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RESEARCH ARTICLE

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Evaluating Bayesian stable isotope mixing models of wild animal diet and the effects of trophic discrimination factors and informative priors

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Abstract

1. Ecologists quantify animal diets using direct and indirect methods, including analysis of faeces, pellets, prey items and gut contents. For stable isotope analyses of diet, Bayesian stable isotope mixing models (BSIMMs) are increasingly used to infer the relative importance of food sources to consumers. Although a powerful approach, it has been hard to test BSIMM performance for wild animals because precise, direct dietary data are difficult to collect.
2. We evaluated the performance of BSIMMs in quantifying animal diets when using $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios from the feathers and red blood cells of common buzzard *Buteo buteo* chicks. We analysed mixing model outcomes with various trophic discrimination factors (TDFs), with and without informative priors, and compared these to direct observations of prey provisioned to chicks by adults at nests, using remote cameras.
3. Although BSIMMs with different TDFs varied markedly in their performance, the statistical package SIDER generated TDFs for both feathers and blood that resulted in model outputs that accorded well with direct observations of prey provisioning. Using feather TDFs derived from captive peregrines *Falco peregrinus* resulted in estimates of diet composition that were also similar to provisioned prey, although blood TDFs from the same study performed poorly. The inclusion of informative priors, based on conventional analysis of pellet and prey remains, markedly reduced model performance.
4. BSIMMs can provide accurate assessments of diet in wild animals. TDF estimates from the SIDER package performed well. The inclusion of informative priors from conventional methods in Bayesian mixing models can transfer biases into model outcomes, leading to erroneous results.

KEYWORDS
animal diet, Bayesian mixing models, Bayesian stable isotope mixing models, informative priors, stable isotopes, trophic discrimination factors

1 | INTRODUCTION

Stable isotope analysis of consumer tissues is an effective indirect method for determining animal diets that, when used in combination with other methods, can provide an estimate of the proportional contributions of food sources (Inger & Bearhop, 2008; Parnell et al., 2013). The method works because naturally occurring variation in the stable isotope ratios of foods is incorporated, with some fractionation, into consumer tissue in a generally predictable manner (Hobson & Clark, 1992). By analysing isotope ratios in the tissues of consumers and their putative foods, it is possible to model isotope mixing and infer the relative importance of food groups to the consumer (Inger & Bearhop, 2008). Recent advances have moved stable isotope mixing models (SIMMs) into a Bayesian framework (BSIMMs), which incorporates uncertainty in parameter estimates and error, and gives probabilistic predictions of diet composition (Moore & Semmens, 2008; Parnell et al., 2013; Phillips et al., 2014). These models also allow prior knowledge to be taken into account, guiding the model fitting process. This inclusion of 'informative priors' from complementary field and dietary information is a widely advocated means of improving SIMM performance (Bond & Diamond, 2011; Moore & Semmens, 2008), particularly where the proportional contribution to ingested items reflects later assimilation of C and N into consumer tissues. Indeed, Derbridge et al. (2015) were unable to reconstruct wolf *Canis lupus* diets from captive feeding trials, without including informative priors. Ecologists have used priors derived from other assessments of diet (Chiaradia, Forero, McInnes, & Ramírez, 2014; Doucette, Wissel, & Somers, 2011), resource availability (Derbridge, Krausman, & Darimont, 2012), prey abundance and handling times (Yeakel et al., 2011). Despite this, the potential influences of informative priors on model outcomes (Chiaradia et al., 2014; Derbridge et al., 2015; Robinson, Franke, & Derocher, 2018) raise concerns that inappropriate priors could confound useful information within the isotopic data (Franco-Trecu et al., 2013).

A further challenge in formulating mixing models is trophic discrimination, which is the change in isotope ratios arising from physiological processes during incorporation of dietary protein into consumer tissue. Trophic discrimination factors (TDFs: $\Delta^{13}C$ and $\Delta^{15}N$ for carbon and nitrogen respectively) account for this change in mixing models and can have a profound influence upon their outcomes (Bond & Diamond, 2011). To derive TDFs, researchers have used values from taxonomically or functionally similar species, often from captive feeding trials, or means from other studies (Caut, Angulo, & Courchamp, 2009). However, TDFs can vary, and hence their estimation can be confounded, with numerous factors including species, nutritional status, tissue type, physiology and diet composition (Caut et al., 2009; Vanderklift & Ponsard, 2003). Although BSIMMs allow for uncertainty in TDFs, the 'true' ranges within which they lie are therefore difficult to determine (Phillips et al., 2014).

If properly implemented, BSIMMs can produce accurate, probabilistic estimates of animal diets (Moore & Semmens, 2008; Parnell et al., 2013), yet concerns have been raised over misuse and sensitivity to input parameters (Boecklen, Yarnes, Cook, & James, 2011; Derbridge et al., 2015; Franco-Trecu et al., 2013; Martínez Del Rio, Wolf, Carleton, & Gannes, 2009). This has led to attempts to evaluate BSIMMs through experimental and observational studies (Derbridge et al., 2012, 2015; Franco-Trecu et al., 2013; Newsome, Collins, & Sharpe, 2015; Resano-Mayor et al., 2014; Weiser & Powell, 2011). Although studies of captive animals in controlled conditions provide a powerful approach to testing mixing model performance (Caut, Angulo, & Courchamp, 2008; Derbridge et al., 2015), they can lack the variation in diet and physiology typical of wild animals (Boecklen et al., 2011). This variation will, amongst other processes, change patterns of nutrient incorporation into different tissues (isotopic routing; Podlesak & McWilliams, 2006). Therefore, model validation in captivity is best complemented by studies in wild systems. Attempts to evaluate BSIMMs in field conditions have almost entirely been constrained to comparing outcomes with those of alternative indirect methods (but see Robinson et al., 2018). While some studies demonstrated similarity between indirect methods and BSIMMs (Newsome et al., 2015; Resano-Mayor et al., 2014), others have biases associated with prey size and digestibility (Franco-Trecu et al., 2013; Tauler-Ametller, Hernández-Matías, Parés, Pretus, & Real, 2018; Weiser & Powell, 2011).

To measure BSIMM performance, a system is required for which accurate dietary data from a direct method can be aligned with stable isotope analysis of tissue integrated over a comparable period. Breeding predatory birds offer such a system, as food is brought to the nest, allowing direct observation and sampling of chick diet (Gaglio, Cook, Connan, Ryan, & Sherley, 2017; Resano-Mayor et al., 2014). Direct observation of feeding at the nest has been aided by remote cameras (Rogers, DeStefano, & Ingraldi, 2005). Although this method can be costly (Tornberg & Reif, 2007) and might include its own biases, such as underestimating small or difficult to identify prey (García-Salgado et al., 2015), dietary estimates from cameras can represent the most complete assessments of raptor diets (García-Salgado et al., 2015; Lewis, Fuller, & Titus, 2004) and have been used to evaluate other analytical methods (Lewis et al., 2004; Selås, Tveiten, & Aanonsen, 2007; Tornberg & Reif, 2007).

We compared predictions from BSIMMs with direct observations of food provisioning at nests of common buzzard *Buteo buteo*. Buzzards are a medium-sized bird of prey (mean = 693 g males and 865 g females) found across much of the Palaearctic (Cramp & Simmons, 1980). In the United Kingdom, the species has rapidly increased in range and density, with breeding densities of >130 pairs per 100 km^2 in some areas (Prytherch, 2013). Their rapid resurgence, coupled with their predatory behaviour (Francksen, Whittingham, & Baines, 2016; Rooney & Montgomery, 2013), has also created specific interest in their dietary habits (Parrott, 2015). In this paper, we present data on buzzard chick diet from direct observations, prey and pellet remains and from stable isotope analysis of tissues from buzzards and their prey. We also assess how TDF choice and informative priors influence stable isotope mixing model outcomes.

2 | MATERIALS AND METHODS

Fieldwork was conducted from May to August 2015 on three study sites in Cornwall, UK (50°21′N, 4°49′W). Habitat on the three sites was similar, comprising comparable proportions of improved pasture and arable, interspersed with woodland patches. Breeding buzzards in southwest England forage over small, well-defined territories (~0.9 km^2; Prytherch, 2013) meaning that within-territory habitat variation is likely to be low. Twenty active buzzard nests were located during the early nesting phase and accessed three times during the nesting season: first to confirm hatching and install cameras, second to sample chicks and third to remove cameras following fledging (Table S1).

Motion-activated cameras (CMOS 380 TVL, HandyKam, Cornwall) were installed on nests between early June and mid-July. Cameras recorded up to five minutes of video when movement was detected (Supporting Information A). Each camera was active over a mean of 15 days (*SD* = 5) encompassing a mean of 207 'hunting hours' (*SD* = 82). The mean age of the oldest chick in the nest during the observation period was 32 days (*SD* = 5). Videos of prey deliveries were watched by a single observer (GS). Where possible, prey items were recorded at species level but were otherwise identified to category. Each item was classed as small, medium or large in relation to the mean size for that species or category (Supporting Information B). For larger prey items (>100 g), the proportion of the whole carcass brought to the nest was noted, as adults often partially consume large prey before returning to the nest (Resano-Mayor et al., 2014). Weights were allocated for each item based on species, size and proportion provisioned. For items that could not be identified, biomass was estimated from the approximate size and the length of time it took to consume (Supporting Information B). The proportion of biomass was estimated for unidentified items but did not feature in further analysis. For each nest, the total estimated biomass of identified prey items was used to calculate the proportional contribution of each prey category to chick diets.

During the three visits to each nest, prey remains and egested pellets were located by searching the nest, tree and a 10 m radius at ground level. Pellets were dissected and the contents sorted by species (or category) and the minimum number of each was identified. When feather remains in pellets could not be identified, size class was estimated from feather size. Remains without edible parts were removed from the nest to avoid recounting. We did not record invertebrates, although they may be an important food source during winter (Tubbs, 1974), as their contribution to chick diet is negligible (Rooney & Montgomery, 2013). Following Resano-Mayor et al. (2014), we estimated prey biomass from the direct observations to convert frequency of occurrence into percentage biomass.

Prior to analysis, data from 'conventional' analytical methods (prey remains and pellet collections) were combined. This approach is commonly used to characterize raptor diets (Rooney & Montgomery, 2013), although the biases from such methods can vary between species (Redpath, Clarke, Madders, & Thirgood, 2001) and years (Francksen et al., 2016) and we acknowledge that combining methods may not always be appropriate. Such datasets will typically overestimate the dietary importance of larger prey items, or those with indigestible parts, while smaller, easily digestible items are underestimated (Francksen et al., 2016; Redpath et al., 2001). In this respect, these methods share several of the same biases as the scat and stomach content–based dietary analyses that have been employed to understand the dietary habits of other taxa (Bowen & Iverson, 2013).

Approximately 0.2 ml of whole blood and four growing or freshly grown body feathers were sampled under licence (Supporting Information C) from chicks that were 18–25 days old. Blood samples were collected into sterile, uncoated syringes, that is, no anticoagulant coatings, and were centrifuged in Eppendorf tubes and red blood cells (RBCs) separated for analysis. Feathers were cleaned with de-ionised water to remove surface contaminants. The turnover rate of RBCs and the age class at which natal down is replaced by body feathers means both RBCs and body feathers will represent chick diets during the early nesting period (Bearhop, Waldron, Thompson, & Furness, 2000; Hobson & Clark, 1993). The majority of the sampled tissue therefore represents dietary information from prior to camera deployment, creating some temporal disparity in our data.

Access to food sources between delivery by the parent and ingestion by the chick is a particular benefit of this system, assuring that tissue samples are more directly representative of those eaten. Therefore, all fresh prey items found within the nest cup were sampled by taking up to 0.5 g of muscle before the remaining prey was returned to the nest. Additional amphibian tissue was collected opportunistically from carcasses found in or near the study area. Tissue samples were immediately put on ice before being stored at −80°C.

2.1 | Stable isotope analysis

Prior to analysis, samples were freeze dried for >48 hr then homogenized and ~0.7-mg aliquots were weighed into tin cups. All stable isotope analyses were carried out using a Sercon INTEGRA2 elemental analyser-isotope ratio mass spectrometer at the University of Exeter. Stable carbon and nitrogen isotope ratios are expressed as δ values and expressed in ‰ where.

$$\delta X = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] * 1{,}000$$

and $X = {}^{15}\text{N}$ or ${}^{13}\text{C}$, R_{sample} = heavy to light isotope ratio derived from the sample, and R_{standard} = heavy to light isotope ratio derived from the Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. To determine accuracy of analysis, IAEA standards of lithium carbonate (LSVEC), CH-6, N-1 and N-2 were analysed at the start and completion of each run. To provide both isotopic reference and drift corrections two alanine standards were placed between no more than eight samples. Based on these within-run standards, analytical precision was ±0.1‰.

We searched the literature for ecologically relevant feather and blood TDFs. We found none for *B. buteo* or other *Buteo* species (Li, Yi, Li, & Zhang, 2001, provide TDFs for *B. hemilasius* but only for muscle). We identified values for feathers and whole blood from two taxonomically similar species: peregrine falcon *Falco peregrinus* (Hobson

& Clark, 1992) and California condor *Gymnogyps californianus* (Kurle et al., 2013). We determined two further sets of values using the R package SIDER (Healy et al., 2018) and by taking the mean (±*SD*) from a dataset of 14 studies reporting TDFs (61 for $\Delta^{13}C$ and 52 for $\Delta^{15}N$) from a total of 25 bird species (Healy et al., 2018). This process resulted in four TDF sources for both feather and whole blood (Table 1).

Only prey items identified to taxonomic order or lower, were included in the direct observations data. For comparison of methods, all datasets were grouped into the same prey categories (Phillips et al., 2014). Only prey categories that comprised >5% biomass from the direct observations were selected for comparison, as the exclusion of uncommon items tends to improve mixing model accuracy (Phillips & Gregg, 2003). For all methodological comparisons, we used biomass rather than frequency of occurrence, as the former provides the best measure of relative importance in diet. Biomass estimates from provisioning observations and conventional methods were calculated for every prey category at each nest. Proportional biomass estimates for the main prey categories at each nest then underwent a bootstrapping procedure (with 1,000 replications) to create distributions that would be comparable with the posteriors produced by BSIMMs.

2.2 | Statistical analysis

R version 3.5.3 (R Core Team, 2019) was used for all analyses. To validate our assumption that red blood cells and feathers contained isotopic information assimilated over comparable time periods, we fitted linear regressions between feather and RBCs $\delta^{15}N$ and $\delta^{13}C$. To analyse variance in $\delta^{15}N$ and $\delta^{13}C$ among prey categories, we used ANOVAs and Tukey's post hoc tests. We used SIMMR v0.4.1 (Parnell & Inger, 2016; Parnell, Inger, Bearhop, & Jackson, 2010), to infer the relative contributions of six prey categories to the diets of buzzard chicks. Models included the mean and standard deviation of $\delta^{15}N$ and $\delta^{13}C$ for the prey categories (Table 2). To account for non-independence of buzzard chicks from the same nest, we used mean $\delta^{15}N$ and $\delta^{13}C$ values per nest.

To test the effects of different TDFs, the model outputs using the four TDF sources were compared to direct observations, using Bhattacharyya's Coefficient (BC). BC varies from 0 (no similarity) to 1 (identical) and, following others (Bond & Diamond, 2011; Catry et al., 2009; Jardine, Bond, Davidson, Butler, & Kuwae, 2015), BC > 0.60 was taken to indicate significant overlap. We conducted pairwise model comparisons for each prey category and used mean BC (±*SD*) as an overall measure. The TDF source that produced the highest mean BC for both feathers and RBCs was used to explore model performance at a finer scale by reconstructing chick diets in individual nests using SIMMRsolo (Parnell & Inger, 2016; Parnell et al., 2010). Separate models were run for RBC and feather samples. The relationships between diet estimates from direct observations and BSIMMs were then tested using Spearman's rank correlation for each prey category. To demonstrate the effect of informative priors on model posteriors, the BSIMMs with the highest mean BC for each tissue were run again with informative priors constructed using the 'simmr_elicit' function from mean proportional biomasses (±*SD*) of each prey category at all 20 nests from the pellets and prey remains dataset.

3 | RESULTS

A total of 334 prey items were identified at 20 nests; 235 prey remains (mean per nest 11.8 ± 5.1 *SD*) and 99 from pellets (5.0 ± 3.2; Table S2). For these conventional methods, rabbit was the most frequently identified prey item (frequency of occurrence for prey remains = 31% and pellets = 37%) and the most important (biomass for prey remains = 37% and pellets = 62%). Informative priors, constructed from analysis of prey remains and pellets, are presented in Table 2.

TABLE 1 Trophic discrimination factors (TDFs) for common buzzards *Buteo buteo* used in Bayesian stable isotope mixing models

	Whole blood		Feather	
Source	$\Delta^{13}C$	$\Delta^{15}N$	$\Delta^{13}C$	$\Delta^{15}N$
Peregrine falcon	+0.2 ± 0.0	+3.3 ± 0.4	+2.1 ± 0.1	+2.7 ± 0.5
California condor	−0.7 ± 0.1	+1.7 ± 0.1	+0.4 ± 0.4	+3.1 ± 0.2
Meta-analysis	+0.4 ± 0.7	+3.1 ± 1.1	+2.2 ± 1.4	+4.1 ± 1.2
SIDER				
Rabbit	+2.3 ± 1.6	+2.8 ± 1.0	+3.3 ± 1.6	+3.7 ± 1.0
Rodents	+2.1 ± 1.6	+3.3 ± 1.0	+3.1 ± 1.6	+4.2 ± 1.0
Shrews and moles	+1.4 ± 1.5	+2.1 ± 1.0	+2.4 ± 1.5	+3.0 ± 1.0
Gamebirds	+1.1 ± 1.5	+2.8 ± 1.0	+2.1 ± 1.5	+3.6 ± 1.0
Corvids	+1.1 ± 1.5	+2.2 ± 1.0	+2.1 ± 1.5	+3.1 ± 1.0
Frogs and toads	+1.6 ± 1.6	+2.8 ± 1.0	+2.6 ± 1.6	+3.6 ± 1.0

Note: TDFs were from taxonomically similar species: peregrine falcon *Falco peregrinus* fed on Japanese quail *Coturnix japonica* (Hobson & Clark, 1992); California condor *Gymnogyps californianus* fed on laboratory rats *Rattus norvegicus* (Kurle et al., 2013), from a meta-analysis of 14 studies reporting TDFs (61 for $\Delta^{13}C$ and 52 for $\Delta^{15}N$) from a total of 25 bird species (Healy et al., 2018) and from prey-specific TDFs estimated through Bayesian inference using the R package 'SIDER' (Healy et al., 2018).

TABLE 2 The stable isotope ratios and informative priors of six main prey categories of common buzzards

	Stable isotope ratios			Informative prior
Prey category	***n***	**$\delta^{15}N \pm SD$**	**$\delta^{13}C \pm SD$**	**$\pm SD$**
Rabbits	24	6.1 ± 1.7	−28.8 ± 0.5	0.523 ± 0.280
Rodents	17	4.2 ± 2.6	−28.3 ± 1.5	0.028 ± 0.035
Shrews and moles	7	9.0 ± 1.7	−25.8 ± 1.0	0.037 ± 0.107
Gamebirds	9	6.3 ± 0.7	−24.7 ± 2.1	0.236 ± 0.235
Corvids	5	8.6 ± 1.5	−25.0 ± 0.6	0.174 ± 0.159
Frogs and toads	7	6.3 ± 1.5	−26.5 ± 0.4	0.002 ± 0.005

Note: Prey categories sampled for isotope ratios were: rabbits (*Oryctolagus cuniculus*), rodents (3 *Apodemus sylvaticus*, 14 *Myodes glareolus/ Microtus agrestis*), shrews and moles (2 *Sorex araneus*, 5 *Talpa europaea*), gamebirds (1 *Alectoris rufa*, 8 *Phasianus colchicus*), corvids (2 *Corvus corone*, 3 Corvidae spp.), frogs and toads (4 *Rana temporaria*, 3 *Bufo bufo*). Informative priors were constructed using the mean proportional biomasses (±*SD*) of the six prey categories at all 20 nests from analysis of buzzard prey remains and pellets.

Nest cameras recorded footage for 4,144 hr over 300 'nest days' (mean = 13.8 ± 4.3 hr per nest per day). A total of 1,409 prey items were recorded (mean = 70.5 ± 30.6 items per nest), of which 1,153 (82%) were identified (Table 3; Table S2). Of 256 that could not be identified, 242 (95%) were categorized as 'unknown small prey' due to their rapid consumption. This category included 104 (43%) deliveries identified as 'small mammals', but where shrews and small rodents could not be distinguished. We were able to identify soft-bodied invertebrates (earthworms) in camera footage but only recorded nine, justifying our exclusion of this prey group. On seven nests, released pheasant poults, identified by clipped primary feathers, were recorded towards the end of the monitoring period. The release date for poults was after isotope samples had been taken from the chicks and so, to allow for comparison of methods, released pheasants were excluded from analysis (camera observations: $n = 39$; conventional methods: $n = 18$). Biomass estimates were obtained for all 1,409 items (Tables S3 and S4). Prey items were grouped by taxonomy and dietary ecology leaving six prey categories comprising >5% biomass that were used for further analyses (Table 3).

We obtained isotope ratio data from RBCs and feathers from 29 buzzard chicks from 20 nests. There was a strong positive relationship between the RBCs and feather isotope ratios for both $\delta^{15}N$ ($R^2 = 0.81$, $p < .001$, slope = 1.28, $SE = 0.12$, intercept = −1.04, $SE = 0.95$) and $\delta^{13}C$ ($R^2 = 0.67$, $p < .001$, slope = 0.87, $SE = 0.11$, intercept = −2.56, $SE = 3.00$). These values may be used to convert between tissue types (Greer, Horton, & Nelson, 2015). Sixty-nine prey tissue samples were collected from the six prey categories (Table 3). There was significant variation among categories in $\delta^{13}C$ ($F_{5,63} = 25.73$, $p < .001$) and $\delta^{15}N$ ($F_{5,63} = 8.87$, $p < .001$). Buzzard chick isotope ratios fell within the range of prey items when TDFs were applied (Figure 1), a necessary condition for SIMMs to produce accurate dietary estimates (Phillips et al., 2014).

The outcomes of BSIMMs varied markedly in their similarity to direct observations of chick provisioning (Table 4; Figure 2; Table S5). The model constructed using buzzard feathers and TDFs from feathers of captive peregrines resulted in a model with the greatest similarity to direct observations, though models using buzzard RBCs and TDFs for bloods from the same peregrine study compared poorly (Table 4; Figure 2; Table S5). Models using TDFs from SIDER had outcomes with high similarity to observed diet for both feather and RBC samples and so this approach was used in further analysis (Table 4; Figure 3). The inclusion of informative priors from analysis of prey remains and pellets markedly reduced the similarity of model outcomes to the direct observations (Table 4; Figure S1; Table S5).

When the mixing models for feathers and RBCs using TDFs from SIDER and no priors were run for each nest, a strong positive relationship was observed between mixing model estimates of chick diet in each nest to those from direct observations, but only for rabbits as the most important prey item (Feather $r_s = 0.79$, $n = 20$, $p < .001$; RBCs $r_s = 0.77$, $n = 20$, $p < .001$; Figure 4).

4 | DISCUSSION

We have used direct observations of wild animal feeding behaviour as a reference against which indirect estimates of diet from stable isotope mixing models and more conventional methods could be compared. Although camera observations are not themselves free from bias (García-Salgado et al., 2015), our approach represents a significant advance from testing mixing model performance by comparison among models (Bond & Diamond, 2011) or other indirect methods (Franco-Trecu et al., 2013; Ramos, Ramírez, Sanpera, Jover, & Ruiz, 2009; Resano-Mayor et al., 2014; Weiser & Powell, 2011). Our results show that, with the right choice of TDFs, and, in this case, by not using informative priors, BSIMMs produced estimates of diet that closely matched direct observations.

The SIDER package was the only TDF source to produce mean similarity coefficients for both tissues that overlapped significantly with direct observations. The accuracy of models for feathers and red blood cells when using SIDER provides evidence of the value of accounting for the numerous sources of variation (phylogeny, tissue type, consumer and source stable isotope ratios) in TDF calculation (Healy et al., 2018). As a result, SIDER TDFs produced higher variances than

TABLE 3 Cumulative frequency and biomass of all prey items provided by adult common buzzards to chicks from video footage from remote cameras on 20 nests

Taxonomic group	Prey category	Species	Frequency of occurrence		Total biomass	
			N	%	g	%
Lagomorpha	**Rabbits**	Rabbit *Oryctolagus cuniculus*	178	12.6	33,156	37.4
Rodentia	**Rodents**	Vole *Myodes glareolus* or *Microtus agrestis*	359	25.5	6,427	7.2
	Rodents	Wood mouse *Apodemus sylvaticus*	49	3.5	1,044	1.2
	Rodents	Rat *Rattus norvegicus*	22	1.6	3,206	3.6
	n/a	Squirrel *Sciurus carolinensis*	9	0.6	3,306	3.7
Soricomorpha	**Shrews and moles**	Mole *Talpa europaea*	59	4.2	5,109	5.8
	Shrews and moles	Shrew Soricidae spp.	66	4.7	470	0.5
Carnivora	n/a	*Mustela nivalis*	6	0.4	352	0.4
Galliformes	**Gamebirds**	Pheasant *Phasianus colchicus*	30	2.1	5,760	6.5
		Released pheasant poults	39	2.8	7,836	8.8
Passeriformes	n/a	Thrush Turdidae spp.	26	1.8	1,984	2.2
	n/a	Unidentified Passeriformes	39	2.8	594	0.7
	Corvids	Corvid Corvidae spp.	30	2.1	4,719	5.3
Columbiformes	n/a	Woodpigeon *Columba palumbus*	7	0.5	1,582	1.8
Accipitriformes	n/a	Buzzard *Buteo buteo*	1	0.1	50	0.1
Gruiformes	n/a	Moorhen *Gallinula chloropus*	1	0.1	230	0.3
Anura	**Frogs and toads**	Frog *Rana temporaria*	104	7.4	2,704	3.0
	Frogs and toads	Toad *Bufo bufo*	108	7.7	3,196	3.6
Squamata	n/a	Slow worm *Anguis fragilis*	2	0.1	26	0.0
	n/a	Grass snake *Natrix natrix*	5	0.4	353	0.4
	n/a	Adder *Vipera berus*	1	0.1	83	0.1
Anguilliformes	n/a	European eel *Anguilla anguilla*	2	0.1	600	0.7
Megadrilacea	n/a	Earthworm	9	0.6	37	0.0
Unidentified		Shrew or small rodent	104	7.4	1,524	1.7
		Bird spp.	1	0.1	250	0.3
		Small (<50 g)	138	9.8	2,236	2.5
		Medium (50–150 g)	10	0.7	1,040	1.2
		Large (>150 g)	4	0.3	800	0.9
Total			1,409	100	88,674	100
Total identified			1,152	82	82,824	93
Total in 6 prey groups			1,005	71	65,790	74

Note: The six most important prey categories are shown in bold. Biomass was estimated for each prey item based on species, size and proportion provisioned (Tables S2 and S3).

those gleaned from studies of captive animals fed controlled diets. This appeared to have improved model fit and accuracy. SIDER is currently limited to mammals and birds and so, for other taxa, we recommend that users either incorporate multiple sources of variance or use larger uncertainties in their TDFs (Granadeiro, Brickle, & Catry, 2014).

When the BSIMMs using SIDER TDFs were applied for models of the importance of rabbits for buzzard chicks in individual nests, there was a significant correlation between model outcomes and direct observations, but a substantial underestimate in the contribution to diet (Figure 4), that was not apparent in the population level analysis. The accuracy with which models predict variation in the importance of rabbits among nests clearly relates to the importance and distinctiveness of prey sources, but, in this case, also to the increased influence of priors on estimates for single nests. BSIMM users for whom intra-population

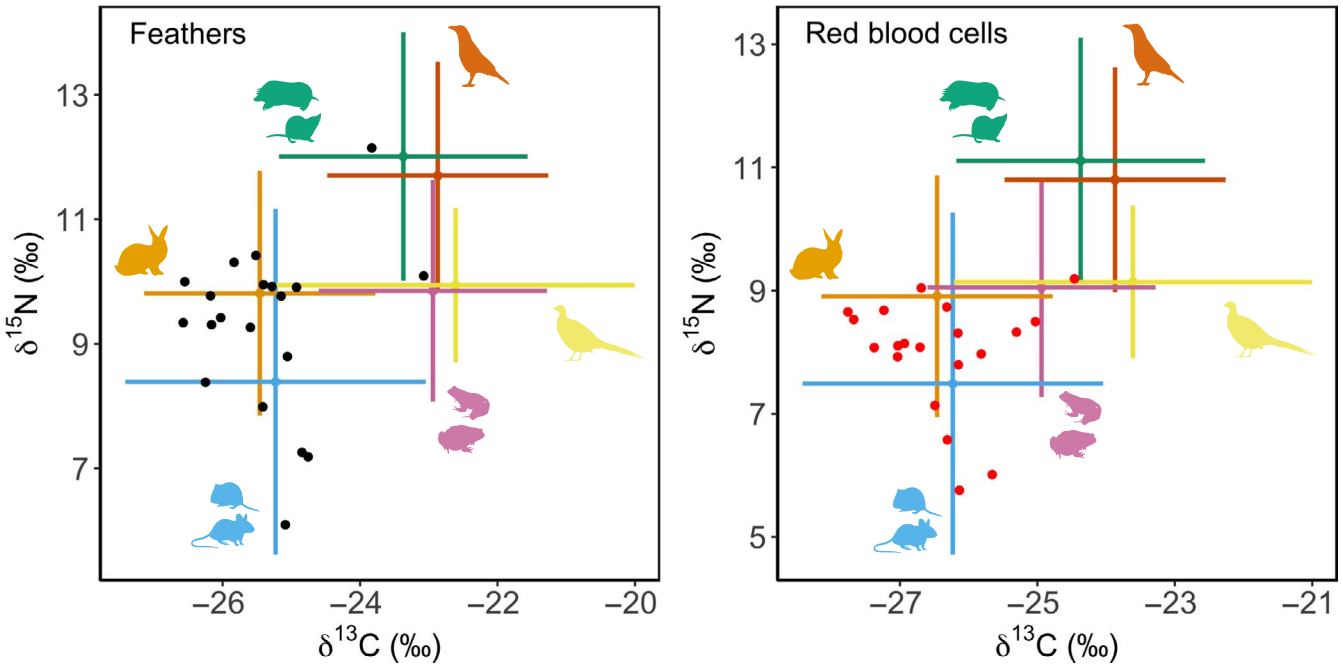

FIGURE 1 Mean stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of tissue samples from 29 common buzzard chicks and their main prey categories. Chicks were from 20 nests. Buzzard samples are feathers and red blood cells. Prey groups are rabbits (light orange), rodents (blue), shrews and moles (green), gamebirds (yellow), corvids (dark orange) and frogs and toads (pink). Bars indicate ± the square root of (prey isotope ratio + prey trophic discrimination factor [TDF] standard deviation). Prey isotope ratios are corrected by prey-specific TDF estimates from the SIDER package (Table 1)

precision (relative importance) is secondary to accurate dietary estimates might wish to use the MixSIAR framework as this allows treatment of individual units as a random effect (Stock et al., 2018; A. Parnell, pers. comm.). We did not observe a significant relationship for other prey categories and there are several plausible explanations. First, there might be dietary items that were underrepresented in camera observations. Second, the contribution that any one food source makes to diet is low, relative to rabbits, impeding the discriminatory power of mixing

TABLE 4 Estimates of diet composition of common buzzard chicks using stable isotope analysis and analysis of prey remains and pellets

					Similarity to direct observations (Bhattacharyya's coefficient)						
Rank	Indirect method	TDF source	Informative priors?	Tissue	Mean ± *SD*	Rabbits	Rodents	Shrews and moles	Game birds	Corvids	Frogs and toads
1	**BSIMM**	**Peregrine**	**No**	**Feather**	**0.734 ± 0.086**	**0.782**	**0.576**	**0.759**	**0.698**	**0.802**	**0.789**
2	**BSIMM**	**SIDER**	**No**	**Feather**	**0.688 ± 0.085**	**0.731**	**0.536**	**0.675**	**0.666**	**0.748**	**0.769**
3	**BSIMM**	**SIDER**	**No**	**RBCs**	**0.665 ± 0.151**	**0.789**	**0.389**	**0.618**	**0.670**	**0.733**	**0.792**
4	**BSIMM**	**Meta-analysis**	**No**	**Feather**	**0.643 ± 0.210**	**0.462**	**0.304**	**0.738**	**0.743**	**0.830**	**0.780**
5	BSIMM	Condor	No	Feather	0.508 ± 0.340	0.021	0.670	0.773	0.125	0.753	0.705
6	BSIMM	Condor	No	RBCs	0.500 ± 0.352	0.009	0.699	0.759	0.087	0.768	0.675
7	BSIMM	Meta-analysis	No	RBCs	0.471 ± 0.334	0.017	0.124	0.689	0.449	0.797	0.751
8	BSIMM	SIDER	Yes (prey/pellet)	RBCs	0.470 ± 0.268	0.528	0.519	0.386	0.458	0.879	0.048
9	BSIMM	Peregrine	No	RBCs	0.443 ± 0.338	0.051	0.140	0.612	0.249	0.800	0.806
10	BSIMM	SIDER	Yes (prey/pellet)	Feather	0.420 ± 0.259	0.293	0.482	0.415	0.476	0.822	0.033
11	Prey/pellet	n/a	n/a	n/a	0.246 ± 0.303	0.752	0.000	0.446	0.043	0.233	0.000

Note: Bayesian stable isotope mixing models (BSIMMs) were run with four sources for trophic discrimination factors (TDFs) and with and without informative priors. Methods are ranked by their similarity to direct observations of prey provisioning by adults to chicks at nests. Similarity was assessed by the mean Bhattacharyya's coefficient (BC), ranging between 0 (no similarity) and 1 (identical). BC > 0.60 is considered significant overlap and methods that produced mean BC values > 0.60 are in bold. RBCs are red blood cells.

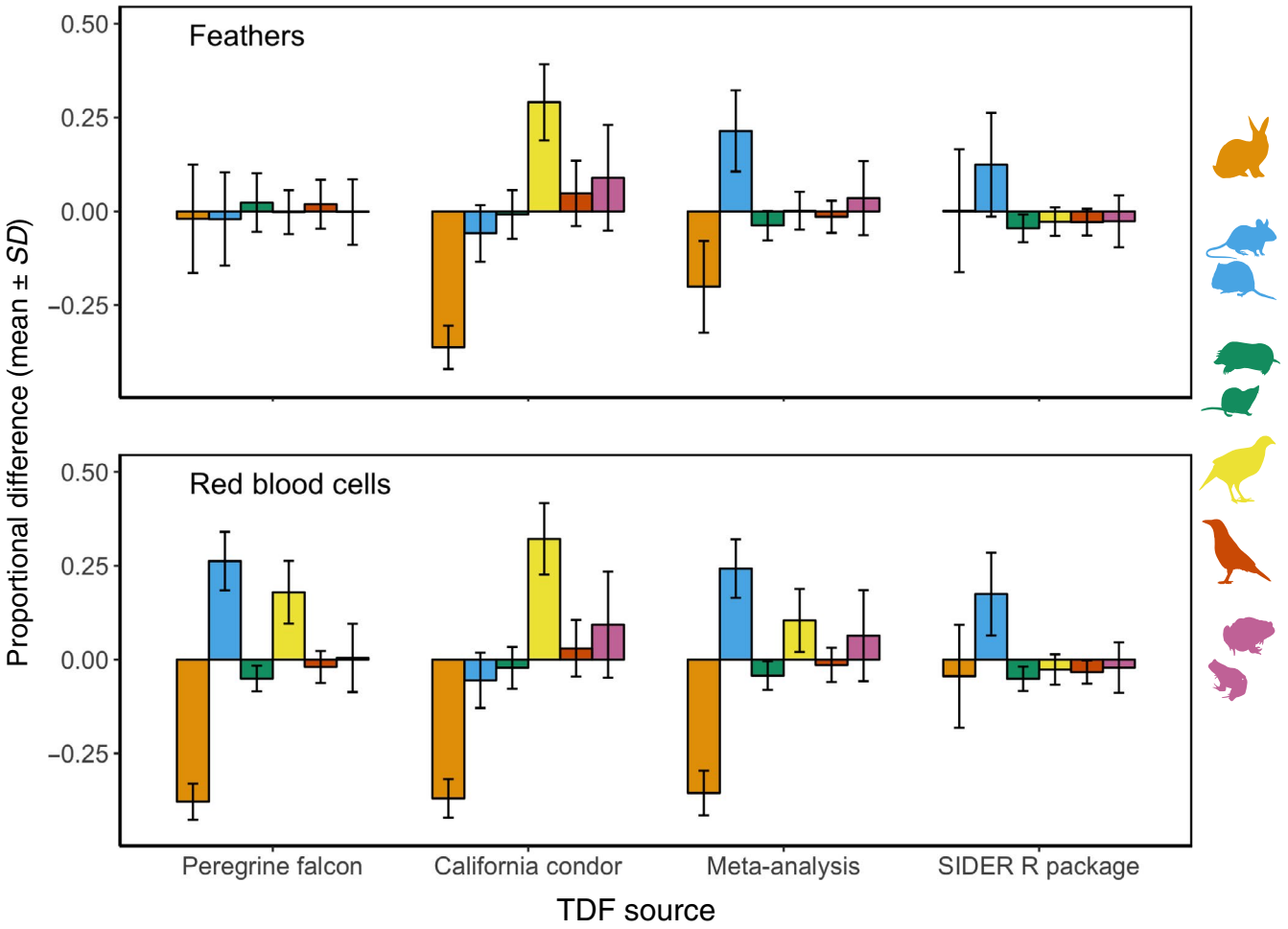

FIGURE 2 Differences in the proportions of each prey category in the diets of common buzzard chicks when estimated by Bayesian stable isotope mixing models and compared to direct observations of prey provisioning. Models use multiple trophic discrimination factors (TDFs) derived from: peregrine falcon fed on Japanese quail, California condor fed on laboratory rats, a meta-analysis of 14 studies from a total of 25 bird species and prey-specific TDFs estimated using the package 'SIDER'. High values indicate large discrepancies. Prey categories are rabbits (light orange), rodents (blue), shrews and moles (green), gamebirds (yellow), corvids (dark orange) and frogs and toads (pink)

models. Third, spatial or temporal mismatch or variation in isotope ratios could reduce fit between prey sources and models at the individual nest level. Finally, model performance is reduced when isotope ratios of prey sources are less distinctive, either because they overlap or lie in-between other sources (Phillips et al., 2014).

Bayesian stable isotope mixing models run with feather isotopes and TDFs derived from captive peregrines produced estimates most similar to direct observations, however, blood TDFs sourced from the same study performed poorly. A potential mechanism for this discrepancy could be tissue-specific differences in physiological processes, such as metabolic rate and isotopic routing (Boecklen et al., 2011), between wild and captive conditions. As a result, studies based on captive feeding trials might produce TDFs that are suitable for one tissue but not another. This would also explain the inability of a recent study (Robinson et al., 2018) to infer the diet of wild peregrines using BSIMMs with blood TDFs from the same source.

Estimates of diet from conventional analysis of prey remains and pellets differed markedly from direct observations and reflected known biases in favour of large, indigestible items and against small, digestible prey. The contribution of amphibians to buzzard diet is a clear example. We, like others (Francksen et al., 2016; Tornberg & Reif, 2007), recorded very few frogs or toads when diet was assessed using prey remains and pellets (mean biomass = 0.2%). However, our direct observations showed amphibians to be important (11.5%) and stable isotope analysis, with TDFs from SIDER, derived similar estimates from both red blood cells (9.7%) and feathers (9.1%).

When priors from analysis of prey remains and pellets were included in the BSIMMs, we observed a substantial reduction in their performance. Model outputs began to reflect the biases within conventional methods, specifically in overestimating the importance of prey with large indigestible remains. We present this result not to show that priors influence posteriors; clearly, this is their purpose (Moore & Semmens, 2008). Rather we highlight how the inclusion of information intended to strengthen models can make them worse if they introduce bias and thereby mask 'real' isotopic variation. One approach for incorporating priors with known biases into BSIMMs could be by expanding their variance or including a bias parameter within the models (Stock et al., 2018). It is trivial to recommend that those considering informative

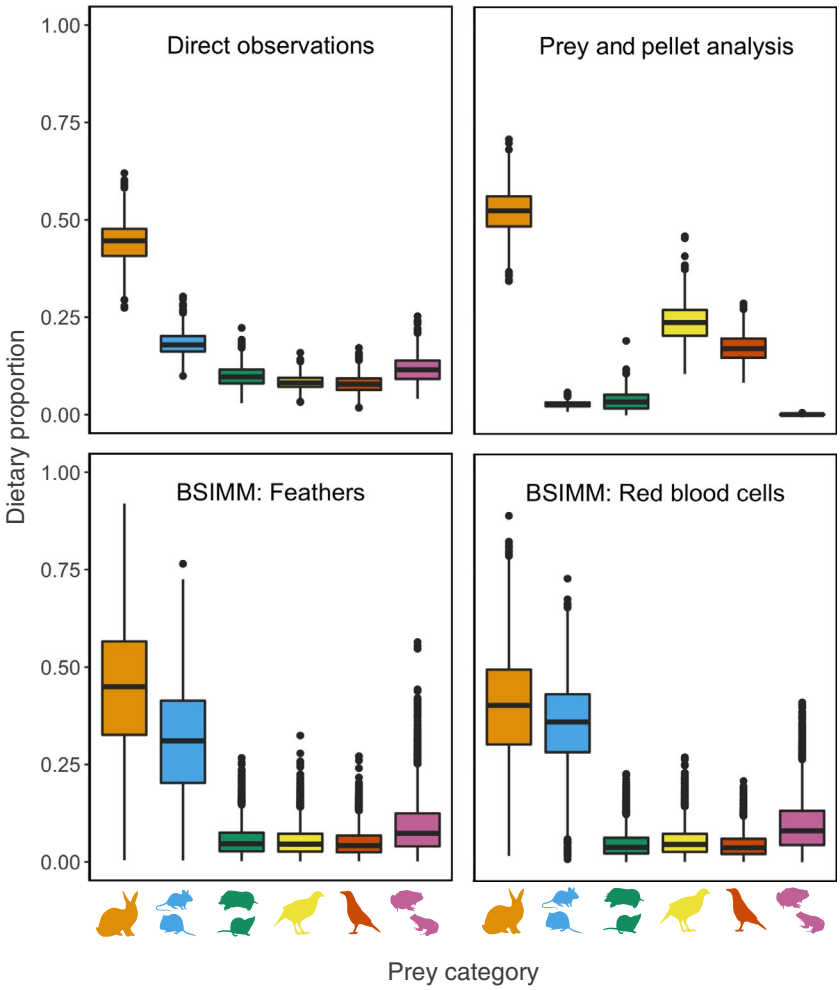

FIGURE 3 Estimates of the composition of the diet of common buzzard chicks. Estimates are derived using direct observations using remote cameras of adults provisioning chicks at the nest, analysis of prey remains and pellets and Bayesian stable isotope mixing models (BSIMMs) run using feathers and red blood cells. Dietary data from direct observations and prey remains analysis are shown as distributions created using a bootstrapping procedure from samples collected from twenty nests. Diet for BSIMMs was inferred using prey-specific trophic discrimination factors from the Bayesian package SIDER without informative priors (see Table 4). Prey groups are rabbits (light orange), rodents (blue), shrews and moles (green), gamebirds (yellow), corvids (dark orange) and frogs and toads (pink)

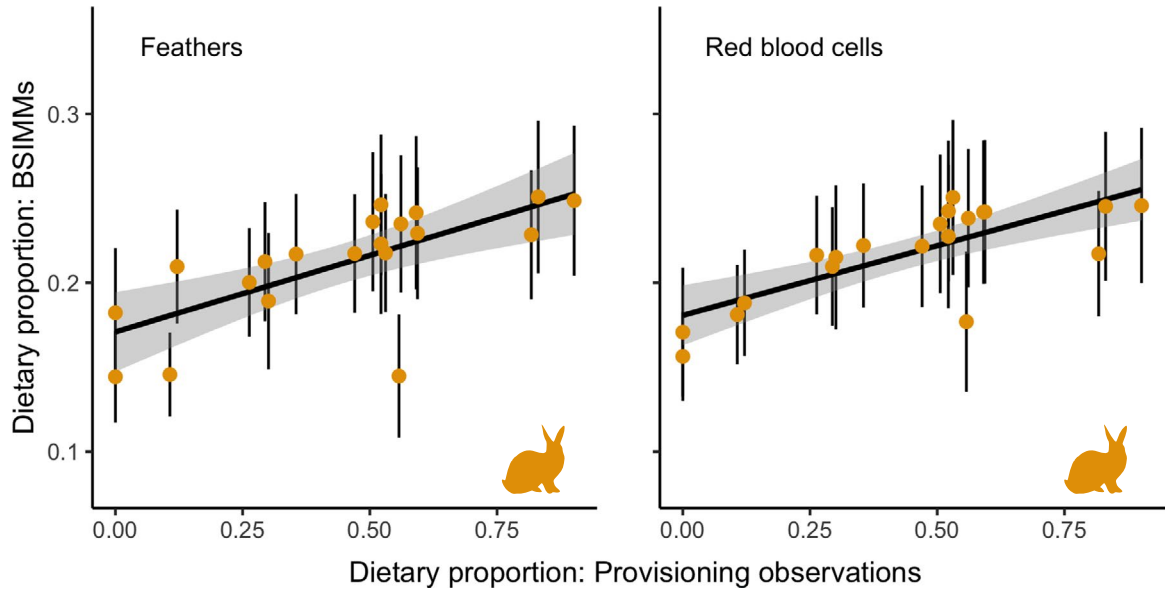

FIGURE 4 Relationships between estimates of the contribution of rabbits to the diets of buzzard chicks from direct observations of provisioning at the nest and Bayesian stable isotope mixing models. Models were run using feathers and red blood cells (feather: $r_s = 0.79$, $n = 20$, $p < .001$; RBC: $r_s = 0.77$, $n = 20$, $p < .001$). trophic discrimination factor estimates were from SIDER. Model estimates are mean proportions (±credibility intervals) for each nest using SIMMRSolo

priors should be confident that their data reflect the current diet of their sample, but in reality such information is often unobtainable or requires extensive additional data. Indeed, could such confirmation be sourced, the benefit of using a BSIMM would be moot.

For dietary studies where direct observations of feeding are not obtainable, the application of stable isotope analysis, with careful deployment of information from conventional methods, can provide a route to identify and account for the biases and shortcomings of both methods. We have demonstrated that, when variation within and among dietary sources is adequately represented and the correct trophic discrimination factors applied, Bayesian stable isotope mixing models are able accurately to infer the relative importance of food sources in wild animal diets.

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AUTHORS' CONTRIBUTIONS

G.J.F.S., S.B., S.M.R., R.I. and R.A.M. conceived ideas and designed methodology; G.J.F.S. collected data; G.J.F.S., C.E.D.G. and M.J.S. analysed data. All authors contributed to drafts and gave approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Repository: https://doi.org/10.5061/dryad.6m905qfvp (Swan et al., 2019).

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SUPPORTING INFORMATION

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