



Skuas (*Stercorarius* spp.) moult body feathers during both the breeding and inter-breeding periods: implications for stable isotope investigations in seabirds

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Seabirds are mostly thought to moult during the inter-breeding period and the isotopic values of their feathers are often therefore assumed to relate to their assimilated diet during such periods. We observed Brown Skuas *Stercorarius antarcticus lonnbergi* and South Polar Skuas *Stercorarius maccormicki* moulting on a breeding site at King George Island, Antarctica. This raises concerns about the reliability of using stable isotopes in feathers to infer feeding localities of birds during the inter-breeding period. We analysed the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of growing and fully grown body feathers collected from the same individuals. For both species, $\delta^{13}\text{C}$ values of growing feathers indicated feeding areas in the Antarctic zone (breeding grounds), whereas most fully grown feathers (100% for South Polar Skuas and 93.3% for Brown Skuas) could be assigned to northern latitudes (non-breeding grounds). However, a few fully grown body feathers of Brown Skuas (6.7% of the feathers, belonging to two birds) showed isotopic values that indicated moult in the Antarctic zone. As the growth period of those feathers was unknown, they could not be used with confidence to depict the foraging behaviour of the birds during the non-breeding period. Although precautions must be taken when inferring dietary information from feathers in seabirds where the moulting pattern is unknown, this study shows that if the development stage of a feather (growing/fully grown) is identified, then dietary information from both breeding and non-breeding seasons can be obtained on the same individual birds.

Keywords: Antarctica, diet, migration, Southern Ocean.

Tissues incorporate into their structures the isotopic composition of the food that animals consume, which in turn reflects their location and trophic level. These features have allowed researchers to analyse stable isotopes for the characterization of both the feeding habitats and the trophic levels of consumers (Hobson *et al.* 1994, Wolf *et al.* 2009, Jaeger *et al.* 2010a). The characteristic turnover rate of the composition of each tissue results in the isotopic pattern of different tissues, allowing the identification of habitats and

diets at different temporal scales (Hobson & Clark 1992, Hobson & Bond 2012, Cherel *et al.* 2014). Among the different tissues, feathers set in their inert structure the isotopic value reflecting diet while they were being synthesized, which remains unchanged once the feathers are fully formed (Hobson & Clark 1992, Bearhop *et al.* 2002). Therefore, the analysis of stable isotopes of feathers allows the identification of the habitat where birds moult and, considering discrimination factors between successive trophic levels, the trophic position of prey during the moulting period (Hobson & Wassenaar 1997, Marra *et al.* 1998, Cherel *et al.* 2014).

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It is broadly accepted that due to the costly energetic requirements of moult and breeding, both processes tend to take place out of phase (Hemborg & Lundberg 1998, Dawson 2008). Furthermore, many long-distance migratory birds moult after breeding or on their wintering sites (Nelson 1979, Löfgren 1984, Schreiber & Burger 2001, Newton 2008). This results in such birds maintaining in their feathers the isotopic signature of the moulting sites, which in many cases are different from the breeding grounds and therefore can be differentiated if the signature of their main prey during these periods is sufficiently different (Hobson & Wassenaar 1997, Jaeger *et al.* 2009, Weimerskirch *et al.* 2015, Cherel *et al.* 2016).

This permanence of the isotopic signature of the moulting sites in feathers is particularly valuable in seabirds, as generally the breeding period is the only stage when they can be sampled. For this reason, if moulting takes place outside the breeding site, stable isotope analysis of feathers has the potential of allowing the identification of the wintering areas and trophic level of the birds during the non-breeding period (Cherel *et al.* 2000, 2014, 2016, Furness *et al.* 2006, Phillips *et al.* 2007). However, the overlap between breeding and moulting increases towards higher latitudes (Newton 2008) and many species start moulting by the end of their breeding period or even completely overlap both processes (Nelson 1979, Schreiber & Burger 2001, Bond *et al.* 2013, Catry *et al.* 2013, Bourgeois & Dromzéé 2014), constituting exceptions to the broadly assumed inter-breeding moult.

Brown Skuas *Stercorarius antarcticus lonnbergi* and South Polar Skuas *Stercorarius maccormicki* breed during the austral summer in the shores of the Antarctic continent and sub-Antarctic Islands and subsequently move northward (Phillips *et al.* 2007, Kopp *et al.* 2011, Weimerskirch *et al.* 2015). Information on the moulting pattern of both species is scarce and is focused mainly on primary feathers (Olsen & Larsson 1997, Newell *et al.* 2013, Votier *et al.* 2015). Both species are expected to undertake the moult of body feathers after the breeding season (Furness 1987, Olsen & Larsson 1997, Phillips *et al.* 2007) but evidence shows that the moulting pattern is highly variable (Votier *et al.* 2015, Weimerskirch *et al.* 2015).

During the austral summer of 2011/2012, individual Brown and South Polar Skuas were recorded moulting body feathers in Potter Peninsula, King George Island, Antarctica. We compare

the isotopic composition of two groups of feathers sampled simultaneously from the same individuals: feathers being grown on the breeding grounds, and fully grown feathers with unknown moult timing. We discuss the implications of this situation when drawing conclusions from the isotopic signatures of feathers when the moulting pattern of the species is unknown.

METHODS

Nine Brown Skuas and 13 South Polar Skuas were handled during the austral summer of 2011/2012 in Potter Peninsula, King George Island, Antarctica. They included three and six moulting Brown and South Polar Skuas, respectively; the birds were adults but only two Brown Skuas were known to be actually breeding. Two growing feathers and a fully grown feather adjacent to those two were taken from the neck and breast of each moulting bird. In addition, three fully grown feathers were taken randomly from the abdomen and back of these birds. Five fully grown feathers were also sampled randomly from the same body parts (neck, breast, abdomen and back) from the other six Brown Skuas and seven South Polar Skuas that were not moulting. Feathers were classified as growing or fully developed according to the presence of their sheath, vascularization or signs of wear.

In the case of fully grown feathers, five feathers per bird were analysed to assess the moulting location and diet of individuals (Jaeger *et al.* 2009). For growing feathers, two per bird were analysed. Feathers were analysed individually and, prior to analyses, were cleaned by immersion in a 2 : 1 chloroform/methanol solution for 3 min followed by two rinses in methanol and then air-dried. Each feather was cut with scissors into small pieces, and a 0.3–0.5 mg subsample was weighed with a microbalance and packed into tin containers. Relative abundance of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) were determined with a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation (in ‰) relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors < 0.15‰ (sd) for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Data were analysed using the `lme` function of the `nlme` package (Pinheiro *et al.* 2016) for R 3.1.2 (R Core Team 2014) to perform a generalized linear mixed model. Models incorporated the kind of feather (growing and fully grown), the species and the interaction between both as explanatory variables for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The same model was used to test for differences between growing and grown feathers from all birds, and in the subset of birds that moulted some feathers in the breeding site. Another model was run to test for differences in the isotopic values of fully grown feathers between birds that moulted and those that did not moult in the breeding site. In all the models the identity of the birds was incorporated as a random effect to avoid the pseudo-replication of feathers taken from the same bird. Values are presented means \pm 1 sd and differences were considered significant at alpha values \leq 0.05.

RESULTS

Tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured on 127 body feathers (51 from Brown Skuas and 76 from South Polar Skuas) including 17 growing feathers (six and 11, respectively). Overall feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values showed a remarkable range of values: $\delta^{13}\text{C}$ ranged from -22.7 to -15.3‰ and from -22.7 to -13.1‰ , and $\delta^{15}\text{N}$ from 8.8 to 19.3‰ and from 9.5 to 18.3‰ in Brown and South Polar Skuas, respectively (Table 1).

The interaction between the kind of feather and the species was not significant in any of the tests. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fully grown feathers differed from those of growing feathers in both when considering all the sampled birds ($\delta^{13}\text{C}$: $t = 7.61$, $P < 0.001$; $\delta^{15}\text{N}$: $t = 2.70$, $P = 0.008$) and when considering only the subsample of birds that moulted some feathers on the breeding site ($\delta^{13}\text{C}$: $t = 5.64$, $P < 0.001$; $\delta^{15}\text{N}$: $t = 2.75$,

$P = 0.009$). There were no differences in the isotopic values of fully grown feathers between the birds that moulted some feathers in the breeding site and those that did not ($\delta^{13}\text{C}$: $t = 0.90$, $P = 0.38$; $\delta^{15}\text{N}$: $t = 0.05$, $P = 0.96$). There were no differences between the species. Three features were noteworthy (Fig. 1). First, growing feathers clustered together and showed little inter-feather isotopic differences when compared with fully grown feathers. Secondly, three fully grown feathers from two Brown Skuas had similar isotopic values to growing feathers. Thirdly, there was a c. 1‰ gap in $\delta^{13}\text{C}$ values, with no body feathers between -21.4 and -20.3‰ ; this gap represents a $\delta^{13}\text{C}$ difference between growing and fully grown feathers.

DISCUSSION

Our work adds evidence for the occurrence of moulting during the breeding season of seabirds (Bond *et al.* 2013, Catry *et al.* 2013, Bourgeois & Dromzeé 2014, Weimerskirch *et al.* 2015) and therefore for the simultaneous presence on the birds of feathers developed during both the breeding and the inter-breeding periods. A positive consequence is that different moulting periods, in habitats with prey with different isotopic signatures, allow the determination of the isotopic signature of the breeding and wintering sites for the same birds using the same tissue. As a negative consequence, this work also warns about the possibility of drawing misleading conclusions from the analysis of feather composition when the moulting pattern is unknown.

As expected, the low $\delta^{13}\text{C}$ values of growing body feathers of Brown and South Polar Skuas reflect the $\delta^{13}\text{C}$ values of the breeding site in Maritime Antarctica (e.g. Hinke *et al.* 2015). In contrast, two possibilities must be considered

Table 1. Isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of fully grown and growing body feathers of adult Brown and South Polar Skuas. Values are means \pm 1 sd with ranges in parentheses.

	N feathers (n birds)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N mass ratio
Brown Skua				
Fully grown	45 (9)	-17.9 ± 1.7 (-22.4 to -15.3)	12.9 ± 3.3 (8.8 – 19.3)	3.12 ± 0.03 (3.05 – 3.19)
Growing	6 (3)	-22.6 ± 0.1 (-22.7 to -22.5)	11.1 ± 0.9 (9 – 11.8)	3.13 ± 0.02 (3.09 – 3.16)
South Polar Skua				
Fully grown	65 (13)	-17.3 ± 1.5 (-20.1 to -13.1)	12.6 ± 2.0 (9.5 – 18.3)	3.13 ± 0.03 (3.07 – 3.24)
Growing	11 (6)	-22.4 ± 0.3 (-22.7 to -21.8)	11.7 ± 0.3 (11.3 – 12.2)	3.13 ± 0.02 (3.10 – 3.16)

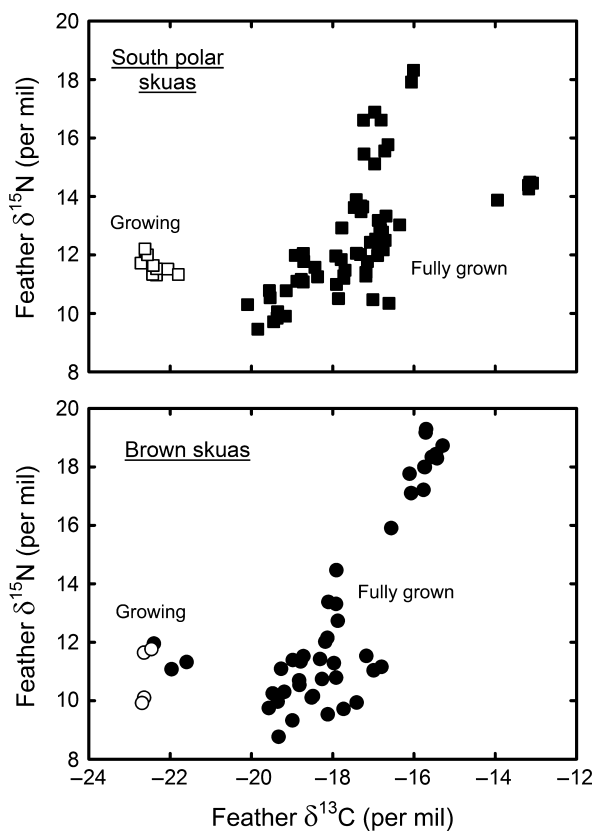


Figure 1. Isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of fully grown (black symbols) and growing (white symbols) body feathers of adult Brown and South Polar Skuas.

when interpreting the isotopic composition of fully grown feathers: (1) if fully grown feathers show a different isotopic signature from the growing ones, it can be assumed that they represent a different site, and hence the habitat and diet/trophic position during the inter-breeding period; and (2) if both fully grown and growing feathers show the same isotopic values, either fully grown feathers could have developed on a wintering site with an isotopic signature similar to that of the breeding ground, or feather growth occurred while on the breeding grounds. Therefore, in the case of both groups of feathers having the same isotopic signatures, the origin of the grown feathers cannot be guaranteed, making it impossible to draw any definite conclusion from them.

In the case of Brown and South Polar Skuas, growing and fully grown feathers had mostly different isotopic signatures. This suggests that each group belongs to the breeding and inter-breeding sites, respectively. However, a few fully grown

feathers of Brown Skuas showed isotopic signatures similar to those of growing feathers, which in this case could suggest that they were grown in the breeding site in the same or a previous season. The standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values also indicates the different origin of both groups of feathers. Fully grown feathers had a much higher standard deviation than growing feathers, which can be related to birds foraging along a broader geographical range and on a wider range of prey items during the inter-breeding season (Bearhop *et al.* 2004, Weimerskirch *et al.* 2015).

For both species, $\delta^{13}\text{C}$ values indicated feeding areas south of the Polar Front in the Antarctic Zone in growing feathers and north of that front in fully grown feathers (Quillfeldt *et al.* 2005, Cherel *et al.* 2006, 2016, Jaeger *et al.* 2010b). The mean $\delta^{13}\text{C}$ value of fully grown feathers of Brown Skuas from Potter Peninsula (-17.9‰) is almost identical to that of the population from South Georgia (-17.8‰ , Phillips *et al.* 2007), suggesting that both populations mainly overwinter in the Sub-Antarctic and Subtropical Zones. However, the high $\delta^{13}\text{C}$ ($> -16\text{‰}$) and $\delta^{15}\text{N}$ ($> 16\text{‰}$) values of some feathers from King George Island indicate that some birds wintered over neritic waters that are marked by elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baseline levels, most likely close to the Patagonian Shelf (Granadeiro *et al.* 2014). South Polar Skuas from King George Island migrate far north, overwintering in the northern hemisphere between 30° and 55°N (Kopp *et al.* 2011). The isotopic values of fully grown body feathers showed large $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations that indicate various moulting habitats, which when compared with ocean isoscapes may suggest locations around 45°N (Graham *et al.* 2010). In addition, the mean South Polar Skua $\delta^{13}\text{C}$ value (-17.3‰) was close to that (-17.7‰) of Atlantic Puffins *Fratercula arctica* from around 47°N (Hedd *et al.* 2010).

Beginning moult as soon as breeding activity stops (Dawson 2008) could be an explanation for finding moulting skuas during the summer time, as most of the sampled birds were not breeding. However, two birds were breeding (one of them was moulting primary feathers), which shows that skuas, like some other seabirds, may moult during their breeding period (Catry *et al.* 2013, Bourgeois & Dromzeć 2014). They therefore simultaneously presented feathers whose isotopic signatures belong to different moulting localities (Fox *et al.* 2007), thus raising the possibility of drawing the

wrong conclusions if the growing feathers are not identified as newly developed. Therefore, this work directs attention towards the condition of development of feathers (through their signs of wear, presence of sheath or vascularization) when sampling species for which the moulting pattern is unknown or can show unexpected changes, in order to avoid assigning wrong origins to the analysed feathers.

In previous studies, analysis of stable isotopes of feathers from adults and chicks has allowed the study of the trophic ecology of birds in two different periods of their annual cycle, namely the interbreeding and breeding periods, respectively (Cherel *et al.* 2000, 2014, Jaeger *et al.* 2010a). The moult of some body feathers in the breeding grounds opens the possibility for studying the trophic ecology of adults in two different periods of the annual cycle for the same individuals, and through the analysis of the same tissue type (feather). Such studies can also be undertaken by measuring stable isotopes on plucked feathers early in the breeding season and collecting the replacement feathers later on (Nisbet *et al.* 2002, Quillfeldt *et al.* 2005). However, this is a more invasive method that requires more than one capture of the birds.

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