

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

4 Matthieu Authier<sup>1,2,6</sup>, Céline Martin<sup>3</sup>, Aurore Ponchon<sup>3,4</sup>, Stephanie  
5 Steelandt<sup>3,5</sup>, Ilham Bentaleb<sup>3</sup>, and Christophe Guinet<sup>1</sup>

6 <sup>1</sup>Centre d'Études Biologiques de Chizé, UPR 1934 du CNRS, 79 360  
7 Villiers-en-Bois

8 <sup>2</sup>École Doctorale Sciences pour l'Environnement Gay Lussac-Université de  
9 Poitiers

10 <sup>3</sup>Institut des Sciences de l'Évolution, UMR 5554 du CNRS, Place E.Bataillon  
11 Bât. 22 / 3e / CC061, 34095 Montpellier Cedex 5

12 <sup>4</sup>Centre d'Écologie Fonctionnelle et Évolutive, UMR 5175 du CNRS, 1919  
13 Route de Mende, F34293 Montpellier Cedex 5

14 <sup>5</sup>Centre d'Études Nordiques, Université de Laval, 2405 rue de la Terrasse,  
15 Québec, Canada G1V0A6

16 <sup>6</sup>authier@cebc.cnrs.fr

17 September 22, 2011

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  $^{14}\text{N}$  is preferentially excreted and the heavier  $^{15}\text{N}$  is preferentially retained, a phenomenon  
59 known as fractionation (Fry, 2006). This differential reactivity results in a predictable  
60 enrichment of the ratio of  $^{15}\text{N}$  to  $^{14}\text{N}$  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  $j^{\text{th}}$  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  $j^{\text{th}}$  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  $j^{\text{th}}$  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  $8 \times 8$   
 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  $3 \times 3$  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  $\Gamma$  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 ( $\Gamma$ ) 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 ( $\alpha_1$ ,  $\alpha_2$  and  $\alpha_4$ ) 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  $\alpha_3$ , 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  $\Gamma$ , 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 ( $\mathbf{T}_{\text{obs}}$ ) to its predicted values  
199 ( $\mathbf{T}_{\text{rep}}$ ) and compute a  $p_{\text{value}}$ :

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

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  $\leq 0$  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  $\varepsilon_i$  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 Micromill<sup>TM</sup> 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  $\delta$  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  $\approx 0.1$  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

<sup>435</sup> consequences of a foraging strategy; thereby harnessing the power of stable isotope analyses.

## 6 Acknowledgements

We would like to thank all volunteers who helped collecting teeth from dead animals found on îles Kerguelen. We thank the Museum National d'Histoire Naturelle (Paris) for kindly providing teeth collected before the population crash. We thank Hubert Vonhof and Els Ufkes for discussing the results. We are also indebted to Christophe Barbraud, Emmanuelle Cam, Luca Börger, two anonymous reviewers and the associate editor for helpful and constructive comments that greatly improved the manuscript. This study is part of a national research program (no. 109, H. Weimerskirch and the observatory *Mammifères Explorateurs du Milieu Océanique*, MEMO SOERE CTD 02) supported by the French Polar Institute (*Institut Paul Emile Victor*, IPEV). The *Territoire des Terres Australes et Antarctiques Françaises* (TAAF), the *TOTAL* Foundation and ANR-VMC 07 IPSOS-SEAL program contributed to this study. The ethics committee of the French Polar Institute (IPEV) approved this study. All animals in this study were cared for in accordance with its guidelines.

## References

- 449  
450 Ambrose, S. (1990) Preparation and Characterization of Bone and Tooth Collagen for Isotopic  
451 Analysis. *Journal of Archaeological Science*, **17**, 431–451.
- 452 Authier, M., Delord, K. & Guinet, C. (2011) Population Trends of Female Elephant Seals  
453 Breeding on the Courbet Peninsula, îles kerguelen. *Polar Biology*, **34**(3), 319–328, doi:  
454 10.1007/s00300-010-0881-1.
- 455 Bailleul, F., Authier, M., Ducatez, S., Roquet, F., Charassin, J.B., Cherel, Y. & Guinet, C.  
456 (2010) Looking at the Unseen: Combining Bio-logging and Stable Isotopes to Reveal a  
457 Shift in the Ecological Niche of a Deep-Diving Predator. *Ecography*, **33**(4), 709–719, doi:  
458 10.1111/j.16000-0587.2009.06034.x.
- 459 Barnard, J., McCulloch, R. & Meng, X. (2000) Modeling Covariance Matrices in Terms of  
460 Standard Deviations and Correlations, with Application to Shrinkage. *Statistica Sinica*, **10**,  
461 1281–1311.
- 462 Barnett, A., Koper, N., Dobson, A., Schmiegelow, F. & Manseau, M. (2010) Using Information  
463 Criteria to Select the Correct Variance-Covariance Structure for Longitudinal Data in Ecology.  
464 *Methods in Ecology and Evolution*, **1**, 15–24, doi:10.1111/j.2041.201X.2009.00009.x.
- 465 Beckage, B., Joseph, L., Belisle, P., Wolfson, D.B. & Platt, W.J. (2007) Bayesian Change-Point  
466 Analyses in Ecology. *New Phytologist*, **174**, 456–467, doi:10.1111/j.1469-8137.2007.01991.x.
- 467 Bellera, C., Hanley, J., Joseph, L. & Albertsen, P. (2008) Hierarchical Changepoint Models  
468 for Biochemical Markers Illustrated by Tracking Postradiotherapy Prostate-Specific Antigen  
469 Series in Men with Prostate Cancer. *Annals of Epidemiology*, **18**(4), 270–282, doi:10.1016/j.  
470 annepidem.2007.10.006.
- 471 Bentaleb, I., Fontugne, M., Descolas-Gros, C., Girardin, C., Mariotti, A., Pierre, C., Brunet,

- 472 C. & Poisson, A. (1998) Carbon Isotopic Fractionation by Phytoplankton in the Southern In-  
473 dian Ocean: Relationship between  $\delta^{13}\text{C}$  of Particulate Organic Carbon and Dissolved Carbon  
474 Dioxide. *Journal of Marine Systems*, **17**, 39–58, doi:10.1534/genetics.110.119305.
- 475 Berkhof, J., van Mechelen, I. & Gelman, A. (2003) A Bayesian Approach to the Selection and  
476 Testing of Mixture Models. *Statistica Sinica*, **13**, 423–442.
- 477 Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charassin, J.B., Roquet, F., Meredith,  
478 M., Thorpe, S., Tremblay, Y., McDonald, B., Park, Y.H., Rintoul, S., Bindoff, N., Goebel,  
479 M., Crocker, D., Lovell, P., Nicholson, J., Monks, F. & Fedak, M. (2007) Variations in Be-  
480 haviour and Condition of a Southern Ocean Top Predator in Relation to *in situ* Oceanographic  
481 Conditions. *Proceedings of the National Academy of Sciences*, **104**(34), 13705–13710.
- 482 Bradshaw, C., Hindell, M., Sumner, M. & Michael, K. (2004) Loyalty Pays: Potential Life  
483 History Consequences of Fidelity to Marine Foraging Regions by Southern Elephant Seals.  
484 *Animal Behaviour*, **68**, 1349–1360, doi:10.1016/j.anbehav.2003.12.013.
- 485 Brodie, C., Leng, M., Casford, J., Kendrick, C., Lloyd, J., Yongqiang, Z. & Bird, M. (2011) Evi-  
486 dence for Bias in C and N Concentrations and  $\delta^{13}\text{C}$  Composition of Terrestrial and Aquatic Or-  
487 ganic Materials Due to Pre-Analysis Acid Preparation Methods. *Chemical Geology*, **282**(3-4),  
488 67–83, doi:DOI:10.1016/j.chemgeo.2011.01.007, URL [http://www.sciencedirect.com/  
489 science/article/pii/S0009254111000222](http://www.sciencedirect.com/science/article/pii/S0009254111000222).
- 490 Budden, M., Havadas, P., Hoffman, L. & Pretz, C. (2007) Generating Valid  $4 \times 4$  Correlation  
491 Matrices. *Applied Mathematics E-Notes*, **7**, 53–59.
- 492 Carleton, S., Kelly, L., Anderson-Sprecher, R. & Martínez del Rio, C. (2008) Should We Use  
493 One-, or Multi-Compartment Models to Describe  $^{13}\text{C}$  Incorporation Into Animal Tissues?  
494 *Rapid Communications in Mass Spectrometry*, **22**, 3008–3014.

- 495 Carleton, S. & Martínez del Rio, C. (2005) The Effect of Cold-Induced Increased Metabolic Rate  
496 on the Rate of  $^{13}\text{C}$  and  $^{15}\text{N}$  Incorporation in House Sparrows (*Passer domesticus*). *Oecologia*,  
497 **144**, 226–232, doi:10.1007/s00442-005-0066-8.
- 498 Chen, Z. & Dunson, D. (2003) Random Effects Selection in Linear Mixed Models. *Biometrics*,  
499 **59**(4), 762–769.
- 500 ChereI, Y. & Hobson, K. (2007) Geographical Variation in the Carbon Stable Isotope Signa-  
501 tures of Marine Predators: a Tool to Investigate Their Foraging Areas in the Southern Ocean.  
502 *Marine Ecology Progress Series*, **329**, 281–287.
- 503 Clark, J. (2005) Why Environmental Scientists are Becoming Bayesians. *Ecology Letters*, **8**,  
504 2–14.
- 505 Cooch, E., Cam, E. & Link, W. (2002) Occam's Shadow: Levels of Analysis in Evolutionary-  
506 Ecology – Where to Next? *Journal of Applied Statistics*, **29**(1 & 4), 19–48, doi:10.1080/  
507 02664760120108421.
- 508 Cowles, M. & Carlin, B. (1996) Markov Chain Monte Carlo Convergence Diagnostics: a Com-  
509 parative Review. *Journal of the American Statistical Association*, **91**(434), 883–904.
- 510 Da-Silva, C., Gomes, A., Martins, E., Bonato, V. & dos Reis, S. (2008) A Bayesian Change-  
511 Point Model for Describing Partial Semelparity of a Neotropical Didelphid Marsupial. *Review*  
512 *of Brazilian Biometry*, **26**(4), 31–44.
- 513 Drago, M., Cardona, L., Crespo, E. & Aguilar, A. (2009) Ontogenic Dietary Changes in South  
514 American Sea Lions. *Journal of Zoology*, **279**, 251–261, doi:10.1111/j.1469-7998.2009.00613.  
515 X.
- 516 Ellison, A. (2004) Bayesian Inference in Ecology. *Ecology Letters*, **7**, 509–520.

- 517 Estrada, J., Rice, A., Natanson, L. & Skomal, G. (2006) Use of Isotopic Analysis of Vertebrae  
 518 in Reconstructing Ontogenetic Feeding Ecology in White Sharks. *Ecology*, **87**(4), 829–834.
- 519 France, R. (1995)  $^{13}$ carbon Enrichment in Benthic Compared to Planktonic Algae: Foodweb  
 520 Implications. *Marine Ecology Progress Series*, **124**, 307–312.
- 521 Fry, B. (2006) *Stable Isotope Ecology*, 1st edn. Springer.
- 522 Gelman, A. (2006) Prior Distributions for Variance Parameters in Hierarchical Models (comment  
 523 on Article by Browne and Draper). *Bayesian Analysis*, **1**(3), 515–534.
- 524 Gelman, A., Jakulin, A., Grazia Pittau, M. & Su, Y.S. (2008) A Weakly Informative Default  
 525 Prior Distribution for Logistic and Other Regression Models. *The Annals of Applied Statistics*,  
 526 **2**(4), 1360–1383.
- 527 Gelman, A., Meng, X.L. & Stern, H. (1996) Posterior Predictive Assessment of Model Fitness  
 528 via Realized Discrepancies. *Statistica Sinica*, **6**, 733–807.
- 529 Gelman, A. & Shalizi, C. (2010) Philosophy and the Practice of Bayesian Statistics. *Working*  
 530 *paper*, Department of Statistics and Department of Political Science, Columbia University,  
 531 URL [http://www.stat.columbia.edu/~gelman/research/unpublished/philosophy.](http://www.stat.columbia.edu/~gelman/research/unpublished/philosophy.pdf)  
 532 pdf.
- 533 Ghosh, P. & Vaida, F. (2007) Random Change-point Modelling of HIV Immunologic Responses.  
 534 *Statistics in Medicine*, **26**, 2074–2087, doi:10.1002/sim.2671.
- 535 Graham, B., Grubbs, D., Holland, K. & Popp, B. (2007) A Rapid Ontogenetic Shift in  
 536 the Diet of Juvenile Yellowfin Tuna from Hawaii. *Marine Biology*, **150**, 647–658, doi:  
 537 10.1007/s00227-006-0360-y.
- 538 Graham, M. (2001) Statistical Significance versus Fit: Estimating the Importance of Individual  
 539 Factors in Ecological Analysis of Variance. *Oikos*, **93**(3), 505–513.

- 540 Guo, X. & Carlin, B. (2004) Separate and Joint Modeling of Longitudinal and Event Time  
 541 Data Using Standard Computer Packages. *The American Statistician*, **58**(1), 1–9, doi:10.1198/  
 542 0003130042854.
- 543 Hall, C., Lipton, R., Sliwinski, M. & Stewart, W. (2000) A Change Point Model for Estimating  
 544 the Onset of Cognitive Decline in Preclinical Alzheimer’s Disease. *Statistics in Medicine*, **19**,  
 545 1555–1566.
- 546 Hebblewhite, M. & Haydon, D. (2010) Distinguishing Technology from Biology: a Critical  
 547 Review of the Use of GPS Telemetry Data in Ecology. *Philosophical Transactions of the*  
 548 *Royal Society London series B*, **365**, 2303–2312, doi:10.1098/rstb.2010.0087.
- 549 Hénaux, V., Powell, L., Hobson, K., Nielsen, C. & LaRue, M. (2011) Tracking Large Carnivore  
 550 Dispersal using Isotopic Clues in Claws: an Application to Cougars across the Great Plains.  
 551 *Methods in Ecology and Evolution*, doi:10.1111/j.2041-210X.2011.00107.x.
- 552 Hobson, K., Piatt, J. & Pitocchelli, J. (1994) Using Stable Isotopes to Determine Seabird Trophic  
 553 Relationships. *Journal of Animal Ecology*, **63**(4), 786–798.
- 554 Hobson, K. & Sease, J. (1998) Stable Isotope Analyses of Tooth Annuli Reveal Temporal Dietary  
 555 Records: an Example Using Steller Sea Lions. *Marine Mammal Science*, **14**(1), 116–129.
- 556 Hobson, K., Wassenaar, L. & Taylor, O. (1999) Stable Isotope ( $\delta d$  and  $\delta^{13}c$ ) are Geographic  
 557 Indicators of Natal Origins of Monarch Butterflies in Eastern North America. *Oecologia*, **120**,  
 558 397–404.
- 559 Horrocks, J. & van Den Heuvel, M. (2009) Prediction of Pregnancy: a Joint Model for Longitu-  
 560 dinal and Binary Data. *Bayesian Analysis*, **4**(3), 523–538, doi:10.1214/09-BA419.
- 561 Huang, S., Meng, S. & Yang, Y. (2010) Assessing the Goodness of Fit of Forest Models Es-

- 562 timated by Nonlinear Mixed-Model methods. *Canadian Journal of Forestry Research*, **39**,  
563 2418–2436, doi:10.1139/X09-140.
- 564 Jaeger, A., Lecomte, V., Weimerskirch, H., Richard, P. & Cherel, Y. (2010) Seabird Satellite  
565 Tracking Validates the Use of Latitudinal Isoscapes to Depict Predators' Foraging Areas in  
566 the Southern Ocean. *Rapid Communication in Mass Spectrophotometry*, **24**, 3456–3460, doi:  
567 10.1002/rcm.4792.
- 568 Jordan, M. (2011) What Are the Open Problems in Bayesian Statistics? *The ISBA Bulletin*, **18**(1),  
569 1–4, URL [www.bayesian.org](http://www.bayesian.org).
- 570 Kelly, J. (2000) Stable Isotopes of Carbon and Nitrogen in the Study of Avian and Mammalian  
571 Trophic Ecology. *Canadian Journal of Zoology*, **78**, 1–27.
- 572 Laws, R. (1952) A New Method of Age Determination for Mammals. *Nature*, **169**(4310), 972–  
573 974.
- 574 Laws, R. (1993) *Antarctic Seals. Research Methods and Techniques*. Cambridge University  
575 Press, chap. 11 - Age Determination. pp. 199–227.
- 576 Link, W. & Barker, R. (2009) *Bayesian Inference with Ecological Applications*. Associated Press,  
577 chap. Individual Fitness. pp. 271–286.
- 578 Louis, T. & Zeger, S. (2009) Effective Communication of Standard Error and Confidence Inter-  
579 val. *Biostatistics*, **10**(1), 1–2.
- 580 Lunn, W., A., T., Best, N. & Spiegelhalter, D. (2000) *WinBUGS - a Bayesian Modelling Frame-*  
581 *work: Concept, Structure, and Extensibility. Statistics and Computing*, **10**, 325–337.
- 582 MacKenzie, K., Palmer, R., Moore, A., Ibbotson, A., Beaumont, W., Poulter, D. & Trueman, C.  
583 (2011) Locations of Marine Animals Revealed by Carbon Isotopes. *Nature Scientific Reports*,  
584 **1**(21), 1–6, doi:10.1038/srep00021.

- 585 Martin, C., Bentaleb, I., Steedlandt, S. & Guinet, C. (2011) Stable Carbon and Nitrogen Isotope  
586 Variations in Canine Dentin Growth Layers of Kerguelen Southern Elephant Seals. *Marine*  
587 *Ecology Progress Series*, **XX**, accepted.
- 588 Martínez Abraín, A. (2010) Statistical Significance and Biological Relevance: a Call for a more  
589 Cautious Interpretation of Results in Ecology. *Acta Oecologica*, **34**, 9–11, doi:10.1016/j.actao.  
590 02.004.
- 591 Matthews, B. & Mazunder, A. (2004) A Critical Evaluation of Intrapopulation Variation of  $\delta^{13}\text{C}$   
592 and Isotopic Evidence of Individual Specialization. *Oecologia*, **140**, 361–371.
- 593 McIntyre, T., de Bruyn, P., Ansorge, I., Bester, M., Bornemann, H., Plötz, J. & Tosh, C. (2010)  
594 A Lifetime at Depth: Vertical Distribution of Southern Elephant Seals in the Water Column.  
595 *Polar Biology*, **33**(8), 1037–1048, doi:10.1007/s00300-010-0782-3.
- 596 McLaren, I. (1993) Growth in Pinnipeds. *Biological Reviews*, **68**, 1–79.
- 597 Mendes, S., Newton, J., Reid, R., Zuur, A. & Pierce, G. (2007) Stable Carbon and Nitrogen  
598 Isotope Ratio Profiling of Sperm Whale Teeth Reveals Ontogenetic Movements and Trophic  
599 Ecology. *Oecologia*, **151**, 605–615.
- 600 Moyes, A. & Doidge, D. (1984) Composition of the Mineral Phase of Dentin in Southern Ele-  
601 phant Seal and Antarctic Fur Seal Teeth. *British Antarctic Survey Bulletin*, **64**, 81–84.
- 602 Muniz-Terrera, G., van den Hout, A. & Matthews, F. (2011) Random Change Point Models:  
603 Investigating Cognitive Decline in the Presence of Missing Data. *Statistics in Medicine*, **30**,  
604 599–610, doi:10.1002/sim.4127.
- 605 Newsome, S., Etnier, M., Monson, D. & Fogel, M. (2009) Retrospective Characterization of  
606 Ontogenic Shifts in Killer Whale Diets via  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  Analysis of Teeth. *Marine Ecology*  
607 *Progress Series*, **374**, 229–242, doi:10.3354/meps07747.

- 608 Newsome, S., Martinìnez del Rio, C., Bearhop, S. & Phillips, D. (2007) A Niche for Isotopic  
609 Ecology. *Frontiers in Ecology and the Environment*, **5**(8), 429–436, doi:10.1890/060150.01.
- 610 O’Hara, R., Cano, J., Ovaskainen, O., Teplitsky, C. & Alho, J. (2008) Bayesian Approaches in  
611 Evolutionary Quantitative Genetics. *Journal of Evolutionary Biology*, **21**, 949–957.
- 612 Peterson, P. & Fry, B. (1987) Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology  
613 and Systematics*, **18**, 293–320.
- 614 Petrovskii, S., Mashanova, A. & Jansen, V. (2011) Variation in Individual Walking Behavior  
615 Creates the Impression of a Lévy Flight. *Proceedings of the National Academy of Sciences  
616 USA*, **108**(21), 8704–8707, doi:10.1073/pnas.1015208108.
- 617 Phillips, D. & Eldridge, P. (2006) Estimating the Timing of Diet Shifts Using Stable Isotopes.  
618 *Oecologia*, **147**, 195–203, doi:10.1007/s00442-005-0292-0.
- 619 Platt, J. (1964) Strong Inference. *Science*, **146**(3642), 347–353.
- 620 Plummer, M., Best, N., Cowles, K. & Vines, K. (2008) *coda: Output Analysis and Diagnostics  
621 for MCMC*. R package version 0.13-2.
- 622 Polischuk, S., Hobson, K. & Ramsay, M. (2001) Use of Stable-Carbon and -Nitrogen Isotopes  
623 to Assess Weaning and Fasting in Female Polar Bears and their Cubs. *Canadian Journal of  
624 Zoology*, **79**, 499–511, doi:10.1139/cjz-79-3-499.
- 625 Popa-Lisseanu, A., Delgado-Huertas, A., Forero, M., Rodríguez, A., Arlettaz, R. & Ibáñez, C.  
626 (2007) Bats’ Conquest of a Formidable Foraging Niche: the Myriads of Nocturnally Migrating  
627 Songbirds. *PLoS One*, **2**(2), e205, doi:10.1371/journal.pone.0000205.g002.
- 628 Post, D. (2002) Using Stable Isotopes to Estimate Trophic Position: Models, Methods and As-  
629 sumptions. *Ecology*, **83**, 703–718.

- 630 Post, D. (2003) Individual Variation in the Timing of Ontogenic Niche Shifts in Largemouth  
631 Bass. *Ecology*, **84**(5), 1298–1310.
- 632 Pourahmadi, M. (2007) Choleski Decompositions and Estimation of a Covariance Matrix: Or-  
633 thogonality of Variance-Correlation Parameters. *Biometrika*, **94**(4), 1006–1013, doi:10.1093/  
634 biomet/asm073.
- 635 Pourahmadi, M. (2010) Covariance Estimation: the GLM and Regularization Perspectives. *Tech-*  
636 *nical report*, URL [www.stat.tamu.edu/~pourahm/STATSCIR.pdf](http://www.stat.tamu.edu/~pourahm/STATSCIR.pdf).
- 637 R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R  
638 Foundation for Statistical Computing, Vienna, Austria, URL <http://www.R-project.org>.  
639 ISBN 3-900051-07-0.
- 640 Rau, G., Riebesell, U. & Wolf-Gladrow, D. (1996) A Model of Photosynthetic  $^{13}\text{C}$  Fraction-  
641 ation by Marine Phytoplankton based on Diffusive Molecular  $\text{CO}_2$  Uptake. *Marine Ecology*  
642 *Progress Series*, **133**, 275–285.
- 643 Rau, G., Sweeney, R. & Kaplan, I. (1982) Plankton  $\frac{^{13}\text{C}}{^{12}\text{C}}$  ratio Changes with Latitude: Differences  
644 between Northern and Southern Oceans. *Deep Sea Research Part I*, **29**(8A), 1035–1039.
- 645 Rau, G., Takahashi, T. & Des Marais, D. (1989) Latitudinal Variation in Plankton  $\delta^{13}\text{C}$ : Implica-  
646 tions for  $\text{CO}_2$  and Productivity in Past Oceans. *Nature*, **341**, 516–518.
- 647 Reich, K., Bjorndal, K. & Bolten, A. (2007) The "Lost Years" of Green Turtles: using Stable Iso-  
648 topes to Study Cryptic Lifestages. *Biology Letters*, **3**, 712–714, doi:10.1098/rsbl.2007.0394.
- 649 Schoeninger, M. & DeNiro, M. (1984) Nitrogen and Carbon Isotopic Composition of Bone Col-  
650 lagen from Marine and Terrestrial Animals. *Geochimica et Cosmochimica Acta*, **48**, 625–639.
- 651 Schulting, R., Blockley, S., Bocherens, H., Drucker, D. & Richards, M. (2008) Stable Carbon and  
652 Nitrogen Isotope Analysis on Human Remains from the Early Mesolithic Site of La Vergne

- 653 (Charente-Maritime, France). *Journal of Archeological Science*, **35**, 763–772, URL [10.1016/](https://doi.org/10.1016/j.jas.2007.06.008)  
654 [j.jas.2007.06.008](https://doi.org/10.1016/j.jas.2007.06.008).
- 655 Semmens, B., Ward, E., Moore, J. & Darimont, C. (2009) Quantifying Inter- and Intra-Population  
656 Niche Variability using Bayesian Hierarchical Stable Isotope Mixing Models. *PLoS One*, **4**(7),  
657 e6187.
- 658 Spiegelhalter, D., Best, T., Best, N. & Lunn, D. (2003) *WinBUGS User Manual version 1.4*. URL  
659 <http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>.
- 660 Spiegelhalter, D., Best, T., Carlin, B. & van der Linde, A. (2002) Bayesian Measures of Model  
661 Complexity and Fit (with Discussion). *Journal of the Royal Statistical Society Series B*, **64**,  
662 583–640.
- 663 Sturtz, S., Ligges, U. & Gelman, A. (2005) R2winbugs: a Package for Running *WinBUGS* from  
664 *R*. *Journal of Statistical Software*, **12**(3), 1–16, URL <http://www.jstatsoft.org>.
- 665 Thums, M., Bradshaw, C. & Hindell, M. (2011) *In-Situ* Measures of Foraging Success and Prey  
666 Encounter Reveals Marine Habitat-Dependent Search Strategies. *Ecology*, **92**, 1258–1270,  
667 doi:10.1890/09-1299.1.
- 668 Treier, S. & Jackman, S. (2008) Democracy as a Latent Variable. *American Journal of Political*  
669 *Science*, **52**(1), 201–217.
- 670 Trull, T. & Armand, L. (2001) Insight into Southern Ocean Carbon Export from the  $\delta^{13}C$  of  
671 Particles and Dissolved Inorganic Carbon using the SOIREE Iron Release Experiment. *Deep-*  
672 *Sea Research Part II*, **48**, 2655–2680.
- 673 Vanderklift, M. & Ponsard, S. (2003) Sources of Variation in Consumer-Diet  $\delta^{15}N$  Enrichment:  
674 a Meta-Analysis. *Oecologia*, **136**(2), 169–182, doi:10.1007/s00442-003-1270-z.

- 675 Vonesh, E., Chinchilli, V. & Pu, K. (1996) Goodness-of-fit in Generalized Nonlinear Mixed-  
676 Effects Models. *Biometrics*, **52**(2), 572–587.
- 677 Vonesh, E., Greene, T. & Schluchter, M. (2006) Shared Parameter Models for the Joint Analysis  
678 of Longitudinal Data and Event Time. *Statistics in Medicine*, **25**, 143–163, doi:10.1002/sim.  
679 2249.
- 680 Wainer, H. (2010) 14 Conversations About Three Things. *Journal of Educational and Be-  
681 havioural Statistics*, **35**(5), 5–25, doi:10.3102/1076998609355124.
- 682 Werner, E. & Gilliam, J. (1984) The Ontogenetic Niche and Species Interactions in Size Struc-  
683 tured Populations. *Annual Review of Ecology and Systematics*, **15**, 393–425.
- 684 West, J., Bowen, G., Cerling, T. & Ehleringer, J. (2006) Stable Isotopes as One of Nature’s  
685 Ecological Recorders. *Trends in Ecology and Evolution*, **21**(7), 408–414.
- 686 Wilske, J. & Arnbom, T. (1996) Seasonal Variation in Vitamin D Metabolites in Southern Ele-  
687 phant Seals (*Mirounga leonina*) Females at South Georgia. *Comparative Biochemistry and  
688 Physiology A*, **114**(1), 9–14.
- 689 Wolf, N., Carleton, S. & Martínez del Rio, C. (2009) Ten Years of Experimental Animal Isotopic  
690 Ecology. *Functional Ecology*, **23**, 17–26, doi:10.1111/j.1365-2435.2008.01529.x.

## 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	‰
$\alpha_1$	-18.4	-18.0	-17.6	11.9	12.1	12.3	‰
$\alpha_2$	0.01	0.21	0.43	-0.79	-0.46	-0.13	‰ per year
$\alpha_4$	-0.42	-0.24	-0.08	0.11	0.20	0.30	‰ per year
$K^\delta$	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;  $\alpha_1$  and  $K^\delta$  the isotopic value and age at the shift respectively, and  $\alpha_2$  and  $\alpha_4$  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%	
$\alpha_1$	1.81	2.88	4.08	0.46	0.72	1.03	Value at Shift
$K^\delta$	1.13	1.56	2.29	1.27	1.60	2.17	Age at Shift
$\alpha_2$	0.18	0.31	0.49	0.19	0.48	0.91	Slope before
$\alpha_4$	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.  $p_{\text{values}}$  of the posterior predictive check are reported on the graph. A  $p_{\text{value}}$  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**

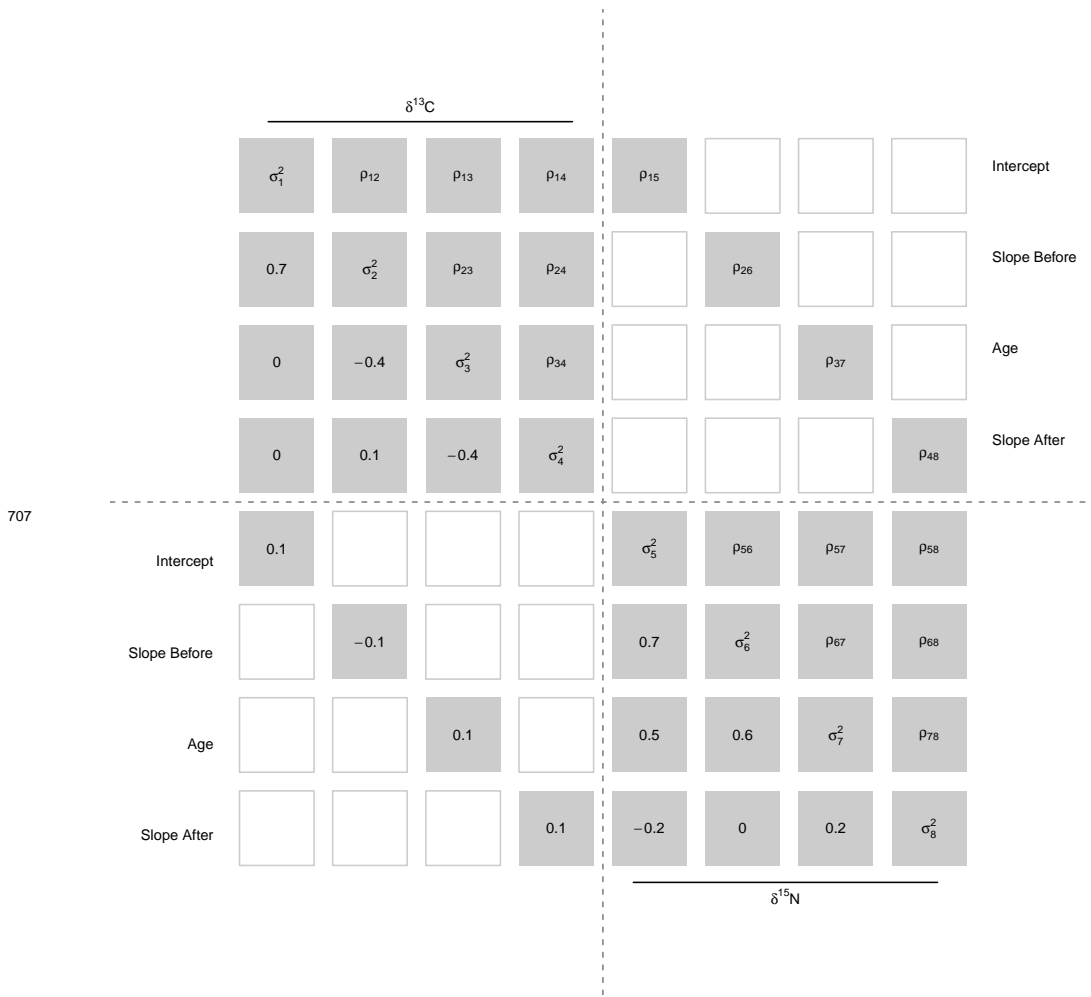
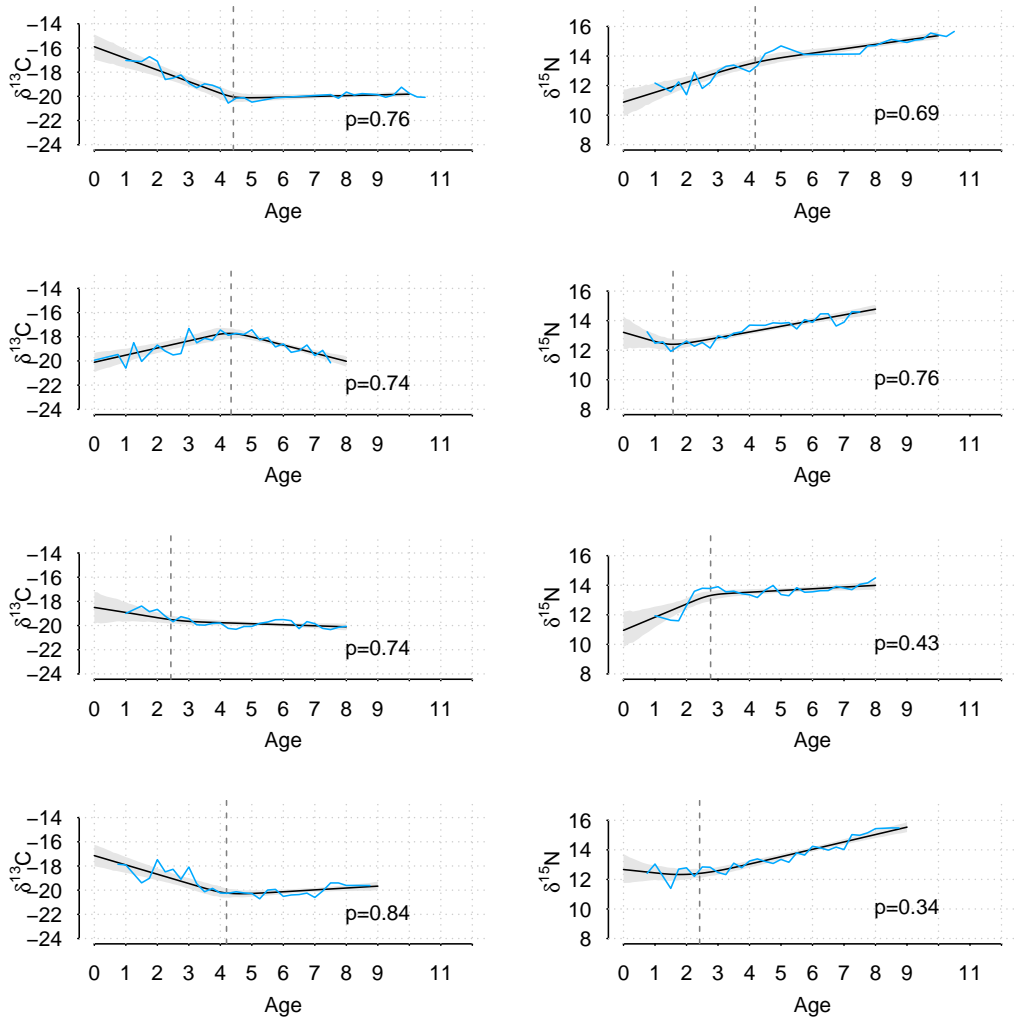


Figure 1

hal-00627200, version 1 - 30 Sep 2011

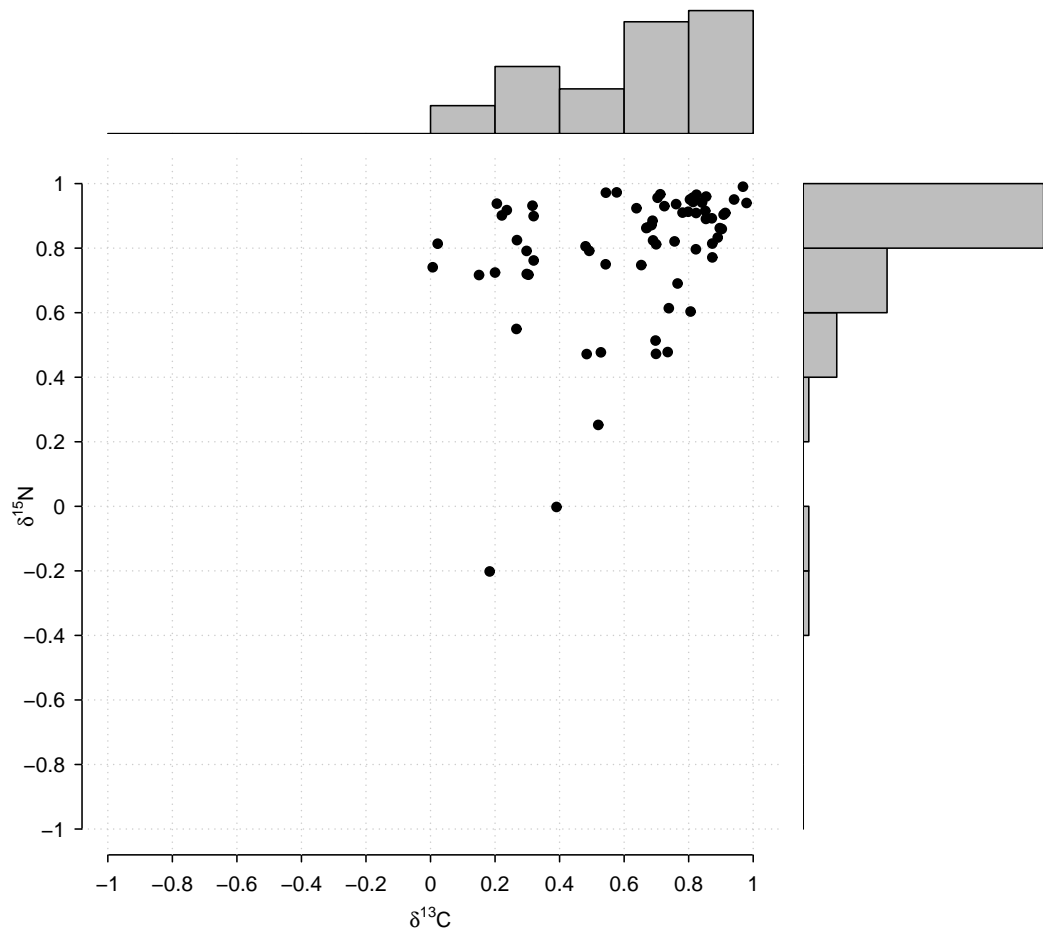


709

710

Figure 2

711



712

Figure 3