Mar Biol (2009) 156:1233–1240
DOI 10.1007/s00227-009-1165-6

ORIGINAL PAPER

Using carbon and nitrogen isotopic values of body feathers to infer inter- and intra-individual variations of seabird feeding ecology during moult

Audrey Jaeger · Pierrick Blanchard · Pierre Richard · Yves Cherel

Received: 9 September 2008 / Accepted: 16 February 2009 / Published online: 10 March 2009

Abstract To determine whether stable isotope measurements of body feathers can be used to investigate the isotopic niche of moulting (inter-nesting) adult seabirds, we examined the stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic composition of body feathers of breeding wandering albatrosses (*Diomedea exulans*) from Crozet Islands, southern Indian Ocean. First we showed that the isotopic composition of body feathers was not significantly different from that of wing feathers, being thus a safe alternative to flight feathers whose collection impairs the birds' flying ability. Second, we looked at the variances in δ^{13}C and δ^{15}N values resulting from the isotopic measurement of a single feather, four different feathers, and a pool of four feathers per bird, to delineate the best isotopic analytical procedure. A two-step protocol is proposed that allows investigating both the intra- and inter-individual components of the niche width of the species. In a first step, isotopic measurements on a single feather per bird are used to define isotopic specialist from isotopic generalist populations. In a second step and for generalist populations only, measurements on additional (three) feathers per bird are used to delineate type A from type B isotopic generalists (Bearhop et al. in J Anim Ecol 73:1007–1012, 2004). Third, from a biological point of view, our data showed different moulting isotopic niches for adult males and females, and also within female wandering albatrosses. Since the isotopic composition of body feathers in this species reflects that of wing feathers, our results suggest that, after validation, body feathers have the potential for investigating the foraging ecology of other Procellariiforms and seabirds during the poorly known inter-nesting period.

Communicated by S. Garthe.

A. Jaeger (✉) · Y. Cherel
Centre d'Etudes Biologiques de Chizé,
UPR 1934 du CNRS, 79360 Villiers-en-Bois, France
e-mail: jaeger@cebc.cnrs.fr

P. Blanchard
Laboratoire Evolution et Diversité Biologique,
UMR 5174 du CNRS, Université Paul Sabatier Toulouse III,
118 Route de Narbonne, 31062 Toulouse Cedex 9, France

P. Richard
Laboratoire Littoral, Environnement et Sociétés,
UMR 6250 du CNRS, Université de La Rochelle,
2 rue Olympe de Gouges, 17000 La Rochelle, France

Introduction

There is an increasing evidence that both environmental variability and human factors during the inter-nesting period shape population dynamics of seabirds (Barbraud and Weimerskirch 2003; Grosbois and Thompson 2005; Rolland et al. 2008). A major obstacle in identifying the underlying biological mechanisms is the lack of information on seabird distribution and ecology during the non-breeding season, when individuals migrate far from their breeding grounds. This is particularly relevant for the conservation of highly pelagic Procellariiforms (albatrosses and petrels), which are among the most threatened taxa of birds (BirdLife International 2008). The stable isotopic analysis of their feathers has become a powerful method to investigate the inter-nesting foraging ecology of adult seabirds (Cherel et al. 2000, 2006; Quillfeldt et al. 2005). Since feather keratin is metabolically inert after synthesis, the isotopic composition of feathers reflects diet during moult (Hobson and Clark 1992; Bearhop et al. 2002), which occurs primarily during the non-breeding period (Warham 1990, 1996; Bridge 2006). Stable carbon (^{13}C/^{12}C, δ^{13}C)

and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) isotope ratios of consumers define their isotopic niche along two dimensions, with $\delta^{13}C$ and $\delta^{15}N$ values reflecting the consumers' foraging habitat and trophic position, respectively (Newsome et al. 2007). Despite the increasing use of the stable isotope method on seabird feathers over recent years, only a few studies investigated the extent to which isotopic signatures vary among and within feather types and no work looked at their consequences on isotopic interpretations.

Most isotopic studies on seabird feathers focused on wing (i.e. primaries and secondaries) and body feathers (Thompson and Furness 1995; Bearhop et al. 2000, Cherel et al. 2006). Wing feathers are sampled either on killed birds (Hebert et al. 2008), on opportunistically collected dead birds (Bearhop et al. 1999; Cherel et al. 2002; Davoren et al. 2002), or, more commonly, on live birds (Cherel et al. 2000, 2008; Hedd and Montevecchi 2006). In many cases, the killing of wild birds cannot be morally defensible, and sampling of wing feathers on live birds is questionable from an ethical point of view because of the resulting impairment of flying ability (Weimerskirch et al. 1995). Also, wing feathers from museum specimens are difficult to procure, while body feathers are generally more readily obtained (Thompson et al. 1995; Norris et al. 2007). Within this context, body feathers offer an alternative to the use of wing feathers. The chronology of body feather moult is often poorly understood, however, and few studies tested the $\delta^{13}C$ and $\delta^{15}N$ values of both body and wing feathers from the same individual seabird to validate their use (Thompson and Furness 1995; Becker et al. 2007).

Stable isotopes are also well suited to investigate the intra- and inter-individual components of niche width, with variance in δ-space among individuals being a useful proxy for niche width (Bearhop et al. 2004; Newsome et al. 2007). The total niche width (TNW) of a population can be partitioned into two components: the within (intra)-individual component (WIC) and the between (inter)-individual component (BIC), such that TNW = WIC + BIC (Bolnick et al. 2003). In most studies using body feathers (Thompson et al. 1995; Bearhop et al. 2000; Cherel et al. 2006), stable isotope measurements were performed on a homogenised pool of several feathers, thus integrating the individual feeding ecology across the entire moult cycle and blurring its spatio-temporal variations. This procedure focuses on the BIC, but not on the WIC component of TNW, while WIC has also important ecological, evolutionary and conservation implications (Bolnick et al. 2003).

The main goal of the present study was to test the use of body feathers of adult seabirds for investigating their foraging ecology during moult. We focused on two methodological considerations to recommend best practices, namely: (1) are the $\delta^{13}C$ and $\delta^{15}N$ values of body feathers identical to those of wing feathers? and (2) what is the appropriate feather sampling and analytical protocol to investigate inter- and intra-individual variations of the isotopic niche? We chose the wandering albatross *Diomedea exulans* as a seabird model because the species disperses widely during the non-breeding period, from tropical to Antarctic waters (Weimerskirch and Wilson 2000). The geographical range of moulting albatrosses therefore spans natural gradients and discontinuities in carbon isotopic composition of oceanic waters that are reflected in the isotopic signatures of seabird tissues (Quillfeldt et al. 2005; Cherel and Hobson 2007), thus potentially inducing large intra- and inter-individual variations in the feather $\delta^{13}C$ values of wandering albatrosses. We also looked at the isotopic niches of female and male wandering albatrosses, because they are known to differ in their feeding ecology, with females favouring foraging in warmer (northern) waters and males in colder (southern) waters (Weimerskirch et al. 1993, 1997; Weimerskirch and Wilson 2000). Since lower-plankton food bases tend to be enriched in ^{13}C relative to higher-latitude waters (François et al. 1993; Trull and Armand 2001), we expected higher feather $\delta^{13}C$ values in females than in males of wandering albatrosses.

Materials and methods

Field study was carried out during the wandering albatross 2003 incubation period (January–March) on Possession Island (46°30′S, 51°45′E), Crozet Archipelago, which is located in the south-western Indian Ocean. According to physical oceanography, the archipelago lies in the middle of the Polar Frontal Zone, between the Subantarctic Front in the north and the Polar Front in the south. The western Indian Ocean is marked by the strong confluence of the Subantarctic and Subtropical Fronts in the north of the archipelago, with subtropical waters being located north of this broad frontal structure (Park and Gambéroni 1997).

Wandering albatrosses are biennal breeders, with parents successful in rearing their single chick breeding in alternate years, while those failing during incubation or during the early stages of the chick-rearing period breeding again the next year (Tickell 1968). In albatrosses, including the wandering albatross (Weimerskirch 1991), all wing, body and tail moult has been at sea between nesting episodes (Warham 1990, 1996). Moult of wing feathers is a long-term process with up to three generations of feathers being present among the primaries (Warham 1990; Weimerskirch 1991). Data on moult of body feathers of Procellariiform seabirds are few, but contour feathers are replaced gradually over several months, and not all necessarily changed each year (Warham 1996).

Feathers were sampled from 23 breeding wandering albatrosses (11 females and 12 males). The tip of two

primaries from two generations (one brown old feather and one black newly moulted feather) and four whole body feathers (randomly sampled on the birds' back) were collected from each individual albatross. Prior to isotopic analysis, feathers were cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol solution following by two successive methanol rinses. Tips of primaries and whole body feathers were then air dried and cut into small fragments. Sub-samples were then weighed (from 0.3 to 0.4 mg) with a microbalance, packed in tin containers, and nitrogen and carbon isotope ratios were subsequently determined by a continuous flow mass spectrometer (Micromass Isoprime) coupled to an elemental analyser (Euro Vector EA 3024). Results are presented in the usual δ notation relative to PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors <0.15‰ and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Data were analyzed using Matlab (7.0), except generalized linear models (GLM) that were performed using Statistica (7.0). Values are mean ± SD.

Results

The isotopic signatures of body feathers and of old and new primaries are showed in Table 1. A generalized linear model with three types of feathers as explanatory variables and individuals as random variables indicated that there was no effect of feather types on $\delta^{13}C$ and $\delta^{15}N$ distributions ($P = 0.452$ and 0.216, respectively).

The isotopic composition of one body feather and of four (pooled or not) body feathers for each individual bird was measured to assess the wandering albatross niche width and its intra- and inter-individual components (following Bolnick et al. 2003), and to compare different analytical protocols (Table 1; Fig. 1). Using one body feather per bird, isotopic variances allowed calculating TNW that amounted to 0.8 and 0.7‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Using a pool of four body feathers per bird, isotopic variances allowed calculating BIC that amounted to 0.4 and 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Accordingly, repeatability (a measure describing the proportion of variance in a character that occurs among rather than within individuals; Lessells and Boag 1987) between four body feathers of each individual was low (0.3 and 0.4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively). Finally, the use of four (not pooled) body feathers per bird indicated that WIC amounted to 0.4‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

Using one randomly selected body feather per bird, females ($n = 11$) and males ($n = 12$) had significantly different $\delta^{13}C$ but not $\delta^{15}N$ values (two-sample t tests, $t = 3.60$ and 1.84, $P = 0.017$ and 0.080, respectively). Pooling the data from the four feathers for each bird and using the resulting average value per bird decreased variances (Table 1; Fig. 1), thus leading again to statistically significant sexual differences in $\delta^{13}C$ but not in $\delta^{15}N$ values ($t = 6.61$ and 1.72, $P < 0.0001$ and $P = 0.103$). Further analysis showed that female birds can be split into two distinct groups according to the isotopic signatures of their feathers (Table 1; Fig. 1). Indeed, three groups of birds were identified by a hierarchical clustering analysis (simple linkage method) using three variables (sex, and the average $\delta^{13}C$ and $\delta^{15}N$ values of four feathers per bird): females (groups 1 and 2), and males (group 3). The three groups segregated by both their $\delta^{13}C$ and $\delta^{15}N$ values (ANOVA, $F_{2,20} = 59.93$ and 19.47, both $P < 0.0001$) (Fig. 2, lower panel). Post hoc

Table 1 Feather $\delta^{13}C$ and $\delta^{15}N$ values of wandering albatross females and males from Crozet Islands

Feather type	Females			Males	Females and males
	Group 1 ($n = 5$)	Group 2 ($n = 6$)	All females ($n = 11$)	Group 3 ($n = 12$)	All birds ($n = 23$)
$\delta^{13}C$ (‰)					
Body feathers ($n = 4$ pooled feathers per bird)	−16.2 ± 0.2	−17.0 ± 0.2	−16.6 ± 0.4	−17.7 ± 0.3	−17.2 ± 0.7
Body feathers ($n = 1$ per bird)	−16.2 ± 0.4	−16.9 ± 0.5	−16.6 ± 0.6	−17.6 ± 0.8	−17.1 ± 0.9
New primaries ($n = 1$ per bird)	−16.7 ± 0.4	−16.9 ± 0.5	−16.9 ± 0.4	−17.4 ± 1.3	−17.2 ± 1.0
Old primaries ($n = 1$ per bird)	−16.9 ± 0.6	−17.6 ± 0.8	−17.2 ± 0.8	−17.9 ± 0.9	−17.6 ± 0.9
$\delta^{15}N$ (‰)					
Body feathers ($n = 4$ pooled feathers per bird)	16.5 ± 0.3	15.3 ± 0.4	15.9 ± 0.7	15.5 ± 0.4	15.6 ± 0.6
Body feathers ($n = 1$ per bird)	16.5 ± 0.5	15.4 ± 0.7	15.9 ± 0.8	15.4 ± 0.6	15.7 ± 0.8
New primaries ($n = 1$ per bird)	15.8 ± 0.9	14.9 ± 1.2	15.3 ± 1.1	15.9 ± 0.9	15.6 ± 1.1
Old primaries ($n = 1$ per bird)	16.1 ± 1.0	15.6 ± 0.9	15.8 ± 0.9	15.5 ± 0.6	15.7 ± 0.8

Values are mean ± SD

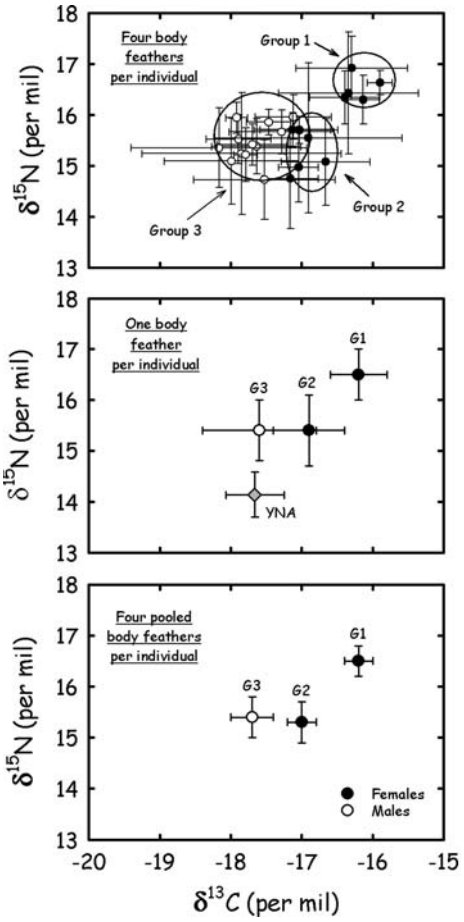

Fig. 1 Body feather δ^{13}C and δ^{15}N values of wandering albatross females and males from Crozet Islands. *Upper panel* mean values of 23 individuals with four body feathers per bird (for groups 1–3, see text); *medium panel* mean values of groups 1–3, with one randomly selected body feather per bird; *lower panel* mean values of groups 1–3, with four pooled body feathers per bird. The signature of chicks of yellow-nosed albatross (YNA) breeding at Amsterdam Island illustrates the δ^{13}C values of a species known to forage in subtropical waters (Pinaud et al. 2005). *G1* group 1, *G2* group 2, *G3* group 3. Values are mean ± SD

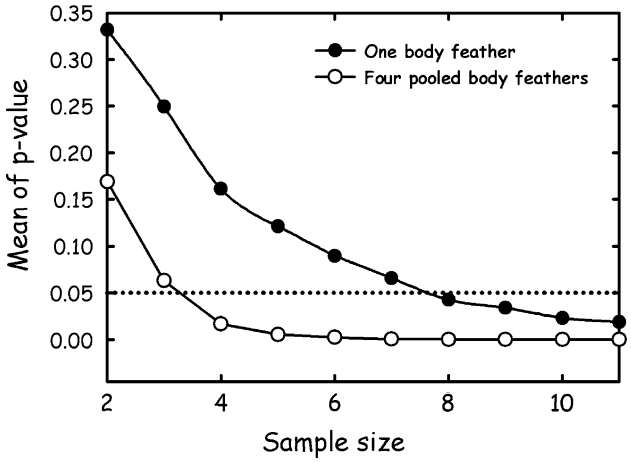

Fig. 2 Mean of *P* value of repetitive *t* tests versus sample size (number of individuals of wandering albatrosses taken randomly). Repetitive *t* tests for different sample sizes were performed on female and male δ^{13}C values of body feathers (δ^{13}C females − δ^{13}C males = 1.1‰), with either one body feather randomly selected per bird (*filled symbols*) or four pooled body feathers per bird (*open symbols*)

Tukey HSD multiple comparison tests indicated that the three groups had statistically different δ^{13}C values, and that δ^{15}N values differed between group 1 females and the two other groups. On the other hand, δ^{15}N values were not significantly different between group 2 females and group 3 males (statistics not shown).

Since variances in isotopic values were higher when using one body feather per individual than with a pool of body feathers, we modelled the minimum number of birds that must be sampled in the field to reach statistical significance ($P < 0.05$; two-sample *t* tests) between sexes. Males and females showed a carbon isotopic difference amounting to 1.1‰. Such a moderate value is higher than analytical errors (Jardine and Cunjak 2005; Mill et al. 2008) and within the range of enrichment factors in ^{13}C between consumers and their diet (McCutchan et al. 2003), being thus about the minimal difference that can be confidently interpreted in terms of biological variations among groups. We considered two different sampling and analytical schedules: firstly the isotopic value of one randomly selected body feather (among the four feathers available per bird), and secondly the average δ^{13}C value of the four body feathers of each bird (corresponding to the sampling of several body feathers in the field that were subsequently pooled before isotopic measurements). Repetitive *t* tests showed that the minimal sample sizes to significantly differentiate females from males were eight and four birds in each group when using the δ^{13}C values of one body feather and four pooled body feathers, respectively (Fig. 2).

Discussion

Body feathers, wing feathers and the non-breeding isotopic niche of albatrosses

The extent to which isotopic signatures vary among the feathers of an individual has clear implications for the use of feathers for isotope measurements. Feathers synthesized at different times of the moult cycle have been used to depict temporal changes in the isotopic niche of adult seabirds during the inter-nesting period and, in rare cases, between the non-breeding and breeding periods (Bearhop et al. 2000; Quillfeldt et al. 2005; Hedd and Montevecchi 2006). Few methodological studies compared the isotopic composition of different feather types from the same individual (Thompson and Furness 1995; Becker et al. 2007).

In a single experimental investigation on captive seabirds kept on a constant diet, no significant variation occurred in the δ^{15}N values of wing and body feathers, but, for an unclear reason, slightly lower δ^{13}C values were found in wing than in body feathers (Becker et al. 2007). As expected in wandering albatrosses, the isotopic composition of wing (both old and new feathers) and body feathers were not statistically different, which is in agreement with all wing, body and tail moult occurring at sea between nesting episodes in albatrosses (Warham 1990, 1996). Hence, body feathers provide a promising alternative to wing feathers to investigate the isotopic niche of moulting albatrosses.

A general prerequisite of the use of body feathers in seabirds is that the overall timing of body and wing feather replacements overlap. At large time scales, seabirds have a range of moulting patterns with wing and body feathers generally occurring during the inter-nesting period, but some species also moult during the breeding season (Warham 1996; Bridge 2006). Consequently, the use of body feathers should be validated for each particular species/group of species. At small time scales, it is likely that different feathers integrate the bird feeding ecology during different time periods because most body feathers do not grow in synchrony and feather types differ greatly in size (e.g. wing vs. body feathers). Within this context, the collection of several body feathers is probably the best non-destructive way to gain isotopic information on the plumage of live birds as a whole (Thompson and Furness 1995, present study). However, moult of body feathers is poorly understood relative to moult of wing feathers (e.g. primaries), thus underlining the need of additional work on the chronology of body feather replacement in seabirds, including Procellariiforms.

Body feathers and inter- and intra-individual niche variations

In seabirds, the usual procedure is to analyse a homogenized sample from several pooled body feathers for each individual (Thompson et al. 1995; Bearhop et al. 2000; Cherel et al. 2006). Indeed, it can be advantageous to analyse a single sample from feathers that is indicative of the isotopic signature of the plumage as a whole for a given individual (Thompson and Furness 1995). From a procedural perspective, this reduces both the time and cost of preparing and analysing samples. From a scientific perspective, the isotopic information of each individual is effectively integrated over the long term. The negative aspects of pooling feathers are, however, twofold. Firstly, a single average isotopic signature for the whole plumage cannot indicate possible distinct isotopic foraging areas during moult. In the extreme, an average isotopic signature can be useless, with no bird moulting in the corresponding isotopic area. Secondly, the within (intra)-individual component (WIC) of the total niche width (TNW) cannot be investigated by using a single average value for the whole plumage. Alternatively, as showed in the present study, measuring the δ^{13}C and δ^{15}N values of several body feathers for each individual allowed determining both WIC and the between (BIC) individual components of TNW for a given population (Bearhop et al. 2004). The procedure, however, increases the number of samples thus consuming both more time and money. A third possibility in analysing feathers is to use the isotopic composition of one body feather per bird only, thus decreasing the sample number. The procedure allows estimating TNW, but with no discrimination between the pooled BIC and WIC. Another disadvantage of analysing a single feather per individual is that variances in δ^{13}C and δ^{15}N values are higher than when working on a sample of pooled feathers per individual, thus partially blurring isotopic segregation between groups (Table 1; Fig. 1, middle and lower panels). Indeed, modelling showed that the number of wandering albatrosses that needed to be sampled before significant differences ($P < 0.05$) between females and males was higher when measuring δ^{13}C values on a single body feather than on a pool of four feathers (Fig. 2).

In summary, neither analysing a pool of body feathers or several body feathers or a single feather for a single individual allow an accurate determination of both BIC and WIC of TNW at low time and money costs. In theory, the procedure must depict the three groups of populations that can be defined from their WIC and BIC. First, low and high BIC values indicate specialist and generalist populations, respectively. Second, generalist populations can be split into type A and type B generalists marked by a low and a high WIC, i.e. individuals all having a wide range of foraging habitats/feeding habits (generalist individuals) and individuals each specializing on a different but narrow range of foraging habitats/feeding habits (specialist individuals), respectively (Bolnick et al. 2003; Bearhop et al. 2004). We consequently suggest the following two-step protocol to investigate both BIC and WIC, and thus TNW of populations of seabirds with a moulting pattern identical to that of the wandering albatross (Fig. 3). The first analytical step involves the measurement of the isotopic composition of a single feather per bird to quantify TNW of the population. If δ^{13}C and δ^{15}N variances are small, indicating an isotopic specialist population, no more measurements are needed, because WIC is almost negligible. A crude limit between small and large variances could be about 1‰, a value higher than analytical errors and that can be confidently interpreted in terms of biological meanings. If δ^{13}C and δ^{15}N variances are large, indicating an isotopic generalist population, WIC must be quantified to characterize type A

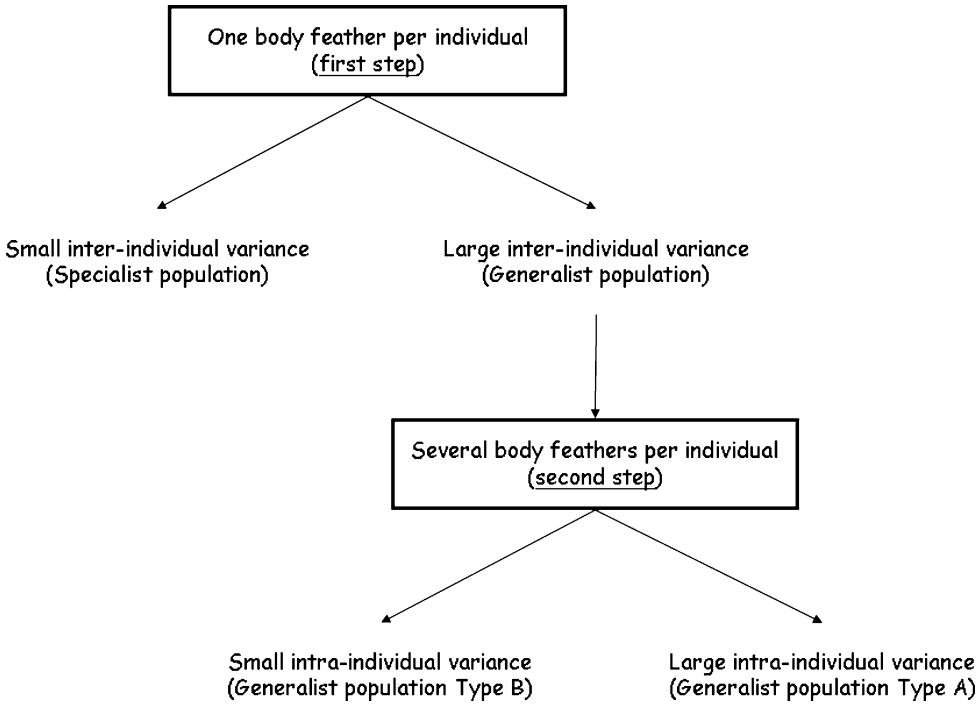

Fig. 3 Two-step analytical procedure enabling the use of stable isotope variance in whole body feathers to infer inter- and intra-individual variation in seabird isotopic niche during moult. The procedure allows to discriminate between isotopic specialist and generalist populations (first step), and between type A and type B generalists (second step). Specialist and generalist populations (types A and B) follow the definitions in Bearhop et al. (2004)

and type B generalists. This can be achieved by measuring the isotopic composition of more feathers per bird, each body feather representing a separate sample (here three additional feathers, thus giving a total of four feathers and thus four separate isotopic measurements per individual). The protocol thus minimizes both the numbers of sampled birds and isotopic measurements, and it maximises the amount of biological information collected from a few feathers only.

Non-breeding isotopic niche of the wandering albatross

Overall, the δ^{13}C values of wandering albatrosses indicate that they mainly foraged outside the Southern Ocean during the non-breeding period. Only a few individual feathers ($n = 14$, about 15%, for a total of 92 feathers) had an isotopic signature indicating moulting in waters south or at the Subtropical Front, and no feather had a very low Antarctic signature (less than −23‰; Quillfeldt et al. 2005; Cherel et al. 2006). The isotopic data are thus in general agreement with the few birds tracked during the inter-nesting period (Nicholls et al. 1995; Prince et al. 1998), but not with some individuals spending most of the time in subantarctic and Antarctic waters (Weimerskirch and Wilson 2000). As expected, males had lower δ^{13}C values than females and all (but one) feathers with a subantarctic origin were from males. Such a sexual spatial segregation agrees with the tracking and observations at sea of wandering albatrosses during both the breeding and non-breeding periods (Weimerskirch and Jouventin 1987; Weimerskirch et al. 1993, 1997; Weimerskirch and Wilson 2000). Interestingly, the δ^{13}C values of male wandering albatrosses were not significantly different from those of the subtropical control group, i.e. chicks of yellow-nosed albatrosses (Fig. 1, middle panel), indicating foraging mainly in oceanic subtropical waters during the inter-nesting period.

A new finding from the present study is that females can be split into two groups according to both their δ^{13}C and δ^{15}N values. The isotopic signature of some females was very close to those of adult yellow-nosed albatrosses from Amsterdam Island and of black-browed albatrosses from Kerguelen Islands (Cherel et al. 2000, authors' unpublished data), suggesting an overall identical moulting area. Indeed, banding recoveries of the three albatross populations showed that some birds visit southern Australian waters during the inter-nesting period (Weimerskirch et al. 1985; Cherel et al. 2000). The second group of females had high δ^{13}C and δ^{15}N values, suggesting they fed in productive neritic waters with different isotopic baseline levels. Overall, feather δ^{13}C values thus support the hypothesis that two types of dispersal occur in wandering albatrosses during the non-breeding season, with some birds visiting neritic waters and others favouring the oceanic domain (Weimerskirch et al. 1985). They furthermore suggest that the former strategy is more common in females and the latter in males. Clearly, however, more information is needed to be precise about the foraging patterns of moulting albatrosses either by comparing the isotopic niches of various populations and species (Cherel et al. 2007) or/and by using

geolocation loggers over the long term (Grémillet et al. 2000; Croxall et al. 2005).

Acknowledgments We thank G. Guillou for running stable isotope samples. The present work was supported financially and logistically by the program REMIGE-ANR Biodiversité 2005-011, the Institut Polaire Français Paul Emile Victor (IPEV, programme no. 109, H. Weimerskirch), and the Terres Australes et Antarctiques Françaises (TAAF).

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