



Bayesian stable isotope mixing models effectively characterize the diet of an Arctic raptor

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Abstract

1. Bayesian stable isotope mixing models (BSIMMs) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ can be a useful tool to reconstruct diets, characterize trophic relationships, and assess spatiotemporal variation in food webs. However, use of this approach typically requires a priori knowledge on the level of enrichment occurring between the diet and tissue of the consumer being sampled (i.e. a trophic discrimination factor or TDF).
2. Trophic discrimination factors derived from captive feeding studies are highly variable, and it is challenging to select the appropriate TDF for diet estimation in wild populations. We introduce a novel method for estimating TDFs in a wild population—a proportionally balanced equation that uses high-precision diet estimates from nest cameras installed on a subset of nests in lieu of a controlled feeding study (TDF_{CAM}).
3. We tested the ability of BSIMMs to characterize diet in a free-living population of gyrfalcon *Falco rusticolus* nestlings by comparing model output to high-precision nest camera diet estimates. We analysed the performance of models formulated with a TDF_{CAM} against other relevant TDFs and assessed model sensitivity to an informative prior. We applied the most parsimonious model inputs to a larger sample to analyse broad-scale temporal dietary trends.
4. Bayesian stable isotope mixing models fitted with a TDF_{CAM} and uninformative prior had the best agreement with nest camera data, outperforming TDFs derived from captive feeding studies. BSIMMs produced with a TDF_{CAM} produced reliable diet estimates at the nest level and accurately identified significant temporal shifts in gyrfalcon diet within and between years.
5. Our method of TDF estimation produced more accurate estimates of TDFs in a wild population than traditional approaches, consequently improving BSIMM diet estimates. We demonstrate how BSIMMs can complement a high-precision diet study by expanding its spatiotemporal scope of inference and recommend this integrative methodology as a powerful tool for future trophic studies.

KEY WORDS

animal diet, arctic, Bayesian stable isotope mixing models, gyrfalcon, nest cameras, raptors, stable isotopes, trophic discrimination factors

1 | INTRODUCTION

Predators play key roles in ecosystem dynamics as top-down regulators of population structure (Holt, 1977) and also act as useful indicators of bottom-up effects (Rodríguez-Estrella et al., 1998). Characterizing how predator diet responds to spatiotemporal shifts in the availability of their prey is crucial for understanding their resilience to environmental change (Schmidt et al., 2012). Arctic ecosystems are at the forefront of anthropogenic climate change, with novel environmental conditions contributing to rapid and large-scale shifts in species distributions, phenology and behaviour (review in Post et al., 2009). As the ranges, phenologies and behaviours of species change, predator-prey relations—along with other ecological interactions—are altered (Thackeray et al., 2016). It is therefore critical to monitor trophic interactions in Arctic ecosystems via dietary analysis of the top predators specializing within those systems, particularly in birds of prey (i.e. raptors; Ims & Fuglei, 2005). Arctic raptor diet studies have done so through the use of nest camera dietary analysis in recent years (e.g. Robinson et al., 2019), which provide high-precision diet estimates for nestlings but are often constrained by sample size and geographic scope. There is an apparent need for a robust methodology to assess spatial and temporal trends in the diet of Arctic raptors. This paper addresses that need by formally evaluating the use of Bayesian stable isotope mixing models (BSIMMs) in a wild population of gyrfalcons *Falco rusticolus*.

Raptor diet studies have traditionally employed the use of direct observation and prey remains/pellet analysis, but in recent years nest cameras have emerged as a more accurate and effective alternative (Lewis et al., 2004). Nest cameras are a useful tool in studying raptor diet and behaviour during the breeding season: motion-activated cameras installed at nesting sites capture prey deliveries (either via video or still image), which are subsequently identified and enumerated to create precise estimates of the proportions of different prey species and categories in the diet (e.g. Robinson et al., 2015). However, this approach requires repeated visits to nesting sites, and even sporadic disturbances early in nesting can influence prey delivery rates and cause nest failure in some species (Harrison et al., 2019). Although nest camera analysis can provide highly accurate estimates of nestling diet at a limited scale, it can underrepresent the contribution of small prey and is often limited in scope due to small sample size; technical failure (e.g. battery/card issues, trigger sensor failure, blocked field of view) can further complicate raptor nest camera studies, effectively reducing sample size by >50% in some cases (e.g. García-Salgado et al., 2015).

Stable isotope approaches provide a complementary methodology to assess broad-scale dietary trends, potentially expanding the spatiotemporal scope of inference that can be obtained from cameras alone (Swan et al., 2020). Stable isotope analysis is a useful and increasingly common method for wildlife diet studies. For example, the isotopic values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) vary among organisms, and are dependent upon their trophic level and basal carbon source (DeNiro & Epstein, 1978, 1981). These values are maintained throughout food webs often resulting in unique

and identifiable positions in isotopic space for different groups of taxa (Hobson & Clark, 1992). By iteratively analysing a consumer's position in isotopic space relative to its diet sources, stable isotope mixing models can estimate the relative importance of sources to a consumer's diet (Parnell et al., 2013). Contemporary BSIMM frameworks (e.g. MixSIAR) contain methods to generate proportional dietary estimates, unifying multiple error structures and allowing for the incorporation of fixed and random effects (Stock et al., 2018).

Bayesian stable isotope mixing models incorporate the following information to generate diet estimates: isotopic values of consumers, isotopic values of source (prey) groups, prior knowledge of expected dietary proportions (i.e. an informative prior) and a trophic discrimination factor (TDF; Parnell et al., 2013). Model performance is reliant upon the careful inclusion of all major source groups for the consumer, and their subsequent grouping into categories that are both ecologically relevant and isotopically differentiable (Phillips et al., 2014). Informative priors are typically generated using another indirect method of diet characterization (e.g. pellet/scat analysis, gut contents, camera data), and have been shown to improve model fit in some instances (e.g. Chiaradia et al., 2014). However, a prior that is either biased or overconfident can mask isotopic variability, thereby generating diet estimates that simply reflect the prior without providing new information about the system (e.g. Robinson et al., 2018). Uninformative priors (i.e. where all prey groups are weighted evenly) have also proven effective in some instances, particularly when accurate priors are unavailable (e.g. Swan et al., 2020).

Diet-tissue discrimination is the process through which the biochemical components of food items change when incorporated into the tissue of consumers, and the application of appropriate TDFs is crucial to the interpretation of stable isotope mixing models (Bond & Diamond, 2011). Many factors influence a consumer's TDF, including its taxon, environment, diet, stage of development and the tissue in question (review in Martínez del Rio et al., 2009). A common approach for the calculation of a TDF is a controlled feeding experiment, wherein a consumer is maintained on a simple diet with a known isotopic signature, and then the consumer's isotopic values are compared against those of its resource (e.g. Carleton & Martínez del Rio, 2010; Hobson & Clark, 1992). This approach has been expanded to include the incorporation of multiple diet items (weighted by proportion) for the calculation of TDFs (Greer et al., 2015). Studies often forgo controlled feeding experiments due to logistical constraints, instead relying upon published TDF values of species that are taxonomically similar to their study organism (e.g. Hedd & Montevercchi, 2006). Choosing or developing an appropriate TDF is fraught with logistical challenges, particularly in wild populations that express wide degrees of variability (Caut et al., 2009).

We introduce a simple and novel method for the estimation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TDFs in wild populations (TDF_{CAM}), applying estimated dietary proportions from high-precision diet data from nest cameras in lieu of the known dietary proportions typical of a traditional controlled feeding study (e.g. Greer et al., 2015). We posit that in situations where high-quality dietary data are available for a subset of the population, the TDF_{CAM} method can be used

to produce more realistic estimates of TDFs in a wild population than traditional approaches, consequently improving BSIMMs diet estimates.

We aimed to test the efficacy of BSIMMs as a method of diet characterization in a wild population, applying a novel method for TDF estimation. We used gyrfalcons as a model organism due to their role as specialist predators in a threatened ecosystem, and due to the availability of high-precision diet data for a subset of the population. First, we generated a TDF_{CAM} from a subset of nestlings, which were then removed from subsequent analysis. Then, we tested BSIMMs using the TDF_{CAM} against published TDF values by comparing model output to high-precision dietary estimates from nest cameras. We also assessed model sensitivity to an informative versus uninformative prior using the same approach. Applying the TDF and prior that corresponded with the top model, we tested BSIMM and nest camera method agreement at three spatiotemporal scales: (a) dietary proportions for individual nest-years; (b) seasonal dietary trends within the brood rearing period and (c) interannual dietary trends. Our case study of an Arctic raptor demonstrates the power and potential of combining the use of nest cameras and BSIMMs to characterize diet in wild populations.

2 | MATERIALS AND METHODS

2.1 | Study design

We studied a gyrfalcon population on the Seward Peninsula on the west coast of Alaska (64°N – 65°N , 164°W – 166°W ; Figure S1). Gyrfalcons are tundra ecosystem specialists occupying a narrow ecological niche across the circumpolar north, and require a high energy input to raise nestlings throughout their 40- to 50-day brood rearing period (from egg hatch to nestling fledge; Booms et al., 2020). This ecosystem is currently undergoing a rapid change in community composition associated with climate change (Post et al., 2009), which has the potential to alter trophic dynamics across the gyrfalcons' range. We use the term 'nest-year' as a sampling unit for this study, which refers to a breeding pair and their young at a nest within a year, which may or may not be independent from nesting sites, territories or breeding pairs across the years of the study. Territories (i.e. nest sites and their surrounding areas) were delineated by a set of decision rules following Anderson et al. (2019).

We monitored and sampled 113 gyrfalcon nestlings at 42 nest-years within 24 discrete territories (2016–2019; Table S1). These were divided into the following subsets: high-confidence nests (HC subset, $n = 20$ nest-years) are those for which we have continuous nest camera diet data from when nestlings hatched to when blood samples were first collected; unknown nests (UNK subset, $n = 20$ nest-years) are those for which we have blood samples but non-existent or incomplete nest camera data; and the TDF subset ($n = 2$ nest-years) had highly reliable nest camera diet data but was analysed separately to generate TDF_{CAM} estimates.

2.2 | Nest cameras

To locate occupied gyrfalcon nests, we conducted large-scale aerial surveys of c. 500 cliffs with potential or historically occupied raptor nesting sites (Figure S1; specific methodology in Robinson et al., 2019). We installed motion-activated cameras (Reconyx Hyperfire I & II) at gyrfalcon cliff nests to quantify and characterize prey deliveries throughout the brood rearing period (following Robinson & Prostor, 2017). We recorded each prey delivery to the lowest possible taxonomic level, and visually estimated the proportion of prey consumed by nestlings (to the nearest 10%), because adults often consume or remove portions of prey items. These percentage values were also used to estimate the size of juvenile prey relative to adult prey for biomass values. We applied mass values from the literature for each prey species (Table S2) and multiplied by per cent consumed to attain a consumed biomass estimate for each delivery. For several prey groups, we applied biomass values derived from specimens we collected rather than using a literature value; either because that species has been shown to vary substantially in biomass across its geographic range (e.g. Arctic ground squirrels; Sheriff et al., 2013) or because we were unable to differentiate between species from a photograph of a partially consumed carcass (e.g. with rock & willow ptarmigan *Lagopus muta* and *Lagopus lagopus*; Table S2).

Prey items were grouped into the following taxonomically and ecologically distinct categories (based on Robinson et al., 2019): ptarmigan (*Lagopus* spp.), Arctic ground squirrels *Urocitellus parryii*, insectivorous birds (shorebirds and passerines), arvicoline rodents (*Microtus*, *Lemmus* and *Myodes* spp.), and jaegers (*Stercorarius* spp.). Prey deliveries of other categories (e.g. ducks and raptors) constituted a small proportion of dietary biomass (<1% combined) and were not considered to be major prey categories for this analysis (Table S2). Prey deliveries that could not be identified to species level were instead assigned to groups (e.g. 'small passerine', 'medium shorebird'), for which we estimated biomass values (Table S2). The proportional contribution (P_{ij}) of each prey category to the nestling's diet was calculated for each nest-year by dividing the sum of that category's biomass by the sum of the total prey biomass consumed by nestlings over the observation period, where (i) represents one of the five prey categories, (j) represents the subset of gyrfalcon nestlings used.

To generate posterior density distributions for our nest camera diet estimates and make them directly comparable to the output of BSIMMs, we bootstrapped 3,000 replicates of dietary proportions for each prey category using the *BAYESBOOT* package in R (Bååth, 2018). To assess the seasonality of gyrfalcon diet from nest camera data, we calculated dietary proportions of each prey category separately for three time intervals corresponding to the following nestling ages: early (1–12 days), intermediate (13–25 days) and late (26–37 days). We analysed the effect of time interval on dietary proportions in a linear mixed model framework with a post hoc Tukey's test using the *LME4* and *MULTCOMP* packages in the R statistical platform (version 4.0.2; Bates et al., 2015; Hothorn et al., 2008; R Core Team, 2020),

treating *Territory* and *Year* as random effects. We applied the same statistical approach to analyse the effect of interannual variability on dietary proportions, treating *Year* as a fixed effect and *Territory* as a random effect. Due to small sample size in 2016, we only included data from 2017 to 2019 in this portion of the analysis.

2.3 | Stable isotope analysis

We collected blood samples from 113 c. 25-day-old gyrfalcon nestlings, a subset of which were resampled when they were c. 35 days old ($n = 28$; Table S1). From each nestling sampled, we collected blood from the brachial vein and immediately deposited it into a heparinized vacutainer. Samples were kept on ice for <6 hr until centrifugation. After removing the plasma, red blood cells were immediately frozen at -20°C until they could be processed for stable isotope analysis.

During the 2018 and 2019 field seasons, we collected 185 muscle samples from prey species representative of five predetermined categories of the gyrfalcon diet (ptarmigan, Arctic ground squirrel, insectivorous birds, arvicoline rodents and jaeger; Table S3). We collected samples from only those species that constituted 95% of each prey category by biomass in the 2014–2015 gyrfalcon diet (Robinson et al., 2019), and our sampling intensity was also reflective of these values. Prey species were sampled with higher frequency dependent on their perceived importance to gyrfalcon diet and relative availability on the landscape, after which values were averaged across species for each prey category. We distributed our sampling efforts across the study site throughout the gyrfalcon brood rearing period. The majority of tissue samples were collected opportunistically from prey remains at raptor nests, but some samples were collected actively via shotgun (9.1% of all samples) or snap-trap (12.9% of all samples) when necessary to account for underrepresented groups. From each prey specimen, we collected c. 1 g of muscle tissue (breast for birds and thigh for mammals) and stored samples at -20°C until they could be processed for stable isotope analysis.

To prepare samples for stable isotope analysis, we freeze dried prey muscle tissue and gyrfalcon red blood cell samples for 48 hr, then ground to a fine powder and subsampled 0.05 g into tins. We analysed carbon and nitrogen stable isotope ratios using a Costech ECS 4010 (Costech Analytical Technologies) connected to a Delta V Plus XP Mass Spectrometer (IRMS; Thermo Fischer Scientific) via a Finnigan Conflo III (Thermo Fischer Scientific). Isotope ratios are expressed as $\delta X\text{‰}$, where $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, and R is a ratio of heavy:light isotopes of a given element. Vienna PeeDee Belemnite and atmospheric nitrogen were used as standards for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively. TDFs are expressed as $\Delta X\text{‰}$, where $\Delta X = (\delta X_{\text{consumer}} - \delta X_{\text{sources}})$. We calibrated our analyses using within-run alkaline peptone standards, achieving an analytical precision estimate of $\pm 0.127\text{‰}$ (nitrogen) and $\pm 0.096\text{‰}$ (carbon) across all runs. Analyses were performed at the Alaska Stable Isotope Facility in the Institute of Northern Engineering (University of Alaska Fairbanks).

2.4 | Estimation of trophic discrimination factors

Because no published values exist for the TDFs of gyrfalcons (or the juveniles of any falconid species) and a controlled feeding experiment was impractical for the scope of this study, we implemented a novel approach for the estimation of TDFs in a wild population. We chose a subset of our study population that exhibited variability in isotopic values and applied a proportionally balanced version of a traditional TDF calculation (Equation 1) using estimated dietary proportions from high-precision nest camera data in lieu of the known proportions typical of a controlled feeding study. We assumed several factors could contribute to the variability in TDFs within the study population: year, nestling age at sampling, differences in diet and distance between nests. Thus, we selected a subset of our population (eight individuals in two nests during different years; Table S1) for which we had precise nest camera dietary data from the time nestlings hatched to when they were sampled, and which exhibited the highest variability of the listed factors. Nestlings at Nest A (2016, sampled at 34 days old) consumed mostly ptarmigan (82.7%), and nestlings at Nest B (2017, sampled at 25 days old) consumed mostly Arctic ground squirrels (55.3%); the nests were also at opposite ends of the study site (81 km apart).

We estimated gyrfalcon TDF_{CAM} for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using the following equation, where (i) represents one of (n) prey categories, (j) represents an individual in the subset of consumers used, (m) is the number of consumers in that subset and (P) is a dietary proportion estimate from nest camera analysis:

$$\begin{aligned} \text{TDF}_{\text{CAM}} \text{ Mean} &= \frac{\sum_{j=1}^m [\delta_j - \sum_{i=1}^n (\text{mean}(\delta_i) \times P_{ij})]}{m} \\ \text{TDF}_{\text{CAM}} \text{ SD} &= \sqrt{\frac{\sum_{j=1}^m (\delta_j - \text{TDF}_{\text{CAM}} \text{ Mean})^2}{m-1}}. \end{aligned} \quad (1)$$

TDF_{CAMs} (Table 1; Figure S2) were then applied to the other nestlings in the population, and the subset of nests used to generate TDF_{CAMs} was excluded from further analysis.

2.5 | Statistical methods

We implemented BSIMMs using the MixSIAR package in R (Stock & Semmens, 2018). The input parameters for the models were the raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of gyrfalcon nestlings, which were tested against the mean and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each of five prey categories (Table S3). All BSIMMs were formulated with 100,000 iterations thinned by 25 and a burn-in of 50,000 with three chains, which were considered to have converged when they passed the Geweke and Gelman–Rubin Diagnostics (following Stock & Semmens, 2018).

To test the sensitivity of BSIMMs to different inputs, we formulated models using different TDFs and prior sets and compared the agreement of their outputs against nest camera dietary

TABLE 1 Summary of trophic discrimination factors and prior sets which were applied to Bayesian stable isotope mixing models. Values for prior sets refer to diet proportions of the five prey categories: PTAR (ptarmigan), AGSQ (Arctic ground squirrel), I. Bird (insectivorous bird), A. Rod (arvicoline rodent), and jaeger

TDF name	$\Delta^{13}\text{C} (\pm SD)$	$\Delta^{15}\text{N} (\pm SD)$	Category	Source		
Peregrine	0.20 ± 0.01	2.70 ± 0.05	CFE ^a	Hobson and Clark (1992)		
Condor	-0.70 ± 0.10	1.70 ± 0.10	CFE ^a	Kurle et al. (2013)		
Snowy owl	0.30 ± 0.20	1.90 ± 0.10	CFE ^a	Therrien et al. (2011)		
SIDER	0.29 ± 1.35	2.28 ± 1.28	SIDER	Healy et al. (2018)		
TDF_{CAM}	0.99 ± 0.17	1.37 ± 0.22	TDF_{CAM}	This paper		
Prior set	PTAR	AGSQ	I. Bird	A. Rod	Jaeger	Source
Informative	0.530	0.362	0.089	0.004	0.015	Robinson et al. (2019)
Uninformative	0.250	0.250	0.250	0.250	0.250	NA (evenly weighted)

^aControlled feeding experiment.

TABLE 2 Ranking of Bayesian stable isotope mixing model performance with Bhattacharyya's coefficient (BC). BC values are displayed for each prey category: PTAR (ptarmigan), AGSQ (Arctic ground squirrel), I. Bird (insectivorous bird), A. Rod (arvicoline rodent) and jaeger. The total BC values are the mean ± SD across categories. Bolded rows are mixing models with a mean BC > 0.6, indicating significant overlap with nest camera data

TDF	Prior	BC (Mean ± SD)	PTAR	AGSQ	I. Bird	A. Rod	Jaeger
TDF_{CAM}	Uninformative	0.730 ± 0.20	0.897	0.636	0.468	0.700	0.947
TDF_{CAM}	Informative	0.413 ± 0.27	0.789	0.194	0.560	0.136	0.384
Snowy owl	Uninformative	0.296 ± 0.36	0.001	0.071	0.281	0.208	0.917
SIDER	Uninformative	0.218 ± 0.35	0.000	0.035	0.057	0.161	0.838
Condor	Uninformative	0.165 ± 0.22	0.008	0.017	0.171	0.079	0.548
Peregrine	Uninformative	0.110 ± 0.20	0.000	0.004	0.000	0.074	0.472

proportions using Bhattacharyya's coefficient (BC; e.g. Swan et al., 2020). BC is a method of analysing overlap in posterior density distributions, and ranges from 0 to 1; in this instance a value of 1 would reflect complete similarity between nest camera estimates and BSIMMs output, 0 would indicate no similarity, and a BC value >0.60 indicates significant overlap between models (Bond & Diamond, 2011). For TDFs, we compared our TDF_{CAM} against reported values from controlled feeding studies of the following taxonomically related or functionally relevant species: peregrine falcon *Falco peregrinus* (Hobson & Clark, 1992), California condor *Gymnogyps californianus*; (Kurle et al., 2013) and snowy owl *Bubo scandiacus* (Therrien et al., 2011; Table 1). We also calculated a TDF for gyrfalcon using the SIDER package in R, which applies a phylogenetic regression model to a database of TDFs published in the literature (Healy et al., 2018). To test model sensitivity to the incorporation of an informative prior, we generated gyrfalcon dietary proportions based on nest camera data for 20 nest-years over the 2014–2015 brood rearing periods on the Seward Peninsula published by Robinson et al. (2019). Proportions were rescaled into Dirichlet hyperparameters before their incorporation into BSIMMs (following Stock et al., 2018). We also generated BSIMMs using uninformative priors where the five prey categories were weighted evenly. After testing six models in a

BC framework (Table 2), we selected the model incorporating the most parsimonious TDF and prior set for use in further analysis.

To analyse spatial, seasonal and interannual variation in diet, we formulated a mixing model using the TDF_{CAM} and uninformative priors (i.e. the top model; Table 2) and applied it to three subsets of gyrfalcon isotope samples using a random and fixed effects framework in MixSIAR. To assess the resolution of BSIMMs at the nest-year scale, we applied the model to the high-confidence subset ($n = 20$ nest-years), with Nest-Year as a fixed effect. We tested for correlations between mean mixing model diet proportions and nest camera diet proportions for each nest-year in each prey category using Pearson's correlation coefficient and linear models. To test for seasonal shifts in prey use, we applied the model to the subset of nestlings that were measured at both c. 25 and c. 35 days of age ($n = 28$ individuals), with Age Group as a fixed effect, nested within Nestling ID as a random effect. We compared modelled dietary proportions of each prey category across the two age classes using a paired t test. To test for interannual differences in prey use, we applied the model to all gyrfalcon nest-years measured at c. 25 days from 2017 to 2019 ($n = 31$ nest-years) with Year as a fixed effect and Territory as a random effect. We compared modelled dietary proportions across 3 years using ANOVA and post hoc Tukey's tests.

3 | RESULTS

3.1 | Nest cameras

From the high-confidence nest camera diet data ($n = 20$ nest-years), we recorded 2,092 prey deliveries (104.6 ± 43.34 deliveries per nest) from the hatch date of the first nestling at each site to the date of first sampling (nestlings 26.4 ± 3.42 days of age), of which a small percentage ($n = 15$; 0.7%) could not be identified to the species level. Gyrfalcon nestlings on the Seward Peninsula consumed primarily ptarmigan (53.14%), but Arctic ground squirrel (22.64%) and insectivorous birds (16.8%) were also important resources during this time interval (Figure 1). In the nest camera data, we found a significant effect of nestling age group on dietary proportions of Arctic ground squirrel ($p < 0.01$), insectivorous birds ($p = 0.024$) and arvicoline rodents ($p = 0.038$), and no significant effect on ptarmigan or jaegers.

Post hoc Tukey's tests indicated the following: younger nestlings ate significantly fewer Arctic ground squirrels and more insectivorous birds and arvicoline rodents than older nestlings (Figure 2A). In the nest camera data, there was significant interannual variability in dietary proportions of arvicoline rodents ($p = 0.037$); they constituted a substantially higher proportion of the diet in 2019 compared to the other years of the study (Figure 3A). There were no significant interannual trends for the other prey groups.

3.2 | Mixing models

There was significant isotopic differentiation in muscle tissue among the five prey categories (MANOVA, $p < 0.01$; Figure 4), with no significant effect of the year the prey tissue was sampled ($p = 0.103$). Post hoc pairwise Tukey's tests indicated no simultaneous overlap

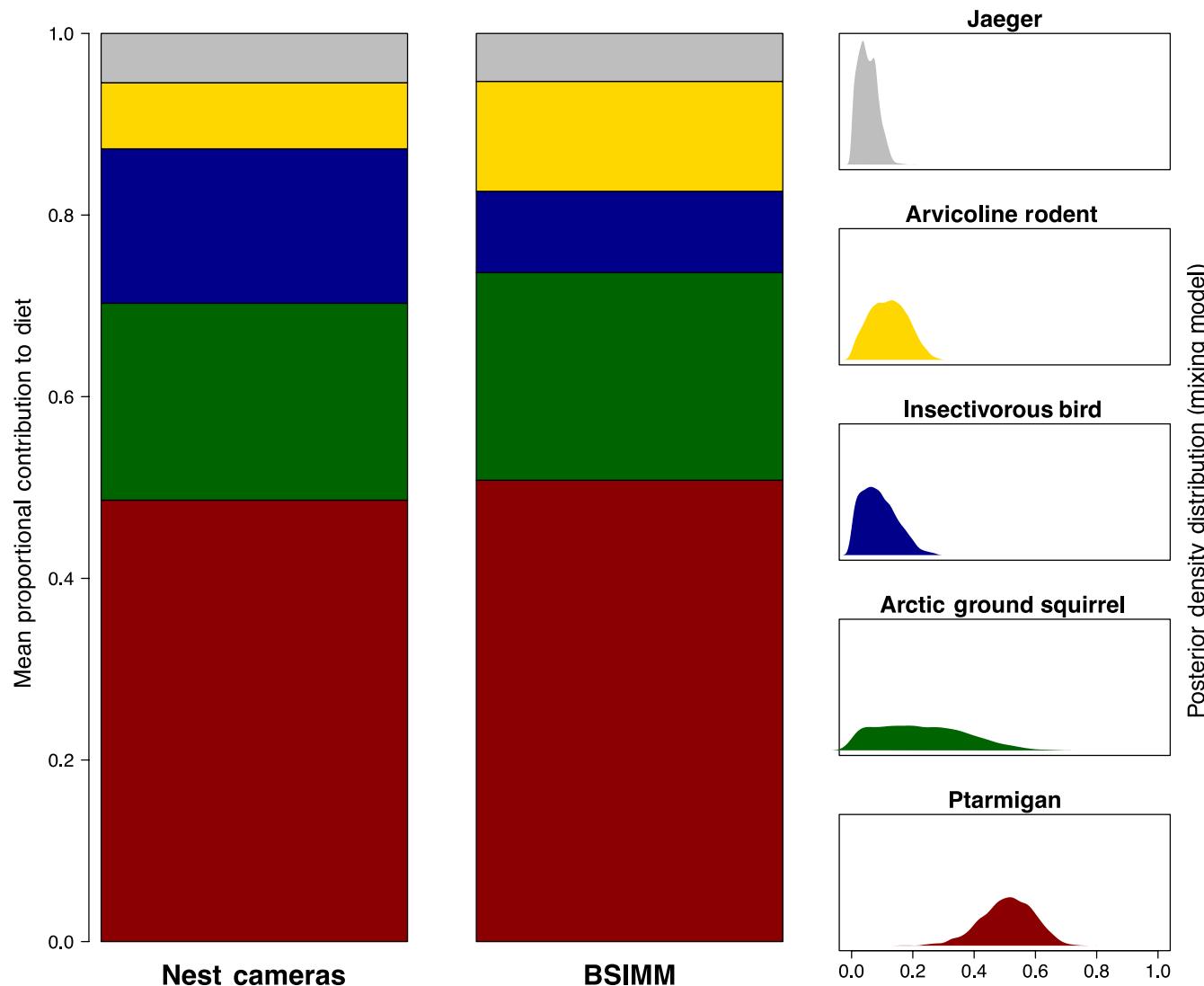


FIGURE 1 The mean proportional contribution of each prey category to gyrfalcon nestling diet on the Seward Peninsula 2016–2019, as inferred from nest cameras and Bayesian stable isotope mixing models (BSIMMs). Mixing model output is from a BSIMM with the HC subset ($n = 58$ nestlings, 20 nest-years) as a consumer group, uninformative priors and our TDF_{CAM} . Nest camera data are from the same subset and time interval. Posterior density distributions generated from the BSIMM are displayed for each prey category

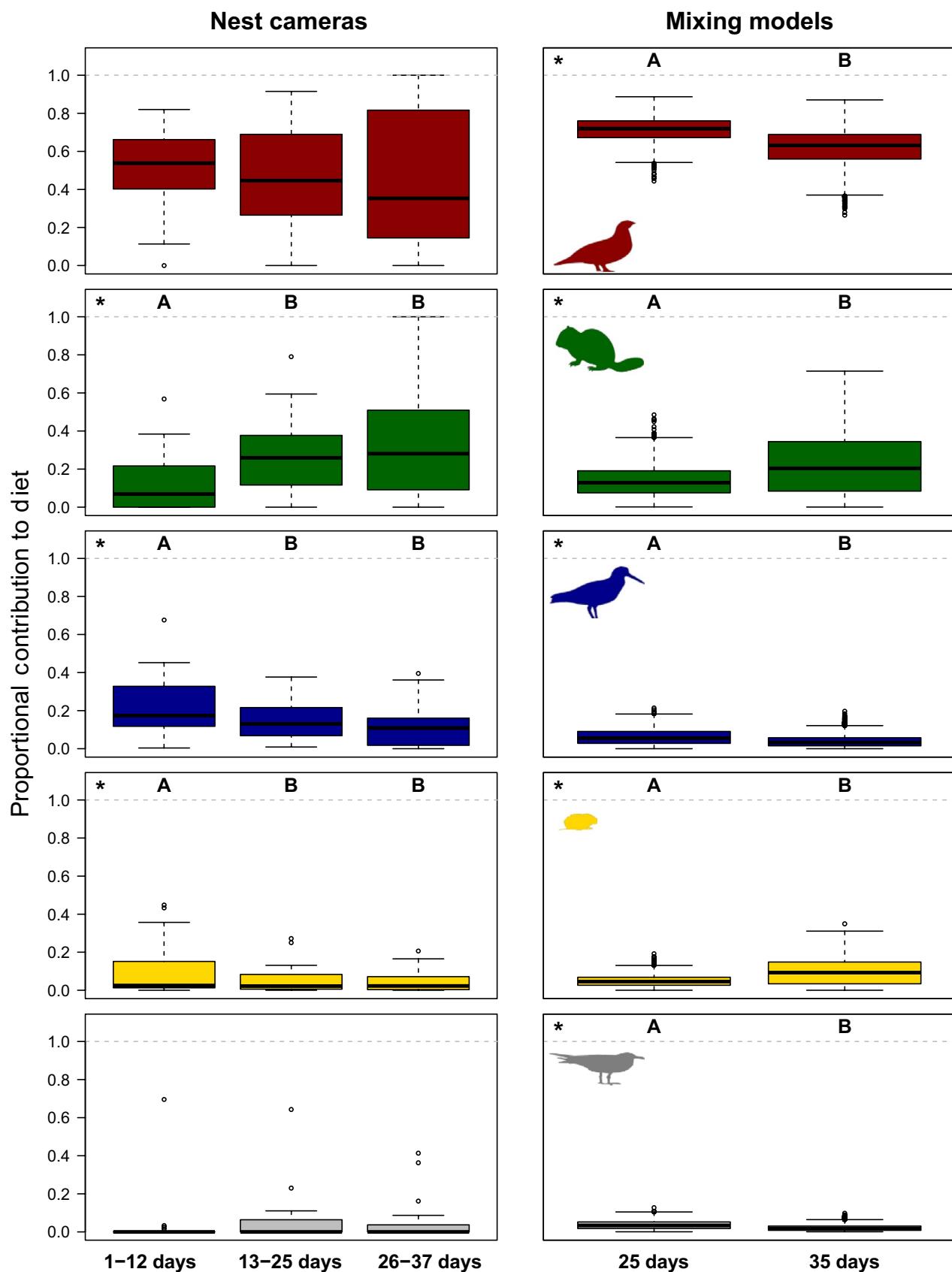


FIGURE 2 Seasonal variation in gyrfalcon diet as indicated by nest camera data ($n = 14$ nestlings) and a Bayesian stable isotope mixing model (BSIMM; $n = 28$ nestlings) on the Seward Peninsula 2017–2018. Round A nestlings were sampled at ~25 days old, and were resampled at ~35 days (Round B). BSIMM was formulated using our TDF_{CAM} , uninformative priors, Round as a fixed effect and Nestling ID as a random effect. Asterisks and letters indicate significant differences between groups from ANOVAs and post hoc Tukey's tests (nest cameras) and paired t-tests (BSIMMs)

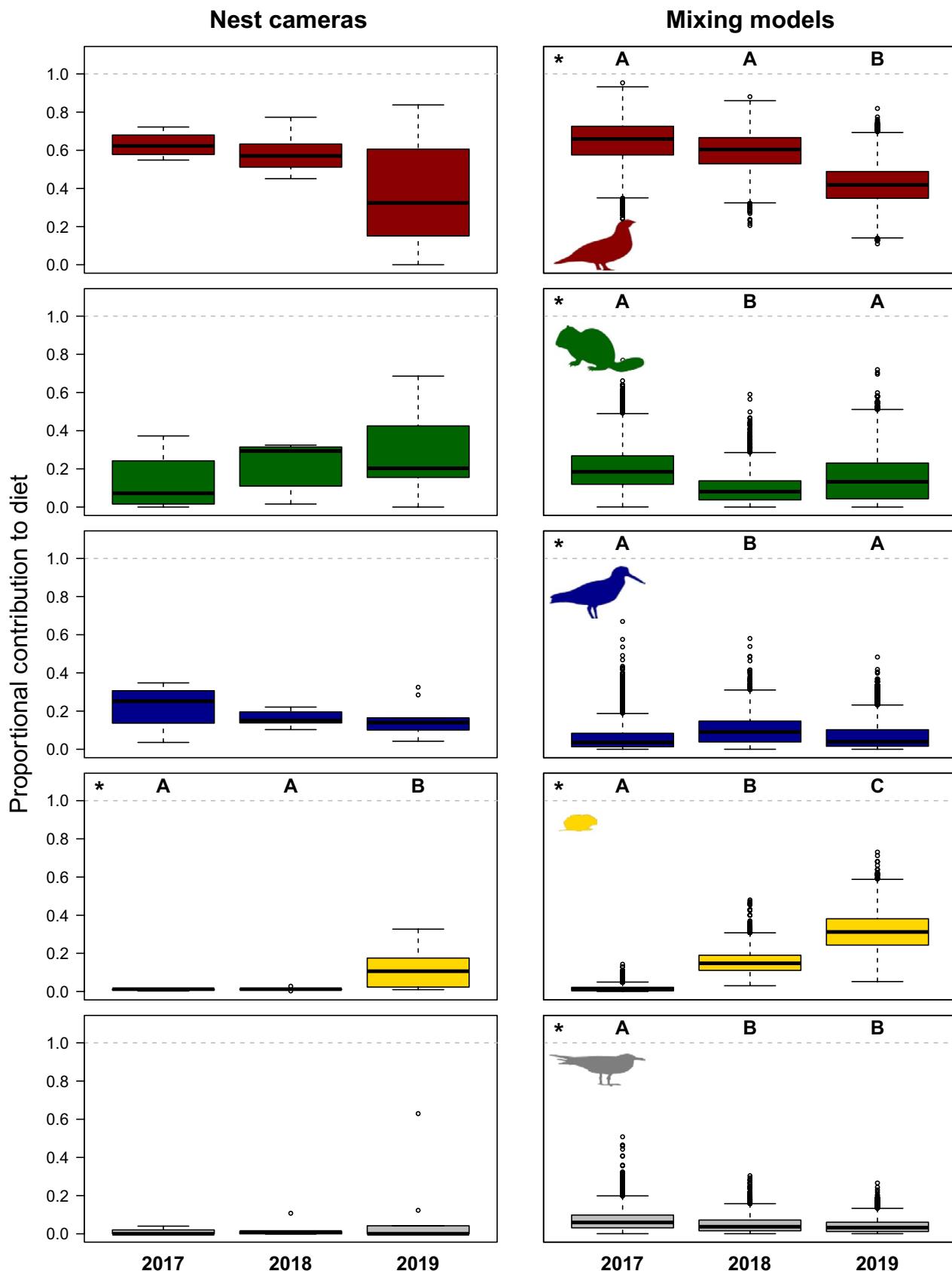


FIGURE 3 Interannual variation in gyrfalcon diet as indicated by nest camera data (HC subset, $n = 19$ nest-years) and a Bayesian stable isotope mixing model (BSIMM; $n = 31$ nest-years) on the Seward Peninsula 2017–2019. Nestlings were in the same age group (~25 days) for all years. BSIMM was formulated using our TDF_{CAM} , uninformative priors, Year as a fixed effect and Territory as a random effect. Asterisks and letters indicate significance between groups from ANOVAs and post hoc Tukey's tests

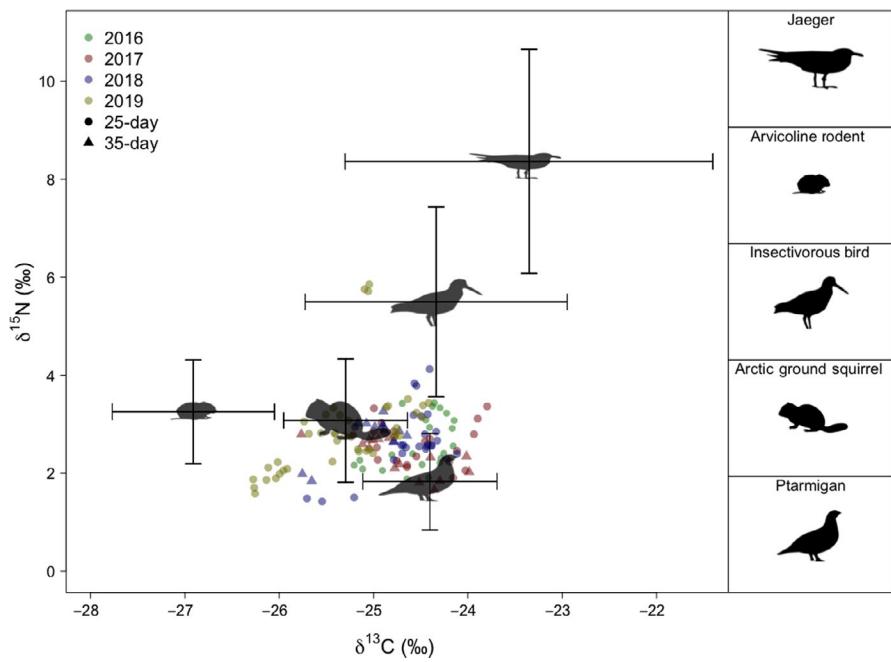


FIGURE 4 Gyrfalcon isotope values (points, $n = 113$) plotted against prey isotope values (silhouettes & bars, $n = 185$), Seward Peninsula 2016–2019. Colours represent year of collection and symbol shapes represent nestling age group. Gyrfalcon isotope values are adjusted using TDF_{CAM} mean values, and error bars around prey categories represent the mean $\pm SD$ of that category's isotope values \pm the TDF_{CAM} SD for that isotope

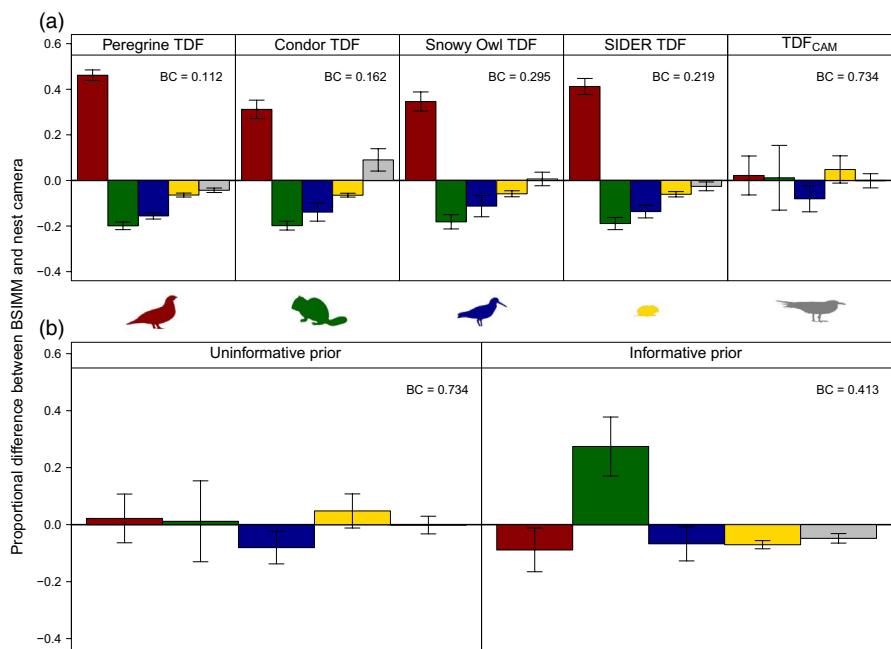


FIGURE 5 (a) The proportional difference between Bayesian stable isotope mixing model (BSIMM) diet estimates and nest camera diet estimates by prey category, comparing models constructed with five unique TDFs (details in Table 1). All models used the high-confidence subset ($n = 58$ nestlings, 20 nest-years) as a consumer group and uninformative priors. Colours correspond to the five prey groups: ptarmigan, Arctic ground squirrel, insectivorous birds, arvicoline rodents and jaegers, shown here as silhouettes. Error bars are $\pm 1 SD$. BC is the corresponding Bhattacharyya's coefficient for each model from Table 2. (b) The proportional difference between BSIMM diet estimates and nest camera diet estimates for each prey category comparing models using uninformative versus informative priors. All models used the high-confidence subset and the TDF_{CAM}

in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between any two categories (ANOVA, Tukey's test, $p < 0.01$). We concluded that each prey category was adequately isotopically differentiable for its use in a BSIMM framework. When BSIMM performance was compared with different TDFs and prior sets, the TDF_{CAM} performed better than all other TDF values tested regardless of which prior set was used, and an uninformative prior performed better than an informative prior (Figure 5; Table 2). We selected this TDF and prior (TDF_{CAM} , uninformative; mean BC = 0.730) for all further BSIMM analyses.

At the nest-year level, there was a strong correlation between modelled and observed mean proportions of ptarmigan ($R = 0.707$, $\beta = 0.611$, $p < 0.01$) and Arctic ground squirrels ($R = 0.579$,

$\beta = 0.562$, $p < 0.01$), a weak non-significant correlation for insectivorous birds ($R = 0.281$, $\beta = 0.297$, $p = 0.229$) and jaegers ($R = 0.22$, $\beta = 0.023$, $p = 0.356$; Figure 6) and no correlation for arvicoline rodents ($R = 0.052$, $\beta = 0.017$, $p = 0.828$). We observed a significant seasonal dietary shift across all prey categories except ptarmigan (paired t test, $p < 0.01$; Figure 2B). We found significant differences between years for each prey category (ANOVA, $p < 0.01$). Post hoc Tukey's tests indicated the following: 2017 had significantly more jaegers and fewer arvicoline rodents than any other year; and 2019 had significantly fewer ptarmigan and more arvicoline rodents than any other year (Tukey's test, $p < 0.01$; Figure 3B).

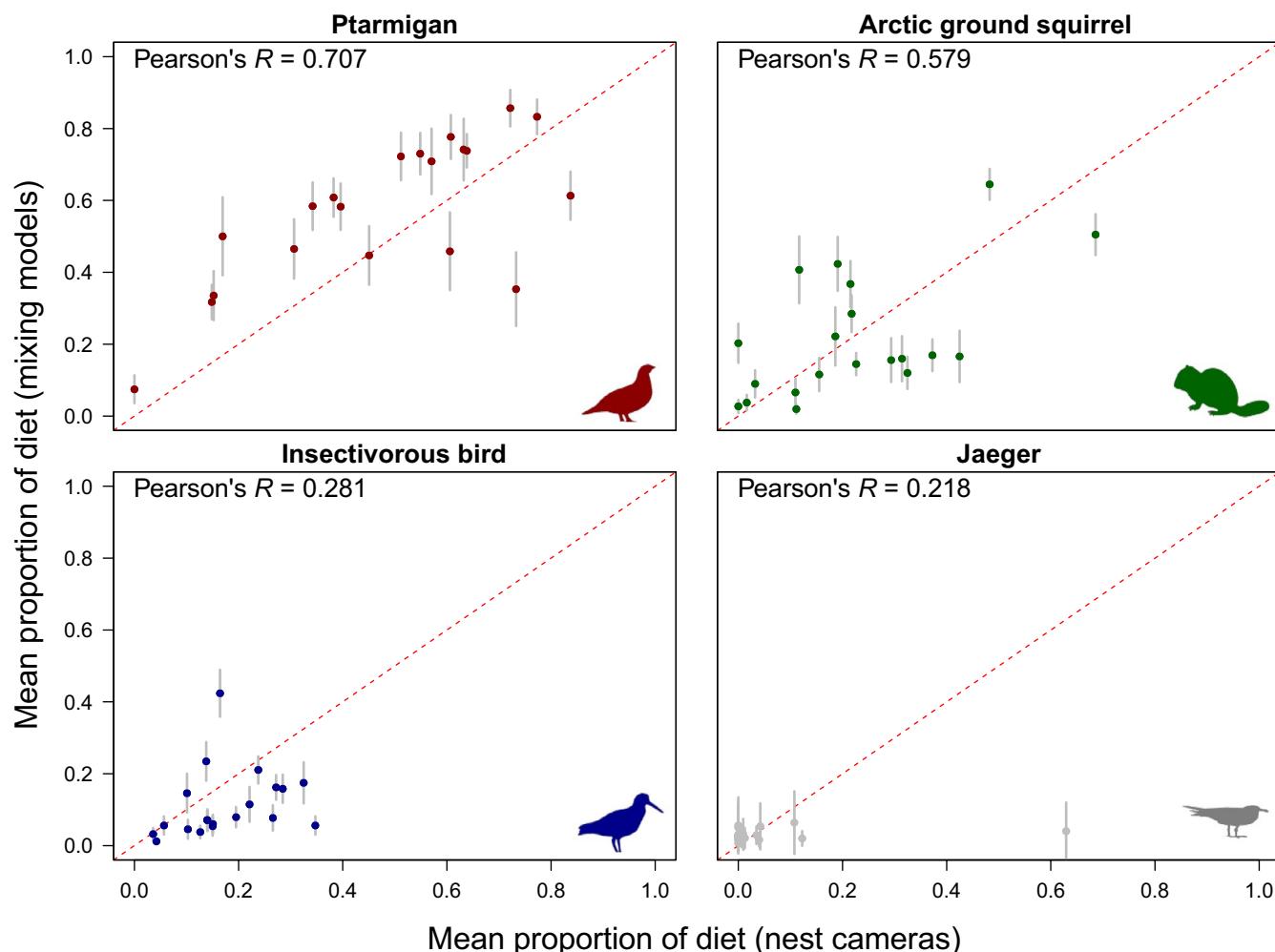


FIGURE 6 Correlations between mean dietary proportion estimates from Bayesian stable isotope mixing model (BSIMM) output and nest cameras for individual nest-years for four prey categories (HC subset, $n = 20$ nest-years); Seward Peninsula gyrfalcon nestling diet 2016–2019. Mixing model output is from a BSIMM with the HC subset as a consumer group, uninformative priors and our TDF_{CAM} treating Nest-Year as a fixed effect. Grey bars represent ± 1 SD estimates for each nest from MixSIAR output. Red dashed line represents a slope of 1. Arvicoline rodents are not shown because there was no discernable correlation for that prey category

4 | DISCUSSION

We found that BSIMM analysis provided accurate estimates of gyrfalcon diet at three spatiotemporal scales consistent with nest camera data, identifying: (a) key components of diet for individual nest-years; (b) seasonal dietary trends within the brood-rearing period and (c) interannual dietary trends. Furthermore, we developed a novel method for TDF estimation in a wild population. BSIMMs formulated with an uninformative prior and TDF_{CAM} had better model agreement than models fit with an informative prior or other TDFs from the literature. We demonstrate how incorporating BSIMMs into a diet study can expand its spatiotemporal scope of inference, as it provides a cost-effective and potentially less time-intensive alternative to other methods of wildlife diet study. We applied this complementary approach to gain novel information about the role of Gyrfalcon trophic ecology in a changing tundra ecosystem.

Our results illustrate the importance of careful selection or estimation of appropriate TDF values in the implementation and interpretation of BSIMMs. Application of TDF values from among the closest taxonomic groups available in the literature into our models would have resulted in the misrepresentation of key diet categories. Specifically, we may have erroneously concluded that this population of gyrfalcons eats almost exclusively ptarmigan during the brood rearing period (Figure 5a; Figure S2b). The SIDER package shows promise as a framework by which to calculate TDFs when they are otherwise unavailable and has produced functional BSIMMs in other systems (e.g. Swan et al., 2020). However, we found our model implemented with a SIDER TDF to be on par with models using values from the literature (Table 2), all of which performed poorly when compared to the TDF_{CAM} we developed.

Although many factors influence discrimination, we suggest that the effects of age might explain the poor performance of models using TDFs derived from prior experimental feeding trials,

because all feeding trials used adult (or fully grown juvenile) raptors. Growth can alter nitrogen-use efficiency, such that growing animals have lower $\Delta^{15}\text{N}$ compared to non-growing individuals (Sears et al., 2009; Williams et al., 2007). Consequently, juveniles often have significantly different TDFs than adults of the same species (reviewed in Martínez del Rio et al., 2009). Specifically, in a controlled feeding study on Japanese quail, growing individuals had $\Delta^{15}\text{N}$ values approximately 1.25‰ lower than non-growing individuals (Hobson et al., 1993). Intriguingly, we see a similar result if we were to compare the $\text{TDF}_{\text{CAM}} \Delta^{15}\text{N}$ generated for rapidly growing gyrfalcon nestlings to a $\Delta^{15}\text{N}$ for adult peregrine falcons ($\Delta\Delta^{15}\text{N} = 1.25\text{‰}$, Table 1). For this reason, we posit that adult and juvenile TDFs may not be directly comparable, and advocate for the estimation of age-class specific TDFs whenever feasible, be it through controlled feeding experiments or via the analysis of high-precision diet data.

We introduce a novel approach to estimate TDFs in a wild population. This approach requires (a) high-precision diet data for a subset of the consumer population, (b) adequate isotopic representation of source groups and (c) careful consideration of factors influencing the variability of isotopic discrimination within the consumer population. Our results demonstrate this method's utility—BSIMM output incorporating our TDF_{CAM} was markedly more similar to nest camera data than any other TDF tested (Figure 5a; Table 2), and produced credible diet estimates for key prey groups at the nest level (Figure 6). This approach could be useful for future studies meeting the above criteria, particularly when relevant literature TDF values are unavailable and conducting a controlled feeding study is infeasible. The TDF_{CAM} equation (Equation 1) could also be adjusted to incorporate variability in high-precision diet estimates (e.g. by having multiple camera data observers to reduce observer bias), and we suggest this approach if proportional dietary estimates are expected to vary substantially by observer.

Uninformed mixing models had better overall method agreement with the camera data than those incorporating the informative priors we generated (Table 2). Models using an informative prior (based on 2014–2015 camera diet data from the same population) overestimated dietary proportions of Arctic ground squirrel, and underrepresented arvicoline rodents and jaegers. Gyrfalcon diet is not static on an interannual or seasonal basis, and changes in response to cyclically available resources (Nielsen & Cade, 1990), which is typical of most wildlife populations. In such dynamic ecosystems, informative priors from the same population in previous years may bias mixing model output due to the differential availability of prey groups between years. We suspect that this disparity in Arctic ground squirrel estimates in the informed model may be an artefact of lower arvicoline rodent abundance in 2014–2015 relative to the years encompassed in this study (Table 1; Table S2). Furthermore, the informative prior reflects gyrfalcon diet over the entire brood rearing period, whereas our stable isotope data is constrained to the first half of the brood rearing period (0–25 days). These results illustrate the importance

of considering interannual and seasonal variability when applying informative priors, and the utility of testing models constructed using different prior sets in a BC framework.

Mixing models predicted the proportion of key prey groups in the gyrfalcon diet in individual nest-years with a relatively high degree of accuracy. Specifically, diet proportions correlated well between methods for the ptarmigan and Arctic ground squirrel categories, which together constituted 70.2% of the diet based on our high-confidence nest camera diet estimates. Generally, the less represented a prey group was in the diet, the less correlated the two outputs became. This could be attributable to the misrepresentation of small diet items in the nest camera data (García-Salgado et al., 2015), inadequate sampling of prey tissues for those groups, or BSIMM results could be biased by mixing space geometry wherein certain prey groups lie between one another (Phillips et al., 2014).

Direct comparison of dietary proportions from BSIMMs and camera data at a fine scale is further complicated by isotopic turnover rates. Isotopic turnover rates (as with TDFs) vary by taxa, diet, environment and growth rate, and the temporal window over which dietary proportions are inferred from the stable isotope ratios of a tissue is dependent upon that tissue's turnover rate (review in Carter et al., 2019). Based on controlled feeding studies in similarly sized birds or by applying regression equations based on a meta-analysis of such studies (Hobson & Wassenaar, 2008), we estimate half-lives of approximately 2 weeks for gyrfalcon red blood cells. Because we analysed a window between hatch and when nestlings were measured at c. 25 days, we suspect that isotopic turnover rates biased our BSIMM diet estimates towards prey items that were more recently consumed. From nest camera data, we found evidence of differential prey use with nestling age, such that older nestlings ate significantly higher proportions of Arctic ground squirrel and fewer insectivorous birds. This seasonality in diet paired with turnover bias could help explain our underestimates of insectivorous birds at the nest-year and population level, along with our overestimates of Arctic ground squirrels when we formulated a BSIMM using informative priors (Figures 1 and 6).

Mixing models detected shifts in prey use on a fine temporal scale consistent with seasonal trends observed in the nest camera data (Figure 2). When gyrfalcon nestlings were resampled 10 days after the initial sampling effort, the BSIMM indicated that the older group had significantly higher dietary proportions of Arctic ground squirrel, arvicoline rodents and jaegers and fewer ptarmigan, insectivorous birds in the diet than the younger group. The directionality of these trends is consistent across both methods for all prey groups except arvicoline rodents, which could be attributed to the reduced ability of nest cameras to detect deliveries of small mammals when nestlings are older. Older nestlings have shorter prey handling times, resulting in fewer motion captures of prey deliveries, particularly for smaller prey items (García-Salgado et al., 2015). In sum, these observed diet shifts likely represent the differential availability and detectability of these prey categories on the landscape at different points of their respective

phenologies. A facultative dietary shift from ptarmigan early in the breeding season to Arctic ground squirrels late in the season has been previously reported for this population, and the ability to detect such seasonal shifts has broad implications for understanding the resilience of gyrfalcons in a changing tundra ecosystem (Robinson et al., 2019).

Our mixing models identified differences in gyrfalcon diet between years at the population level consistent with interannual trends in the camera data (Figure 3). Most notably, they indicated that arvicoline rodents were significantly more abundant in the 2019 diet than in other years and may constitute a substantial portion of the diet. Lemmings and voles fluctuate cyclically in tundra ecosystems, and their years of abundance are typically associated with elevated reproductive success of their predators (Kausrud et al., 2008). Our rodent trapping efforts for this study indicated that 2019 was a year of high arvicoline rodent abundance on the Seward Peninsula compared to other years; capture success rates were 0.008 individuals/trap night in 2018, and 0.183 individuals/trap night in 2019. Previous gyrfalcon diet studies have not identified arvicoline rodents to be an important diet item in most systems (summarized in Booms et al., 2020), but small mammals are likely to be underrepresented using traditional methods of diet characterization such as prey remains/pellet analysis (Lewis et al., 2004), and nest cameras (García-Salgado et al., 2015). Our results indicate that arvicoline rodents may be more important to gyrfalcon diet in our system than previously assumed, particularly during years of high abundance. Climate change is contributing to the increased irregularity (Kausrud et al., 2008) or collapse (e.g. Schmidt et al., 2012) of arvicoline rodent cycles across the circumpolar north, impacting the population dynamics of the predator guild that relies on them. Thus, we recommend that in the future, gyrfalcon and other Arctic raptor studies consider arvicoline population dynamics when analysing predator response to changing Arctic ecosystems.

The methodological approach we applied in this study, while robust, is not without its limitations and assumptions. Crucially, it requires some prior knowledge of the consumer's diet in the system, both to construct informative priors (if desired), and to ensure the adequate sampling of all major source groups for the consumer. We elected to evenly weight all of our specimens collected within a prey category (rather than evenly weighting each species within a category), because we obtained more samples for species that were more abundant in the system. For example, the mean isotope values for collected ptarmigan were biased by the larger number of willow ptarmigan collected (relative to rock ptarmigan), but this bias was also reflected in ptarmigan remains taken from gyrfalcon nests. In the absence of information on relative abundance, it may be advantageous to weight each species equally within a prey group. Isotopic values of source groups can vary substantially on a rather small geographic and temporal scale (e.g. Baltensperger et al., 2015), and it is therefore important that source isotope values be considered study site specific. Thus, our isotopic prey map for the Seward Peninsula should not be directly applied to other tundra ecosystems but could

be used to generate diet estimates for other members of the food web within the system (e.g. other raptors). This approach could allow for a cross-comparative dietary analysis of multiple species within the predator guild, so long as their samples were collected contemporaneously.

The TDF_{CAM} approach also requires that a subset of the population have high-precision diet data available via another method, which can also serve as a control against which the BSIMM output is tested. This method is not limited to raptors; we anticipate this technique could be readily applied to other systems in which central place foragers feed whole prey to their young (e.g. some seabirds and insectivorous songbirds). Although we used nest cameras, this approach could be further extended to other methods of high-precision diet quantification across taxonomic groups (e.g. direct observation, camera collars), so long as they can be applied to a time interval consistent with the turnover time of the chosen tissue used in stable isotope analysis. For example, we do not advocate for developing TDFs based on gut contents, which would only reflect the most recent meal and suffer from well-described biases associated with the retention of hard parts and the rapid digestion of soft-bodied organisms. Rather than relying solely on mixing model output, we advocate for an integrative approach which combines the high precision of nest camera diet analysis with the broader spatiotemporal reach of BSIMMs.

Here we demonstrate how BSIMMs can be used in conjunction with nest cameras to draw new inference on spatiotemporal patterns in the diet of an Arctic raptor. Collectively, our results indicate a high degree of individual, seasonal and interannual variability in the diet of gyrfalcons, a species often considered to be a dietary specialist. In situations where a subset of high-precision dietary data are available, BSIMMs can be validated by estimating and comparing different inputs (such as TDFs and informative priors) before their application to a larger sample. Although this study used raptor nest camera data as a model, this integrative approach could be readily applied to other organisms and methods of high-precision diet quantification, thereby representing a powerful tool for future wildlife diet studies.

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AUTHORS' CONTRIBUTIONS

D.L.J., C.T.W., D.L.A., T.L.B. and M.T.H. conceived ideas and designed methodology; D.L.J., M.T.H. and T.L.B. collected data; D.L.J. and C.T.W. analysed the data; D.L.J. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.6m905qfxs> (Johnson et al., 2020); no location data will be provided for raptors as specified by Alaska state law.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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