value (1×10^6 replicates) is the result of a Fisher's exact test.

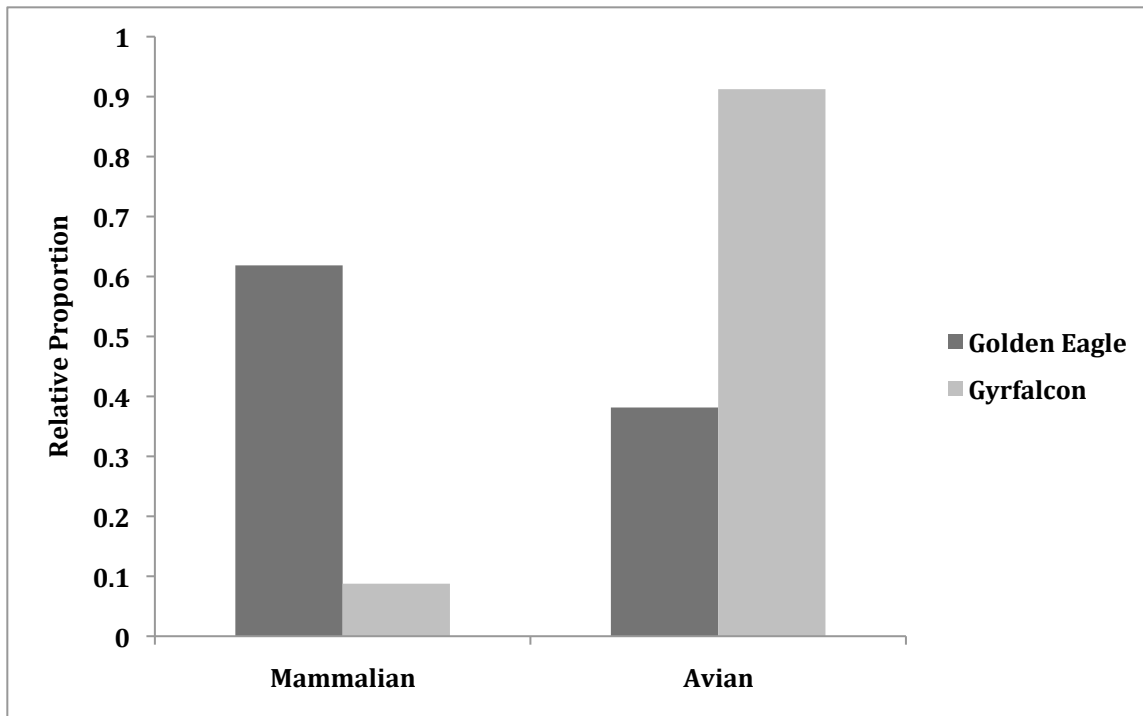


Figure 7. Bar graph of the relative proportions of the minimum number of mammalian and avian prey items for the diets of Golden Eagles and Gyrfalcons on the Seward Peninsula, AK, 2014. $P < 0.001$. P -value is the result of a Fisher's exact test.

Table 1. Minimum number of prey items, prey biomass, and relative prey biomass for the 14 prey categories comprising the diet of Golden Eagles on the Seward Peninsula, AK, 2014.

Prey Category¹	Minimum Number of Prey Items	Prey Biomass (g)	Relative Prey Biomass (%)²	Sources of Body Mass Estimates³
Sciuridae <i>Urocitellus parryii</i>	222	158281.56	56.78	1
Galliformes Phasianidae <i>Lagopus spp.</i>	79	43118.99	15.47	2, 3, 4, 5, 6, 7, 8
Passeriformes Turdidae <i>Turdus migratorius</i> <i>Oenanthe oenanthe</i> Calcariidae <i>Plectrophenax nivalis</i> Corvidae <i>Corvus corax</i>	31	3653.53	1.31	9, 10, 11, 12, 13, 14, 15, 16, 17, 18
Anseriformes Anatidae <i>Branta Hutchinsii</i> <i>Aythya marila</i>	21	25124.45	9.01	19, 20, 21, 22, 23
Charadriiformes Laridae <i>Stercorarius spp.</i> <i>Larus sp.</i> Charadriidae <i>Pluvialis sp.</i> Scolopacidae <i>Gallinago delicata</i>	13	6811.02	2.44	24, 25, 26, 27, 28, 29, 30, 31, 32, 33
Cricetidae <i>Lemmus spp.</i> <i>Dicrostonyx groenlandicus</i> <i>Microtus spp.</i>	7	470.39	0.17	46
Leporidae <i>Lepus othus</i>	4	19200.00	6.89	46
Cervidae <i>Rangifer tarandus</i>	4	-	-	46
Mustelidae <i>Mustela spp.</i>	2	110.75	0.04	46

Erethizontidae	1	10750.00	3.86	46
<i>Erethizon dorsatum</i>				
Accipitriformes	1	4229.25	1.52	34, 35
Accipitridae				
<i>Aquila chrysaetos</i>				
Gruiformes	1	3705.00	1.33	36
Gruidae				
<i>Grus canadensis</i>				
Gaviiformes	1	3325.45	1.19	37, 38, 39,
Gaviidae				40, 41, 42,
<i>Gavia sp.</i>				43, 44, 45
Canidae	1	-	-	46
<i>Canis sp.</i>				
Total	388	278780.39	-	-

¹ avian order and mammalian family. Other taxonomic classifications represent prey identified to aid in estimating biomass

² prey biomass for each prey category divided by total prey biomass

³ see Appendix

Table 2. Diversity indices, number of effective prey categories, and results of modified *t*-tests for Golden Eagles at successful and unsuccessful nest sites and Golden Eagles and Gyrfalcons on the Seward Peninsula, AK, 2014.

	Simpson's Index (<i>D</i>)	<i>1/D</i>	Shannon's Index (<i>H</i>)	<i>e^H</i>	Modified <i>t</i>-Test Result
Successful	0.38	2.6	1.34	3.8	
Unsuccessful	0.37	2.7	1.39	4.0	p > 0.05
Golden Eagle	0.38	2.6	1.34	3.8	
Gyrfalcon	0.51	1.9	0.96	2.6	p < 0.05

Table 3. Mean prey mass, results of *t*-tests, *d/w* ratios, and Piankas' indices for Golden Eagles at successful and unsuccessful nest sites and Golden Eagles and Gyrfalcons on the Seward Peninsula, AK, 2014.

	Prey Mass (g) ($\mu \pm SD$)	Transformed Prey Mass <i>ln</i>(g) ($\mu \pm SD$)	<i>t</i>-Test Result	<i>d/w</i>	Piankas' Index
Successful	671.1 \pm 478.70	6.26 \pm 0.871			
Unsuccessful	858.7 \pm 1170.93	6.40 \pm 0.885	p = 0.17	0.16	99%
Golden Eagle	665.6 \pm 484.58	6.25 \pm 0.868			
Gyrfalcon	407.5 \pm 194.75	5.72 \pm 1.00	p < 0.001	0.57	45%

APPENDIX

Sources of Prey Body Mass Estimates

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