

1 Breaking the sticks: a hierarchical change-point model
2 for estimating ontogenetic shifts with stable isotope
3 data

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18 **Abstract**

19 1. Stable isotopes are increasingly used in ecology to investigate ontogenetic shifts

20 in foraging habitat (via $\delta^{13}\text{C}$) and in trophic level (via $\delta^{15}\text{N}$). These shifts are in
21 essence an individual-level phenomenon, requiring repeated measures throughout the
22 life of individuals, that is longitudinal data. Longitudinal data require in turn
23 specifying an appropriate covariance structure. Here we present a hierarchical model
24 to jointly investigate individual ontogenetic shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

- 25 2. In a Bayesian framework, we used a Cholesky decomposition for estimating a
26 moderately-sized covariance matrix, thereby directly estimating correlations between
27 parameters describing time-series of isotopic measurements. We offer guidelines on
28 how to select the covariance structure.
- 29 3. The approach is illustrated with a hierarchical change-point (or broken stick) model
30 applied to a data set collected on Southern Elephant Seals, *Mirounga leonina*.
31 Ontogenetic shifts in foraging habitat, following a juvenile and variable stage, were
32 detected and interpreted as fidelity to a foraging strategy; while ontogenetic shifts in
33 trophic level were more likely the result of complete independence from maternal
34 resources followed by a gradual increase in trophic level as seals aged.
- 35 4. Specifying both an appropriate covariance and mean structure enabled us to draw
36 strong inferences on the ecology of an elusive marine predator, and has wide
37 applicability for isotopic ecology provided repeated isotopic measurements are
38 available.

39 1 Introduction

40 The use of stable isotopes in ecology is expanding rapidly (Kelly, 2000; Newsome *et al.*, 2007;
41 West *et al.*, 2006; Wolf *et al.*, 2009). This inexpensive technique has become extremely popular
42 to investigate various phenomena, from migration (Hobson *et al.*, 1999) to diet estimation
43 (Semmens *et al.*, 2009). A recent application is the detection of temporal shifts in a species' diet
44 (Phillips & Eldridge, 2006; Popa-Lisseanu *et al.*, 2007), and more specifically of changes in

45 trophic level throughout the life of an individual, that is the detection of ontogenetic shifts
46 (Estrada *et al.*, 2006; Post, 2003). An ontogenic shift is defined as *the patterns in an organism's*
47 *resource use that develop as it increases in size from birth or hatching to its maximum* (Werner
48 & Gilliam, 1984). In their review on ontogenetic shifts, Werner & Gilliam (1984) focused on
49 changes in habitat use and trophic level, both of which are apprehended in isotopic ecology via
50 carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes respectively.

51 Carbon isotopes are used for identifying carbon sources and fluxes within ecosystems (Kelly,
52 2000; Peterson & Fry, 1987; West *et al.*, 2006). Natural gradients in carbon isotopes occur
53 between terrestrial and marine food webs (Schoeninger & DeNiro, 1984; Hobson *et al.*, 1994),
54 between inshore and offshore waters (Rau *et al.*, 1982; Hobson *et al.*, 1994), between benthic
55 and pelagic foodwebs (France, 1995) or between low and high latitudes water masses (Rau
56 *et al.*, 1982, 1989). The nitrogen isotopic ratio is a reflection of the trophic level of organisms
57 (Post, 2002; Vanderklift & Ponsard, 2003). Because the lighter isotope is usually more reactive,
58 ^{14}N is preferentially excreted and the heavier ^{15}N is preferentially retained, a phenomenon
59 known as fractionation (Fry, 2006). This differential reactivity results in a predictable
60 enrichment of the ratio of ^{15}N to ^{14}N from preys to consumers (Kelly, 2000).

61 A large number of studies looking at ontogenic shifts concerns species with “cryptic lifestages”,
62 in particular marine organisms such as turtles (Reich *et al.*, 2007), fish (Estrada *et al.*, 2006;
63 Post, 2003) or marine mammals (Drago *et al.*, 2009; Hobson & Sease, 1998; Mendes *et al.*,
64 2007; Newsome *et al.*, 2009). In some studies, repeated isotopic measurements were available
65 for the same individual using so-called archive tissues, because they are metabolically inert after
66 synthesis, such as vertebrae (Estrada *et al.*, 2006), or teeth (Hobson & Sease, 1998; Mendes
67 *et al.*, 2007; Newsome *et al.*, 2009). These studies addressed the estimation of a change-point in
68 the time-series of isotopic measurements, yet they typically pooled data from all individuals to
69 infer a population-level change-point, or ontogenetic shift. For example, Newsome *et al.* (2009)
70 fitted a 4 parameters logistic model to estimate a change in dentin $\delta^{15}\text{N}$ of Californian Killer

71 Whales (*Orcinus orca*) after weaning. The model is fit at the population level, that is assuming
72 all individuals experienced an ontogenetic shifts at the same age, despite apparent individual
73 heterogeneity in the raw plot (their Figure 2a). Ignoring individual heterogeneity when it is in
74 fact present may hinder our ability to draw accurate inferences (Cooch *et al.*, 2002; Petrovskii
75 *et al.*, 2011). In addition, the change-point is often treated as known even when it was first
76 estimated from the same data. Unless a profile likelihood approach is used, no confidence
77 interval for the change-point is usually reported, and all subsequent inferences are conditional
78 on the point estimate for the change-point.

79 Stable isotopes in ecology of wild animals are often hailed as a powerful technique. Yet,
80 inferences are typically drawn from statistical analyses that tend to 1) emphasize testing over
81 estimation and goodness-of-fit (Graham, 2001; Martínez Abraín, 2010); and 2) focus on the
82 mean response at the expense of variability (but see Hénaux *et al.* (2011)). In the case of
83 detecting an ontogenetic shift, the problem is clearly one of estimation: when does an organism
84 change its habitat use or trophic level? Further questions may arise as to what are the
85 ecological, life-history and ultimately population consequences of such an individual change
86 (Werner & Gilliam, 1984; Graham *et al.*, 2007). This paper thus deals with the problem of
87 estimating individual ontogenetic shifts with longitudinal isotopic data, that is repeated
88 measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on the same organism throughout its life. We present a
89 Bayesian change-point model to jointly estimate individual ontogenetic shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.
90 Our aim is to bring forward to a larger audience the vast literature on change-point models
91 (Beckage *et al.*, 2007; Hall *et al.*, 2000; Muniz-Terrera *et al.*, 2011; Ghosh & Vaida, 2007), and
92 how to fit them using the *BUGS* language (Lunn *et al.*, 2000).
93 Change-point, or broken-stick, models aim at finding an abrupt rupture in a time-series. The
94 time-series is assumed to be the juxtaposition of piece-wise linear homogeneous segments, each
95 segment separated from the next by a change-point. Such models have been used in
96 epidemiology to infer the onset of cognitive decline (Hall *et al.*, 2000; Muniz-Terrera *et al.*,

2011), of prostate cancer (Bellera *et al.*, 2008) or of HIV immunologic response decline (Ghosh & Vaida, 2007). In ecology, Beckage *et al.* (2007) used a change-point model to study allometric relationships between tree height and tree diameter or to study seedling recruitment with respect to canopy cover along a transect; while Da-Silva *et al.* (2008) studied post-reproductive survival in a partially semelparous marsupial. These models are very flexible as they allow specifying different probability distributions to describe different parts of a time series. Change-point models thus seem appropriate to describe ontogenetic shifts (e.g. Post (2003)), but are not prescriptive. Other models (for example Newsome *et al.* (2009)) may prove useful when investigating ontogenic shifts. Our aims here are to expose the use of powerful statistical tools to help ecologists drawing strong inferences (Platt, 1964). We will illustrate our methodology with an example using data on Southern Elephant Seals *Mirounga leonina*.

1.1 Southern Elephant Seal Example

Southern Elephant Seals are marine carnivores with a very elusive lifestyle since they can spend more than 80% of their lifetime at sea (McIntyre *et al.*, 2010). Where they are foraging remained a mystery until the advent of miniaturized electronic tags (Biuw *et al.*, 2007). Seals from îles Kerguelen (49°30' S, 69°30' E) in the Southern Indian Ocean show a dual foraging strategy: animals forage either in Antarctic waters or in polar frontal waters (Bailleul *et al.*, 2010). Across the Southern Ocean, $\delta^{13}\text{C}$ decreases with increasing latitude (Bentaleb *et al.*, 1998; Trull & Armand, 2001). Carbon stable isotopes can thus help identify the foraging areas of marine predators: a relative difference of $\approx 2\text{‰}$ is expected between the two strategies (Cherel & Hobson, 2007; Jaeger *et al.*, 2010). Processes underlying carbon isotopic fractionation in marine foodwebs are briefly reviewed in MacKenzie *et al.* (2011) and a model for fractionation is described in Rau *et al.* (1996).

With Southern Elephant Seals, we were interested in answering the following questions:

- 121 • Are seals faithful to a foraging strategy (Bradshaw *et al.*, 2004)?
- 122 • When do they become faithful?
- 123 • Are ontogenic shifts in carbon (foraging habitat) and nitrogen (trophic level) isotopes
- 124 concomitant?
- 125 • Are there notable sex differences?
- 126 • Can we detect differences in stable isotope values before and after the 1970s population
- 127 crash (Authier *et al.*, 2011)?

128 **2 Material & Methods**

129 **2.1 Notations and Assumptions**

130 Throughout we will assume the data are composed of N measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on m
 131 different individuals. For the j^{th} individual, there are n_j measurement, such that $N = \sum_{j=1}^m n_j$.
 132 These measurement are collected along some biologically-meaningful ordered scale such as age
 133 (or size). This scale is assumed continuous for convenience. We will also posit that a piecewise
 134 linear, or broken-stick model, provides an adequate description of the data, although this may be
 135 relaxed to consider non-linear functions as well. With the broken-stick model, we will denote
 136 by $K_j^{\delta^{13}\text{C}}$ ($K_j^{\delta^{15}\text{N}}$) the age of the j^{th} individual when an ontogenetic shift in foraging habitat
 137 (trophic level) occurs.

138 **2.2 Model Building**

139 The time-series of isotopic measurements for the j^{th} individuals is then modelled as:
 140 for $i \in [1 : n_j]$

$$\delta^{13}\text{C}_{i,j} = a_{1,j} + (\text{Age}_{i,j} - e^{a_{3,j}}) \times \begin{cases} a_{2,j} + \varepsilon_{i,1}, & \text{Age}_{i,j} \leq e^{a_{3,j}} \\ a_{4,j} + \varepsilon_{i,2}, & \text{Age}_{i,j} > e^{a_{3,j}} \end{cases} \quad (1)$$

141 where

$$\left\{ \begin{array}{l} a_{1,j} = \text{isotopic value at ontogenetic shift} \\ a_{2,j} = \text{slope before the ontogenetic shift} \\ a_{3,j} = \log(K_j^{\delta^{13}\text{C}}) \\ a_{4,j} = \text{slope after the ontogenetic shift} \\ \varepsilon_{i,1} \sim \mathbf{N}(0, \sigma_{\delta^{13}\text{C},1}) \text{ are the residuals before the ontogenetic shift} \\ \varepsilon_{i,2} \sim \mathbf{N}(0, \sigma_{\delta^{13}\text{C},2}) \text{ are the residuals after the ontogenetic shift} \end{array} \right.$$

142 and $\sigma_{\delta^{13}\text{C}}$ is the residual standard deviation, which is allowed to be different before and after the
 143 ontogenetic shift. A logarithmic transformation is used to guarantee positive values for all $K_j^{\delta^{13}\text{C}}$
 144 or $K_j^{\delta^{15}\text{N}}$. We implicitly assume that only the consumer, not its prey, can experience an isotopic
 145 shift, but the model cannot be used to distinguish between these two alternatives (Matthews &
 146 Mazunder, 2004).

147 The individual coefficients $a_{k \in [1:4],j}$ are assumed to be exchangeable and drawn from a
 148 multivariate normal distribution of vector mean $\alpha_{k \in [1:4]}$ and covariance matrix of dimension 4:

$$\begin{pmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{pmatrix}_j \sim \text{MVN} \left(\begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \\ \alpha_4 \end{bmatrix}, \begin{bmatrix} \sigma_1^2 & \sigma_{1,2} & \sigma_{1,3} & \sigma_{1,4} \\ \sigma_{2,1} & \sigma_2^2 & \sigma_{2,3} & \sigma_{2,4} \\ \sigma_{3,1} & \sigma_{3,2} & \sigma_3^2 & \sigma_{3,4} \\ \sigma_{4,1} & \sigma_{4,2} & \sigma_{4,3} & \sigma_4^2 \end{bmatrix} \right) \quad (2)$$

149 This formulation allows to directly estimate correlations between parameter of interest via the
 150 covariance matrix. For example, one could be interested to assess whether an ontogenetic shift
 151 occurs later or earlier depending on the steepness of the slope $a_{2,j}$. The interpretation of such
 152 correlations would depend on the biology of the studied organism.

153 The same broken-stick model can be applied to $\delta^{15}\text{N}$: this model then calls for the estimation of

154 two independent covariance matrices each of dimension 4: one for $\delta^{13}\text{C}$ and one for $\delta^{15}\text{N}$
 155 (hereafter referred to as $2 \times 4 \times 4$). An obvious question is whether ontogenetic shifts in $\delta^{13}\text{C}$ and
 156 $\delta^{15}\text{N}$ are simultaneous or correlated. Answering this question requires the estimation of
 157 covariance matrix \mathbf{V} of dimension 8, as represented on Figure 1 (this model is referred to as 8×8
 158 hereafter).

159 Specifying the covariance structure of a model has generally received less attention than
 160 specifying its mean response, but the problem is no less relevant (Pourahmadi, 2010).

161 Estimating a covariance matrix of size greater than 2 is a challenge: in addition to the usual
 162 restriction to lie between -1 and 1 , correlations are jointly constrained. For example, with a
 163 3×3 covariance matrix, $\rho_{1,2}$ and $\rho_{1,3}$ can take any value between -1 and 1 , but $\rho_{2,3}$ must then
 164 conform to the following constraints for the matrix to be positive-definite and invertible
 165 (Budden *et al.*, 2007):

$$166 \rho_{1,2}\rho_{1,3} - \sqrt{(1 - \rho_{1,2}^2)(1 - \rho_{1,3}^2)} \leq \rho_{2,3} \leq \rho_{1,2}\rho_{1,3} + \sqrt{(1 - \rho_{1,2}^2)(1 - \rho_{1,3}^2)}$$

167 Estimating a matrix such as represented in Figure 1 presents some additional challenges since
 168 some elements are constrained to be 0. We opted for a Cholesky decomposition of \mathbf{V} into a
 169 diagonal matrix Γ and a lower triangular matrix L with 1s on the diagonal:

$$\mathbf{V} = \Gamma L L^T \Gamma \quad (3)$$

170 There are several Cholesky decompositions, all of which guarantee positive-definiteness
 171 (Pourahmadi, 2007), but equation 3 neatly separates standard deviation (Γ) and correlation
 172 ($L L^T$) parameters (Barnard *et al.*, 2000; Chen & Dunson, 2003). It becomes possible to force
 173 some correlations to be 0 and impose the desired structure for \mathbf{V} .

174 In a Bayesian framework, priors need to be specified on each of the parameters. We used
 175 weakly-informative priors: for parameters on the same scale as the data (α_1 , α_2 and α_4) we
 176 used normal priors with a large variance. For the parameter governing the distribution of ages at

177 ontogenetic shifts, a logarithmic transformation in equation 1 guarantees positive values for all
178 $K_j^{\delta^{13}\text{C}}$ or $K_j^{\delta^{15}\text{N}}$. For the parameter α_3 , we used a Student- t prior (with location, scale and
179 degrees of freedom set to 0, 10 and 7 respectively (Gelman *et al.*, 2008)). For modelling \mathbf{V} , we
180 used the priors similar to those of Chen & Dunson (2003): independent Half-Normal priors of
181 mean 0 and standard deviation 1.5 for the elements, $\gamma_{p \in [1:8]}$, of the diagonal matrix Γ , and
182 independent normal priors of mean 0 and standard deviation 0.5 for the elements, $\lambda_{p \in [2:8], q < p}$, of
183 L . A prior covariance matrix of dimension 4 (8) with such a specification is depicted on Figure
184 S1 (Figure S3). This prior gives reasonable values (that is between 0 and 10) for the variances
185 of the $a_{i,j}$, but can be altered depending on the studied organisms. It is also somewhat
186 conservative as most of the probability mass for variance parameters is put on values less than 5.
187 This prior thus reflects skepticism for large differences between individuals. Uniform priors
188 were put on the residual standard deviations (Gelman, 2006).

189 2.3 Model Selection

190 With hierarchical models, model selection is a challenge and several methods have been
191 suggested, such as DIC (Spiegelhalter *et al.*, 2002; Barnett *et al.*, 2010); but there is currently no
192 consensus (Jordan, 2011). We choose to avoid using the DIC because of drawbacks such as lack
193 of invariance to reparametrization (Spiegelhalter *et al.* (2002) and the following discussion). In
194 fact, DIC was computed but yielded non-sensical results for the estimated number of parameters
195 when the Cholesky decomposition was used (see Table S2). To select an appropriate model, we
196 focused on Posterior Predictive Checks (Gelman *et al.*, 1996; Berkhof *et al.*, 2003) wherein
197 each fitted model is used to predict (hypothetical) repetitions of the data set. From this
198 hypothetical dataset, we compared an observed summary statistic (\mathbf{T}_{obs}) to its predicted values
199 (\mathbf{T}_{rep}) and compute a p_{value} :

$$p_{\text{value}} = Pr(\mathbf{T}_{\text{rep}} > \mathbf{T}_{\text{obs}}) \quad (4)$$

200 A p_{value} close to 0.5 tells us of a good fit ($\mathbf{T}_{rep} \approx \mathbf{T}_{obs}$), while an extreme p_{value} (0 or 1) betrays
 201 a major model misfit. We chose the range of observed isotopic values as discrepancy statistics
 202 to assess model fit. The rationale for choosing the range as a test statistic is the following: if a
 203 change-point is necessary to describe the time-series of isotopic measurement, the range of
 204 predicted value is likely to be underestimated when fitting a model with no change-point. The
 205 tip of the broken stick will be missed by a simple linear regression, hence an underestimation of
 206 the range. Posterior Predictive Checks can be used to test whether a broken-stick model is
 207 justified or to select a covariance structure. For example, we can compare the covariance
 208 structure depicted in Figure 1 with a simpler structure where the matrix is block diagonal with
 209 no correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (that is, $\rho_{1,5} = \rho_{2,6} = \rho_{3,7} = \rho_{4,8} = 0$ in Figure 1).

210 2.4 Checking Model Fit

211 Once a model has been selected, it is crucial to check model fit (Gelman & Shalizi, 2010).
 212 Therefore model fit was assessed for each individual using a goodness-of-fit statistic for
 213 non-linear models (Vonesh *et al.*, 1996; Huang *et al.*, 2010). This concordance coefficient is
 214 denoted r_c and varies between -1 and 1 , with values ≤ 0 betraying a complete lack of fit
 215 (Vonesh *et al.*, 1996; Huang *et al.*, 2010). This concordance coefficient assesses the fit of the
 216 model at the individual level (Huang *et al.*, 2010), and is computed as follow, with j denoting an
 217 individual:

$$r_{c_j} = 1 - \frac{\sum_{i=1}^{n_j} (\mu_{i,j} - \delta_{i,j})^2}{\sum_{i=1}^{n_j} (\delta_{i,j} - \bar{\delta}_j)^2 + \sum_{i=1}^{n_j} (\mu_{i,j} - \bar{\mu}_j)^2 + n_j(\bar{\delta}_j - \bar{\mu}_j)^2} \quad (5)$$

$$\text{where } \begin{cases} \mu_{i,j} = a_{1,j} + (Age_{i,j} - K_j) \times \begin{cases} a_{2,j}, & Age_{i,j} \leq K_j \\ a_{4,j}, & Age_{i,j} > K_j \end{cases} \\ \bar{\delta}_j = \mathbf{E}(\delta_{i,j}) = \frac{\sum_{i=1}^{n_j} \delta_{i,j}}{n_j} \\ \bar{\mu}_j = \mathbf{E}(\mu_{i,j}) = \frac{\sum_{i=1}^{n_j} \mu_{i,j}}{n_j} \end{cases}$$

218 $\bar{\delta}_j$ and $\bar{\mu}_j$ are the means of the observed and fitted values respectively, while the numerator in
 220 equation 5 is the sum of squared-residuals ε_i for the j^{th} individual. In the next section, we will
 221 apply the above methodology to a “real-life” case.

222 2.5 Southern Elephant Seal Data

223 Teeth were collected from elephant seals that died of natural causes on îles Kerguelen. Canines
 224 grow continuously throughout the whole life without closing of the pulp cavity, allowing for age
 225 determination (Laws, 1952, 1993). Canines from 47 males and 20 females were analyzed and
 226 sampled for isotopic analysis. 18 teeth were sampled on animals that died before a population
 227 crash in the 1970s, while the remaining 49 were sampled in the 2000s, after the population had
 228 stabilized (Authier *et al.*, 2011).

229 Each tooth was cut longitudinally and observed under diffused light to count growth layers. The
 230 alternate pattern of two opaque and two translucent growth layers corresponds to the annual
 231 biological cycle of Southern Elephant Seals (Laws, 1952). Translucent bands are enriched in
 232 vitamin D and synthesized when seals are ashore to breed and to moult, while opaque ones are
 233 synthesized when at sea (Wilske & Arnbohm, 1996). Within a year, a Southern Elephant Seal
 234 comes onshore to breed, returns to the sea, then comes onshore to moult before another trip at
 235 sea. Thus each growth layer was assumed to correspond to one forth of a year (Martin *et al.*,
 236 2011). Each growth layer was sampled for 1 mg of bulk dentin using a MicromillTM sampler
 237 (ISEM, Université de Montpellier 2). Organic matter $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of the bulk
 238 dentine were measured with an elemental analyzer (EA-IRMS, Euro-Vector EA 3000) coupled

239 to a continuous flow mass spectrometer (Optima-Micromass) at the Université de Montpellier 2.
240 As a recent study raised concerns about non-linear offsets of organic %C, %N and $\frac{C}{N}$ after acid
241 treatment (Brodie *et al.*, 2011), we forwent any acid (or demineralization) treatment prior to
242 isotopic measurement. As a result, the measured $\delta^{13}C$ is a mixture of organic carbon with a
243 small amount of inorganic carbon. To test the impact of the inorganic fraction, Martin *et al.*
244 (2011) compared acid-treated and untreated samples but found no differences ($\pm 0.02\%$).
245 Schulting *et al.* (2008) found similar $\frac{C}{N}$ ratios between bulk dentin and collagen, with a lower
246 carbon and nitrogen contents in bulk dentin most likely due to the mineral fraction. Here we
247 assumed that the impact of the mineral fraction is negligible. If not, relative trends (see Results)
248 should be unaffected under the assumption of a systematic bias.

249 Stable isotopic signatures are presented in the usual δ notation (in ‰) relative to Pee Dee
250 Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$ respectively. Typical precisions for isotopic
251 measurement were 0.20 ‰ for both carbon and nitrogen. We used $\frac{C}{N}$ ratio thresholds of bone
252 and tooth collagen (2.9 to 3.6) as criteria for the identification of diagenetic alteration
253 (Ambrose, 1990); assuming that total dentin, whose organic phase is mainly collagen and water
254 (Moyes & Doidge, 1984), has the same $\frac{C}{N}$ ratio than bone and tooth collagen. 1,590 samples
255 were analyzed, but 176 were discarded because of anomalous $\frac{C}{N}$ ratios, yielding a final sample
256 size of 1,414 (1,115 from males and 299 from females) analyses from 67 individuals (47 males
257 and 20 females). The first $\delta^{15}N$ value of each time-series was also removed as it is clearly a
258 reflection of maternal diet (Hobson & Sease, 1998; Martin *et al.*, 2011). Summary statistics of
259 the data are available in Table S1 and depicted in Figure S2. It should be stressed that females
260 are under-represented in this data set, and that samples collected from dead females on beaches
261 were biased toward young females. Thus time-series of isotopic measurement were usually
262 shorter for females (Table S1). We fitted the model defined by equation 1 to these data.

263 To answer questions about any differences between males and females, or between animals
264 living before and after the population crash, we can easily modify the hierarchical change-point

265 model defined by equation 1 by further specifying that the vector of means ($\alpha_{k \in [1:4]}$) depends on
266 the sex of seals and whether they lived *before* or *after* the population crash:

$$267 \quad a_{k \in [1:4],j} = \alpha_{1,k} + \alpha_{2,k} * \text{Sex}_j + \alpha_{3,k} * \text{Crash}_j + \eta_{k,j}$$

268 where the individual-level residuals $\eta_{k,j}$ are drawn from a multivariate normal distribution of
269 mean 0 and covariance matrix \mathbf{V} (see equation 3).

270 **2.6 Software**

271 All models were fitted with *winBUGS* (Spiegelhalter *et al.*, 2003) called from *R* (R
272 Development Core Team, 2009) with the package *R2WinBUGS* (Sturtz *et al.*, 2005). We used
273 normal priors for regression parameter on the natural scale and Student priors with 7 degrees of
274 freedom (Gelman *et al.*, 2008) for regression parameters on the log scale. Three chains were
275 initialized with overdispersed starting values. After appropriate burn-in (200,000 iterations) and
276 thinning of the chains (1 value every 200 iterations stored), convergence was assessed using the
277 Gelman-Rubin convergence diagnostic (Cowles & Carlin, 1996) with the *coda* package
278 (Plummer *et al.*, 2008). Posterior mean (or median when posterior distributions were
279 asymmetric) with 95% Highest Probability Density (HPD) intervals are reported as
280 2.5% *Mean* 97.5% following Louis & Zeger (2009). Inferences are based on a posterior sample of
281 3,000 iterations. Annotated *BUGS* code is available in the Appendix, along with an *R* script and
282 a simulated data set.

283 **3 Results**

284 **3.1 Model Selection and Fit**

285 A hierarchical change-point model provided an adequate fit to the elephant seal isotopic data
286 (Figures 2 & 3). Ontogenetic shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were generally supported, except

287 for short time-series and a few individuals. The broken-stick model provided a better fit than a
 288 null model with no change-point. The model with the most complex covariance structure (8x8
 289 model) did not greatly improve predictive ability (Table 1). Moreover, the estimated
 290 correlations $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were small, with a posterior mean of ≈ 0.1 in absolute magnitude
 291 (Figure 1). Results from the hierarchical model with no correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are
 292 thus reported, although results from the other hierarchical model were very similar. There was
 293 no statistical support for distinguishing between sexes or between individuals sampled *before* or
 294 *after* the population crash (Supplementary Figures 4 & 5): the posterior distribution of
 295 regression coefficients for both factors was as diffuse as that of its prior and included 0.

296 3.2 Ontogenetic Shifts

297 Results for the selected hierarchical change point model are summarized in Tables 2 & 3. The
 298 residual variances for both isotopes were larger before the ontogenetic shift (Table 2). We found
 299 individual heterogeneity in all four parameters $a_{k \in [1:4]}$: all variance components were well
 300 estimated (Table 3, Supplementary Figure 3). The estimated age at ontogenetic shift was larger
 301 for $\delta^{13}\text{C}$ values (3.2 years) than for $\delta^{15}\text{N}$ values (1.9 years, Table 2). This difference was
 302 statistically significant at the 5% level. $\delta^{13}\text{C}$ values at ontogenetic shifts were more variable
 303 than $\delta^{15}\text{N}$ values, but the variability in age at ontogenetic shift was similar for the two elements
 304 (Table 3). There is a sign reversal in slopes before and after the ontogenetic shift in both carbon
 305 and nitrogen isotopes (Table 2): the slope was positive and then negative for $\delta^{13}\text{C}$ and the
 306 opposite for $\delta^{15}\text{N}$. Slopes were more variable before than after the ontogenetic shift for both
 307 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Table 3). There was respectively a small and no correlation between
 308 slopes before and after the change-point in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figure 1).

4 Discussion

4.1 Southern Elephant Seal Foraging Ecology

Using as an example the Southern Elephant Seal, a species with a cryptic life-style, we analyzed stable isotope data with a hierarchical change-point model to draw inferences on its foraging habits and its trophic level. Despite the on-going “biologging” revolution, some questions are still not easily addressed with miniaturized tags (Hebblewhite & Haydon, 2010). For example, equipping a large enough (in the statistical sense) sample of individuals with expensive data recorders that may be lost is usually not an option. For this reason, carbon and nitrogen stable isotopes are no longer studied in ecology as a complementary “side-kick” to biologging, but in their own right (Newsome *et al.*, 2007; Wolf *et al.*, 2009). We were interested in inferring the foraging behaviour of Southern Elephant Seal using repeated measurements of dentin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values over the whole life of individuals. Using a hierarchical change-point model, we estimated ontogenetic change-points in both foraging habitats and in trophic level, and found that there was individual variability in both the trajectory and timing of shifts.

Our modelling approach proved fruitful to investigate some aspects of the ecology of Southern Elephant Seals. In particular, our selected model answered all five questions we asked. After a juvenile stage characterized by a large residual variance, Southern elephant seals became faithful to a foraging strategy. Inferences drawn from longitudinal isotopic data are in agreement with those of biologging studies (Bradshaw *et al.*, 2004), but the former involved a larger sample over a longer time-period than the latter. This commitment to a foraging strategy occurred at an early age, on average at about 3 years, but there was substantial individual heterogeneity (Table 3, Figures 2, S6 & S7). An ontogenetic shift in $\delta^{15}\text{N}$ was also detected, but this shift occurred earlier (around 1.9 year-old on average).

The ontogenetic shifts we identified can be the result of several processes, such as complete independence from maternal resources acquired before weaning (Hobson & Sease, 1998;

334 Polischuk *et al.*, 2001) or a shift in foraging habitat (interfrontal *versus* Antarctic waters) and
335 trophic level (Bailleul *et al.*, 2010). If the estimated shift solely resulted from a decay of
336 maternal resources, we would not expect a difference in residual variances before and after a
337 shift. In the case of Southern Elephant Seals, not only residual variances, but also slope
338 variances were larger before the shift (Tables 2 & 3). This pattern may be interpreted as an
339 individual switching from a very variable state to a more stable one, or in other words for
340 carbon isotopes, in seals becoming faithful to a foraging strategy. The posterior mean for the
341 marginal slope after the ontogenetic shift was negative, which we interpreted as individuals
342 foraging in Antarctic waters. These seals have to haul out on îles Kerguelen for reproduction
343 and moulting, and they are very likely to feed on the way (Thums *et al.*, 2011), thus diluting a
344 “pure” Antarctic signature for $\delta^{13}\text{C}$. Hence a negative slope, as the Antarctic signal becomes
345 preponderant over the years. The estimated individual variability showed that some slopes after
346 the shift were null or slightly positive, which can be a reflection of seals foraging always in the
347 same water mass, for example, in pelagic waters of the Polar Front (Bailleul *et al.*, 2010).
348 Finally, a few individuals had a large positive slope before the shift and a shift late in life. The
349 large positive slope before the shift may be a reflection of seals foraging on the Kerguelen
350 Plateau (Bailleul *et al.*, 2010), which has an enriched $\delta^{13}\text{C}$ signature compared to pelagic water
351 masses (Cherel & Hobson, 2007); before switching to an alternative strategy.

352 Concerning trophic level inferred from $\delta^{15}\text{N}$ values, the shift occurred on average earlier than
353 for the $\delta^{13}\text{C}$ data (Table 2). Slopes before the shift were negative, yet they reversed sign after.
354 Their magnitude also halved before and after the shift, with very few individual variability left
355 after the shift (Table 3). This pattern suggested the shift in $\delta^{15}\text{N}$ values to mostly reflect the
356 gradual decay of maternal influence on $\delta^{15}\text{N}$ (Hobson & Sease, 1998), followed by a gradual
357 elevation in the trophic web as seals grew in size. Growth is indeterminate in these seals: they
358 keep growing until their death although growth is very slow in adults (McLaren, 1993). This
359 continuous growth means that older seals can physically catch bigger preys, which may explain

360 why we observed a gradual elevation in trophic levels. Additionally, the large energy stores
361 males must accumulate before the breeding season may also drive a shift toward large and
362 energetically profitable preys. Residual variances were also larger before than after the shift but
363 the decrease was not as dramatic as for $\delta^{13}\text{C}$ values (Table 2). Thus this shift may mostly reflect
364 complete independence from maternal inputs.

365 This pattern of an elevation in trophic level with age (Figure 2) does not conflict with blood
366 isotopic data for males, but was not expected for females: in a previous study, Bailleul *et al.*
367 (2010) collected blood samples on juvenile males and on adult females. This study evidenced
368 an elevation in $\delta^{15}\text{N}$ with increasing snout-to-tail length, a proxy for age, only in juvenile males.
369 This discrepancy probably results from the imbalance of the female data compared to males:
370 few time-series for females spanned more than 4 years (Table S1, Figures S6 & S7). The limited
371 number time-series spanning more than 4 years means that the male pattern largely dominates
372 the population-level pattern in our hierarchical model. Thus blood isotopic data is more reliable
373 to infer the female pattern (Bailleul *et al.*, 2010), although the dentin isotopic analysis suggested
374 that a few females too underwent an elevation in trophic position as they aged (that is,
375 individuals with increasing slope after the ontogenetic shift; Figures 2, S6 & S7).

376 **4.2 Modelling strategy**

377 The explicit modelling of correlations between parameters governing a broken-stick model for
378 both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values allowed us to investigate whether ontogenetic shifts in foraging
379 habitat and trophic level were concomitant. There was a very small positive correlation between
380 the ages at shift. The explicit incorporation of this correlation into the model did not
381 substantially improve its predictive ability for $\delta^{13}\text{C}$ or for $\delta^{15}\text{N}$ values (Table 1). There seemed
382 to be such a large variability in individual trajectories of foraging strategy and trophic level in
383 this population that there is no meaningful 'average' $\delta^{13}\text{C}$ profile associated with an 'average'
384 $\delta^{15}\text{N}$ profile.

385 Finally, the hierarchical modelling approach enabled us to assess whether there were differences
386 between sexes and between seals living before and after a population crash. The data at hand
387 suggested none (Figures S4 and S5), but the Bayesian framework is explicit about inferences
388 being drawn conditional on the observed data. Thus, failure to detect any differences in this
389 peculiar data set may stem for the imbalance between males and females (respectively 70%
390 *versus* 30% of seals), and between animals living before and after the population crash
391 (respectively 28% *versus* 72% of seals).

392 We believe that the piecewise linear formulation of our change-point model is biologically
393 sound for this species since the change-points reflect life-history events such as complete
394 independence from maternal resources or commitment to a foraging strategy. This assumed
395 model suggested gradual changes after a shift (non-null slopes), which we deemed to be
396 reasonable with longitudinal isotopic data. The interpretation of isotopic data in ecology
397 crucially depends on the rate of tissue turn-over/synthesis, and the accuracy (not the precision)
398 of isotopic data can be quite crude depending on the sampled tissue. Turn-over rates may be
399 very short for some tissues (for example blood plasma), but one order of magnitude larger for
400 others (for example claws) (Carleton *et al.*, 2008). These rates also scale with body mass
401 (Carleton & Martinez del Rio, 2005), which may allow to use experimentally-estimated rates
402 from one species on similar-sized species. However, this is still somewhat of a blackbox for
403 wild animals (Wolf *et al.*, 2009).

404 Assumptions are unavoidable, but the Bayesian framework is very flexible, allowing to fit
405 models to peculiar data sets rather than “adjusting the data to fit the model”. The broken-stick
406 model we assumed reasonable for Southern Elephant Seal need not be so for other species.

407 With little modification in the prior specification of the covariance matrix, non-linear functional
408 responses such as a logistic curve, which also has 4 parameters, can be easily fitted. However, a
409 logistic curve carries also assumptions such as symmetry and asymptotic isotopic values at the
410 end of the time scale. Finally, the broken-stick model was useful for estimating individual shifts

411 for Southern Elephant Seals, but it did not accommodate cyclic-patterns discernible during the
412 first years in some individuals (Figure S6). The broken-stick model lumped these cycles into a
413 residual variance which was larger in early life compared to late life.

414 **5 Conclusions**

415 Carbon and nitrogen stable isotope analyses are a powerful technique to peek into the ecology
416 of cryptic species: even a cursory glance at the plethora of studies using this technique cannot
417 fail to notice how often “stable isotopes revealed” biological surprises. The technique is hailed
418 as powerful, which it is even more so conditional on using statistical analyses specifically
419 designed to investigate a particular question (see for example Hénau *et al.* (2011)). Here, we
420 presented a hierarchical model to investigate individual patterns of ontogenetic shifts in
421 foraging habitat and trophic level (Werner & Gilliam, 1984). The most important aspect of the
422 model is not the specification of the mean response, which can readily be modified to conform
423 to the biology of the studied species, but of the covariance structure. The methodology we
424 outlined can be useful for researchers interested in drawing inferences at the individual level
425 (Cooch *et al.*, 2002; Semmens *et al.*, 2009). Bayesian methods allow to fit with relative ease
426 complex models, and thereby to accommodate the (usually complex) structure of ecological
427 data (Ellison, 2004; Clark, 2005). This move towards Bayesian methods is not confined to
428 ecology (Link & Barker, 2009; O’Hara *et al.*, 2008) or even the biological sciences (Treier &
429 Jackman, 2008; Wainer, 2010). Rather, it stems for a growing realization that uncertainties need
430 to be quantified and to flow freely across different levels of an analysis to avoid overconfident
431 claims. As more data become available, more complex models can also be fit to refine our
432 knowledge (Gelman & Shalizi, 2010). The modelling approach outlined here can be further
433 extended to incorporate, for example, a survival analysis (Guo & Carlin, 2004; Horrocks & van
434 Den Heuvel, 2009; Vonesh *et al.*, 2006) of Southern Elephant Seals to assess the life-history

⁴³⁵ consequences of a foraging strategy; thereby harnessing the power of stable isotope analyses.

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7 Tables

Model	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
8x8	0.85	0.73
2x4x4	0.84	0.69
Null	0.69	0.58

Table 1: Posterior Predictive Checks. The statistic considered is the range of isotopic values and the reported p_{values} are the probability that the predicted range exceeds the observed one. The percentage of individuals with a $0.1 < p_{value} < 0.9$ is reported for both carbon and nitrogen isotopic time-series. Broken-stick models decreased the proportion of individuals with extreme p_{values} : a broken-stick model was appropriate for most individuals. There was however little support for an increase in covariance complexity: overall changes in $\delta^{13}\text{C}$ were not correlated with changes in $\delta^{15}\text{N}$.

Parameter	$\delta^{13}C$			$\delta^{15}N$			Unit
	2.5%	Mean	97.5%	2.5%	Mean	97.5%	
$\sigma_{\epsilon,1}$	0.75	0.81	0.86	0.46	0.52	0.57	‰
$\sigma_{\epsilon,2}$	0.29	0.32	0.35	0.33	0.36	0.39	‰
α_1	-18.4	-18.0	-17.6	11.9	12.1	12.3	‰
α_2	0.01	0.21	0.43	-0.79	-0.46	-0.13	‰ per year
α_4	-0.42	-0.24	-0.08	0.11	0.20	0.30	‰ per year
K^δ	2.2	3.2	4.2	1.3	1.9	2.4	years

Table 2: Estimated marginals from a broken-stick model fit to the Southern Elephant Seal data. $\sigma_{\epsilon,1}$ and $\sigma_{\epsilon,2}$ are respectively the residual standard deviations before and after the shift; α_1 and K^δ the isotopic value and age at the shift respectively, and α_2 and α_4 the slopes before and after the shift respectively.

Variance	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			Interpretation
	2.5%	Median	97.5%	2.5%	Median	97.5%	
α_1	1.81	2.88	4.08	0.46	0.72	1.03	Value at Shift
K^δ	1.13	1.56	2.29	1.27	1.60	2.17	Age at Shift
α_2	0.18	0.31	0.49	0.19	0.48	0.91	Slope before
α_4	0.03	0.20	0.41	0.04	0.08	0.13	Slope after

Table 3: Estimated individual-level variances in all 4 parameters governing the broken-stick model fit the Southern Elephant Seal data. Medians are reported instead of means because some posterior distributions were slightly asymmetric.

8 Figure Captions

Figure 1: Covariance matrix for a joint broken-stick model of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Light gray squares symbolize free parameters to estimate from the data, whereas squares left blank represent parameters with no biological interpretation that are thus constrained to 0. Estimated mean correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ parameters for the Southern Elephant Seal example are shown below the diagonal.

Figure 2: Broken-stick model fitted to 4 individual time-series of isotopic measurements. Each row corresponds to a different individual. $\delta^{13}\text{C}$ ($\delta^{15}\text{N}$) profiles are depicted on the left (right) panel. p_{values} of the posterior predictive check are reported on the graph. A p_{value} close to 0.5 signals a good-fit.

Figure 3: Assessing the fit of the selected model (2x4x4). Distributions of individual-level concordance coefficients, r_c are reported for both $\delta^{13}\text{C}$ (x-axis) and $\delta^{15}\text{N}$ (y-axis) values.

706 **9 Figures**

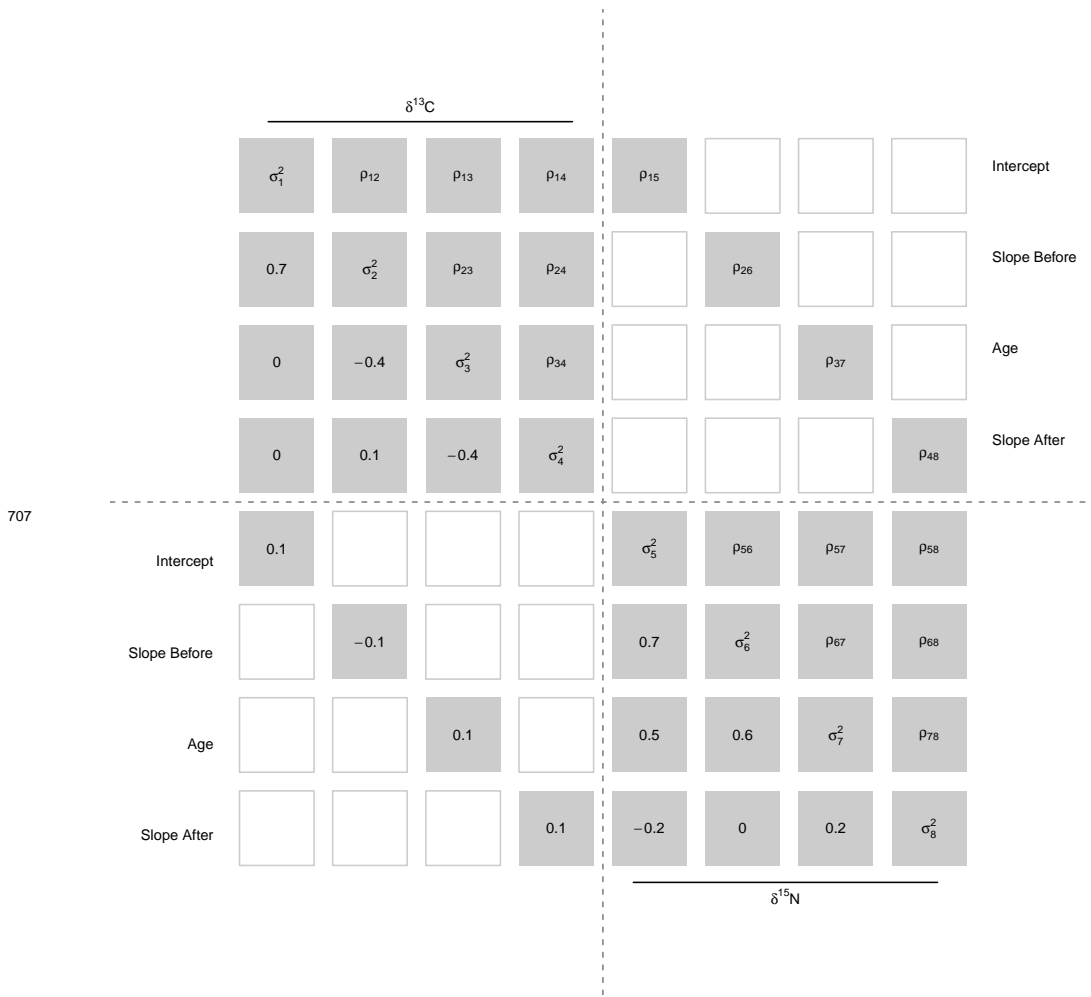
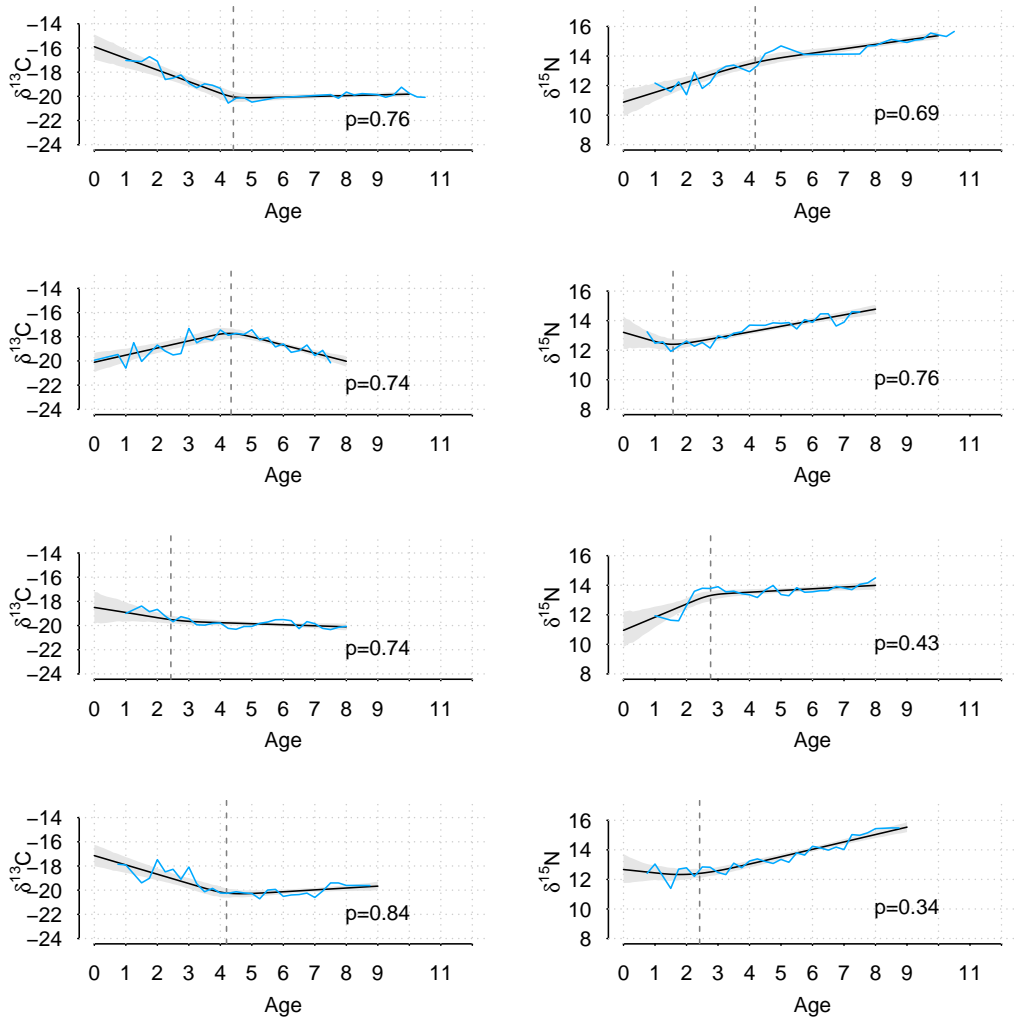


Figure 1

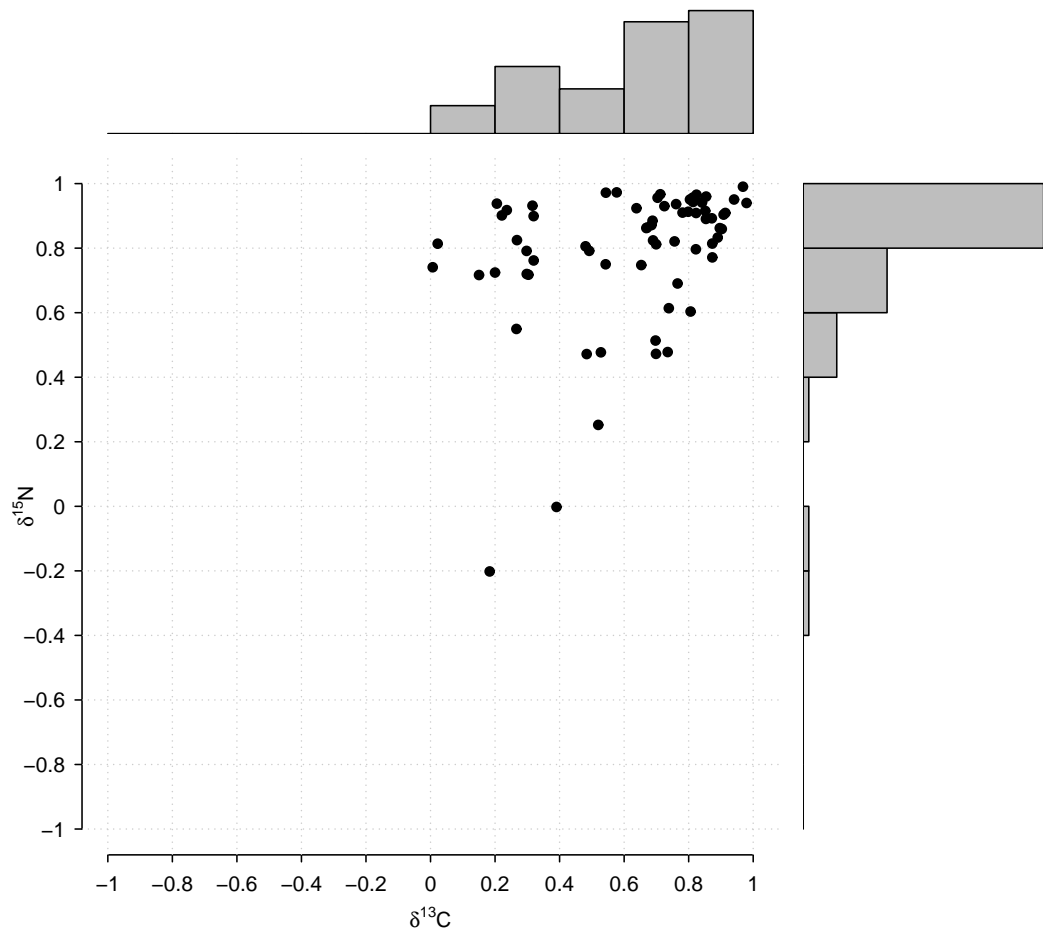


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Figure 2

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Figure 3