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DIETARY PLASTICITY IN A SPECIALIST PREDATOR, THE GYRFALCON (*FALCO RUSTICOLUS*): NEW INSIGHTS INTO DIET DURING BROOD REARING

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ABSTRACT.—Climate and landscape change are expected to affect species' distributions and interactions, with potentially harmful consequences for specialist predators. Availability of optimal prey can affect reproductive success in raptors, especially in the Arctic, where dramatic differences in prey availability occur both within and between years. However, behavioral responses of dietary specialist, resident predators such as Gyrfalcons (*Falco rusticolus*) to changes in prey availability remain poorly understood. To improve understanding of how climate-driven changes in prey availability may affect diet of avian predators in the Arctic, we characterized Gyrfalcon diet on the Seward Peninsula, Alaska, in 2014 and 2015 from images representing 2008 prey items obtained by motion-activated cameras at 20 nests. We documented two important dietary shifts: the proportion of ptarmigan (Willow Ptarmigan [*Lagopus lagopus*] and Rock Ptarmigan [*L. muta*]) in the diet declined throughout the brood-rearing period in both years, and also differed between years. In both cases, ptarmigan were replaced by Arctic ground squirrels (*Urocitellus parryii*) in the diet. Despite shifts in prey composition, dietary breadth did not change, which revealed a facultative shift in prey use in which Gyrfalcons relied on prey of large size rather than prey of a particular taxon. We describe previously undocumented prey-use patterns during Gyrfalcon breeding, specifically an interchange between two prey species that are keystones in tundra ecology. These results are important for informing predictive models of climate change and adaptive species management plans. Further study of the interchange between prey types described in this study can strengthen insight into key ecosystem processes, and the cause and effect of potential decoupling of predator-prey interactions.

KEY WORDS: *Gyrfalcon*; Falco rusticolus; Lagopus *spp.*; *Alaska*; *Arctic ground squirrel*; *climate change*; *diet*; *ptarmigan.*

PLASTICIDAD EN LA DIETA DE UN DEPREDADOR ESPECIALISTA, *FALCO RUSTICOLUS*: NUEVAS PERSPECTIVAS SOBRE SU ALIMENTACIÓN DURANTE LA CRÍA DE LA NIDADA

RESUMEN.—Es de esperar que tanto el clima como los cambios en el paisaje afecten las distribuciones y las interacciones de las especies, a veces con consecuencias potencialmente perjudiciales, sobre todo para los

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depredadores especialistas. La disponibilidad de presas óptimas puede afectar el éxito reproductivo de las rapaces, especialmente en el Ártico, donde se registran diferencias dramáticas en la disponibilidad de presas a lo largo del año y entre años. Sin embargo, es muy poco lo que sabemos sobre las respuestas comportamentales de los depredadores residentes con dietas especializadas, como *Falco rusticolus*, frente a los cambios en disponibilidad de presas. Para entender mejor cómo los cambios en la disponibilidad de presas resultante de modificaciones climáticas afectan la dieta de los depredadores de aves en el Ártico, investigamos la dieta de *F. rusticolus* en la Península Seward, Alaska, en 2014 y 2015 a partir de 2008 presas identificadas en 20 nidos y por medio de imágenes obtenidas usando cámaras activadas por movimiento. Registramos dos cambios importantes en la dieta de esta especie: 1) la proporción de lagópodos (*Lagopus lagopus* y *L. muta*) en la dieta disminuyó a lo largo del período de cría de la nidada en ambos años y 2) también varió entre años. En ambos casos, los lagópodos fueron reemplazados por ardillas terrestres del Ártico (*Urocitellus parryii*). A pesar de los cambios en la composición de la dieta, su amplitud no varió, lo que reveló un cambio discrecional en el uso de presas en el cual *F. rusticolus* se apoyó en presas de gran tamaño más que en presas pertenecientes a un taxón específico. Describimos patrones de consumo de presas previamente no registrados durante el período de cría de *F. rusticolus*, específicamente un intercambio entre dos especies de presas que son clave en la ecología de la tundra. Estos resultados son importantes para desarrollar modelos predictivos de cambio climático y planes de manejo adaptativos de especies. El estudio adicional del intercambio entre tipos de presas descripto en este trabajo puede fortalecer el entendimiento de los procesos claves del ecosistema, y la causa y efecto del desacoplamiento potencial de las interacciones depredador-presa.

[Traducción del equipo editorial]

Climate-induced changes in the Arctic are affecting ecosystem function (Post et al. 2009, Kortsch et al. 2015, Frainer et al. 2017) and disrupting life history strategies and important species interactions (Ims and Fuglei 2005, Hunter et al. 2010, Smith et al. 2010). Disruption to life histories of key ecosystem members, such as apex predators, may have important implications for their status in tundra ecology because population stability of predators often depends on population trends of prey species (Krebs et al. 2001, Sinclair and Krebs 2002, Barraquand et al. 2014). Under predicted climate-change scenarios in the Arctic, population trends of many species will become less cyclic and pronounced (Gilg et al. 2009), which may disrupt predator-prey interactions and decouple ecosystem dynamics (Bretagnolle and Gillis 2010, Mossop 2011, Schmidt et al. 2012).

The effects of climate-induced changes may be particularly pronounced for specialist species (Hayhow et al. 2015, Kellermann and van Riper 2015). The Gyrfalcon (*Falco rusticolus*) is considered a true specialist in terms of both habitat and diet. A year-round resident of Arctic tundra in much of its range, the Gyrfalcon is a dietary specialist that relies heavily on ptarmigan (*Lagopus* spp.; Cade 1960, Nielsen and Cade 1990, 2017, Huhtala et al. 1996, Nielsen 1999, 2003, Nyström et al. 2005), although exceptions to these generalizations are known (Burnham and Burnham 2011). Because of the Gyrfalcon's specialized diet, predicted climate-change effects in the Arctic, including increases in shrub cover (Zhang et al. 2013) and the resulting impacts on ptarmigan distribution (Virkkala et al. 2008, Lehikoinen et al. 2014), may potentially influence Gyrfalcon populations. Although behavioral responses of avian predators to boom-and-bust prey cycles have been studied in the Arctic (Gilg et al. 2009, Schmidt et al. 2012, Barraquand et al. 2014, Pokrovsky et al. 2014), the behavioral responses to changes in prey availability of dietary specialist, resident predators such as the Gyrfalcon remain poorly understood. A better understanding of Gyrfalcons' ability to modify prey use in response to changing prey availability is necessary to model the effects of predicted climate change on this species and on ecosystem function in Arctic tundra.

To provide important information to further understand the role of Gyrfalcons in tundra ecosystems, better predict climate change effects on Gyrfalcon populations, and further determine Gyrfalcon dependence on ptarmigan, we conducted the first large-scale, camera-based study of Gyrfalcon diet aimed to analyze trends in prey use during two breeding seasons in western Alaska. We focused on the brood-rearing period to capture peak resource requirements to understand the importance of prey types during this period (Collopy 1984, Holthuijzen 1990) and to detect potential changes in prey use. We designed our study to test whether patterns in prey use reflect (1) ecosystem phenology (i.e., changes in prey availability over time) and correlate with calendar date (hereafter referred to as the

Ecosystem Phenology Hypothesis [EPH]), or (2) the developmental and energetic needs of growing nestlings, which correlate with nestling age (hereafter referred to as the Developmental Phenology Hypothesis [DPH] or Nestling Age Hypothesis). The distinction between these two hypotheses is important in the context of climate change because dietary habits associated with nestling development may be less plastic, whereas dietary habits that follow system phenology may be adaptable to changing prey landscapes. We hypothesized that patterns in prey use are best explained by the EPH. Specifically, we predicted three patterns associated with phenology during brood-rearing. First, we predicted a decrease in ptarmigan in Gyrfalcon diet because changes in ptarmigan behavior and appearance at the onset of their nesting period reduce their availability as prey (Hannon et al. 1998). Second, we predicted a decrease in the use of large prey items in Gyrfalcon diet as use of ptarmigan declined, and as alternative, migratory prey species of smaller body mass become more available. Third, we predicted that an increase in Gyrfalcon diet breadth would occur during the brood-rearing period as ptarmigan use decreased and use of alternative prey increased.

METHODS

Study Area. The study area covered 14,150 km^2 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 31–39) occupied nesting territories (Bente 2011).

Nest Treatment. To locate nesting Gyrfalcons, we conducted occupancy surveys in 2014 and 2015 using a Robinson R-44 helicopter (Robinson Helicopter Company, Torrence, CA, USA). We considered a nest occupied if it contained eggs, young, an incubating bird, or a mated pair on or near the nest (following Franke et al. 2017). After we determined Gyrfalcon occupancy, we installed Reconyx PC800 (Reconyx Inc., Holmen, WI, USA) 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, five received cameras in both 2014 and 2015. Installation of cameras and methods for data collection followed those described in Robinson and Prostor (2017). We prioritized camera installation in nests with eggs; however, in some cases we installed cameras after hatch for nests discovered with nestlings during occupancy surveys.

Data Analysis. We catalogued prey items from nest camera images and classified items to the lowest taxonomic level possible. To avoid double-counting, we counted whole or headless prey as one item and noted individual parts delivered during a 24-hr period, because they may represent a single prey item. We also noted the condition of any prey removed by adults because Gyrfalcons are known to cache prey (Booms and Fuller 2003). We assigned average mass values to identified mammals (Kays and Wilson 2009) and birds (Sibley 2014) for biomass calculations. We assigned biomass for young or partially grown prey 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 variation in Arctic ground squirrel (*Urocitellus parryii*) mass across its distribution, we calculated an average mass for Alaska squirrels from Sheriff et al. (2013). We estimated mass values for unknown items by comparing them visually to the size of a known item (e.g., an avian prey item approximately the size of a Lapland Longspur [*Calcarius lapponicus*] received a mass assignment of 27 g) following Booms and Fuller (2003).

To assess the completeness of diet sampling, we constructed a rarefaction curve using EstimateS software (Colwell 2013) and adopted the 100 sample-order randomization. Rarefaction curves represent the cumulative means of resampling 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 approach an asymptote represents the number of samples (individual prey items for this study) required to capture all species in the Gyrfalcon diet for our study area, and indicates that sampling is sufficient for further statistical inference (Anderson 2009, Wirta et al. 2015, Robinson 2017).

To evaluate the important drivers for influencing changes in prey use we organized prey items in two ways: biomass categories (prey size) and prey-type categories. Biomass categories were based on the biomass range catalogued in the diet: small (<200 g), medium (201–400 g), and large (>400 g). Prey types were organized into seven ecologically meaningful prey categories following Robinson et al.

(2015): ptarmigan (Willow Ptarmigan [*Lagopus lagopus*] and Rock Ptarmigan [*L. muta*]), shorebird, passerine, jaeger (*Stercorarius* spp.), squirrel (Arctic ground squirrel [*Urocitellus parryii*]), microtine, and other (raptor [Accipitriformes and Strigiformes], waterfowl [Anseriformes], and seabird [Alcidae]). We lumped raptor, waterfowl, and seabird because these items constituted very small contributions by number to the overall diet. We placed items we could not identify to these groups in one of two categories: unknown bird or unknown.

To test our predictions from the Ecosystem Phenology and Developmental Phenology Hypotheses, we organized proportion of total biomass of prey size and type categories by ordinal date as a measure of phenology, and nestling age as a measure of nestling development into 5-d periods (hereafter referred to as "5-d period" and "age," respectively). For both "5-d period" and "age" we plotted percent contribution by prey type and biomass category in a vertical bar chart to illustrate the change in prey use across time. We calculated diet breadth using the standardized version of Levin's Index of Diet Breadth (Hurlbert 1978). We calculated diet breadth for each nest using the seven ecologically relevant prey categories by "5-d period" and "age" to illustrate the change in prey use across these two temporal scales.

Statistical Analysis. We created generalized linear mixed models (GLMMs) using the package lme4 in the statistical platform R 3.2.3 (Bates et al. 2015, R Core Team 2015) with a binomial distribution and log link to test the EPH and DPH. All models included nest as a random intercept to control for the expected variation between nests, and year as a fixed effect to control for differences between years. We included "5-d period" and "age" as predictors of whether an individual prey was of size class large, and whether a prey item was a ptarmigan. We created linear mixed models (LMMs) using the package lme4 with log link and nest as a random variable to control for the expected variation between nests, year as a fixed effect to control for differences between years, and "5-d period" and "age" as predictors of diet breadth. We used an information-theoretic approach to evaluate models and to test parameter support against the intercept-only model (Burnham et al. 2011). We 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 with $\Delta AIC < 2$ of the best model (Burnham and Anderson 2002). We 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 its 85% confidence interval did not contain zero. We note that inference from this study would be no different had we used more traditional 95% confidence intervals. We carried out all analyses in the statistical platform R 3.2.3 (R Core Team 2015).

RESULTS

Overall Diet Composition. We placed cameras in 23 nests, but due to camera failure and nest failure prior to hatch, cameras did not capture prey deliveries at three nests; therefore, we quantified diet at 20 nests. We documented 2008 prey items (Table 1), of 40 species and 15 families over two breeding seasons. Of the recorded prey items, we identified 99% to categories used for analysis (i.e., 1% were placed in the category "unknown"). Mean total biomass per nest was 40.4 kg. After 1000 prey detections, the rate at which species were added to the total number of recorded species decreased to three species per 200 prey items (Fig. 1). Approximately one additional species was added to the total detected in the diet after 1600 prey detections, indicating that additional sampling would have little effect on the overall diet description. Thus, sampling effort was adequate for a full characterization of species composition in the Gyrfalcon diet during brood-rearing.

Ptarmigan represented 52% of overall prey biomass, followed by squirrel (36%), and shorebird (Table 1). However, diet composition differed between years, with ptarmigan exceeding 75% of the diet in 2014, and squirrel exceeding 50% of the diet in 2015 (Fig. 2).

Temporal Change in Prey Use. Of three models that compared temporal effects on the proportion of ptarmigan in the diet, the top model contained the predictor "5-d period," the fixed effect "year," and the random intercept "nest" (Table 2). All other models had $\Delta AIC > 2$ (Age $\Delta AIC = 6.66$; Table 2) from the top model, and thus we considered them to be uninformative. The variable "5-d period" was associated with the proportion of ptarmigan in the overall diet, because the proportion of ptarmigan decreased by "5-d period" ($\beta = -0.14$, CI = –0.17, –0.11); Fig. 3). The proportion of ptarmigan in the diet decreased by "5-d period" as the season

Table 1. Summary of prey types (40 total species) catalogued from motion-activated cameras installed at 20 Gyrfalcon nests during the brood-rearing period in 2014 and 2015 on the Seward Peninsula, Alaska. Information regarding species identified and items identified to lowest taxonomic level possible are given by number of items, total biomass estimated, and percent of total biomass estimated. Species are listed in order of total biomass contribution observed in all years. Biomass assignment varies, and is estimated on a per-prey-item basis.

	2014			2015			ALL YEARS		
PREY CATEGORY	*n*	TOTAL BIOMASS (g)	% BIOMASS	*n*	TOTAL BIOMASS (g)	% BIOMASS	*n*	TOTAL BIOMASS (g)	% BIOMASS
Birds									
Ptarmigan	520	250,975	75.6	367	170,115	35.7	887	421,090	52.1
Jaeger	4	929	0.3	38	11,400	2.4	42	12,329	1.5
Shorebird	99	19,101	5.8	154	29,175	6.1	253	48,276	6.0
Passerine	55	1788	0.6	169	10,624	2.2	224	12,412	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	11,202.5	1.4
Subtotal birds	729	280,587.5	84.6	781	228,112	47.9	1510	508,699.5	62.9
Mammals									
Squirrel	69	49,197	14.8	343	243,488	51.1	412	292,685	36.2
Microtine	1	80	0.0	53	3107	0.7	54	3187	0.4
Subtotal mammals	70	49,277	14.9	396	246,595	51.7	466	295,872	36.6
Unknown	17	1947	0.6	15	1866.5	0.4	32	3813.5	0.5
Total	**816**	**331,811.5**		**1191**	**476,573.5**		**2008**	**808,385**	

advanced during both years, corresponding with an increase in the contribution of squirrel (Fig. 4). In 2014, this decrease was less substantial and ptarmigan remained the most common prey type throughout the brood-rearing period, but in 2015 this

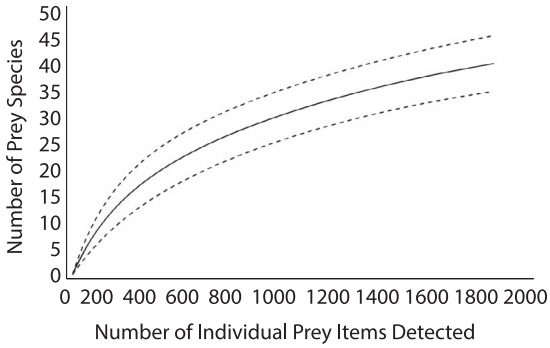

Figure 1. Rarefaction curve illustrating the effect of each additional prey species to the overall species total in the Gyrfalcon diet on the Seward Peninsula, Alaska. In the range from 1600 to 1800 detections, approximately one additional species was detected in the overall diet, meaning that sampling was sufficient for the purpose of the current study.

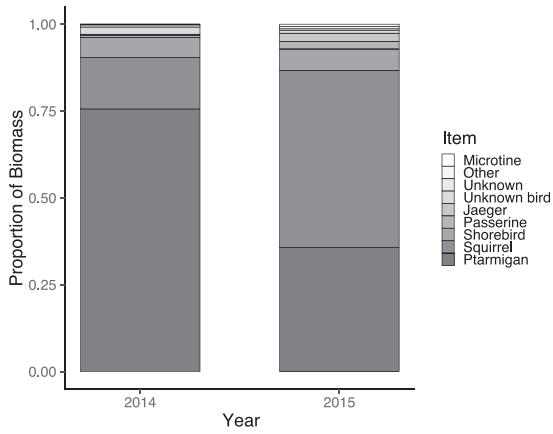

Figure 2. Proportion of biomass contribution of prey items to Gyrfalcon diet during brood rearing on the Seward Peninsula, western Alaska, in 2014 (n=10 nests) and 2015 (n=10 nests). In 2014, ptarmigan constituted the majority of the diet, with ground squirrels and shorebirds as other primary contributors to total biomass. In 2015, ground squirrels constituted the majority of the diet, with ptarmigan, shorebirds, jaegers, and passerines as other main contributors to total biomass.

Table 2. AIC (Akaike's Information Criterion) model selection criteria for models of Gyrfalcon diet that explore the role of "5-d period" (Ecosystem Phenology Hypothesis) and "age" (Nestling Age Hypothesis/Developmental Phenology Hypothesis) in Gyrfalcon diet by the proportion of ptarmigan and the proportion of size class large in the diet during the 2014 and 2015 breeding seasons in western Alaska. The variable "5-d period" showed the strongest association with the proportion of ptarmigan (AIC weight = 0.97), and the proportion of size class large (AIC weight = 0.89) in the diet, supporting the Ecosystem Phenology Hypothesis.

MODEL AND VARIABLES	K	ΔAIC[a]	AIC WEIGHT[b]	CUMULATIVE WEIGHT[c]	DEVIANCE
Proportion of Ptarmigan					
5-d period	4	0.00	0.97	0.97	2311
Age	4	6.66	0.03	1.00	2318
Intercept only	3	34.60	0.00	1.00	2348
Size class "large"					
5-d period	4	0.00	0.89	0.89	2467
Age	4	5.35	0.06	0.96	2472
Intercept only	3	6.01	0.04	1.00	2475

[a] ΔAIC = a measure of each model relative to the top model.
[b] AIC weight = the "weight of evidence" in favor of a given model being the best approximating model in the set.
[c] Cumulative weight = the cumulative sum of the AIC weight scores including each preceding model.

decrease resulted in a mid-season switch to squirrel as the most common prey type (Figs. 2, 4).

The top model of temporal effects on the proportion of size class "large" in the diet contained the predictor "5-d period" and the random intercept "nest" (Table 2). All other models were ΔAIC > 2 (Age ΔAIC = 5.35; Table 2) from the top model, and thus we considered them to be uninformative. The variable "5-d period" was also associated with the proportion of the size class "large," such that the proportion of large prey decreased by 5-d period as the season advanced (β = –0.06, CI = –0.09, –0.03; Fig. 3). The proportion of size class "large" to the diet decreased slightly by 5-d period, but throughout the season size class "large" remained as the most common size class (Fig. 3).

The top models of temporal effects on diet breadth with "5-d period" and "age" as predictors were the null models, which contained only the fixed effect of "year" and the random intercept "nest" (Table 3). However, in both instances, the model including "5-d period" or "age," respectively, received weak support, suggesting a weak association between diet breadth and time.

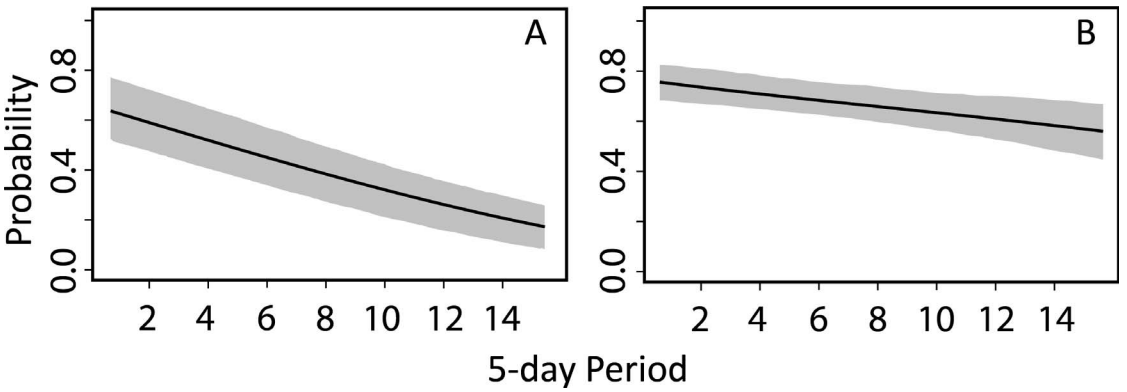

Figure 3. Top Generalized Linear Mixed Models (GLMM) from AIC model selection that support the Ecosystem Phenology Hypothesis, and best explained the effects of system phenology on Gyrfalcon diet by (A) the proportion of ptarmigan and (B) the proportion of the size class "large" as prey types in the diet during the 2014 and 2015 breeding seasons in western Alaska. Grey shading indicates the 85% confidence interval. The variable "5-d period" was negatively associated with both the probability of ptarmigan as a prey item (β = –0.14, 85% CI = –0.17, –0.11) and the probability of prey items of the size class "large" (β = –0.06, 85% CI = –0.09, –0.03).

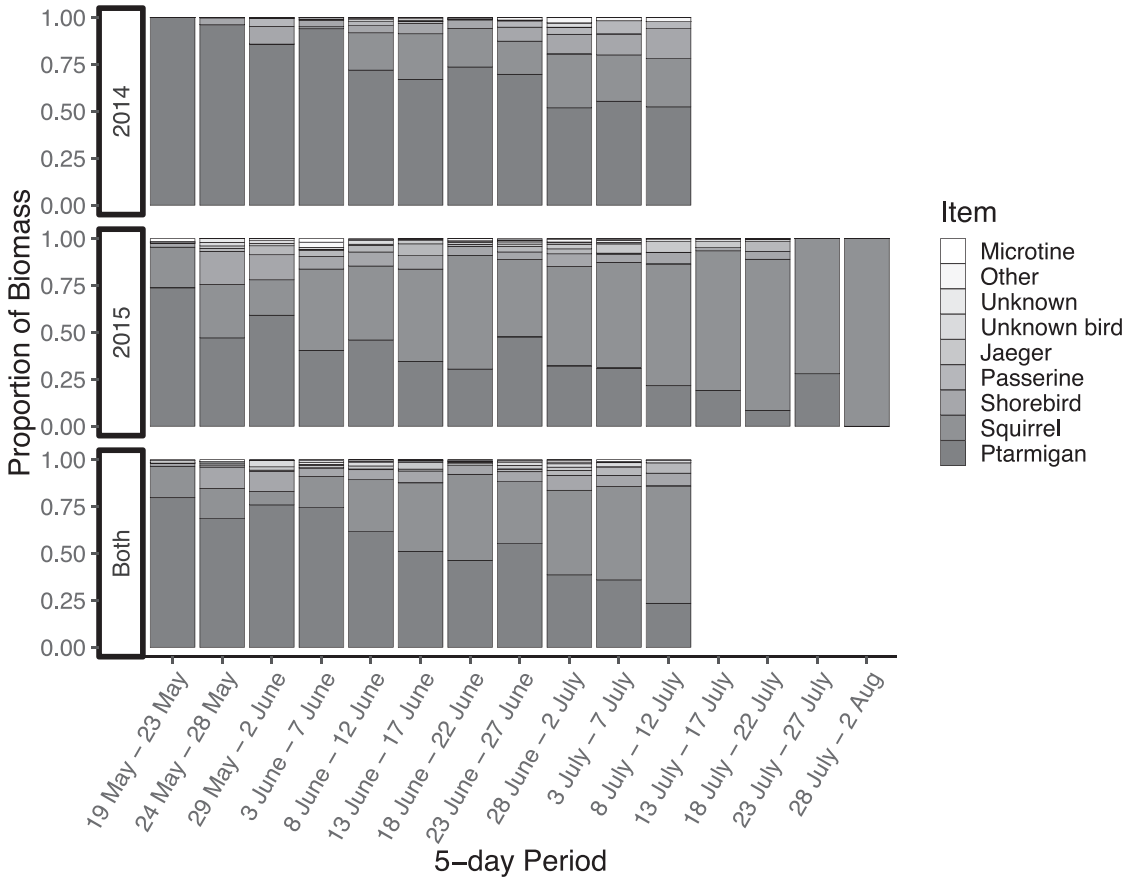

Figure 4. Change in the proportion of prey items in the Gyrfalcon diet by 5-d period over the course of two breeding seasons on the Seward Peninsula, Alaska: 2014 (top), 2015 (middle), and both years (bottom) as determined by prey items catalogued using nest cameras in 20 nests (10 in 2014, 10 in 2015). Proportion of ptarmigan decreased by 5-d period in both 2014 and 2015.

Table 3. AIC model selection criteria for models of Gyrfalcon diet that explore the role of ecosystem phenology ("5-d period") and the role of nestling age in diet breadth of Gyrfalcons during the brood-rearing period during the 2014 and 2015 breeding seasons in western Alaska. In both cases, the intercept-only model was the best-supported model, indicating that neither 5-d period nor age were associated with diet breadth.

MODEL AND VARIABLES	K	ΔAIC[a]	AIC WEIGHT[b]	CUMULATIVE WEIGHT[c]	DEVIANCE
Ecosystem phenology					
Intercept only	4	0.00	0.71	0.71	23.6
5-d period	5	1.79	0.29	1.00	23.8
Nestling age					
Intercept only	4	0.00	0.66	0.66	−379.6
Age	5	1.30	0.34	1.00	−380.3

[a] ΔAIC = a measure of each model relative to the top model.
[b] AIC weight = the "weight of evidence" in favor of a given model being the best approximating model in the set.
[c] Cumulative weight = the cumulative sum of the AIC weight scores including each preceding model.

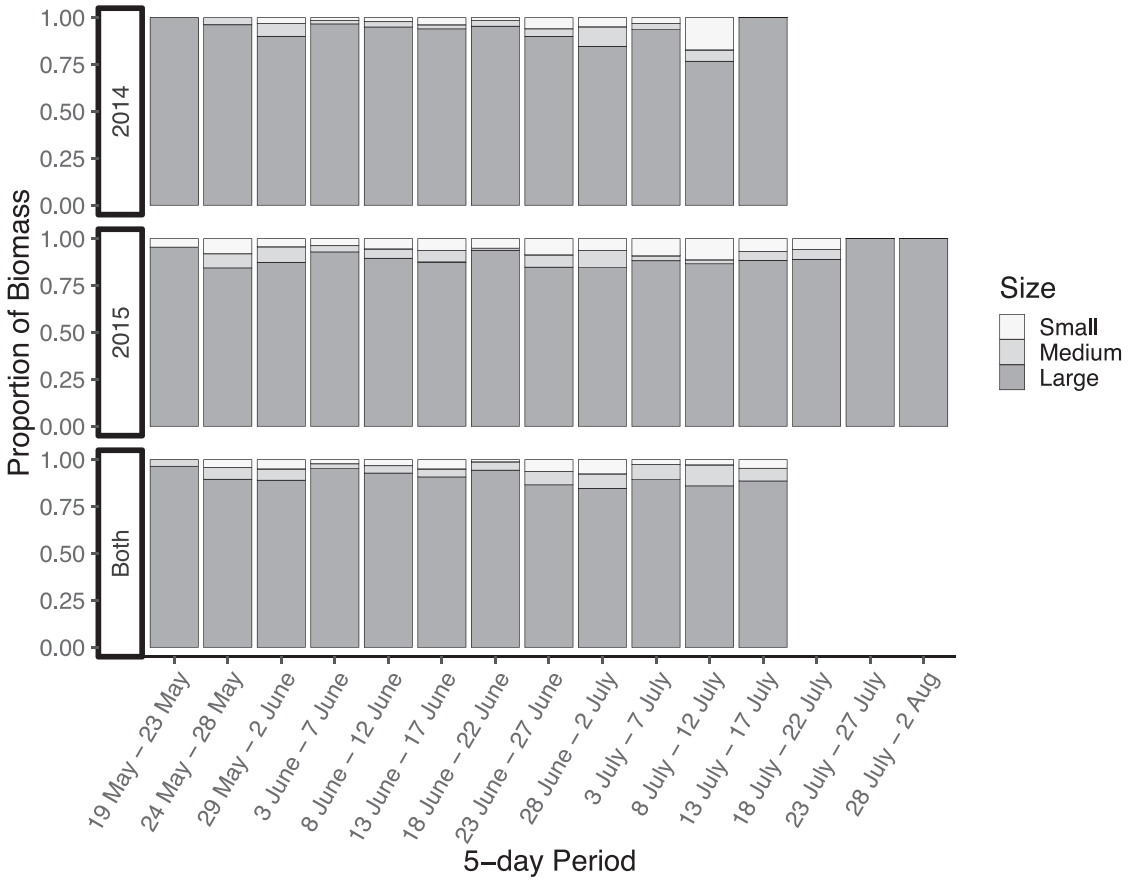

Figure 5. Change in the proportion of Gyrfalcon prey items in each biomass category by 5-d periods across the brood-rearing period on the Seward Peninsula, Alaska: 2014 (top), 2015 (middle,) and both years (bottom). Generally, the same patterns appear between years: a shift to a larger prey type (ground squirrel) as the season advanced, but with a less substantial shift in 2014 when ptarmigan were the most common prey type in the diet.

DISCUSSION

We found that changes in use of ptarmigan and large prey types over time were best explained by the Ecosystem Phenology Hypothesis. Our results indicated that changes in prey use were related to calendar date (ecosystem phenology) and not nestling age (developmental phenology). Although the models supported a decrease in the use of both ptarmigan and large prey types over time, large items remained the most used prey type throughout the brood-rearing period, whereas ptarmigan did not. Consequently, diet breadth remained unchanged, in contrast to our prediction that diet breadth would increase over time. We further observed two important trends in prey use: (1) a mid-season shift in dominant prey type from ptarmigan to squirrel occurred in both years, and (2) a switch in dominant prey type occurred between years from ptarmigan in 2014 to squirrel in 2015.

In contrast to their established recognition as ptarmigan specialists, Gyrfalcons in our study were facultative specialists on large prey types (e.g., prey >400 g) during the brood-rearing period. The observation that Gyrfalcons switched predominant prey type within and between years suggests that Gyrfalcon prey-use patterns depend on seasonal and annual availability of optimal prey types. Previous studies that have investigated inter-seasonal shifts in nestling diet have demonstrated the influence of the division in parental roles, in which dietary changes in prey size and type were explained not by prey availability, but by shifts in parental roles associated

with a decrease in nestling dependency (Steen et al. 2010, Sonerud et al. 2014a, 2014b). Although the trends in our data may have been influenced by a division in parental roles, our results indicate that changes in dietary habits are better explained by ecosystem phenology than by nestling age. Because a facultative specialist selects prey based on availability (Glasser 1982), the inclusion of an optimal prey type in the diet depends on its availability, and that of other optimal prey. As the availability of prey types changes, the optimal diet could switch from specialization on one food type to another with or without increases in diet breadth (Pyke 1984), as we observed in this study. Therefore, the seasonal and annual shifts from ptarmigan to squirrel that we observed likely reflect changes in prey availability, which may be a function of either absolute prey abundance or variation in prey susceptibility to predation. For ptarmigan, vulnerability to predation varies by sex and age over the course of the summer (Nielsen and Cade 1990, 2017, Nielsen 1999). During courtship, male ptarmigan perform conspicuous displays, and they retain their white winter plumage against a landscape that is largely brown in color, thus rendering them susceptible to predation. As nesting begins, adult ptarmigan molt into their cryptic summer plumage, breeding displays and courtship behaviors decrease, and both male and female ptarmigan become less conspicuous (Hannon et al. 1998). Additionally, such shifts in prey availability may include seasonal and interannual differences in squirrel abundance (Carl 1971, Green 1977, Batzli and Sobaski 1980) that influence their role in Gyrfalcon diet (Poole and Boag 1988). Because we did not conduct concurrent prey surveys with our dietary observations, we were unable to assess the relative effects of changes in prey behavior or abundance on their incidence in the diet. We therefore encourage future researchers to couple analyses of temporal dietary trends in nesting Gyrfalcon with temporal prey trends in the surrounding area to further understand Gyrfalcon prey use and its connection to fluctuations in prey populations.

Because Gyrfalcon prey use in this study consisted predominately of shifts between two prey types, shifts in prey use may signal the ramifications of trophic cascades in Arctic tundra and should be considered in climate-change scenarios for this ecosystem. For instance, the contribution of squirrel as an alternative prey type may stabilize Gyrfalcon populations in western Alaska during lows in ptarmigan population cycles. Populations of specialist predators often fluctuate with populations of preferred prey species, whereas generalist predators are more numerically stable because they are capable of switching prey type in response to fluctuations in prey abundance (Korpimäki 1985, Korpimäki and Norrdahl 1989, Redpath and Thirgood 1999, Redpath et al. 2001). In Iceland, Gyrfalcons undergo regular fluctuations in reproductive rate following the population cycles of Rock Ptarmigan (Nielsen 2011). In western Canada, a collapse in Willow Ptarmigan population cycles is thought to be responsible for a decline in numbers of breeding Gyrfalcons (Mossop 2011). On the Seward Peninsula, Gyrfalcon breeding numbers have fluctuated little over time (Bente 2011). Additionally, in other parts of Alaska, the number of occupied territories has also remained relatively stable over time with no obvious regular or cyclic pattern (Mindell et al. 1987, Mindell and White 1988). The lack of appreciable population cycles of Gyrfalcons in western Alaska supports the premise that Arctic ground squirrels maintain predator population stability (Korpimäki et al. 1990, Kurki et al. 1997).

Our study illustrates an important relationship involving three keystone members of Arctic ecosystems—two ecosystem engineers (Tape et al. 2010, Christie et al. 2011, Wheeler and Hik 2012) that are members of the prey guild, and one apex predator. This relationship presents an opportunity for studying the effects of climate change on ecosystem functioning in Arctic tundra (Watson et al. 2011, Wheeler and Hik 2012). For instance, under some climate change scenarios ptarmigan may become functionally less available to Gyrfalcon through two mechanisms: (1) increases in the height, density, and distribution of shrub cover could increase the number of refugia from predation; and (2) range shifts or reductions could alter the distribution of ptarmigan within the range of the Gyrfalcon (Virkkala et al. 2008, Mossop 2011, Lehikoinen et al. 2014). Climate change is also predicted to impact the distribution of Arctic ground squirrels through a multitude of factors related to its habitat associations (Barker and Derocher 2010, Wheeler and Hik 2012), where effects may be negative (e.g., increases in shrub cover) or positive (e.g., increases in forbs; Wheeler et al. 2015). Thus, although our results provide important information on the phenology and role of each important prey type in Gyrfalcon breeding ecology, the effects of climate change on the relationship between these three important

ecosystem members remain uncertain. This uncertainty underscores the importance of continued research on this aspect of Gyrfalcon life history to expand understanding of the effects of global change on key interactions in tundra ecology.

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