Isotopic Niche Partitioning and Individual Specialization in an Arctic Raptor Guild

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Abstract

Intra- and inter-specific resource partitioning within predator communities is a fundamental component of trophic ecology, and one proposed mechanism for how populations partition resources is through individual niche variation. The Niche Variation Hypothesis (NVH) predicts that interindividual trait variation leads to functional trade-offs in foraging efficiency, resulting in populations comprised of individual dietary specialists. A modified version of the NVH [mNVH] predicts niche specialization is plastic and responsive to fluctuating resource availability. We quantified niche overlap and tested the mNVH within an Arctic raptor guild, focusing on three species that employ different foraging strategies: Golden Eagles (generalists); Gyrfalcons (facultative specialists); and Rough-legged Hawks (specialists). Tundra ecosystems exhibit cyclic populations of arvicoline rodents (lemmings and voles), providing a unique system under which to examine interannual fluctuations in predator resource availability. Using blood $\delta^{13}C$ & $\delta^{15}N$ values from 189 raptor nestlings on Alaska's Seward Peninsula (2014–2019), we calculated isotopic niche width and used Bayesian stable isotope mixing models (BSIMMs) to characterize individual specialization and test the mNVH. We observed a high degree of isotopic niche overlap between the three species and variable trophic responses to different stages of the arvicoline rodent cycle. Elevated arvicoline rodent abundance corresponded to reduced niche overlap among species and increased individual specialization in Golden Eagles and Gyrfalcons. Further, Gyrfalcons displayed a positive relationship between individual specialization and population niche width on an interannual basis consistent with the mNVH. Our findings suggest plasticity in niche specialization may reduce intra- and inter-specific resource competition under dynamic ecological conditions.

Introduction

Trophic ecology is largely centered on the concept of a realized trophic niche –described as all resources an organism actually consumes– which is inherently community-dependent and limited both by local resource availability and inter- and intra-specific competition (Hutchinson 1957). Analyzing trophic niche width can reveal spatial and temporal patterns in resource use, determine the degree of dietary generalism or specialization for a population, and serve as a metric of resource competition (Schoener 1982). Characterizing changes in an organism's trophic niche in response to dynamic ecological conditions can illuminate its role in greater ecosystem function as well as indicate its resilience to environmental change.

Two predominant paradigms exist to explain how a population may alter its trophic niche in response to variable environmental conditions: Optimal Foraging Theory (OFT; Macarthur & Pianka 1966), and the Niche Variation Hypothesis (NVH; Van Valen 1965). Classic OFT postulates that stabilizing selection leads to the evolution of behavioral strategies that maximize the net rate of energy intake – resulting in preferred diets that are consistent across all individuals within a population (Pyke et al. 1977). Conversely, the NVH posits that populations are comprised of individuals that specialize on different subsets of available diet items, and thus a generalized population's niche width reflects the combined niches of many individual specialists (Bolnick et al. 2002). Although the NVH was initially postulated in the context of evolved individual specialization in populations via destabilizing selection (Van Valen 1965), niche variation can also arise as a plastic response to variability in resource abundance, potentially acting as a mechanism for avoiding resource competition (mNVH [modified NVH]; Svanbäck & Bolnick 2005; Svanbäck & Bolnick 2007). Under increased resource abundance, populations aligning with the mNVH paradigm are predicted to expand their niche via increased individual dietary specialization as a greater diversity of prey becomes available (Bolnick et al. 2007).

Individual specialization is an important driver of food web dynamics in a variety of taxa (reviewed in: Bolnick et al. 2003). The degree to which populations exhibit individual specialization under the NVH/mNVH paradigm is largely dependent upon that population's degree of intraspecific trait variation associated with different phenotypes, experience, and personalities (Bolnick et al. 2011; Toscano et al. 2016). Species that are long-lived, exhibit some degree of site and pair fidelity, occupy upper trophic levels, and express the ability to learn complex behavior are expected to have high degrees of individual specialization (Araújo et al. 2008). On an interspecific basis, generalist species are more likely to fall under the NVH paradigm than specialists which may be more constrained in these phenotypic or behavioral traits (Bison et al. 2015; Maldonado et al. 2017). Evaluating whether a population exhibits individual specialization in alignment with the mNVH has meaningful implications for its ecological resilience, resource competition, and resultant food web dynamics (Bolnick et al. 2002).

The Arctic raptor guild comprises the upper trophic level in tundra ecosystems, wherein several species coexist through slight differences in their realized niche space – theoretically partitioning resources via small differences in phenology, life history strategy, morphology, and foraging behavior. Arctic tundra ecosystems are characterized by pulses in resource availability, often connected to the abundance of cyclic populations of arvicoline rodents (lemmings & voles; *Myodes, Microtus, and Lemmus spp.).* Highs and lows within these population cycles have effects that reverberate through the food web, directly affecting the predator guild that relies on them and indirectly influencing predation pressure on alternate prey species (Ims and Fuglei 2005). Although raptors exhibit characteristics that we may expect to be consistent with the NVH (e.g., Araujo et al. 2008), many raptor dietary studies have largely ignored the implications of individual specialization on their trophic ecology (but see Steenhof & Kochert 1988; L'Herault et al. 2013). Further, Arctic raptor dietary studies typically focus on a single species, thus the trophic dynamics of sympatric species remain largely understudied, particularly under varying degrees of resource availability.

To evaluate niche partitioning within the Arctic raptor guild, we focus on three sympatric species with different foraging strategies: the Golden Eagle (*Aquila chrysaetos*; a dietary generalist; Katzner et al. 2020); the Gyrfalcon (*Falco rusticolus*; a facultative specialist; Booms et al. 2020); and the Rough-legged Hawk (*Buteo lagopus*; a dietary specialist on arvicoline rodents; Bechard et al. 2020). Although these species nest sympatrically and their diets overlap to some extent, it remains unclear how interspecific competition and niche partitioning may influence their trophic ecology (Poole & Bromley 1988, Dalerum et al. 2016). By focusing on the trophic ecology of Arctic raptors under dynamic ecological conditions (i.e., fluctuating arvicoline rodent abundance), we seek to evaluate niche partitioning under the mNVH paradigm, thereby characterizing their behavioral plasticity and providing broader context for the tundra food web.

Methods for estimating trophic niche space have advanced over recent years with the integration of stable isotope approaches, resulting in the concept of an “isotopic niche” (Bearhop et al. 2004). Variation in the stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) exists among taxa, resulting in a position in isotopic space linked to their basal carbon source and trophic level (e.g., Bearhop et al. 2004). Thus, individuals and populations will occupy different isotopic space based on the resources they consume, making an organism’s isotopic niche a useful proxy for its trophic niche (e.g., Herrera & Rodríguez 2013). Isotopic niche width can be directly estimated and compared across communities via the calculation of stable isotope Bayesian ellipses (Jackson et al. 2011). Further, by iteratively analyzing a consumer’s isotopic position relative to that of its resources, Bayesian stable isotope mixing models (BSIMMs) can generate proportional dietary estimates (e.g., *MixSIAR*, Stock and Semmens 2016). Together, these methods create a framework to quantitatively analyze isotopic niche dynamics and estimate which resources may be driving them. Resulting proportional diet estimates can be used to distinguish within-individual from between-individual components of the diet to address broad trophic hypotheses associated with individual specialization (i.e., the mNVH).

We quantified the isotopic niche space of the three focal raptor species by analyzing nestling blood samples to generate Bayesian standard ellipses, which were then compared across years with fluctuating resource availability. We further produced proportional dietary estimates for each species in a BSIMM framework and used them to assess the degree of individual dietary specialization within each population. We predicted the standard ellipse area (SEA; a measure of isotopic niche size) would reflect the predominate foraging strategies of each species such that Rough-legged Hawks would have the smallest SEA, Golden Eagles would have the largest, and Gyrfalcons would be intermediate. The focal raptor populations were expected to hold some degree of individual (nest-level) diet specialization, and we predicted that the strength of that specialization would vary both on a generalist-specialist gradient between species and as a plastic response to interannual fluctuations in resource availability. We tested the NVH in the raptor guild and predicted that its support would be more likely in species exhibiting higher dietary flexibility (Golden Eagles and Gyrfalcons) than our dietary specialist (Rough-legged Hawks). For Golden Eagles and Gyrfalcons, population niche width was expected to expand due to increased individual specialization on different foraging niches, reducing intraspecific competition. Finally, we hypothesized that this niche variation may also mitigate interspecific competition among the raptor guild such that higher resource diversity (i.e., a high arvicoline rodent year) creates the ecological opportunity for increased individual specialization, thereby reducing overall niche overlap as individuals specialize on different components of the food web.

Methods

Study area

Jiangsu, in the eastern province of China, with an area of 40,000 square miles and a population of about 80 million (ranked fifth most populated amongst the provinces in China). As of December 31, 2020, Jiangsu Province had more than 600 confirmed cases of COVID-19, and several studies reported the presence of different types of natural focus diseases in Jiangsu province[18, 19, 20, 21], At present, Jiangsu Province has not published an article about the impact of COVID-19 on natural focus disease. Therefore, it is of great value to find the impact of COVID-19 on routine surveillance of natural focus diseases.

Data collection

We collected the reported cases of natural focus diseases (brucellosis, malaria, hemorrhagic fever with renal syndrome[HFRS], dengue, Severe Fever With Thrombocytopenia Syndrome[SFTS], Rabies, Tsutsugamushi and Japanese encephalitis [JE]) from 2015-2020 and data of the confirmed COVID-19 patients from January 22, 2020 to December 31, 2020 in Jiangsu Province by referring to the Health Records of Jiangsu Provincial Center for Disease Control and Prevention (Jiangsu Provincial CDC). The confirmed patients of COVID-19 were diagnosed based on the criterion of World Health Organization (WHO) interim guidance[22]. This study was approved by the Ethical Committee of Jiangsu provincial CDC. All data analyzed were anonymized.

ARIMA model fitting and prediction

Due to the seasonal characteristics of natural focus diseases in Jiangsu Province (except for dengue), ARIMA(p, d, q) × (P, D, Q) s was adopted for natural focus diseases(ARIMA(p, d, q) model was adopted for dengue). Use the autocorrelation and partial autocorrelation features to identify the model, test the significance of the established model parameters, and analyze the residuals between the value of model fitted and reported, make ACF diagrams and PACF diagrams for the residual sequence, and use the Box-Ljung residual white noise test method to determine whether the residual sequence is a white noise sequence, if P0.05, then residual is a white noise sequence, indicated that the established model is suitable and can be used for prediction.

Statistical analysis

The data were entered in Microsoft Excel 2019 (Microsoft Crop., USA). Nonparametric tests were used to analyze the difference between the reported incidence and the predicted incidence in 2020, difference between reported incidence in 2020 and previous four years, difference between the duration from illness onset date to diagnosed date(DID) in 2020 and the previous four years. The determination coefficient (R^2) was used to evaluate the goodness of fit of the model simulation, regression analysis was used to calculate R^2. Statistical analyses and establishment of ARIMA model were conducted with SPSS 13.0 software (IBM Corp., Armonk, NY, USA), and GraphPad Prism 7.0 (GraphPad Software, La Jolla, CA).

Results

We analyzed 189 raptor nestling red blood cell samples (Supplemental Table 1) for $\delta^{13}C$ and $\delta^{15}N$ and generated Bayesian ellipses to characterize their isotopic niche space and overlap (Fig. 1; Table 1). Across years, population niche width (as measured by the SEA) differed among species consistent with our initial predictions: Golden Eagles had the largest isotopic niche, Gyrfalcons were intermediate, and Rough-legged Hawks had the smallest isotopic niche. Golden Eagles had a significantly larger SEA than both Gyrfalcons and Rough-legged Hawks (90% CI - GOEA: 1.56–2.59, GYRF: 0.93–1.55, RLHA: 0.42–1.19; Fig. 1 inset).

Table 1
Overlap in isotopic niche space based on estimates of standard eillipse area between the three focal raptor species (Golden Eagles [GOEA]; Gyrfalcons [GYRF]; Rough-legged Hawks [RLHA]) in all years (top three lines) and broken into individual years (for sample sizes, see Table 1).

Year	Species 1	Species 2	Mean Overlap (%)	Overlap Area (‰^{2})	Species 1 (%)	Species 2 (%)
ALL	GYRF	GOEA	61.2	5.6	76.7	46.1
ALL	GYRF	RLHA	41.4	2.4	32.8	49.9
ALL	GOEA	RLHA	44.2	3.0	63.2	25.1
2016	GYRF	GOEA	57.7	2.5	85.6	29.7
2017	GYRF	GOEA	24.6	1.2	40.9	8.1
2018	GYRF	GOEA	62.4	2.5	57.1	67.8
2018	GYRF	RLHA	28.3	0.5	10.8	45.7
2018	GOEA	RLHA	43.2	0.7	18.8	67.5
2019	GYRF	GOEA	54.5	5.0	55.8	53.3
2019	GYRF	RLHA	29.5	1.3	14.7	44.5
2019	GOEA	RLHA	9.9	0.4	4.8	15.0

To assess the effects of interannual variation on isotopic niche size and position, we created Bayesian ellipses and calculated SEA for each cohort (sample sizes Supplemental Table 1; Fig. 2). Arvicoline rodent trapping success increased 20-fold between 2018 and 2019 (Supplemental Table 6), indicating that 2019 was a high year in the arvicoline cycle. The Golden Eagle isotopic niche was smallest in 2018 and largest in 2019 (90% CI – 2017: 1.20–3.95; 2018: 0.24–1.02; 2019: 1.03–6.90). Gyrfalcons had the largest isotopic niche in 2019, with credible intervals that did not overlap with 2016 or 2017 (90% CI – 2016: 0.23–0.74; 2017: 0.20–0.79; 2018: 0.37–1.16; 2019: 0.87–2.20). Rough-legged Hawks did not substantially differ in SEA between 2018 and 2019, but there was a noticeable shift in niche space toward arvicoline rodents in 2019 with only 17.81% overlap between the two years (Fig. 2).

There was a high degree of isotopic niche overlap between the three species and among years (Table 1), with Gyrfalcons and Golden Eagles overlapping more with each other (61.20%) than either species did with Rough-legged Hawks (41.37% and 44.16% respectively). Because isotopic niche area changed on an interannual basis for each species, there were some instances where the proportional niche overlap (%) decreased although the overlap area (‰^{2}) increased. Comparing 2018 (lower arvicoline rodent year) to 2019 (higher arvicoline rodent year), Golden Eagle isotopic niche space overlapped substantially less with Rough-legged Hawks (2018: 43.2%; 2019: 9.9%) and slightly less with Gyrfalcons (2018: 62.4%; 2019: 54.5%). Niche overlap remained relatively consistent between Rough-legged Hawks and Gyrfalcons across years (2018: 28.3%; 2019: 29.5%). All three species overlapped in their total isotopic niche space by 7.4% in 2018 and 2.9% in 2019.

The isotopic niche (SEA) reflected the trophic niche (Shannon Index; based on nest camera data) for the subset of Gyrfalcon nestlings for which contemporaneous data existed (Supplemental Fig. 7; Supplemental Table 4). Specifically, the 2019 Gyrfalcon subset had a significantly larger niche relative to other years based on the nest camera data (2017: 1.02–1.14; 2018: 0.98–1.14; 2019: 1.46–1.59); whereas stable isotope SEA data for the same subset of Gyrfalcons showed a similar pattern although the 90% credible intervals overlapped.

There was substantial isotopic differentiation between the seven prey categories used in BSIMMs (Supplemental Table 2). The isotopic composition of muscle tissues differed among the seven prey categories (MANOVA, $p < 0.01$; Fig. 1), with no significant effect of collection year ($p = 0.114$). Post-hoc pairwise Tukey's tests indicated no simultaneous overlap in δ13C and δ15N between any two categories (ANOVA, Tukey's test, $p < 0.01$) with the exception of hares, which overlapped with arvicoline rodents (δ13C $p = 0.799$; δ15N $p = 0.977$) and Arctic ground squirrels (δ13C $p = 0.196$; δ15N $p = 0.99$). We concluded that each prey category was adequately isotopically differentiable for its use in a BSIMM framework, but that care should be taken interpreting the output with regards to hares.

We further characterized trophic niche dynamics in the raptor guild using proportional diet estimates for each nest from BSIMMs (sample sizes Supplemental Table 1; Supplemental Table 7; Supplemental Fig. 8). Golden Eagle diet was relatively consistent throughout the course of the study, indicating that Arctic ground squirrels were their most important resource, followed by hares and ptarmigan. Modelled Gyrfalcon diet indicated a heavy reliance on ptarmigan, and a sharp increase in arvicoline rodents in 2019 (to 26% ± 11%), and Rough-legged Hawks similarly showed a dramatic increase in arvicoline rodent reliance from 2018 (34% ± 11%) to 2019 (73% ± 14%; Supplemental Table 7; Supplemental Fig. 8).

We found significant interannual variability in individual specialization for each raptor species. For Golden Eagles, individual specialization was significantly lowest in 2016 and highest in 2019; Gyrfalcons also had the highest degree of individual specialization in 2019; and Rough-legged Hawks significantly decreased from 2018 to 2019. We then examined whether individual specialization (E index) increased with population niche width (SEA) at a greater rate than expected by chance, consistent with predictions of the mNVH (Fig. 3). Golden Eagles had a lower degree of individual specialization than would be expected by chance, and there was no significant difference between the slopes of the empirical and null models ($p = 0.47$). Gyrfalcons had a significantly positive relationship between individual specialization and isotopic niche width (ß=0.12, R^2 = 0.96, p = 0.02), but the slope of the empirical model was not significantly different from that of the null model (p = 0.14). When we further tested this relationship in Gyrfalcons using a larger sample of dietary data from nest cameras (n = 58 nest-years 2014–2019; Supplemental Table 5), we similarly found a significant positive relationship between individual specialization (E Index) and population niche width (Shannon Index; ß=0.52, R^2 = 0.96, p < 0.01), and the slope was significantly higher than that of the null model (p < 0.01), consistent with the mNVH (Fig. 4).

Discussion

Our analysis of stable isotope Bayesian ellipses and subsequent BSIMMs revealed a large degree of isotopic niche overlap between Golden Eagles, Gyrfalcons, and Rough-legged Hawks in the first comparative dietary study of its kind for a guild of raptors. Isotopic niche width (SEA) generally reflected each species' expected foraging niche (Fig. 1 inset), and responses to interannual resource availability varied by species (Fig. 1; Table 1). Following our predictions, interspecific isotopic niche overlap decreased under high arvicoline rodent abundance, coinciding with elevated individual specialization for species exhibiting greater dietary flexibility (Golden Eagles and Gyrfalcons). Further, our findings supported the mNVH in Gyrfalcons – individual specialization within the population was higher than expected by chance and positively correlated with trophic niche width on an interannual basis (Fig. 4). Our findings point to niche variation as an important aspect of Arctic raptor trophic ecology, which may reduce niche overlap and promote population stability under dynamic ecological conditions.

Characterizing the role of individual specialization in a population's trophic dynamics is important for our understanding of functional ecology because it can greatly affect ecological processes ranging from resource competition to climate change resilience (Bolnick et al. 2003). Under the classic OFT paradigm, populations are relatively canalized in their foraging behaviors, which maximizes the net rate of energy intake at the cost of heightened intraspecific resource competition and reduced heterogeneity (MacArthur & Pianka, 1966). For instance, Jesmer et al. (2020) found that although the dietary niche breadth of large ruminants increases with food limitation, it does so via increased diet breadth of individuals, consistent with OFT, rather than through increased individual specialization. They attribute this pattern to population-level homogeneity in the physiological and cognitive requirements of their study species (moose; *Alces alces*). Although recent models postulate how individual specialists may operate within an OFT framework, they do not fully explain how they arise and are maintained within populations (Svänback & Bolnick, 2005). Conversely, individual niche specialization (under the mNVH paradigm) is predicted to persist and be most prevalent in populations which exhibit intraspecific trait variation, ultimately resulting in different individual foraging strategies/preferences based on phenotype (Bolnick et al. 2003), personality (Toscano et al. 2016), or learned foraging behavior (Araujo et al. 2008). We predicted that the mNVH would be supported in the Arctic raptor guild because their high cognitive capacity, parental care, and social learning (Kitowski, 2009) create conditions under which individual differences in foraging strategies may arise. The presence of prey population cycles may further promote the persistence of individual specialization within long-lived tundra predator populations – one foraging strategy may confer high reproductive success in one phase of the cycle but lead to nest failure in the subsequent phase.

Several underlying traits may have contributed to the varying degrees of individual specialization observed between the three species: phenotypic variation in plumage coloration, territory/pair fidelity, and the cognitive capacity for learning new foraging behaviors. Gyrfalcons are highly phenotypically variable in their plumage coloration (ranging from dark brown to white; Booms et al. 2020) that could affect their detectability by certain prey species and drive individual variation in foraging strategies (e.g., Bolnick et al. 2011). Whereas Golden Eagles and Rough-legged Hawks migrate south for the winter, Gyrfalcon pairs stay on or near their home-ranges year-round (Eisaguirre et al. 2016), which may facilitate learning specialized foraging behaviors specific to their home-ranges. Use of Gyrfalcons in the sport of falconry has also revealed they can be trained to hunt prey they would not encounter in the wild (Cade 1982), further highlighting their individual capacity for learning complex foraging behavior. Based on these same criteria, Rough-legged Hawks were expected to have the lowest degrees of inter-individual variation in foraging strategy: they are more phenotypically similar and as a migratory and semi-nomadic species, they likely have the lowest rates of site/pair fidelity (e.g., Bechard et al., 2020). Because specialists are often more constrained than generalists in certain traits that can limit inter-individual variation in foraging strategy (e.g., Bolnick et al., 2003), we further expected Rough-legged Hawks to operate under the classic OFT paradigm. Golden Eagles are long-lived dietary generalists, exhibit territory and pair fidelity in our study system, and have clearly displayed the ability to learn complex foraging behavior on an individual basis (e.g., knocking goats from cliffs and fishing; reviewed in Katzner et al. 2020). We predicted that Golden Eagles would follow the mNVH based on these traits, but instead found that they display lower degrees of individual specialization than would be expected by chance.

Our finding that Golden Eagles did not fall under the mNVH may have an ecological explanation, or alternatively, could be attributed to methodological difficulties associated with constructing BSIMMs for a generalist species. In our study system, prey groups occupy different temporal niches (e.g., strictly diurnal ground squirrels and ptarmigan [Williams et al., 2017; Rierth & Stokkan 1998]; nocturnal arvicoline rodents; [Peterson & Batzli 1975]). Golden Eagles may require a broad temporal foraging window to meet the nutritional needs of their growing young, potentially necessitating that each individual or pair within the population broaden their trophic niche as a result. Alternatively, this finding could have an analytical basis: BSIMM estimates for Golden Eagles were more sensitive to an informative prior (Supplemental Fig. 4) and had lower between-year sample sizes than the other two species, both of which may have had a homogenizing effect on modeled inter-individual diets. We suspect this sensitivity is attributable to the isotopic mixing space: the main discrepancies were between modelled proportions of hares and Arctic ground squirrels which overlapped in isotopic space. Furthermore, Golden Eagles (as an opportunistic dietary generalist) proved to be generally difficult to analyze in a BSIMM framework simply because they eat so many different prey types. Although we included source values from their main prey categories (Supplemental Table 2; Herzog et al. 2019), underrepresented groups outside of the mixing space could have influenced fine-scale Golden Eagle diet estimates and resulting individual specialization metrics. Since Gyrfalcons and Rough-legged Hawks were less sensitive to an informative prior and have prey groups that are better isotopically characterized for this study, we are more confident in our BSIMM diet estimates for those species than the diet estimated for Golden Eagles.

Interspecific niche overlap was lowest among the raptor guild under high arvicoline rodent abundance (2019; Table 1), suggesting that individual niche variation may play a role in mediating interspecific resource competition. The consequences of individual specialization are typically discussed in the context of intraspecific competition (e.g., Bolnick et al. 2005; Xia et al. 2020), but the same patterns may hold true for niche dynamics at an interspecific level (e.g., Bison et al. 2015; Maldonado et al. 2017). Under the concept of ecological opportunity, a population's degree of individual specialization increases with higher resource diversity (Roughgarden 1974). A peak of cyclic arvicoline rodents in tundra ecosystems increases the diversity of the raptor prey base: both directly increasing rodent density but also indirectly increasing the density and reproductive success of their specialist predators which these raptors may also consume (Therrien et al. 2014; e.g., in our system; Long-tailed Jaegers [*Stercorarius longicaudus*], Short-eared Owls [*Asio flammeus*], Short-tailed Weasels [*Mustela erminea*]). As predicted, a high arvicoline rodent year (2019) corresponded with higher degrees of individual specialization for Gyrfalcons and Golden Eagles as individuals had a broader prey base from which to sample. BSIMM output indicates that some Gyrfalcon pairs remained ptarmigan specialists (constituting up to 89 ± 5% of the diet), whereas others relied more heavily on arvicoline rodents directly (up to 62 ± 5%), and still others capitalized on arvicoline rodent predators (up to 19 ± 5%; Supplemental Table 8). We suspect Gyrfalcons in our study system may fall under a "competitive refuge" model (described by Svanbäck & Bolnick 2005), wherein individuals within the population share top-ranked prey (e.g., ptarmigan) but have different rankings for lower-tier resources based on efficiency tradeoffs associated with their phenotypes or learned foraging behaviors. Which alternative resources Gyrfalcons specialize on could be partially attributable to variable availability of localized prey groups around nest sites across a heterogeneous landscape. Although Golden Eagles likely did not consume arvicoline rodents, the other members of the raptor guild did, which may have reduced predation pressure on the other prey groups (e.g., Ims & Fuglei 2005), facilitating Golden Eagle niche variation. Rough-legged Hawks displayed the opposite trend, reducing inter-individual specialization in 2019 as each individual was better able to capitalize upon their preferred resource (consistent with a traditional OFT response). Collectively, these disparate foraging strategies resulted in reduced niche overlap between the three raptor species under higher resource diversity, highlighting the complex roles population cycles can play in tundra food webs.

Along with directly mitigating resource competition, niche variation may promote population stability under dynamic ecological conditions by buffering against the loss (or periodic unavailability) of specific habitats or resources (Bolnick et al. 2003). This is particularly pertinent in Arctic tundra ecosystems, which are undergoing rapid change due to anthropogenic global warming that is causing unprecedented and unpredictable effects on ecosystem-level processes (review in Post et al. 2009). Arvicoline rodent population cycles are collapsing and dampening across Europe and the Arctic (Ims et al. 2008), illuminating the need to study food web dynamics in systems where these cycles are still intact. Our findings indicate that although arvicoline rodent abundance is directly important to its specialist predators (i.e., Rough-legged Hawks and some individual Gyrfalcons) it also may indirectly widen the available prey base for other members of the predator guild, allowing for reduced resource competition via niche variation. Although previous studies have hypothesized that dampened arvicoline rodent cycles influence the population dynamics of their specialist predators (e.g., Fufachev et al. 2019), we provide evidence that other members of the predator guild will also be affected in their trophic dynamics. Further work linking individual specialization to reproductive success and territory characteristics will be crucial in furthering our understanding of predator population resilience in a changing Arctic.

Declarations

Author Contributions: DLJ and CTW conceived the manuscript and analyzed the data. DLJ, DLA, MTH, and TLB conducted fieldwork. DLJ wrote the manuscript; other authors provided editorial advice.

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Data Archiving Statement: Data (except nest locations) and code available from the Dryad digital repository (submission upon acceptance with a one-year embargo); no location data will be provided for raptors as specified by Alaska state law.

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Figures

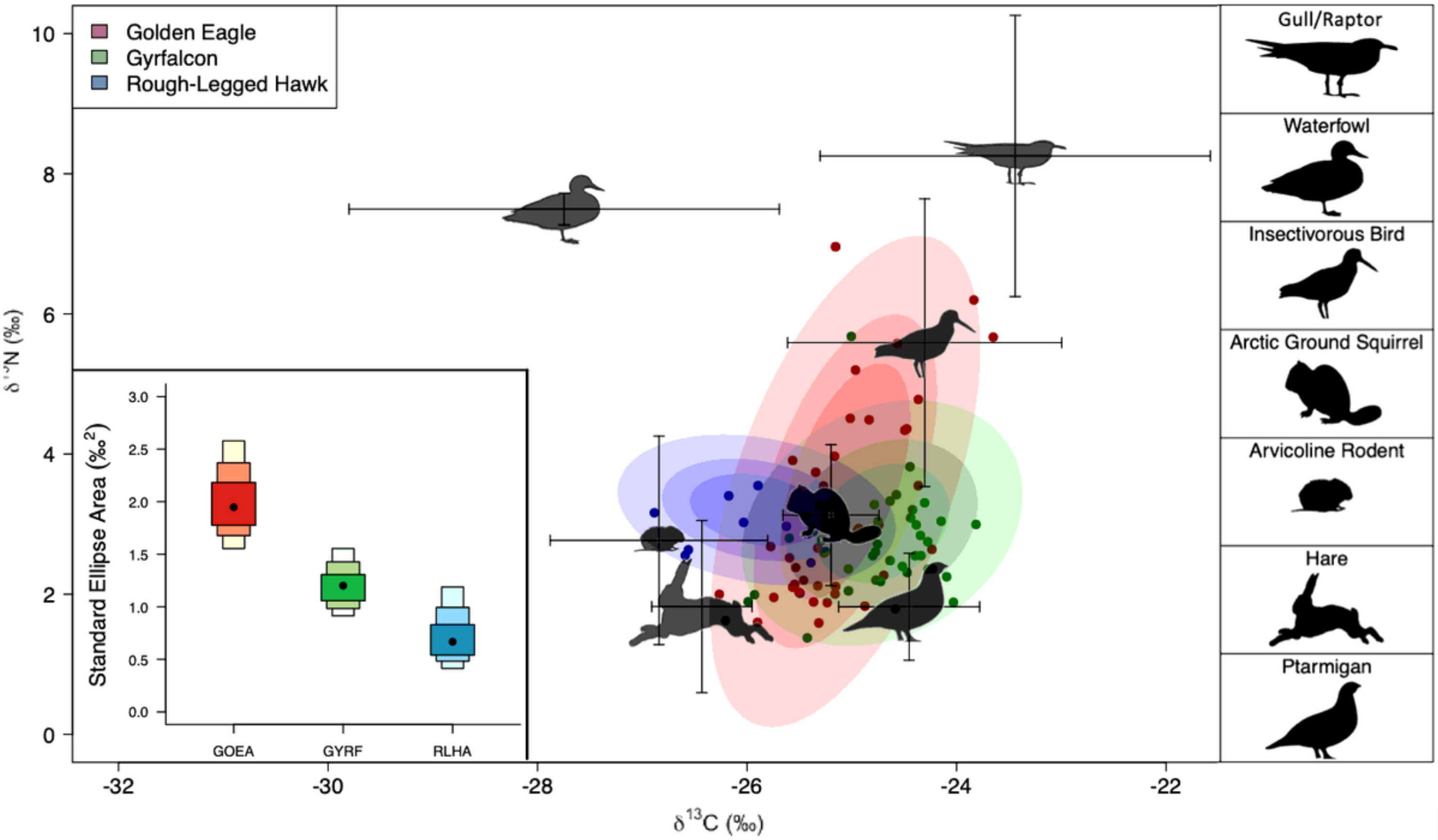

Figure 1

Isotopic mixing space and Bayesian ellipses for the three focal raptor species. Colored points are stable isotope values for each nest-year for each species, Seward Peninsula 2014-2019 (sample sizes; Supplemental Table 1). Shaded ellipses and boxes correspond to 50%, 75%, and 90% credible intervals of standard ellipse area for each raptor species across the years sampled. Silhouettes correspond to stable isotope values from each of seven prey categories, displayed as mean ± 1 SD (sample sizes; Supplemental Table 1). Raptor isotope values are adjusted using TDFCAM mean values, and the TDFCAM SD is added to the error bar of each prey species. Inset (bottom left) represents numerical estimates of standard ellipse area for each raptor species.

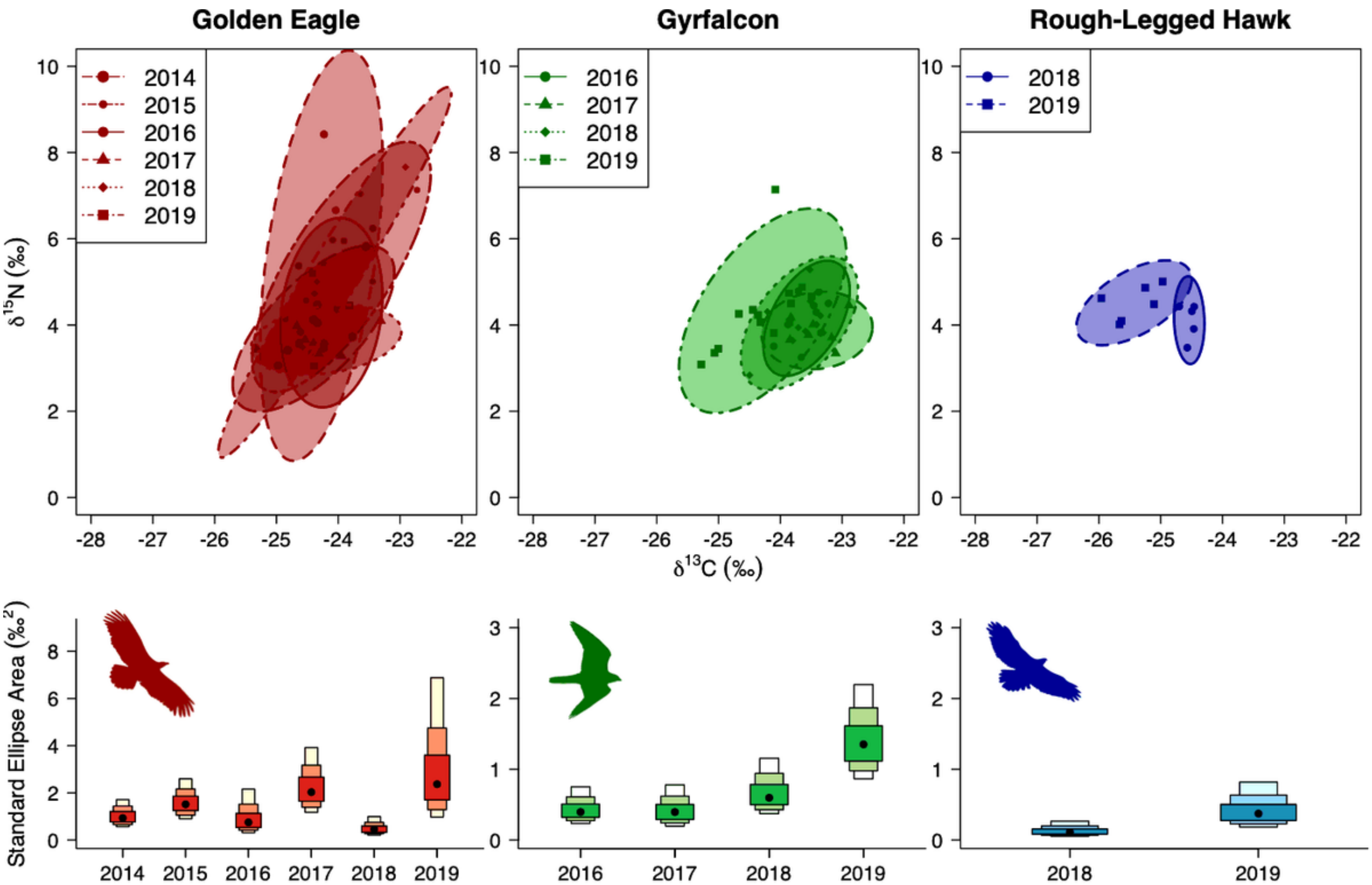

Figure 2

Stable isotope Bayesian ellipses (95% credible intervals) and standard ellipse area (SEA) for raptors on the Seward Peninsula (2014-2019; sample sizes [nest-years] Supplemental Table 1). On upper ellipse plots, different shapes and line types correspond to samples from different years, and darker shaded regions indicate isotopic niche overlap between years. On lower SEA density plots, points indicate the mean SEA estimate and colored boxes correspond to 50%, 75%, and 90% credible intervals respectively.

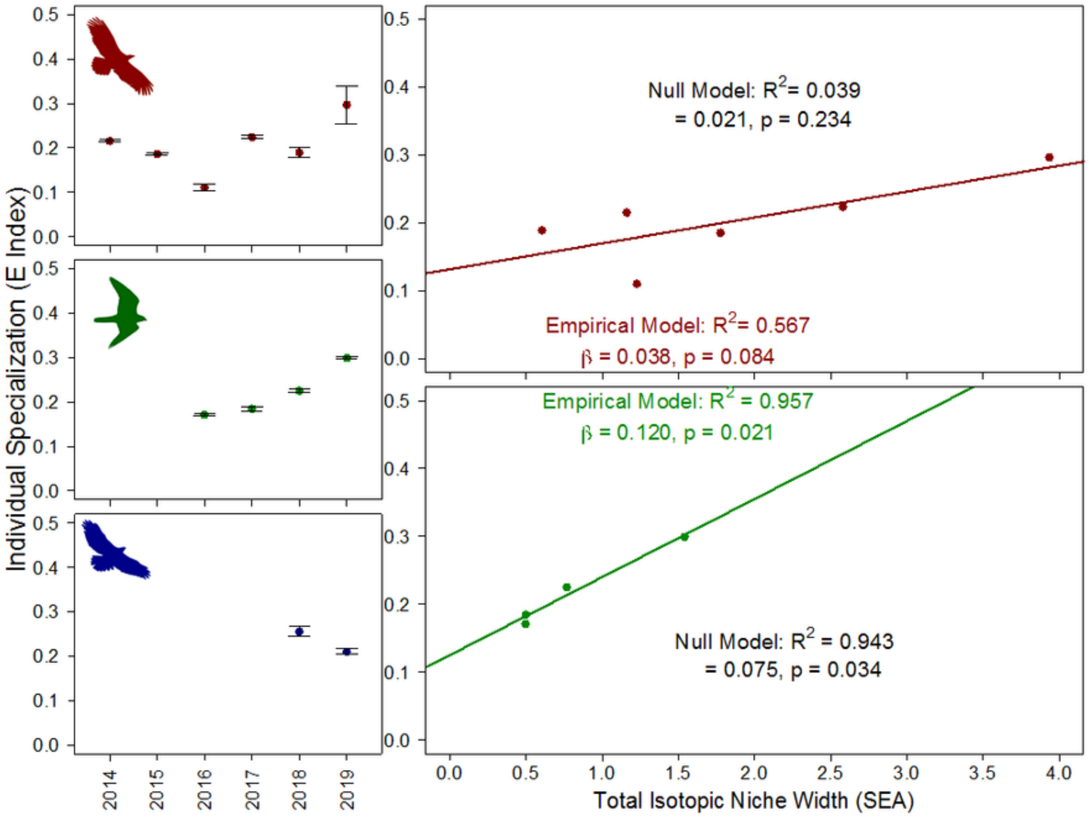

Figure 3

Individual specialization (E Index) for each of the focal raptor species in each year during the brood rearing period on the Seward Peninsula, as inferred from stable isotope data (n=95 nest-years, 2014-2019; Supplemental Table 1). In left panels, error bars represent 95% confidence intervals. Right panels indicate the relationship between individual specialization and total trophic niche width (SEA) with empirical linear models (colored lines) and null models (grey lines). The top right (red) panel is Golden Eagle data, and the bottom right (green) panel is Gyrfalcon data. Each point represents population-level data from each year.

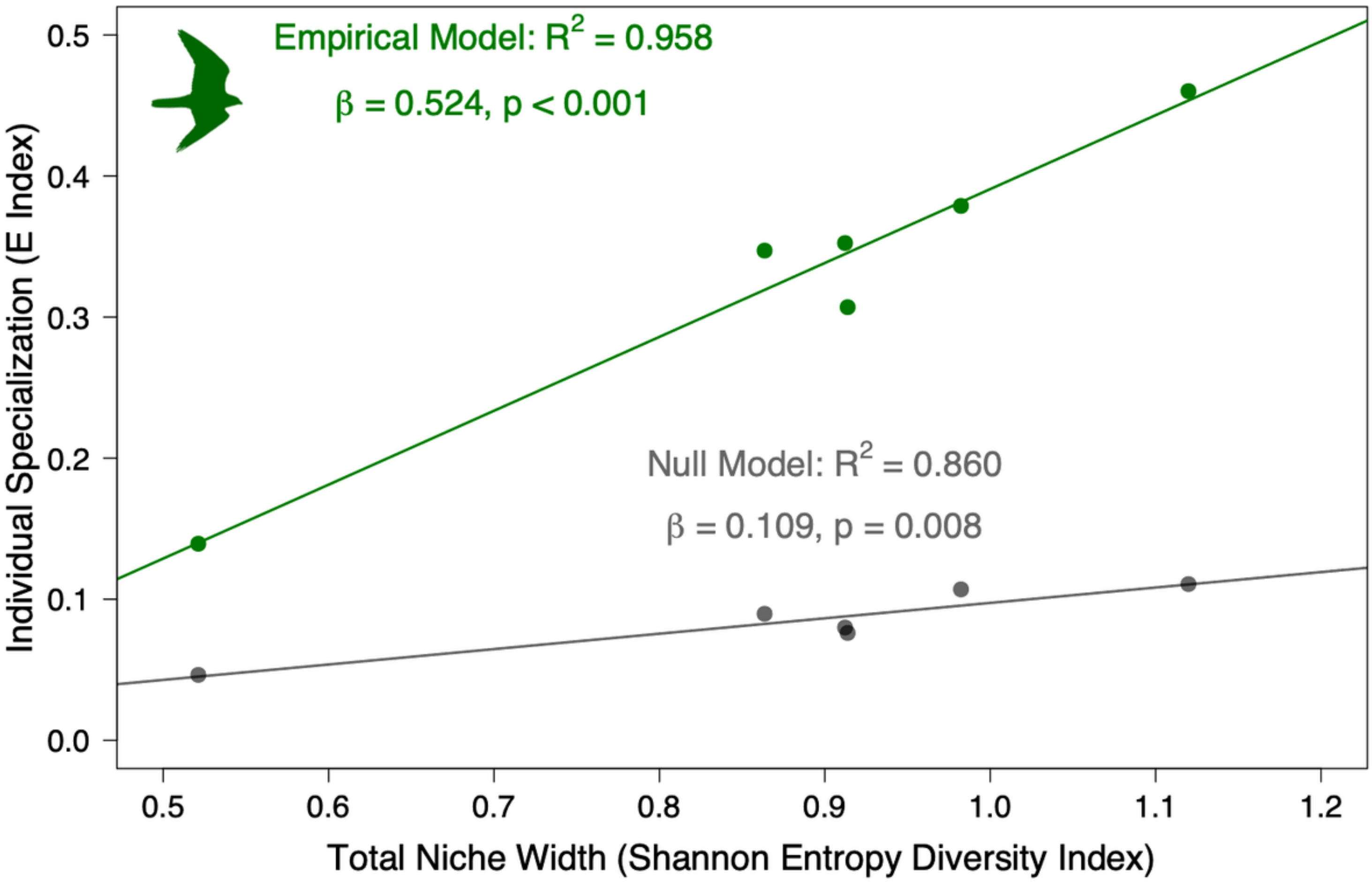

Figure 4

The relationship between individual specialization (E index) and total niche width (Shannon Entropy Diversity Index) for Gyrfalcons on the Seward Peninsula, as inferred from nest camera data (n=58 nest-years, 2014-2019; Supplemental Table 5). Each point represents population-level data from each year. The slope of the empirical linear model (green line) is significantly different from that of the null model (gray line), consistent with the mNVH.

Supplementary Files

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