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Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors

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Abstract. Stable isotopes are now used widely in ecological studies, including diet reconstruction, where quantitative inferences about diet composition are derived from the use of mixing models. Recent Bayesian models (MixSIR, SIAR) allow users to incorporate variability in discrimination factors (Δ^{13}C or Δ^{15}N), or the amount of change in either δ^{13}C or δ^{15}N between prey and consumer, but to date there has been no systematic assessment of the effect of variation in Δ^{13}C or Δ^{15}N on model outputs. We used whole blood from Common Terns (*Sterna hirundo*) and muscle from their common prey items (fish and euphausiids) to build a series of mixing models in SIAR (stable isotope analysis in R) using various discrimination factors from the published literature for marine birds. The estimated proportion of each diet component was affected significantly by Δ^{13}C or Δ^{15}N. We also use recently published stable-isotope data on the reliance of critically endangered Balearic Shearwaters (*Puffinus mauretanicus*) on fisheries discards to show that discrimination factor choice can have profound implications for conservation and management actions. It is therefore crucial for researchers wishing to use mixing models to have an accurate estimate of Δ^{13}C and Δ^{15}N, because quantitative diet estimates can help to direct future research or prioritize conservation and management actions.

Key words: assumptions; conservation; discrimination factor; management; MixSIR; mixing model; Puffinus mauretanicus; *sensitivity analysis; SIAR; stable isotope;* Sterna hirundo.

INTRODUCTION

The use of stable-isotope ratios of carbon and nitrogen in ecological studies has increased substantially over the last 20 years (Inger and Bearhop 2008, Martínez del Rio et al. 2009). Despite this, the ability to use stable isotopes to estimate the contribution of various prey sources to a consumer's diet using stable-isotope mixing models has received comparatively little attention (e.g., Phillips and Gregg 2001, 2003, Moore and Semmens 2008, Parnell et al. 2010). As a consequence, the sources of variability that contribute to mixing-model output remain largely unexplored.

Discrimination factors, or the amount of change in isotope ratios as they are incorporated from prey into the consumers' tissue (also called "fractionation factors," "diet-to-tissue discrimination," "trophic discrimination factors," or "enrichment factors"), are cited frequently as the weakest link in the application of stable-isotope mixing models to ecological questions of diet reconstruction (Gannes et al. 1997, Wolf et al. 2009). Determining discrimination factors accurately in vertebrates, such as mammals or birds, can be particularly challenging because individuals must be held on an isotopically fixed diet in captivity for lengthy periods of time. For example, there are fewer than 20 published pairs of discrimination factors for marine birds (Bond and Jones 2009), and fewer than 70 for birds in general (Table 1; see Caut et al. 2009), but the application of stable isotopes to ecological questions is widely prevalent in avian ecology. Furthermore, if discrimination factors are specific to the consumer, tissue, and diet (DeNiro and Epstein 1981, Vanderklift and Ponsard 2003, Caut et al. 2008), then the use of surrogate or proxy discrimination factors (those published for other species or, less commonly, tissues) may not be appropriate for species or tissues where the specific discrimination factor is unknown.

Moore and Semmens (2008) and Parnell et al. (2010) developed two programs that implement a Bayesian approach to stable-isotope mixing models. Aside from the mathematical advantages of using a Bayesian method, these programs provide several advances over previous modeling approaches (e.g., Isosource; Phillips and Gregg 2003), including the ability to account for variation in discrimination factors and to incorporate prior information. In MixSIR (Moore and Semmens 2008) and SIAR (Parnell et al. 2010), users are able to specify separate discrimination factors and their standard deviation for each prey source. This ability to account for variability in the prey mixture is a significant

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TABLE 1. Discrimination factors for piscivorous marine birds used in Bayesian models MixSIR and SIAR (stable isotope analysis in R), with values based on the range of values from the published literature.

Consumer species	Prey species	Discrimination factor ± SD (‰) Δ^{13}C	Discrimination factor ± SD (‰) Δ^{15}N	Source
King Penguin	Atlantic herring and capelin	−0.81 ± 0.3	+2.07 ± 0.26	Cherel et al. (2005)
Great Skua	sprat	+1.1 ± 0.4		Bearhop et al. (2002)
Great Skua	sprat	+2.1 ± 0.4		Bearhop et al. (2002)
Ring-billed Gull	perch		+1.4 ± 0.1	Hobson and Clark (1992)
Ring-billed Gull	perch		+3.1 ± 0.2	Hobson and Clark (1992)
Rhinoceros Auklet	silverside		+3.49 ± 0.25	Sears et al. (2009)

Notes: Discrimination factors Δ^{13}C and Δ^{15}N are the changes in isotope ratios (δ^{13}C and δ^{15}N) between prey and the consumer. Scientific names are: King Penguin, *Aptenodytes patagonicus*; Great Skua, *Stercorarius skua*; Ring-billed Gull, *Larus delawarensis*; Rhinoceros Auklet, *Cerorhinca monocerata*; Atlantic herring, *Clupea harengus*; capelin, *Mallotus villosus*; sprat, *Sprattus sprattus*; perch, *Perca flavescens*; and silverside, *Menidia menidia*.

advance in the application of such models to ecological field data.

Despite the recent advances, there has been no assessment of the effect of varying the magnitude of discrimination factors on the output of mixing-model programs, a current deficiency in their application (Martínez del Rio et al. 2009), or on the ability to compare the output from competing Bayesian mixing models. Bayesian models have greater statistical power, allow users to incorporate variation in discrimination factors and prior information, and are therefore preferable to non-Bayesian approaches (Link and Barker 2010). The goals of this study were therefore: (1) to investigate how the output changes with a change in the magnitude of the discrimination factors and (2) to demonstrate how changes in discrimination factors can potentially affect management and conservation decisions.

MATERIALS AND METHODS

Common Tern data

As part of another study (Bond and Diamond 2009), we collected stable carbon and nitrogen isotope data from the whole blood of adult Common Terns (*Sterna hirundo*) and from the muscle tissue of their major associated prey: "hake" (white hake *Urophycis tennuis*, silver hake *Merluccius bilinearis*, and four-bearded rockling *Enchelyopus cimbrius*), Atlantic herring (*Clupea harengus*), krill (*Meganyctiphanes norvegica*), and larval hake/herring. Collections were made on Machias Seal Island, New Brunswick, Canada (44°30′ N, 67°06′ W). For collection, preparation, and lab analysis, we direct the reader to Bond and Diamond (2009). Briefly, prey items were collected from birds that regurgitated when handled, and from prey items found dropped in the colony. Samples were dried and lipids were extracted from the prey muscle tissue (Bligh and Dyer 1959) prior to stable-isotope analysis. Lipids are depleted in ^{13}C relative to either carbohydrates or proteins (DeNiro and Epstein 1977), and because lipid content can vary greatly among individuals, sexes, and species, it is recommended that lipids be removed (Bond and Jones 2009). Blood samples were frozen in the field and were dried prior to analysis.

We defined discrimination factors as

$$\Delta X = \delta X_{\text{consumer}} - \sum\nolimits_1^i \left(\frac{\delta X_{\text{prey}_i} \times M_i}{\sum\nolimits_1^i M_i}\right)$$

where ΔX is either Δ^{13}C or Δ^{15}N, δX represents either δ^{13}C or δ^{15}N, and M_i is the dry mass of prey species i. Note that δ^{13}C and δ^{15}N are actual isotope values measured in prey and consumer, whereas Δ^{13}C and Δ^{15}N are the change in isotope ratios between prey and the consumer. From the published literature, we selected discrimination factors (and their standard deviation as a measure of uncertainty) for whole blood in piscivorous birds. We ran simulations using a variety of discrimination factors. All values and associated error for Δ^{13}C

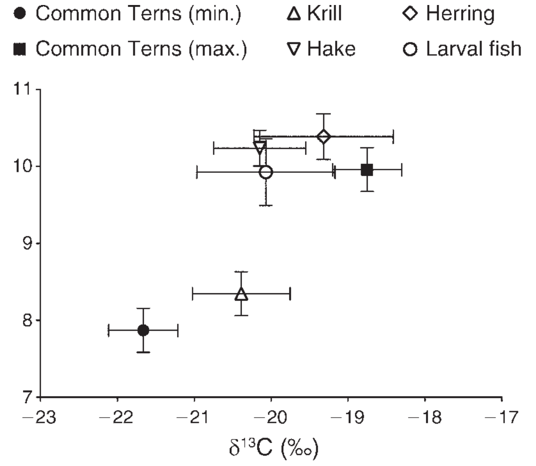

FIG. 1. Stable-isotope ratios (with 95% CI) in whole blood of Common Terns (*Sterna hirundo*), corrected for discrimination factors, and in muscle from common prey types. The two values for Common Terns represent extremes (minimum and maximum) in discrimination factors (Δ^{13}C, −0.81‰, +2.1‰; Δ^{15}N, +1.4‰, +3.49‰; see Table 1). Note that δ^{13}C and δ^{15}N are actual isotope values measured in prey and consumer, whereas Δ^{13}C and Δ^{15}N are the change in isotope ratios between prey and the consumer.

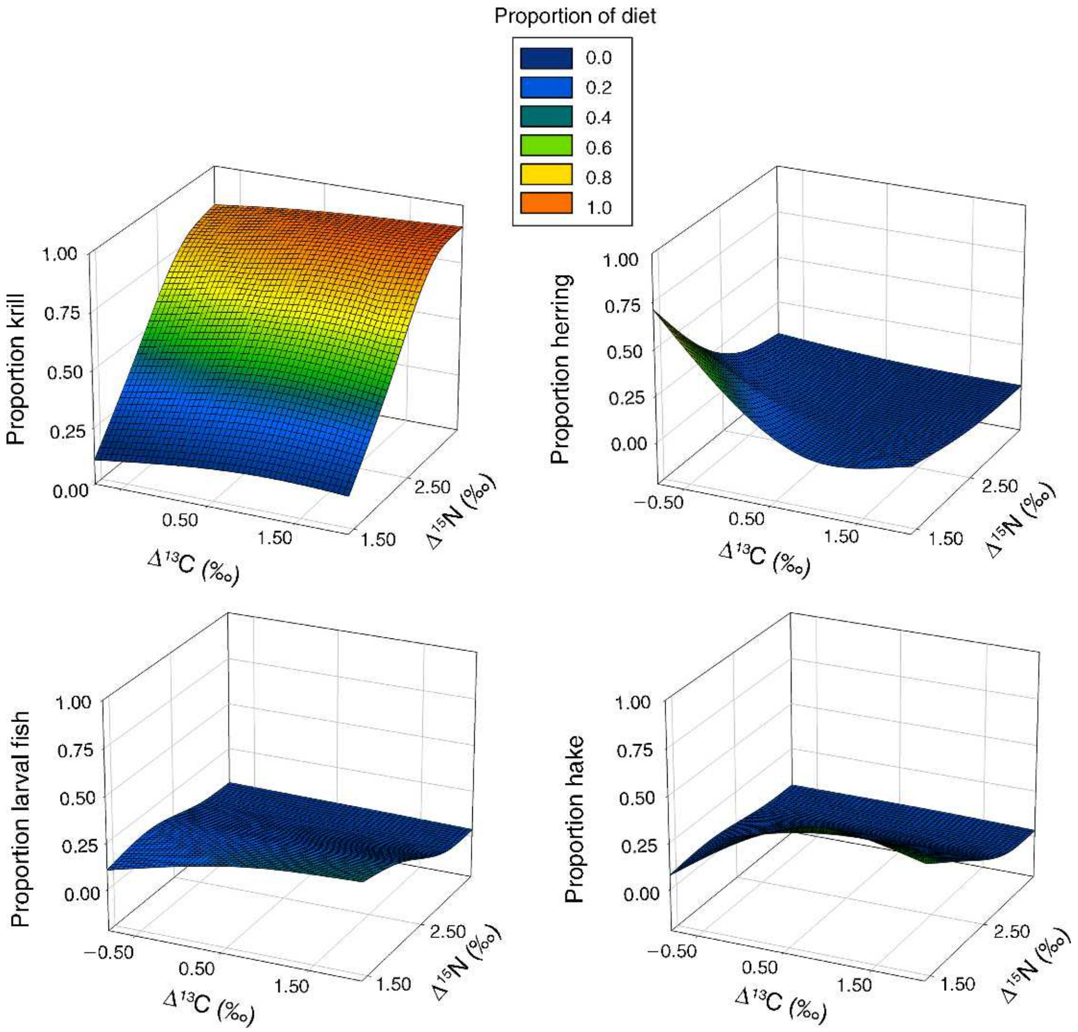

FIG. 2. Variation in estimated contribution of four prey groups (krill, herring, larval fish, and hake) to the diet of Common Terns caused by changing isotope discrimination factors. Colors and the *y*-axis indicate the proportional contribution of each prey group with varying nitrogen (*z*-axis) and carbon (*x*-axis) discrimination factors.

and Δ^{15}N were taken from published studies where captive seabird populations were held on an isotopically constant diet; we chose values that spanned the range of values over all studies (for Δ^{13}C, −0.81–2.1‰; for Δ^{15}N, 1.1–3.49‰; Table 1).

Model programs and statistical analysis

In the mixing-model program SIAR (stable isotope analysis in R), we ran 1 million iterations, thinned by 15 and with an initial discard of the first 40 000, resulting in 64 000 posterior draws. When the model has difficulty differentiating among possible sources, the posterior samples for the source contributions are likely to be correlated. We assessed model fit by examining the *P* value of the highest correlation in each model. This was repeated for each set of discrimination factors. We obtained identical results (not shown) when we performed similar analyses using another Bayesian mixing model (MixSIR; Moore and Semmens 2008) that is structurally very similar.

The SIAR output gives a joint posterior distribution for the vector of proportional contributions of each prey group that is a Dirichlet distribution (Parnell et al. 2010), which is multivariate and continuous. To compare model output among competing models (i.e., different sets of discrimination factors), we calculated Bhattacharyya's Coefficient, BC, for the first 5000 iterations of each pairwise comparison (Bhattacharyya 1943, Rauber et al. 2008). BC is analogous to other indices of dietary overlap such as the Horn-Morisita Index, where $0 \leq \text{BC} \leq 1$, BC = 1 indicates complete similarity between distributions and BC = 0 indicates complete dissimilarity (Horn 1966, Kailath 1967). BC > 0.60 indicated significant overlap between models (Catry et al. 2009). We present the median BC with 95% confidence intervals derived from the 5000 iterations.

TABLE 2. Bhattacharyya's coefficients (BC) for pairwise model comparisons of SIAR mixing-model output of Common Tern (*Sterna hirundo*) diet.

Model values for $\Delta^{13}C$, $\Delta^{15}N$ (‰)	Model values for $\Delta^{13}C$, $\Delta^{15}N$ (‰)							
	−0.81, 3.49	−0.81, 2.07	−0.81, 3.1	−0.81, 1.4	1.1, 3.49	1.1, 2.07	1.1, 3.1	1.1, 1.4
−0.81, 3.49		0.257	0.500	0.114	0.467	0.262	0.493	0.114
−0.81, 2.07	0.03–0.74		0.292	0.399	0.189	0.272	0.213	0.202
−0.81, 3.1	0.08–0.94	0.04–0.72		0.125	0.488	0.293	0.510	0.134
−0.81, 1.4	0.01–0.47	0.06–0.81	0.01–0.42		0.078	0.106	0.086	0.112
1.1, 3.49	0.06–0.93	0.02–0.54	0.07–0.93	0.01–0.27		0.262	0.531	0.110
1.1, 2.07	0.03–0.72	0.03–0.81	0.04–0.75	0.01–0.43	0.03–0.70		0.297	0.455
1.1, 3.1	0.08–0.93	0.03–0.55	0.08–0.93	0.01–0.28	0.09–0.94	0.04–0.71		0.130
1.1, 1.4	0.01–0.45	0.02–0.75	0.01–0.46	0.01–0.53	0.01–0.40	0.07–0.86	0.02–0.43	
2.1, 3.49	0.05–0.93	0.02–0.48	0.07–0.92	0.01–0.24	0.08–0.94	0.03–0.61	0.07–0.94	0.01–0.34
2.1, 2.07	0.03–0.74	0.04–0.90	0.04–0.73	0.01–0.55	0.03–0.67	0.09–0.97	0.04–0.68	0.06–0.88
2.1, 3.1	0.07–0.94	0.02–0.51	0.07–0.93	0.01–0.27	0.09–0.95	0.03–0.64	0.09–0.95	0.01–0.38
2.1, 1.4	0.01–0.47	0.03–0.82	0.01–0.46	0.02–0.72	0.01–0.38	0.06–0.83	0.01–0.38	0.10–0.96

Notes: Discrimination factors for whole blood were taken from published studies of captive piscivorous bird populations (see Table 1). Two discrimination factors (for C and N) are required by the models. To compare model output, for example, the BC between model $\Delta^{13}C = -0.81$‰, $\Delta^{15}N = 3.49$‰ and model $\Delta^{13}C = 2.1$‰, $\Delta^{15}N = 3.1$‰ is 0.485, indicating nonsignificant overlap between model output. BC = 0 indicates no overlap between distributions (and consequently, different posterior probabilities of prey composition), and BC = 1 indicates complete overlap; BC > 0.60 is considered significant overlap. Median BC is presented above the diagonal, and 95% confidence intervals from 5000 iterations are presented below the diagonal.

Finally, we plotted the estimated median contribution of each prey source to the terns' diet as a function of both carbon and nitrogen discrimination factors using a three-dimensional heat map where blue represented a contribution of 0% and red a contribution of 100%.

Balearic Shearwater data and management implications

To show how discrimination factors can affect management decisions and applied conservation, we considered the case of the Balearic Shearwater (*Puffinus mauretanicus*) in the Mediterranean Sea. Recently, Navarro et al. (2009) used the mixing-model program Isoerror (Phillips and Gregg 2001) to estimate the contribution of fisheries discards to the critically endangered Balearic Shearwater, and determined that fisheries discards played a large role in the pre-breeding diet of adult shearwaters. Navarro et al. (2009) used whole-blood and fish muscle discrimination factors determined by an observational study of wild Yellow-legged Gulls (*Larus michahellis*; Ramos et al. 2009). No discrimination factors have been published for the Order Procellariiformes. We used the data presented in Navarro et al. (2009) and, following the same procedure as outlined for Common Terns in the Bay of Fundy, we used SIAR to examine the influence of discrimination factors on the estimated reliance of male Balearic Shearwaters on fisheries discards (demersal prey sources) during the pre-incubation period, again using BC.

RESULTS

Common Tern whole blood and prey type stable-isotope values are presented in Fig. 1 and a summary of the estimates of Common Tern diet composition is presented in Fig. 2. Correlations among Common Tern posterior samples for source contributions were moderate (0.3–0.7) because of similar $\delta^{13}C$ and $\delta^{15}N$ values of hake and herring. In general, there was very low overlap among models with different discrimination factors. The highest median BC for the Common Tern data was 0.59, and most BC values were <0.40 (Table 2). Model performance was generally better for male pre-breeding Balearic Shearwaters (source correlations generally were <0.5). As with Common Terns, discrimination factors influenced model output significantly (where BC > 0.60), although there was generally more overlap in model output among models with similar discrimination factors (Fig. 3, Table 3).

DISCUSSION

Our results show the importance of using appropriate discrimination factors in using stable carbon and nitrogen isotope mixing models for animal diet reconstruction. In the vast majority of cases, species-specific discrimination factors are not available, forcing researchers to compromise and estimate a discrimination factor based on those from species that are similar, either ecologically or taxonomically. Some aspect of this variation may also be caused by variation in either consumer or source isotope ratios, and further systematic investigation is required to assess the importance of these sources of variation on model output.

Depending on the set of discrimination factors chosen, our estimates of Common Tern diet were significantly different (where BC > 0.60). For example, the median estimated percentage of krill ranged from 10.8% ($\Delta^{13}C = -0.81$‰, $\Delta^{15}N = 1.4$‰) to 90.7% ($\Delta^{13}C = 2.1$‰, $\Delta^{15}N = 3.49$‰) in SIAR (Fig. 2). This can have consequences not only for ecological investigations, but also for management decisions, because seabirds are used frequently as indicators of prey abundance and as indicators of the health of the oceanic domain (Cairns 1987, Furness and Camphuysen 1997). Although touted as a "fairly routine" method for assessing seabird diet (Barrett et al. 2007), the proper interpretation of stable-

TABLE 2. Extended.

Model values for $\Delta^{13}C$, $\Delta^{15}N$ (‰)			
2.1, 3.49	2.1, 2.07	2.1, 3.1	2.1, 1.4
0.450	0.257	0.485	0.118
0.148	0.344	0.180	0.288
0.450	0.292	0.488	0.136
0.063	0.140	0.074	0.178
0.510	0.241	0.535	0.099
0.206	0.585	0.249	0.418
0.508	0.274	0.549	0.116
0.083	0.466	0.103	0.585
	0.188	0.523	0.071
0.02–0.57		0.226	0.459
0.09–0.94	0.03–0.61		0.091
0.01–0.32	0.07–0.86	0.01–0.33	

isotope results and careful construction of models are challenges for those not thoroughly and intimately familiar with the stable-isotope literature (Bond and Jones 2009).

In our reexamination of stable-isotope data from Balearic Shearwaters, we found that, depending on the set of discrimination factors used, the median proportion of demersal prey (interpreted as reliance on fisheries discards) of males during the pre-incubation period ranged from 2% to 56%, as compared with the original estimate of 59% in Navarro et al. (2009). For females, our median estimates ranged from 4% to 41%, as compared with the original estimate of 23%. The discrimination factors used by Navarro et al. (2009) were within the range of those used in our simulations, and although there may be differences based on the model structure (SIAR vs. IsoError), we believe that our

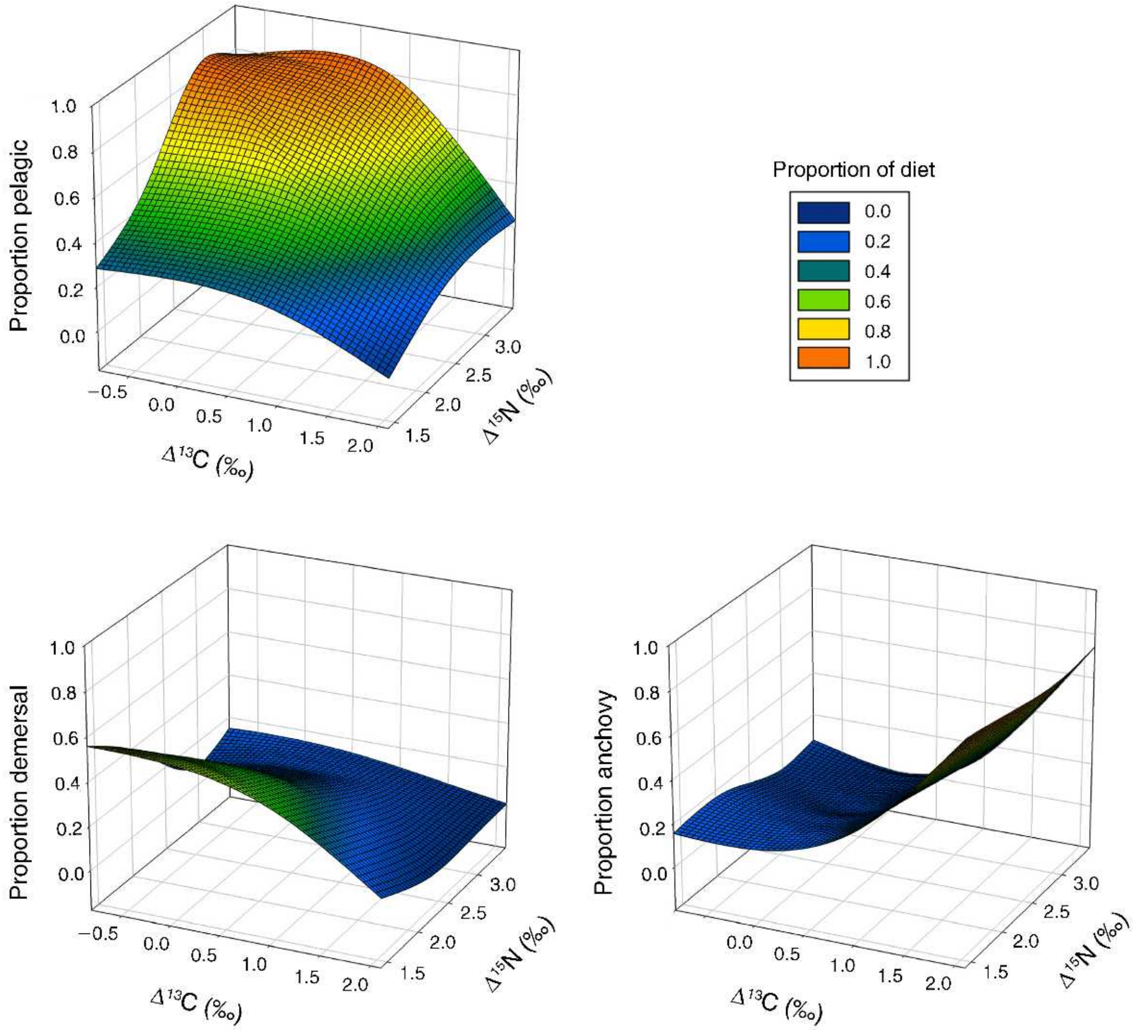

FIG. 3. Variation in estimated contribution of three prey groups (pelagic fishes, demersal fishes, and anchovies) in the pre-incubation diet of male Balearic Shearwaters (*Puffinus mauretanicus*) caused by changing isotope discrimination factors. Colors and the *y*-axis indicate the proportional contribution of each prey group with varying nitrogen (*z*-axis) and carbon (*x*-axis) discrimination factors. Original data are from Navarro et al. (2009).

TABLE 3. Bhattacharyya's coefficient for pairwise model comparisons of SIAR mixing-model output of male Balearic Shearwater (*Puffinus mauretanicus*) diet.

Model values for $\Delta^{13}C$, $\Delta^{15}N$ (‰)	Model values for $\Delta^{13}C$, $\Delta^{15}N$ (‰)							
	−0.81, 3.49	−0.81, 2.07	−0.81, 3.1	−0.81, 1.4	1.1, 3.49	1.1, 2.07	1.1, 3.1	1.1, 1.4
−0.81, 3.49		0.508	0.805	0.396	0.567	0.494	0.595	0.337
−0.81, 2.07	0.12–0.88		0.608	0.769	0.707	0.950	0.816	0.839
−0.81, 3.1	0.19–0.99	0.12–0.95		0.489	0.583	0.592	0.643	0.426
−0.81, 1.4	0.07–0.79	0.19–0.98	0.09–0.87		0.466	0.813	0.574	0.878
1.1, 3.49	0.11–0.97	0.20–0.93	0.11–0.98	0.11–0.77		0.752	0.943	0.525
1.1, 2.07	0.12–0.83	0.37–0.99	0.13–0.92	0.26–0.98	0.30–0.94		0.860	0.900
1.1, 3.1	0.13–0.95	0.31–0.96	0.14–0.99	0.18–0.84	0.46–0.99	0.55–0.98		0.640
1.1, 1.4	0.07–0.67	0.28–0.99	0.09–0.79	0.24–0.99	0.16–0.79	0.52–0.99	0.28–0.87	
2.1, 3.49	0.02–0.53	0.05–0.78	0.02–0.58	0.03–0.59	0.12–0.81	0.09–0.68	0.11–0.79	0.07–0.64
2.1, 2.07	0.02–0.48	0.06–0.86	0.02–0.56	0.05–0.68	0.14–0.71	0.12–0.72	0.13–0.72	0.11–0.72
2.1, 3.1	0.02–0.52	0.05–0.76	0.02–0.57	0.03–0.54	0.12–0.90	0.08–065	0.10–0.80	0.06–0.59
2.1, 1.4	0.01–0.29	0.04–0.72	0.01–0.37	0.04–0.85	0.12–0.83	0.08–0.67	0.06–0.52	0.11–0.83

Notes: BC = 0 indicates no overlap between distributions (and consequently, different posterior probabilities of prey composition), and BC = 1 indicates complete overlap; BC > 0.60 is considered significant overlap. Median BC is presented above the diagonal, and 95% confidence intervals from 5000 iterations are presented below the diagonal.

simulation highlights the need for greater attention to the ecological assumptions of mixing models and the use of discrimination factors from different species. Seabirds can, to varying degrees, rely on fisheries discards, and changes in discard rates or composition can alter species' demography, behavior, and diet (Furness 2003, Votier et al. 2004), which will influence management actions and priorities. Our results have clear implications for the conservation and management of this critically endangered species because it is now unclear how heavily Balearic Shearwaters rely on fisheries discards.

It is possible for isotope modeling programs to have difficulty resolving source contributions when the isotope ratios of all sources fall within a narrow range, such as in our data set (ranges of 1.5–2.0‰). Furthermore, when the differences between consumer and diet isotope ratios are larger, the error associated with using estimated discrimination factors is likely to be small (Martínez del Rio et al. 2009). Because the data in this study were collected from the field, these results should be a reasonable and realistic scenario for those using any Bayesian mixing-model program (e.g., MixSIR or SIAR). Finally, the addition of field observations and additional dietary information will strengthen model output and interpretation and should be included when possible.

In summary, we found that the most statistically advanced isotope mixing models are highly sensitive to the discrimination factors used in model construction. We therefore recommend that researchers make use of the currently held captive individuals and research centers to perform isotope discrimination studies on their species of interest, that they incorporate additional foraging data sets, and that those wishing to implement these models consult or collaborate with scientists familiar with stable-isotope analysis, model construction, and interpretation.

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Table 3. Extended.

Model values for $\Delta^{13}C$, $\Delta^{15}N$ (‰)			
2.1, 3.49	2.1, 2.07	2.1, 3.1	2.1, 1.4
0.152	0.151	0.147	0.092
0.331	0.409	0.298	0.308
0.154	0.165	0.146	0.109
0.226	0.326	0.200	0.344
0.486	0.467	0.476	0.476
0.364	0.457	0.335	0.349
0.441	0.470	0.426	0.255
0.306	0.449	0.267	0.477
	0.772	0.822	0.261
0.20–0.99		0.723	0.458
0.22–0.99	0.16–0.98		0.219
0.04–0.80	0.08–0.93	0.03–0.70	

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