Mar Biol (2008) 155:593–598
DOI 10.1007/s00227-008-1048-2

ORIGINAL PAPER

Differences in stable isotopes in blood and feathers of seabirds are consistent across species, age and latitude: implications for food web studies

Petra Quillfeldt · Leandro Bugoni · Rona A. R. McGill · Juan F. Masello · Robert W. Furness

Received: 29 April 2008 / Accepted: 20 August 2008 / Published online: 12 September 2008
© The Author(s) 2008. This article is published with open access at Springerlink.com

Abstract Stable isotopes of growing feathers and blood both represent assimilated diet, and both tissues are used to study the diet and foraging distribution of marine and terrestrial birds. Although most studies have assumed that both tissues represent a difference of one trophic level to diet, the enrichment factors of blood and feathers may differ, especially where endogenous reserves are used as precursors during feather synthesis. In this study, we compare carbon and nitrogen stable isotopes of blood and simultaneously growing feathers of five species of Procellariiformes, representing five genera, different geographical regions and different life stages (chicks and adults). In all species, feathers were enriched in ^{15}N and ^{13}C compared with blood. Isotopic values of carbon and nitrogen were correlated in different tissues growing simultaneously for most species analyzed, suggesting that mathematical corrections could be used to compare different tissues. Our results imply that more care needs to be taken when comparing stable isotope signatures across studies assuming different tissues are equivalent indicators of trophic ecology.

Communicated by R. Lewison.

P. Quillfeldt (✉) · J. F. Masello
Max-Planck-Institut für Ornithologie,
Vogelwarte Radolfzell, Schlossallee 2,
78315 Radolfzell, Germany
e-mail: petra.quillfeldt@gmx.de

L. Bugoni · R. W. Furness
Institute of Biomedical and Life Sciences,
Graham Kerr Building, University of Glasgow,
Glasgow G12 8QQ, UK

R. A. R. McGill
Scottish Universities Environmental Research Centre,
East Kilbride, Glasgow G75 0QF, UK

Introduction

Recent developments in our knowledge about the natural distribution of stable isotopes in marine food webs have provided us with a useful tool to study movements and the trophic level at which seabirds feed, which can be applied when more direct studies are impossible (e.g., Cherel et al. 2005a, 2006; Quillfeldt et al. 2005; Bearhop et al. 2006; Gladbach et al. 2007). In particular, carbon stable isotope ratios can reflect foraging locations (reviewed in Rubenstein and Hobson 2004), while nitrogen isotope ratios become enriched in ^{15}N with trophic level by approximately 3.0–5.0‰ (Minagawa and Wada 1984, Owens 1987) and δ^{15}N can thus indicate trophic position and be used to infer dietary composition (e.g., Hobson and Welch 1992; Hobson et al. 2000; Forero et al. 2005). Depending on the tissue chosen, dietary information spanning different temporal scales can also be obtained (Hobson and Clark 1992a).

The stable isotope approach is especially useful for studies of diet and foraging areas outside the breeding season, when pelagic birds are not usually accessible for sampling using traditional methods (Barrett et al. 2007). A number of studies have made use of the fact that the molting period is in this time, and thus, feathers grown by adult seabirds reflect the diet in the interbreeding period (e.g., Nisbet et al. 2002; Quillfeldt et al. 2005; Cherel et al. 2006; Gladbach et al. 2007). To assess diet and foraging areas during the breeding season, on the other hand, several tissues can be sampled non-destructively, including blood and feather samples of chicks and adults. However, due to the specific metabolic processes involved in tissue synthesis, different tissues may differ in their isotopic enrichment factor relative to the diet (e.g., Hobson and Clark 1992a).

As noted by several authors (Bearhop et al. 2000a; Cherel et al. 2005a, b), differences in isotopic discrimination

among tissues are a potential problem when comparing different tissue types. Temporal studies comparing the blood (representing the breeding season) and feathers (representing the interbreeding season) of adult seabirds are dependent on the assumption that isotope analyses of the two tissues provide directly comparable dietary proxies. However, most researchers working in the field of isotope ecology are aware that the enrichment factors of blood and feathers may differ when endogenous reserves are used as precursors during feather synthesis (Cherel et al. 2005a) or when blood contains ^{15}N-depleted uric acid (Bearhop et al. 2000b). Thus, most studies have limited their analysis to either blood or feathers, but have assumed both tissues to represent a difference of one trophic level to diet. A few studies have directly compared feather and blood isotope values (e.g., Podlesak et al. 2005; Bearhop et al. 2006), mainly on the assumption that the influence of tissue specific fractionation is small compared to the effect they aimed to measure.

The aim of this study is to compare the carbon and nitrogen stable isotope values of blood and simultaneously growing feathers of five species of Procellariiformes in order to test for differences in isotopic tissue discrimination between tissues. We also hope that by testing the basis of assumptions that are often made in dietary studies regarding the equivalence of different tissues, we can help clarify if blood or feather is the optimal tissue to sample. We also consider the limitations of extrapolating different-tissue stable isotope comparisons within temporal studies or between studies using feather and studies using blood.

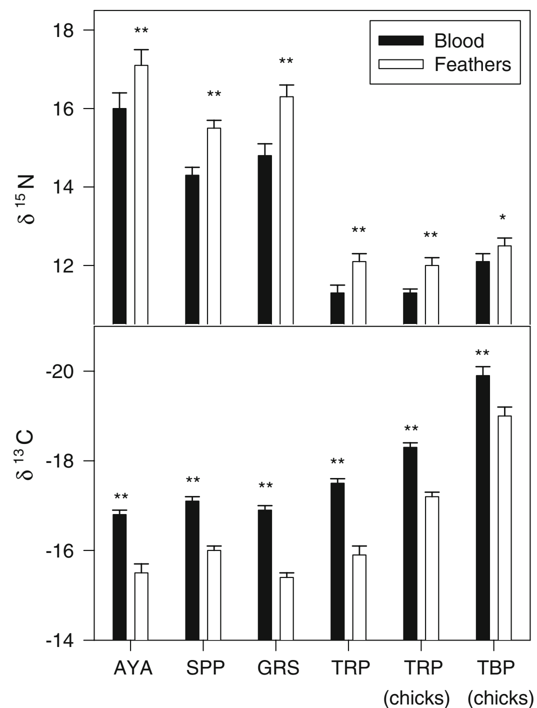

Fig. 1 Carbon and nitrogen stable isotopes (means ± SE) of seabird blood and growing feathers, representing similar time periods. For sample sizes see Table 2

Materials and methods

Study site, species and sampling

Species, abbreviations used in Fig. 1 and sampling locations are listed in Table 1, for sample sizes see Table 2.

Great shearwaters *Puffinus gravis*, Atlantic Yellow-nosed albatrosses *Thalassarche chlororhynchos* and Spectacled petrels *Procellaria conspicillata* were sampled in the Southwestern Atlantic Ocean off the Brazilian coast, onboard fishing vessels from February to June 2006. Birds scavenging discards were attracted to the vessel and trapped with a cast net as described by Bugoni et al. (2008b). Blood was collected from the tarsal vein using a 2-ml disposable syringe and needle. Growing body feathers, i.e., still with blood in the calamus, from the breast and dorsum were collected and stored dry in sealed plastic bags. This sample includes immature as well as breeding and non-breeding adults.

Trindade petrels *Pterodroma arminjoniana* were sampled in breeding colonies of Trindade Island (*c*. 20°30′S–29°19′W), where there is a population estimated at 1,130 breeding pairs (Luigi et al. 2008). Blood and growing feathers were collected from December 2006 to April 2007 and

Table 1 Species, abbreviations used in Fig. 1 and sampling locations of the Procellariiformes included in the present study

Species	Abbreviation	Age and sample location
Atlantic Yellow-nosed albatross *Thalassarche chlororhynchos*	AYA	Adults and immatures (at sea SW Atlantic)
Spectacled petrel *Procellaria conspicillata*	SPP	Adults and immatures (at sea SW Atlantic)
Great shearwater *Puffinus gravis*	GRS	Adults and immatures (at sea SW Atlantic)
Trindade petrel *Pterodroma arminjoniana*	TRP	Breeding adults (colonies Trindade Island)
Trindade petrel *Pterodroma arminjoniana*	TRP	Chicks (colonies Trindade Island)
Thin-billed prion *Pachyptila belcheri*	TBP	Chicks (colonies New Island, Falkland Islands)

Table 2 Carbon stable isotopes (means ± SE) of seabird blood and growing feathers, representing similar time periods, and individual differences between the simultaneously sampled tissues (means ± SE)

Species	Age	$\delta^{13}C$				
		Blood	Feathers	Paired differences	Pair-wise test	Correlation
Thalassarche chlororhynchos	Adults ($N = 15$)	−16.8 ± 0.1	−15.5 ± 0.2	1.3 ± 0.1	$t = 17.1$, $P < 0.001$	$R = 0.894$, $P < 0.001$
Procellaria conspicillata	Adults ($N = 21$)	−17.1 ± 0.1	−16.0 ± 0.1	1.1 ± 0.1	$t = 13.2$, $P < 0.001$	$R = 0.807$, $P < 0.001$
Puffinus gravis	Adults ($N = 15$)	−16.9 ± 0.1	−15.4 ± 0.1	1.4 ± 0.1	$t = 18.0$, $P < 0.001$	$R = 0.749$, $P = 0.001$
Pterodroma arminjoniana	Adults ($N = 18$)	−17.5 ± 0.1	−15.9 ± 0.2	1.5 ± 0.2	$t = 7.7$, $P < 0.001$	$R = 0.036$, $P = 0.888$
Pterodroma arminjoniana	Chicks ($N = 15$)	−18.3 ± 0.1	−17.2 ± 0.1	1.2 ± 0.2	$t = 7.1$, $P < 0.001$	$R = 0.080$, $P = 0.776$
Pachyptila belcheri	Chicks ($N = 17$)	−19.9 ± 0.2	−19.0 ± 0.2	0.9 ± 0.1	$t = 13.9$, $P < 0.001$	$R = 0.912$, $P < 0.001$

preserved in the same way described above. Four adults were sampled during chick feeding stage, whereas 14 were prospecting birds, but both groups were sampled over the same time period despite differences in breeding stage as the species nests throughout the year (Luigi et al. 2008). During the prospecting period (i.e., before the pre-laying exodus, which lasts usually 2 months), adults are frequently in final moult stage, with some growing body feathers still present (Luigi et al. 2008). Chicks were sampled following the same procedure, and full grown or growing body feathers of the definitive plumage were collected. One chick was 40-days-old and others were 70–100 days old, so close to fledging, which occurs about the 95th to 100th day (Luigi et al. 2008). The half-life of isotope turnover of avian whole blood has been determined to be 11.4 days for quail (Hobson and Clark 1992a), and so represents the same time window as growth of new body feathers, as these feathers are 20–30 mm long and growth rate of feathers in birds varies from 2.5 to 10 mm per day (Langston and Rohwer 1996).

Feather and blood samples from chicks of Thin-billed prions *Pachyptila belcheri* were collected as part of ongoing studies of their breeding biology at New Island Nature Reserve, Falkland Islands (e.g., Quillfeldt et al. 2003, 2006, 2007a, b, c). The present study includes samples collected from 40-day-old chicks during the breeding seasons 2004–2005 ($N = 7$) and 2005–2006 ($N = 10$). Birds were captured by hand and blood samples (0.2–0.4 ml) were collected from the brachial vein using heparinized capillaries within 2 min from burrow opening to the end of blood sampling. Blood samples were immediately transferred to 0.5-ml tubes and kept on ice until centrifugation. Plasma (used for hormone analyses, e.g., Quillfeldt et al. 2006, 2007c) and blood cells (used in the present analysis) were stored frozen in separate 0.5-ml tubes at −20°C. Undertail covert feathers of chicks were collected shortly before fledging by gentle pulling and placed in individual sealed plastic bags. The first tail feathers of chicks including the tail coverts start to emerge after 3 weeks of age (e.g., Strange 1980; "at 22 days the sheaths of the rectrices can be felt protruding"), therefore the distal parts of these feathers represent the middle of the nestling growth period of 50–56 days. The half-life of isotope turnover of avian red blood cells was 29.8 days in crows *Corvus brachyrhynchos* (Hobson and Clark 1993) and 10.9 days for Yellow-rumped warblers *Dendroica coronata* (Podlesak et al. 2005). The red blood cell samples collected from Thin-billed prion chicks therefore represented the diet ingested ca. 2–4 weeks before the sampling at 20 days, i.e., at the same time as the analyzed feather parts.

Sample preparation and stable isotope analysis

Feathers were cut into small fragments using stainless steel scissors, and whole blood and red blood cells (RBC) were freeze-dried and ground. Carbon and nitrogen isotope analyses were carried out on 0.65–0.7 mg aliquots of homogenized powder, weighed into tin cups.

Carbon and nitrogen isotope ratios were measured simultaneously by continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a Costech Elemental Analyser (EA) linked to a Thermo Finnigan Delta Plus XP Mass Spectrometer. Two laboratory standards were analyzed for every ten unknown samples, allowing any instrument drift over a typical 14-h run to be corrected. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards V-Pee Dee belemnite (carbon) and AIR (nitrogen), according to the following equation $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Based on internal standards (tryptophan), the analytical precision (± 1 SD) was estimated as ±0.18‰ and ±0.17‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively.

Data analysis

Statistical tests were performed in Sigma Stat 2.03. All tests used pair-wise data for each individual, carried out sepa-

rately for each species and age group. Sample sizes are given in Table 2.

Results

In all species and age groups, the feathers were enriched in ^{15}N and ^{13}C compared with blood (Table 2; Fig. 1). The differences ranged between 0.4 and 1.5‰ for δ^{15}N and between 0.9 and 1.6‰ for δ^{13}C (Table 2; Fig. 1). In all species except Trindade petrels, the δ^{15}N and δ^{13}C values of feathers and blood samples were highly correlated in individuals (Table 2, Table 3).

Discussion

Our study shows differences between the carbon and nitrogen stable isotopes of blood and simultaneously growing feathers of five species of Procellariiformes, representing five genera. We found that feathers were consistently enriched in ^{15}N and ^{13}C compared with blood in all species.

This is in line with previous studies that reported differences in isotope values between blood and feathers (e.g., Hobson and Clark 1992b; Bearhop et al. 2000a; Cherel et al. 2005a, b). However, the present approach is novel in that it used simultaneously collected samples from wild birds in their natural habitat, and exhibiting their natural foraging behaviors. In contrast, previous studies did not sample the same individuals simultaneously (e.g., Cherel et al. 2005a; Bearhop et al. 2000a, for simultaneously sampled hydrogen see Langin et al. 2007). Further, studies with simultaneous sampling, to our knowledge, have been carried out only in captive birds thus far (Hobson and Clark 1992b; Cherel et al. 2005b, but see Bugoni et al. 2008a).

The most likely explanation for increased ^{15}N and ^{13}C isotope enrichment in feathers compared to blood are metabolic differences. These may be found in the different protein sources (several proteins in blood, keratin in feathers) and differences would also appear if endogenous reserves are used as precursors during feather synthesis (e.g., Cherel et al. 2005a). For example, a large difference between ^{15}N enrichment factors of whole blood and feathers may indicate that most amino acids available for keratin synthesis are provided by endogenous reserves. Conversely, almost identical and low ^{15}N enrichment factors in whole blood and feathers may suggest a dietary origin of feather amino acids (Cherel et al. 2005a).

The presence of uric acid, which is ^{15}N depleted (Petersen and Fry 1987), has also been suggested as a cause of isotopic differences between blood and feathers. Bearhop et al. (2000b) found that uric acid removal in Great skua *Stercorarius skua* blood increased the measured δ^{15}N by 1.2‰, while δ^{13}C was not affected. As Cherel et al. (2005a) pointed out, the effect of uric acid is likely to be minimal because of the small amount of uric acid in blood, compared to protein (Garcia-Rodriguez et al. 1987; Boismenu et al. 1992). Higher values might be found, however, in times of high protein turnover such as during growth in chicks (Bearhop et al. 2000b and references therein). In the present study, both the nitrogen and carbon isotope ratios were lower in blood than in feathers, indicating that uric acid is not the only source for the observed difference between tissues. In Thin-billed prions, blood cells rather that whole blood were analyzed, and as uric acid is present in the plasma, it should not interfere with the measurements in this case. In fact, we found that the difference between δ^{15}N of blood and feathers was smallest in Thin-billed prions (0.4‰), and the difference was statistically significant ($P = 0.021$) rather that highly significant ($P < 0.001$) as in all other species. Thus, when the separation of plasma is possible, this may be a good way to exclude uric acid as an error source and allow better comparison between blood and feathers from the same species.

In four of five species in this study, δ^{15}N and δ^{13}C values of feathers and blood samples from individual birds were highly correlated. There was one exception of this pattern. In Trindade petrels, we observed a correlation only for

Table 3 Nitrogen stable isotopes (means ± SE) of seabird blood and growing feathers, representing similar time periods, and individual differences between the simultaneously sampled tissues (means ± SE)

Species	Age	δ^{15}N				
		Blood	Feathers	Paired differences	Pair-wise test	Correlation
Thalassarche chlororhynchos	Adults ($N = 15$)	16.0 ± 0.4	17.1 ± 0.4	1.1 ± 0.2	$t = 6.2, P < 0.001$	$R = 0.765, P < 0.001$
Procellaria conspicillata	Adults ($N = 21$)	14.3 ± 0.2	15.5 ± 0.2	1.2 ± 0.1	$t = 9.7, P < 0.001$	$R = 0.819, P < 0.001$
Puffinus gravis	Adults ($N = 15$)	14.8 ± 0.3	16.3 ± 0.3	1.5 ± 0.2	$t = 6.2, P < 0.001$	$R = 0.765, P < 0.001$
Pterodroma arminjoniana	Adults ($N = 18$)	11.3 ± 0.2	12.1 ± 0.2	0.8 ± 0.1	$t = 5.2, P < 0.001$	$R = 0.709, P < 0.001$
Pterodroma arminjoniana	Chicks ($N = 15$)	11.3 ± 0.1	12.0 ± 0.2	0.7 ± 0.2	$t = 4.0, P = 0.001$	$R = 0.278, P = 0.316$
Pachyptila belcheri	Chicks ($N = 17$)	12.1 ± 0.2	12.5 ± 0.2	0.3 ± 0.1	$t = 2.5, P = 0.021$	$R = 0.859, P < 0.001$

adults and only for nitrogen. It is tempting to suggest that this may have resulted from a large variation in foraging areas over a short time, as the Trindade petrel is the only tropical species in our dataset. In tropical species, foraging occurs over vast oceanic areas, and thus there may be more short-term variation in diet, as well as individual metabolic differences (e.g., in the use of internal stores during feather growth). Foraging trips by Trindade petrel parents vary from hours to weeks (Luigi et al. 2008), which could suggest that chicks use both diet and endogenous stores for tissue formation, depending on feeding frequencies. Thus the lack of intertissue correlations of carbon and nitrogen isotope values could reveal individual differences according to nutritional status.

In the present study, the difference between blood and simultaneously grown feathers was remarkably similar across five species of Procellariiformes representing five genera (Fig. 1), despite differences in ecology and geographical regions. It was also in the range of the difference found for captive King *Aptenodytes patagonicus* and Rockhopper *Eudyptes chrysocome* penguins, where Cherel et al. (2005b) found difference of 1.5 and 1.7‰ for δ^{15}N, and between 0.9 and 1.1 ‰ for δ^{13}C.

In deciding which tissue type is more reliable, both tissue types have error sources. In blood, variable content of uric acid and lipids is of concern, but this may be avoided if red blood cells can be used rather than whole blood, which may also be beneficial in many studies because red blood cells sample a much longer time window than plasma (e.g., Podlesak et al. 2005). In feathers, the variable use of endogenous reserves during feather growth has to be taken into account, especially of certain amino acids such as sulphur-containing amino acids (cysteine and methionine) that are abundant in keratin but may be scarce in recently ingested food, such that feather stable isotopes may also be biased. For chicks the role of stored reserves is not usually a major concern, although this needs to be confirmed in species undergoing mass recession during the growth of the feathers, as is the case in Procellariiformes. The best solution may be the analysis of both blood and growing feather so that the two together give a better indication than either tissue alone.

We suggest that future studies consider the following: (i) Sample both tissues if possible to overcome limitations of each. (ii) Use similar tissues to compare temporal patterns when possible, e.g., compare moult feathers with regrowths in the breeding season. (iii) RBC may be preferable to whole blood or plasma, by avoiding uric acid effects on nitrogen isotope ratios, (iv) Correlation between isotopic values of different tissues of similar age should be addressed, which could provide arithmetic corrections and make comparisons across tissues viable. (v) More research is needed on metabolic differences between chick and adults, as well as studies addressing differences in chick and adult diets in the nesting period. (vi) Avoid preserving tissues with preservatives containing the stable isotopes to be analyzed, such as ethanol or heparin for determination of SI of carbon in blood.

Acknowledgments We are grateful to the following organizations that facilitated fieldwork: New Island Conservation Trust, Projeto Albatroz, captain and crew of fishing vessel 'Ana Amaral' and the Brazilian Navy. NERC funded the isotope analysis. We would like to acknowledge financial support by DFG, Germany (Qu 148/1-ff), and New Island Conservation Trust. Fieldwork at New Island was approved by the Falkland Islands Government (Environmental Planning Office) and in Brazil by environmental agency (IBAMA) through permits No. 0128931BR, No. 203/2006, No. 02001.005981/2005, No. 023/2006, No. 040/2006 and No. 1282/1, and International Animal Health Certificate No. 0975–06. The Scottish Executive-Rural Affairs Directorate also kindly provided us the permit POAO 2007/91 to import samples into Scotland. LB received a CAPES Scholarship.

Open Access This article is distributed under the terms of the Creative Commons Attribution Noncommercial License which permits any noncommercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

References

Barrett RT, Camphuysen K, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S et al (2007) Diet studies of seabirds: a review and recommendations. ICES J Mar Sci 64:1675–1691. doi:10.1093/icesjms/fsm152

Bearhop S, Phillips RA, Thompson DR, Waldron S, Furness RW (2000a) Variability in mercury concentrations of great skuas *Catharacta skua*: the influence of colony, diet and trophic status inferred from stable isotope signatures. Mar Ecol Prog Ser 195:261–268. doi:10.3354/meps195261

Bearhop S, Teece MA, Waldron S, Furness RW (2000b) Influence of lipid and uric acid on δ^{13}C and δ^{15}N values of avian blood: implications for trophic studies. Auk 117:504–507. doi:10.1642/0004-8038(2000)117[0504:IOLAUA]2.0.CO;2

Bearhop S, Phillips RA, McGill R, Cherel Y, Dawson DA, Croxall JP (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Mar Ecol Prog Ser 311:157–164. doi:10.3354/meps311157

Boismenu C, Gauthier G, Larochelle J (1992) Physiology of prolonged fasting in Greater Snow Geese (*Chen caerulescens atlantica*). Auk 109:511–521

Bugoni L, McGill RAR, Furness RW (2008a) Effects of preservation methods on stable isotopes signatures in bird tissues. Rapid Commun Mass Spectrom 22:2457–2462. doi:10.1002/rcm.3633

Bugoni L, Neves TS, Peppes FV, Furness RW (2008b) An effective method for trapping scavenging seabirds at sea. J Field Ornithol 79(3):308–313. doi:10.1111/j.1557-9263.2008.00178.x

Cherel Y, Hobson KA, Bailleul FR, Groscolas R (2005a) Nutrition, physiology, and stable isotopes: new information from fasting and molting penguins. Ecology 86:2881–2888. doi:10.1890/05-0562

Cherel Y, Hobson KA, Hassani S (2005b) Isotopic discrimination between food and blood and feathers of captive penguins: Implications for dietary studies in the wild. Physiol Biochem Zool 78:106–115. doi:10.1086/425202

Cherel Y, Phillips RA, Hobson KA, McGill R (2006) Stable isotope evidence of diverse species-specific and individual wintering

strategies in seabirds. Biol Lett 2:301–303. doi:10.1098/rsbl.2006.0445

Forero MG, Gonzalez-Solis J, Hobson KA, Doncazar JA, Bertellotti M, Blanco G et al (2005) Stable isotopes reveal trophic segregation by sex and age in the southern giant petrel in two different food webs. Mar Ecol Prog Ser 296:107–113. doi:10.3354/meps296107

Garcia-Rodriguez T, Ferrer M, Carrillo JC, Castroviejo J (1987) Metabolic responses of *Buteo buteo* to long-term fasting and refeeding. Comp Biochem Physiol A 87:381–386. doi:10.1016/0300-9629(87)90139-3

Gladbach A, McGill RAR, Quillfeldt P (2007) Foraging areas of Wilson's storm-petrel *Oceanites oceanicus* in the breeding and inter-breeding period determined by stable isotope analysis. Polar Biol 30:1005–1012. doi:10.1007/s00300-007-0258-2

Hobson KA, Clark RG (1992a) Assessing avian diets using stable isotopes I. Turnover of ^{13}C in tissues. Condor 94:181–188. doi:10.2307/1368807

Hobson KA, Clark RG (1992b) Assessing avian diets using stable isotopes II. Factors influencing diet-tissue fractionation. Condor 94:189–197. doi:10.2307/1368808

Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. Auk 110:638–641

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using δ^{13}C and δ^{15}N analysis. Mar Ecol Prog Ser 84:9–18. doi:10.3354/meps084009

Hobson KA, Sirois J, Gloutney ML (2000) Tracing nutrient allocation to reproduction with stable isotopes: a preliminary investigation using colonial waterbirds of Great Slave Lake. Auk 117:760–774. doi:10.1642/0004-8038(2000)117[0760:TNATRW]2.0.CO;2

Langin KM, Reudink MW, Marra PP, Norris DR, Kyser TK, Ratcliffe LM (2007) Hydrogen isotopic variation in migratory bird tissues of known origin: implications for geographical assignment. Oecologia 152:449–457. doi:10.1007/s00442-007-0669-3

Langston NE, Rohwer S (1996) Molt-breeding tradeoffs in albatrosses: life story implications for big birds. Oikos 76:498–510. doi:10.2307/3546343

Luigi G, Bugoni L, Fonseca-Neto FP, Teixeira DM (2008) Biologia e conservação do petrel-de-trindade, *Pterodroma arminjoniana*, na ilha da Trindade, Atlântico sul. In: Mohr LV, Castro JWA, Costa PMS, Alves RJV (eds) Ilhas oceânicas brasileiras: da pesquisa ao manejo, vol. 2. Ministério do Meio Ambiente, Brasília

Minagawa M, Wada E (1984) Stepwise enrichment of δ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim Cosmochim Acta 48:1135–1140. doi:10.1016/0016-7037(84)90204-7

Nisbet ICT, Montoya JP, Burger J, Hatch JJ (2002) Use of stables isotopes to investigate individual differences in diets and mercury exposures among Common terns *Sterna hirundo* in breeding and wintering grounds. Mar Ecol Prog Ser 242:267–274. doi:10.3354/meps242267

Owens NJP (1987) Natural variation in ^{15}N in the marine environment. Adv Mar Biol 24:389–451. doi:10.1016/S0065-2881(08)60077-2

Petersen BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320. doi:10.1146/annurev.es.18.110187.001453

Podlesak DW, McWilliams SR, Hatch KA (2005) Stable isotopes in breath, blood, feces and feathers can indicate intra-individual changes in the diet of migratory songbirds. Oecologia 142:501–510. doi:10.1007/s00442-004-1737-6

Quillfeldt P, Masello JF, Strange IJ (2003) Breeding biology of the Thin-billed prion P*achyptila belcheri* at New Island, Falkland Islands, in the poor season 2002/2003: egg desertion, breeding success and chick provisioning. Polar Biol 26:746–752. doi:10.1007/s00300-003-0544-6

Quillfeldt P, McGill RAR, Furness RW (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. Mar Ecol Prog Ser 295:295–304. doi:10.3354/meps295295

Quillfeldt P, Masello JF, Strange IJ, Buchanan KL (2006) Begging and provisioning of Thin-billed prions *Pachyptila belcheri* is related to testosterone and corticosterone. Anim Behav 71:1359–1369. doi:10.1016/j.anbehav.2005.09.015

Quillfeldt P, Strange IJ, Masello JF (2007a) Sea surface temperatures and behavioural buffering capacity in Thin-billed prions *Pachyptila belcheri*: breeding success, provisioning and chick begging. J Avian Biol 38:298–308

Quillfeldt P, Strange IJ, Segelbacher G, Masello JF (2007b) Male and female contributions to provisioning rates of Thin-billed prions *Pachyptila belcheri* in the South Atlantic. J Ornithol 148:367–372. doi:10.1007/s10336-007-0138-0

Quillfeldt P, Poisbleau M, Chastel O, Masello JF (2007c) Corticosterone in Thin-billed prion *Pachyptila belcheri* chicks: diel rhythm, timing of fledging and nutritional stress. Naturwissenschaften 94:919–925. doi:10.1007/s00114-007-0275-6

Rubenstein DR, Hobson KA (2004) From birds to butterflies: animal movement patterns and stable isotopes. Trends Ecol Evol 19:256–263. doi:10.1016/j.tree.2004.03.017

Strange I (1980) The Thin-billed prion, *Pachyptila belcheri*, at New Island, Falkland Islands. Gerfaut 70:411–445