

Moult of three Tristan da Cunha seabird species sampled at sea

LEANDRO BUGONI^{1,2}, LILIANA C. NAVES^{2,3} and ROBERT W. FURNESS¹

¹College of Medical, Veterinary and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK

²Institute of Biological Sciences, Waterbirds and Sea Turtle Laboratory, Universidade Federal do Rio Grande - FURG. CP 474, CEP 96.203-900, Rio Grande, RS, Brazil

³Current address: Alaska Department of Fish and Game, Division of Subsistence, 333 Raspberry Road, Anchorage, AK 99518, USA
lbugoni@pq.cnpq.br

Abstract: Primary, tail and body moult of three seabirds from Tristan da Cunha archipelago were studied by castnetting offshore south Brazil from February 2006 to August 2007. Timing, duration and synchronization of primary and tail moult are described relative to the annual calendar. Body moult overlapped breeding in Atlantic yellow-nosed albatrosses (*Thalassarche chlororhynchos*), but tail and primary moult did not. Spectacled petrels (*Procellaria conspicillata*) had protracted body moult, whereas primary and tail moult were completed by August. We documented onset of primary moult during chick-rearing in spectacled petrels and great shearwaters (*Puffinus gravis*) of unknown breeding status, and suggest that the south-west Atlantic Ocean holds important numbers of moulting birds of both species during the summer–early autumn. The albatrosses and the spectacled petrels replaced rectrices alternately. Great shearwaters replaced rectrices outward, starting at the central pair. Primary, tail and body moult largely overlap in all three species, suggesting that the metabolic costs of primary moult may not be overly restrictive. Metabolic and nutritional ability to afford simultaneous moult of different feather tracts support the idea that impaired flight caused by wing moult is a strong factor driving no overlap of primary moult and breeding.

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Introduction

Detailed knowledge of moult patterns at the species and population level is needed for a better understanding of life history traits, energy budget strategies and consequences of human activities on bird populations. Knowledge on the timing, duration and sequence of feather replacement is also essential to effectively design sampling and to interpret results of studies using feathers as biogeochemical markers. Analysis of stable isotopes, trace elements and contaminants in feathers can identify trophic relationships and ecological processes in breeding, migration and wintering areas (Gómez-Díaz & González-Solís 2007, Leat *et al.* 2013).

In general, birds tend not to overlap demanding activities such as breeding, migration and moult (Payne 1972, Langston & Rohwer 1996, Rohwer *et al.* 2011). The total moult cost has various components: i) metabolic and nutritional costs of growing new feathers (Lindström *et al.* 1993), ii) impaired flight performance caused by loss of wing and tail area (Bridge 2009), iii) increased predation risk (Slagsvold & Dale 1996), and iv) impaired thermoregulation (Payne 1972). Feather growth rate seems physiologically constrained, which causes moult to extend over long periods, especially for large birds because large feathers take longer to grow (Rohwer *et al.* 2009).

Consequently, large birds either simultaneously shed all flight feathers becoming temporarily flightless or have complex moult strategies, i.e. do not renew all feathers each year, probably due to life history trade-offs involving breeding, migration, moult and ecological factors (Bridge 2006, Rohwer *et al.* 2009). The relative importance of moult cost elements and their interactions with limited feather growth rate are poorly understood. Moult studies have focused on primary replacement, precluding a better understanding of how costs of replacing other feather tracts affect moult strategies.

Procellariiformes are extremely pelagic and usually moult during the non-breeding period. Capture of seabirds at sea allows sampling moult in pelagic species away from breeding grounds (Bugoni *et al.* 2008). However, because of difficulties in sampling pelagic birds at sea, most moult studies have been conducted on breeding grounds, when wing moult is usually inactive in breeding birds (Furness 1988, Prince *et al.* 1993, Allard *et al.* 2008). Moult data have been opportunistically collected in birds washed ashore (Bugoni *et al.* 2007), fisheries bycatch (Edwards & Rohwer 2005), museum collections and observation of live birds at distance (Watson 1971, Brown 1988). Despite much progress in the last 20 years, moult ecology in pelagic seabirds is poorly known. A review of seabird moult data could not

find any information for around 25% of all species, most of these occurring in South America and Asia (Bridge 2006). Furthermore, a large diversity of moult strategies (timing, duration and sequence of feather replacement) makes it difficult to generalize patterns across species and to develop a consistent moult terminology (Bridge 2011).

Albatrosses have a general divergent primary moult pattern: p8–p10 moult outward sequentially (p1 is the innermost and p10 the outermost primary) and the inner primaries moult inward, maybe in stepwise waves (two or more non-adjacent feathers grow simultaneously and yet create only small gaps in the wing surface). Albatrosses usually do not moult primaries while breeding (Furness 1988, Prince *et al.* 1993, Langston & Rohwer 1996, Edwards 2008), but the black-browed albatross (*Thalassarche melanophris* Temminck) may start moult late in the chick-rearing period (Catry *et al.* 2013). Non-breeding albatrosses may replace all primaries in a moult season, but breeding albatrosses may take two or more years to replace all primaries with moult suspension during breeding. Adults with accumulated moult deficit may skip a breeding season to catch up with moult in a sabbatical year (Langston & Rohwer 1996) and birds with worn feathers have an increased likelihood of failing their breeding attempt (Rohwer *et al.* 2011).

Petrels and shearwaters usually complete an annual, sequential primary moult outward from p1 to p10 (Marchant & Higgins 1990). Petrels frequently start primary moult during breeding, making it possible to study primary moult at breeding grounds (Hunter 1984, Barbraud & Chastel 1998). The shorter inner primaries usually shed almost simultaneously and the longer outer primaries shed one or two at a time.

Within general moult patterns, the timing and frequency of feather replacement at the species, population and individual level may vary depending on migratory strategies, colony location, ecological conditions and individual status (Alonso *et al.* 2009, Catry *et al.* 2013). Tropical and subtropical shearwaters may start primary moult during breeding, such as Cory's shearwaters (*Calonectris borealis* del Hoyo & Collar) breeding in the Azores and Berlengas (Alonso *et al.* 2009). However, breeding great shearwaters (*Puffinus gravis* O'Reilly) in Tristan da Cunha are thought to delay moult until arrival in wintering grounds in the north-west Atlantic, although these are high-latitude, trans-equatorial migrants (Brown 1988). Moult timing can also markedly differ in closely-related species: breeding southern fulmars (*Fulmarus glacialis* (Smith)) start primary moult during egg incubation while breeding northern fulmars



Fig. 1. Moulting great shearwater (*Puffinus gravis*) photographed at sea in southern Brazil. The image shows differences between new (p1–p8) and old (p9–p10) primaries and new (r1) and old (r2–r6) rectrices.

(*Fulmarus glacialis* (L.)) start primary moult after chick fledging (Barbraud & Chastel 1998, Allard *et al.* 2008).

Previous studies have not identified different moult patterns in males and females (Furness 1988, Prince *et al.* 1993, Allard *et al.* 2008), except in the wandering albatross (*Diomedea exulans* L.) which shows pronounced sexual dimorphism (Weimerskirch 1991).

This study provides information on moult of multiple feather tracts (primaries, rectrices and body feathers of head, back and belly) for Atlantic yellow-nosed albatrosses (*Thalassarche chlororhynchos* Gmelin), spectacled petrels (*Procellaria conspicillata* (Gould)) and great shearwaters captured at sea, largely during the non-breeding period, offshore Brazil (south-west Atlantic Ocean). The main objective of this study was to provide a comparative assessment of timing of moult among species and sex, discussed in relation to annual life cycle, including breeding and migration. This study is relevant because little (Atlantic yellow-nosed albatross and great shearwater) or no (spectacled petrel) moult information is available for these species during the austral spring and summer. The three species are endemic to Tristan da Cunha and Gough Island (central southern Atlantic Ocean), although great shearwaters also have a small population (50–100 pairs) on the Falkland (Malvinas) Islands (Woods & Woods 1997). These species breed during the austral spring and summer. Adults arrive in Tristan da Cunha and Gough Island in late August/September and egg laying occurs from mid-September to November (Rowan 1951). Hatching occurs in late November to mid-December for Atlantic yellow-nosed albatrosses and spectacled petrels, and in January for great shearwaters. Chicks of spectacled petrels fledge by March (Ryan & Moloney 2000), chicks of Atlantic yellow-nosed albatrosses in April (Cuthbert *et al.*

2003) and of great shearwaters in mid-May while adults depart in April (Cuthbert 2005).

Material and methods

Study area and bird capture at sea

Birds were captured and sampled for moult on the Brazilian continental shelf and shelf break, within 25°–35°S and 41°–52°W. This region is under the influence of the Subtropical Convergence, where the warm Brazilian Current running southward meets the cold Falkland/Malvinas Current running northward. This highly productive region is a feeding ground for an abundant and diverse bird fauna (Neves *et al.* 2006). Bird captures were carried out from two fishing boats targeting tuna (*Thunnus* spp.), sharks (mainly blue shark *Prionace glauca* (L.)) and swordfish (*Xiphias gladius* L.) using hook-and-line and pelagic longline. Birds were attracted to the boat by chumming, using fishing discards, and birds on the water were captured by a castnet thrown from the boat (Bugoni *et al.* 2008). Bird captures were conducted in cruises in February (two cruises), April (one cruise), May–June (one cruise) 2006, and late July–August 2007 (two cruises). The sample also included a few birds incidentally caught by fishing gear in February–June 2006.

Moult scores

Petrels and albatrosses moult primaries in a symmetrical manner; therefore moult scores for p1–p10 were recorded for the right wing only (Harris 1973, Hunter 1984, Furness 1988, Prince *et al.* 1993, Allard *et al.* 2008, Rohwer *et al.* 2011). All rectrices from the left (L) and

Table 1. Primary, tail and body moult of Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*), spectacled petrel (*Procellaria conspicillata*) and great shearwater (*Puffinus gravis*) sampled offshore south Brazil.

Age, moult state and timing related to breeding cycle	n	Number of primaries per bird (mean ± SD)			Number of rectrices per bird (mean ± SD)			Active body moult (% of birds)		
		Growing	Old	New	Growing	Old	New	Head	Neck	Belly
Atlantic yellow-nosed albatross										
a. Adult, chick-rearing (Feb; Table IIa)	13	0.0 ± 0.0	1.5 ± 2.9	8.5 ± 2.9	0.0 ± 0.0	6.5 ± 6.2	5.5 ± 6.2	0	8	39
b. Adult, late fledging/non-breeding (Apr–Aug; Table IIb)	4	2.3 ± 1.5	1.5 ± 2.4	6.8 ± 1.7	2.3 ± 1.3	7.0 ± 4.8	2.8 ± 5.5	0	50	100
c. Immature, chick-rearing (Feb; Table IIc)	7	2.0 ± 1.0	1.0 ± 2.4	7.0 ± 2.9	3.8 ± 2.0	6.3 ± 5.3	2.4 ± 5.3	43	100	100
d. Immature, non-breeding (Apr–Aug; Table II d)	9	0.0 ± 0.8	5.7 ± 4.4	4.3 ± 4.3	5.0 ± 2.0	4.3 ± 5.2	4.9 ± 3.8	33	89	88
Spectacled petrel										
a. Active primary moult, chick-rearing (Feb; Table IVa)	35	3.1 ± 0.6	1.0 ± 1.6	6.0 ± 1.5	3.8 ± 3.4	9.0 ± 5.0	2.5 ± 4.9	76	81	75
b. Complete primary moult and continuation of tail moult, non-breeding (Apr–Aug; Table IVb)	11	0.0 ± 0.0	0.0 ± 0.0	10.0 ± 0.0	3.8 ± 1.6	0.7 ± 2.1	9.5 ± 3.8	75	83	81
c. Start of primary moult, non-breeding (Apr–Jun; Table IVc)	18	4.0 ± 1.1	2.6 ± 1.9	3.7 ± 2.6	2.8 ± 2.7	8.6 ± 5.0	2.7 ± 5.1	89	83	89
Great shearwater										
a. No active primary and tail moult (Feb–Jun)	22	0.0 ± 0.0	10.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	12.0 ± 0.2	0.0 ± 0.0	18	9	68
b. Early primary and tail moult, chick-rearing (Feb; Table Vb)	28	3.1 ± 0.9	5.1 ± 2.2	1.7 ± 2.1	1.7 ± 0.6	11.2 ± 1.3	0.2 ± 0.6	82	89	100
c. Late primary moult, non-breeding (Apr–Jun; Table Vc)	17	1.5 ± 0.5	2.1 ± 1.9	6.6 ± 1.8	2.2 ± 0.8	8.2 ± 1.1	2.6 ± 1.5	24	35	71

Table II. Moulting scores of primaries and rectrices (number of cases of each score) of the Atlantic yellow-nosed albatross. Relative frequency of occurrence (FO%) = total number of cases divided by (number of feathers in tract × number of birds sampled).

Score	Primaries (right wing)										FO%	Left rectrices					Right rectrices					FO%			
	1	2	3	4	5	6	7	8	9	10		6	5	4	3	2	1	1	2	3	4		5	6	
a. Adult, chick-rearing (Feb, <i>n</i> = 13)																									
0	1	1	1	1	1	1	1	4	4	4	14.6	7	7	7	7	7	7	7	7	7	7	7	7	7	53.8
1											0														0
2											0														0
3											0														0
4											0														0
5	12	12	12	12	12	12	12	9	9	9	85.4	6	6	6	6	6	6	6	6	6	6	6	6	6	46.2
Mean	4.6	4.6	4.6	4.6	4.6	4.6	4.6	3.5	3.5	3.5		2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	
b. Adult, late fledging/non-breeding (Apr–Aug, <i>n</i> = 4)																									
0			1	1				1	1	2	15.0	3	2	3	2	3	2	2	2	2	2	3	2	58.3	
1									1	1	5.0						1		1	1				6.3	
2								1	1		5.0		1		1						1			8.3	
3								1			2.5													2.1	
4			1					1			5.0						1							2.1	
5	4	4	2	3	4	4	4		1	1	67.5	1	1	1	1	1		1	1	1	1	1	1	22.9	
Mean	5.0	5.0	3.5	3.8	5.0	5.0	5.0	2.3	2.0	1.5		1.3	1.8	1.3	1.8	1.3	1.3	2.0	1.5	1.5	1.8	1.3	1.8		
c. Immature, chick-rearing (Feb, <i>n</i> = 7)																									
0			1	1	1	1	1		1	1	10.0	4	5	3	5	4	2	2	4	4	3	4	4	52.4	
1		1				1					2.9			1	2	1	2	2		3	1	1	1	16.7	
2			1							2	4.3			1			1	1						3.6	
3								1	1	2	5.7	2									1		1	4.8	
4		1							2	2	7.1		1									1		2.4	
5	7	5	5	6	6	5	6	6	3	0	70.0	1	1	2		2	2	2	3		2	1	1	20.2	
Mean	5.0	4.3	3.9	4.3	4.3	3.7	4.3	4.7	3.7	2.6		1.6	1.3	1.9	0.3	1.6	2.0	2.0	2.1	0.4	2.0	1.4	1.3		
d. Immature, late fledging/non-breeding (Apr–Aug, <i>n</i> = 9)																									
0	4	5	5	5	5	6	6	5	5	5	56.7	3	3	3	3	3	5	4	3	3	3	3	3	36.1	
1											0		2		1					1		1	1	6.5	
2											0													0	
3											0			1		1		2	1		2			6.5	
4											0	1	2	1	1	1	1			1		3		10.2	
5	5	4	4	4	4	3	3	4	4	4	43.3	5	2	4	4	4	3	3	4	5	3	2	5	40.7	
Mean	2.8	2.2	2.2	2.2	2.2	1.7	1.7	2.2	2.2	2.2		3.2	2.2	3.0	2.8	3.0	2.1	2.3	2.7	3.2	2.4	2.6	2.9		

right (R) halves of the tail were scored (r1 is the central pair and r6 the outermost pair). Scores were based on feather appearance (old or new, Fig. 1) and stage of development: 0 = old feather, 1 = feather missing or new feather in pin, 2 = new feather emerging from sheath up to one-third grown, 3 = new feather one- to two-thirds grown, 4 = new feather more than two-thirds grown with waxy sheath remains at its base, or 5 = new feather fully grown without waxy sheath remains at its base (Ginn & Melville 1983). Old feathers were distinguished from new fully grown ones by having faded colour, duller brightness and abraded tips (Fig. 1). However, it was sometimes difficult to distinguish old and new feathers, especially in birds not in active moult showing only one apparent feather generation. Additionally, in birds captured by castnetting the plumage may be wet and in disarray. This scoring method documents only one category of old feathers. Therefore, the occurrence of more than two generations of primaries in albatrosses is not discussed. Despite careful consideration of scores during data collection, this scoring limitation may also have caused scoring error when outer

primaries, which are more subject to decay, looked older than inner primaries although they could belong to the same generation. Body moult on head, back and belly was defined as active if at least five growing feathers were located in these areas; otherwise body moult was defined as inactive.

Data analysis

Moult data were tabulated as the number of cases of each score (0–5) per feather (p1–p10, r6 R and L). The frequency of occurrence (FO) of each score was calculated as FO = total number of cases ÷ (number of feathers in tract × number of birds sampled). A subscript 0–5 is used to indicate the moult score. The mean number of new, old and growing feathers was also analysed. Body moult was analysed as the proportion of birds with active moult in the head, back and belly.

The sequence of replacement of rectrices was analysed for birds with active tail moult or a combination of old and new rectrices. Birds with only new or old rectrices

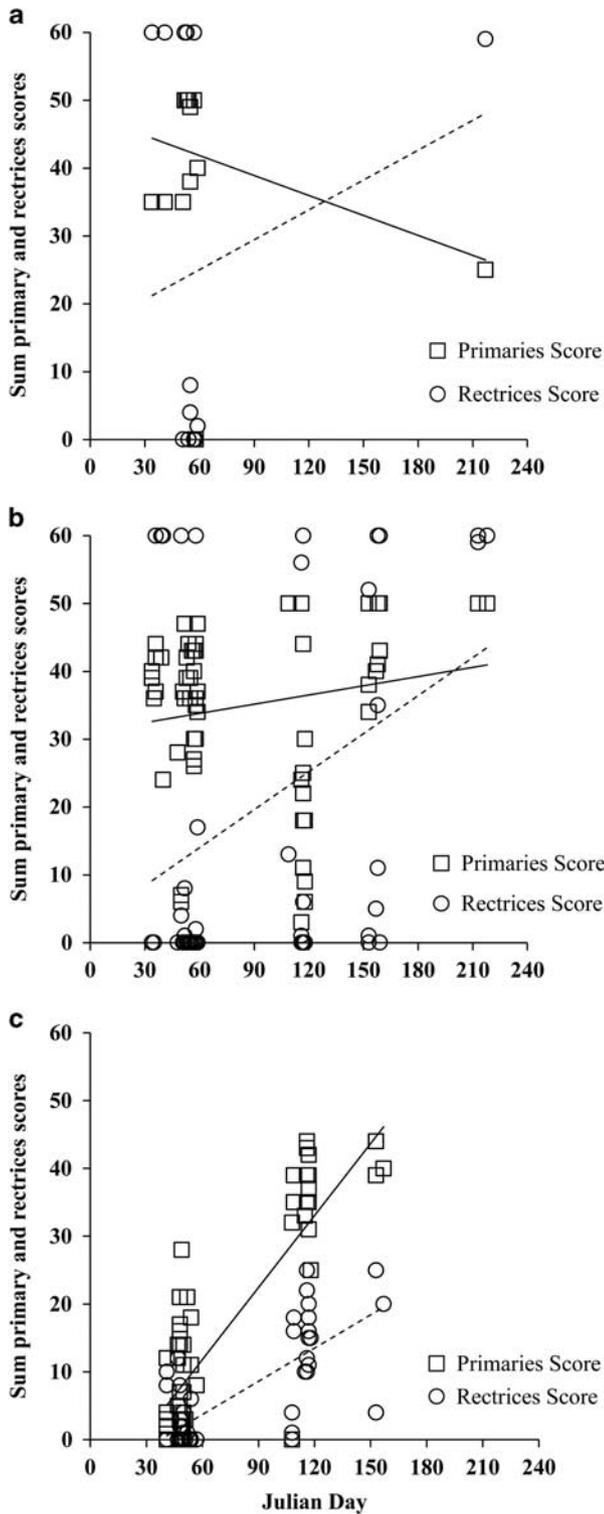


Fig. 2. Relationships between Julian day and total moult scores of primaries (up to 50, continuous line) and rectrices (up to 60, dashed line). **a.** Atlantic yellow-nosed albatross, **b.** spectacled petrel, and **c.** great shearwaters.

were not included in this analysis because these birds do not provide information on moult sequence. Birds were sorted in approximate ascending order of tail moult scores (from 1–5) to depict tail moult progression. Based on the sample for Atlantic yellow-nosed albatrosses and spectacled petrels, tail moult progress was defined as early (only one or two fully grown new rectrices) or late (three or more fully grown new rectrices).

A difficulty of sampling moult away from breeding colonies is that age and breeding status are usually unknown, as opposed to moult data collected at breeding colonies in the context of banding and monitoring programmes. Hatch-year and immature Atlantic yellow-nosed albatrosses (up to 6 years old) were aged based on bill colour (Bugoni & Furness 2009), and the specific age of adults (older than 6 years) was not defined. Spectacled petrels and great shearwaters cannot be easily aged based on characteristics of plumage and bare parts. Petrels and shearwaters sampled in February–June with no active moult were defined as ‘first-year juveniles’; however, this may have included some successful breeding adults in February. No such assumption was made for birds sampled in July–August because they could have been adults which had completed moult.

Sex was determined by PCR amplification of CHD genes and sex-related differences were tested for the timing of moult and synchronization between primary and tail moult.

Pearson’s correlation coefficient for relationships between total moult scores for primaries and rectrices were calculated to assess synchronization in moult of these feather tracts. Correlation coefficient for relationships between Julian day and moult scores for primaries and rectrices were also calculated to assess overlap between moult and breeding activities. Only birds in active primary and/or tail moult were included in these analyses (i.e. birds with at least one feather scored 1–4). Hatch-year birds were not included because they are unlikely to have active primary and tail moult. Analyses were carried out combining males and females for each of the three studied species and for females and males separately (sample size for albatrosses was insufficient to analyse sexes separately). There was an indication of synchronization between primary and tail moult for spectacled petrels in the non-breeding period, therefore correlation coefficients between these tracts were calculated for this category of birds. Statistical significance was determined after Bonferroni correction for multiple comparisons, derived from the α level (0.05) divided by the number of comparisons. In the moult synchronization analysis, the number of comparisons was eight, thus correlations were statistically significant if $P < 0.006$. In the analysis of overlap between moult and breeding activities, moult scores and Julian days were $\log + 1$ transformed and the number of comparisons was 18, thus correlations were statistically significant if $P < 0.003$.

Table III. Relationships between Julian day and moult scores of primaries and rectrices of the Atlantic yellow-nosed albatross, spectacled petrel and great shearwater. Data were log +1 transformed and Bonferroni correction for multiple comparisons applied; correlations are statistically significant if $P < 0.003$.

Julian day vs. moult score	Atlantic yellow-nosed albatross			Spectacled petrel			Great shearwater		
	<i>r</i>	<i>P</i>	<i>n</i>	<i>r</i>	<i>P</i>	<i>n</i>	<i>r</i>	<i>P</i>	<i>n</i>
Primaries, sexes combined	-0.30 ^a	0.111	30	0.00	0.980	64	0.51	< 0.0001	55
Rectrices, sexes combined	0.39 ^a	0.034	30	0.32	0.010	64	0.76	< 0.0001	55
Primaries, females	– ^b	– ^b	– ^b	0.30	0.232	18	0.55	0.0014	31
Primaries, males	-0.09 ^c	0.794	11	-0.10	0.522	46	0.64	0.0008	24
Rectrices, females	– ^b	– ^b	– ^b	0.31	0.206	18	0.71	< 0.0001	31
Rectrices, males	-0.06	0.872	11	0.35	0.018	46	0.74	< 0.0001	24

^aAll birds with active moult pooled, i.e. immatures and adults.

^bSmall sample size for adult females precluded analysis.

^cAdults (4+ years) only. Sample size for immatures (2–4 years old) precluded analysis of the group.

Results

Atlantic yellow-nosed albatross

Adult and immature Atlantic yellow-nosed albatrosses were sampled in February (chick-rearing), late April (late fledging) and May–August (non-breeding). Due to small sample sizes, data for late fledging and non-breeding were combined.

Adults sampled during chick-rearing ($n = 13$) had a lower frequency of body moult than adults sampled during late fledging/non-breeding and immatures, and no active primary and tail moult (Tables I & IIa). Nine of these adults had all primaries scored as new, three had new p1–p7 and old p8–p10, and one had all primaries scored as old ($FO_5 = 85\%$). Six of these adults

had all rectrices scored as new and seven had all rectrices scored as old ($FO_5 = 46\%$).

Adults sampled in late fledging/non-breeding ($n = 4$) had most inner primaries new ($FO_5 = 68\%$), had old or growing outer primaries p8–p10 ($FO_{1-4} = 18\%$), and were in active tail moult ($FO_{1-4} = 19\%$, Tables I & IIb).

Immatures sampled during chick-rearing ($n = 7$) were moulting one or two of the three outer primaries p8–p10; two birds were also moulting p2 and/or p3 (mean number of growing primaries = 2.0, max = 4, $FO_{1-4} = 20\%$; Tables I & IIc). Six of these immatures had active tail moult ($FO_{1-4} = 28\%$) and a high proportion of old rectrices ($FO_0 = 52\%$, mean number of growing rectrices = 3.8, max = 6).

Table IV. Moult scores of primaries and rectrices (number of cases of each score) of the spectacled petrel sampled offshore south Brazil. Relative frequency of occurrence ($FO\%$) = total number of cases divided by (number of feathers in tract × number of birds sampled).

Score	Primaries (right wing)										FO%	Left rectrices					FO%	Right rectrices					FO%	
	1	2	3	4	5	6	7	8	9	10		6	5	4	3	2		1	1	2	3	4		5
a. Active primary moult, chick-rearing (Feb, $n = 35$)																								
0				1	2	2	2	7	9	19	12.0	24	26	25	26	26	25	26	27	25	26	25	24	74.8
1	3	1	1				1	4	4	13	11.4	2	1	1	1					1	1	2	2	3.2
2		1			1	2	1	7	5	1	5.1													0
3				1	1	1	6	3	6	2	5.7	1			1			1				1		1.2
4		1	1		3	3	8	10	2		8.0			1										0.2
5	32	32	33	33	28	26	14	4			57.7	7	7	7	7	7	7	7	7	7	7	7	7	20.6
Mean	4.7	4.8	4.9	4.8	4.5	4.3	3.6	2.5	1.4	0.6		1.1	1.0	1.1	1.0	1.1	1.1	1.1	1.0	1.1	1.0	1.1	1.1	1.1
b. Complete primary moult and continuation of tail moult, non-breeding (Apr–Aug, $n = 11$)																								
0											0		1	1		1	1		1	1		2		6.1
1											0		1		1		1	2		1	1			5.3
2											0													0
3											0		1		1					1			1	3.8
4											0	1	1		2				1			1	1	5.3
5	11	11	11	11	11	11	11	11	11	11	100	10	7	10	9	7	9	9	8	9	10	7	10	79.5
Mean	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0		4.9	3.9	4.5	4.5	4.2	4.2	4.3	4.3	4.2	4.6	3.8	4.9	
c. Start of primary moult, non-breeding (Apr–Jun, $n = 18$)																								
0	1				1	1	6	11	13	14	26.1	13	14	13	13	13	12	10	13	13	13	14	13	71.3
1	2	3	2	3	4	9	5	1	1	3	18.3	1		1	1			2	1	1	1		1	4.6
2		1	2	2	5	1	1	1	2	1	8.9													0
3				3	1	1	1	3	2		6.1						2	1						1.4
4	2	2	1	2	1	1	2	2			7.2													0
5	13	12	13	8	6	5	3				33.3	4	4	4	4	4	4	5	4	4	4	4	4	22.7
Mean	4.2	4.1	4.2	3.6	2.8	2.4	1.8	1.1	0.6	0.3		1.2	1.1	1.2	1.2	1.2	1.4	1.7	1.2	1.2	1.2	1.1	1.2	

Table V. Moulting scores of primaries and rectrices (number of cases of each score) of the great shearwater sampled offshore south Brazil. Relative frequency of occurrence (FO%) = total number of cases divided by (number of feathers in tract × number of birds sampled).

Score	Primaries (right wing)										FO%	Left rectrices					Right rectrices					FO%		
	1	2	3	4	5	6	7	8	9	10		6	5	4	3	2	1	1	2	3	4		5	6
b. Early primary and tail moult, chick-rearing (Feb, $n = 28^a$)																								
0			2	13	19	24	27	28	27	28	60.0	27	27	27	27	23	17	18	26	27	27	27	27	92.6
1	14	11	13	8	7	3	1				20.4				3	4	4	1					3.7	
2	1	4	1	2	1						3.2						1	1					0.6	
3	1	2	6	3		1					4.6						1	3					1.2	
4	2	2	1	1	1						2.5												0	
5	10	9	5	1				1			9.3			1	4	1							1.9	
Mean	2.8	2.8	2.2	1.1	0.5	0.2	0.0	0.0	0.2	0.0		0.0	0.0	0.0	0.0	0.3	1.0	0.7	0.0	0.0	0.0	0.0	0.0	
c. Late primary moult, non-breeding (Apr–Jun, $n = 17$)																								
0							1	4	10	15	17.6	17	17	16	10	9		1	8	13	14	17	17	68.1
1	1					1	1	2	4	1	5.9			1	3	1	2	3		1	1			5.9
2							1	2	1	1	2.9									1	1			1.0
3								3	1		2.4				2				2					2.0
4					1		2	2			0.9				1				1					1.0
5	16	17	17	17	16	16	12	4	1		68.2			4	4	15	13	6	2	1			22.1	
Mean	4.8	5.0	5.0	5.0	4.9	4.8	4.2	2.5	0.8	0.2		0.0	0.0	0.1	1.4	1.8	4.5	4.0	2.4	0.8	0.5	0.0	0.0	

^aTail moult scores are available for 27 out of 28 birds in moult state 'b'.

Immatures sampled during late fledging/non-breeding ($n = 9$) had no active primary moult and similar proportions of primaries scored as old and new (FO₀ = 57%, FO₅ = 43%; Tables I & II). Three of these birds had all rectrices scored as old, one had all rectrices new, and the other five birds were in advanced tail moult.

The total moult scores for primaries and rectrices were negatively correlated, but this correlation was not significant ($r = -0.48$, $n = 16$, $P = 0.06$, critical $P < 0.006$). Correlations between moult scores and Julian day were non-significant for primaries and rectrices when considering males and females combined, or when considering males separately (sample size insufficient to assess females separately; Fig. 2a, Table III).

Spectacled petrel

All spectacled petrels sampled in February (late chick-rearing) had active primary moult, most had old rectrices (although seven birds had all rectrices scored as new), and a few were starting tail moult (defined as moult state 'a', $n = 35$; Tables I & IVa). Birds sampled in April–August (non-breeding) were divided in two moult states. Birds in moult state 'b' (April–August) had new primaries and no active moult, advanced tail moult or all rectrices new ($n = 11$, Tables I & IVb). Birds in moult state 'c' (April–June) had active primary moult and tail old or starting moult ($n = 18$, Tables I & IVc). The moult state 'b' probably represented a later stage (progression over time) of state 'a', and these moult states may represent birds in similar age and/or breeding status. On the other hand, it seems that moult state 'c' involved a later start of primary and tail moult, probably after fledging, and may refer to birds of age and/or breeding status differing from

birds represented in moult status 'a' and 'b'. A correlation between total primary and tail scores was not found in birds sampled in the non-breeding period ($r = 0.21$, $P = 0.33$, $n = 23$; moult states 'a', 'b' and 'c' combined).

In general, primary moult was sequential and progressed outward from p1 to p10. Seven birds had one of the four inner primaries scored higher than its adjacent inner feather (e.g. 4552110000) and two other birds in early primary moult had p1–p6 scored 1 or 2, suggesting simultaneous shedding of inner primaries. Active head, belly and back moult were observed in all three moult states, and most birds had moult in at least two body areas, suggesting that body moult largely overlaps primary and tail moult (Table I).

Total moult scores for primaries and rectrices were not correlated when considering sexes combined ($r = 0.00$, $P = 0.98$, $n = 57$), or when considering females ($r = -0.25$, $P = 0.35$, $n = 16$) and males ($r = 0.09$, $P = 0.50$, $n = 41$) separately. There was a tendency for a positive correlation between moult scores versus Julian day in some categories of birds, but correlations were not statistically significant (Fig. 2b, Table III).

Great shearwater

Great shearwaters were sampled in February (chick-rearing), late April (late chick-rearing/fledging) and early June (non-breeding). In the sample, 67% of birds were in active primary moult and 43% were also in active tail moult (Tables I and V). Only a few great shearwaters were seen in July–August (none captured) and all birds closely seen had new primaries, rectrices and body coverts. Three moult states were identified: a) no active

Table VI. Tail moult sequence in the Atlantic yellow-nosed albatross. Each line corresponds to an individual bird. Dataset includes birds in active tail moult or a combination of old and new rectrices (no birds with identical scores were originally present in the sample). Birds were sorted from top to bottom based on the prevalence of low to high moult scores (0–5).

Individual bird	Sampling date	Left rectrices, moult scores						Right rectrices, moult scores					
		6	5	4	3	2	1	1	2	3	4	5	6
1	10 Feb 2006	0	0	0	0	0	1	0	0	0	0	0	0
2	26 Feb 2006	0	0	0	0	0	0	1	0	0	1	0	0
3	28 Apr 2006	0	0	0	0	0	1	0	1	0	0	0	0
4	24 Apr 2006	0	2	0	2	0	0	0	0	0	2	0	2
5	26 Feb 2006	0	0	1	0	0	2	2	0	1	0	1	0
6	24 Apr 2006	0	0	0	0	0	0	3	0	1	0	0	0
7	23 Feb 2006	3	0	2	0	1	5	1	5	0	3	0	3
8	28 Apr 2006	5	1	3	5	3	5	3	3	5	3	1	5
9	19 Apr 2006	4	1	5	1	5	0	5	5	4	1	5	1
10	26 Feb 2006	3	5	5	1	5	1	5	5	1	5	5	1
11	10 Feb 2006	5	4	5	1	5	5	5	5	1	5	4	5
12	24 Apr 2006	5	5	4	5	4	0	0	1	5	5	4	5
13	25 Apr 2006	5	4	5	5	5	4	3	5	5	5	4	5
14	06 Jun 2006	5	4	5	4	5	5	5	5	5	3	4	5
15	05 Aug 2007	5	5	5	5	5	4	5	5	5	5	5	5

primary and tail moult (except by one bird with r1L scored 1), old primaries and rectrices (FO₀ = 100%, moult score table not presented; February *n* = 9, April *n* = 12, June *n* = 1) and active body moult mostly at belly (68%, Table I), b) early primary and tail moult (February *n* = 28) (mean growing primaries = 3.1, max = 5; mean growing rectrices = 1.7, max = 3) and active moult in at least two body areas (Table I), and c) late primary moult (April *n* = 14, June *n* = 3) (mean growing primaries = 1.5, max = 2; mean growing rectrices = 2.2, max = 4) and active body moult less prevalent than in state 'b' (Table I).

There were strong, positive correlations between total moult scores of primaries and rectrices when considering

both sexes combined ($r = 0.78$, $P < 0.0001$, $n = 44$) and when considering females ($r = 0.79$, $P < 0.0001$, $n = 27$) and males ($r = 0.78$, $P = 0.0003$, $n = 17$) separately. Primary and tail moult progressed from February to June, indicated by significant positive correlations between feather moult scores and Julian day (Fig. 2c, Table III).

Primary moult was sequential and proceeded outward from p1 to p10. Five out of 28 birds in early primary moult had one of the four inner primaries scored higher than its adjacent inner feather and eight other birds had at least p1–p3 scored 1 or 2, suggesting simultaneous shedding of inner primaries. The scores of p7–p10 in active moult frequently varied by two or more units,

Table VII. Tail moult sequence in the spectacled petrel. Each line corresponds to an individual bird. Dataset includes birds in active tail moult or a combination of old and new rectrices (no birds with identical scores were originally present in the sample). Birds were sorted from top to bottom based on the prevalence of low to high moult scores (0–5).

Individual bird	Sampling date	Left rectrices, moult scores						Right rectrices, moult scores					
		6	5	4	3	2	1	1	2	3	4	5	6
1	26 Apr 2006	0	0	0	0	0	0	1	0	0	0	0	0
2	25 Jun 2006	0	0	0	1	0	0	0	0	0	0	0	0
3	21 Feb 2006	0	0	0	0	0	1	0	0	0	0	0	0
4	21 Feb 2006	1	1	0	1	0	1	0	0	1	1	1	1
5	27 Feb 2006	1	0	0	0	0	0	0	0	0	0	0	1
6	07 Jun 2006	0	0	1	0	1	3	3	1	1	0	0	1
7	24 Apr 2006	1	0	0	0	0	3	1	0	0	1	0	0
8	28 Feb 2006	3	0	1	0	3	0	3	0	3	0	1	3
9	19 Apr 2006	4	0	0	3	0	0	1	0	0	1	0	4
10	19 Feb 2006	0	0	4	0	0	0	0	0	0	0	0	0
11	06 Jun 2006	0	0	0	0	0	0	5	0	0	0	0	0
12	07 Jun 2006	5	1	5	1	5	1	1	5	1	5	0	5
13	02 Jun 2006	5	3	5	5	3	5	5	3	5	5	3	5
14	26 Apr 2006	5	4	5	5	4	5	5	4	5	5	4	5

Table VIII. Tail moult sequence in the great shearwater. Each line corresponds to an individual bird. Dataset includes birds in active tail moult or a combination of old and new rectrices (birds with identical scores originally present in the sample are presented side by side, e.g. birds #2 and #3, #4 and #5). Birds were sorted from top to bottom based on the prevalence of low to high moult scores (0–5).

Individual bird	Sampling date	Left rectrices, moult scores						Right rectrices, moult scores					
		6	5	4	3	2	1	1	2	3	4	5	6
1	19 Feb 2006	0	0	0	0	0	0	1	0	0	0	0	0
2	21 Feb 2006	0	0	0	0	0	1	0	0	0	0	0	0
3	18 Apr 2006	0	0	0	0	0	1	0	0	0	0	0	0
4	19 Feb 2006	0	0	0	0	0	1	1	0	0	0	0	0
5	17 Feb 2006	0	0	0	0	0	1	1	0	0	0	0	0
6	18 Feb 2006	0	0	0	0	1	1	0	0	0	0	0	0
7	02 Jun 2006	0	0	0	1	0	1	1	0	1	0	0	0
8	18 Apr 2006	0	0	0	1	0	1	0	0	0	2	0	0
9	19 Feb 2006	0	0	0	0	0	2	2	0	0	0	0	0
10	17 Feb 2006	0	0	0	0	0	0	3	0	0	0	0	0
11	23 Feb 2006	0	0	0	0	0	3	3	0	0	0	0	0
12	10 Feb 2006	0	0	0	0	1	5	1	0	0	0	1	0
13	17 Feb 2006	0	0	0	0	0	5	3	0	0	0	0	0
14	25 Apr 2006	0	0	0	0	0	5	5	0	0	0	0	0
15	26 Apr 2006	0	0	0	0	0	5	5	0	0	0	0	0
22	10 Feb 2006	0	0	0	0	5	5	0	0	0	0	0	0
17	27 Apr 2006	0	0	0	0	1	5	5	0	0	0	0	0
16	16 Feb 2006	0	0	0	0	1	5	5	1	0	0	0	0
18	26 Apr 2006	0	0	0	1	0	5	1	0	5	0	0	0
19	19 Apr 2006	0	0	0	0	3	5	5	3	0	0	0	0
20	27 Apr 2006	0	0	0	0	3	5	5	3	0	0	0	0
21	19 Apr 2006	0	0	0	0	4	5	5	4	0	0	0	0
23	28 Apr 2006	0	0	0	0	5	5	5	0	0	0	0	0
24	27 Apr 2006	0	0	0	0	0	5	5	5	0	0	0	0
25	06 Jun 2006	0	0	0	0	5	5	5	5	0	0	0	0
26	02 Jun 2006	0	0	0	5	5	5	5	5	0	0	0	0
27	27 Apr 2006	0	0	0	5	0	5	5	5	0	0	0	0
28	27 Apr 2006	0	0	0	5	0	5	1	0	2	5	0	0
29	26 Apr 2006	0	0	0	5	0	5	5	5	5	0	0	0
30	26 Apr 2006	0	0	1	0	5	5	5	5	0	1	0	0

suggesting that the outermost primaries shed more discretely than inner primaries.

Tail moult

Atlantic yellow-nosed albatrosses (Table II) and spectacled petrels (Table IV) started tail moult at the end of primary moult, while tail moult in great shearwaters started while inner primaries were moulting (Table V). In albatrosses and petrels, the mean number of growing rectrices was 3.5–3.8 in both the early (one or two fully grown new feathers) and late (three or more fully grown new feathers) moult stages. Growing rectrices were interspaced with fully grown ones (scores 0 or 5), and small rectrices (scores 1 and 2) were next to large ones (scores 3, 4, 5, 0) (exceptions were observed in only one albatross and two spectacled petrels; Tables VI and VII). During the period represented in the sample, tail moult in albatrosses (7.0 months) and spectacled petrels (3.5 months) included the whole tail and reached a mean of 6.5 and 7.5 fully grown rectrices. For albatrosses and petrels, it was not

possible to clearly identify moult sequence(s) based on the number of cases each rectrix was among the first ones to shed.

The definition of ‘early’ and ‘late’ tail moult based on the sample of Atlantic yellow-nosed albatross and spectacled petrel seemed to not apply to the moult pattern of great shearwaters, at least for the period represented in this sample (February–June, chick-rearing and non-breeding). However, these moult progress categories were still useful to compare tail moult patterns among the studied species. In the great shearwater, the mean number of growing rectrices was 1.9 in the early moult and 2.0 in the late moult, progressing from summer to early winter. In all great shearwaters ($n = 30$, Table VIII), the moult started in the central pairs of rectrices. In the 3.5 months represented in the sample, the moult progressed outwards from r1 to r3 in most birds, reaching a mean of 3.9 new fully grown rectrices. Because the sample included mostly shearwaters in early tail moult (22 birds had moult only in the first or first and second pairs of rectrices), it is not clear whether the moult progresses sequentially towards outer rectrices

or tends to alternate feather pairs, as observed in the spectacled petrel and Atlantic yellow-nosed albatross samples.

Discussion

The data presented here for Atlantic yellow-nosed albatrosses supports previous knowledge on moult patterns in albatrosses: i) primary moult does not overlap breeding (Furness 1988, Prince *et al.* 1993, Weimerskirch 1991, Edwards 2008), ii) p8–p10 constitutes a moult series (Harris 1973, Prince *et al.* 1993), iii) replacement of p8–p10 proceeds outward, and iv) several patterns of moult are possible according to age (immatures, adults) and breeding status (breeders, failed breeders, sabbaticals).

This study provided new information on the timing of tail and body moult. Tail moult did not overlap breeding in the Atlantic yellow-nosed albatross and birds supposed to be breeding adults had a lower occurrence of body moult than birds supposed to be immatures and non-breeding adults. Timing of tail and body moult in Atlantic yellow-nosed albatrosses may be related to a long breeding season, which may require a higher degree of overlap of activities at times of abundant food resources. Costs of tail moult may be smaller than primary moult, at least in terms of loss of flight efficiency.

Scoring of primaries and rectrices of the Atlantic yellow-nosed albatross presented some potential difficulties. Around 50% of adults sampled during chick-rearing had all rectrices scored as new and the other half had all rectrices scored as old. Furthermore, most adults had primaries scored as new (Table II). However, during chick-rearing, breeding birds would be expected to have a relatively high proportion of old primaries. This reported occurrence of old and new primaries and rectrices may reflect: i) non-differentiation of more than one generation of old feathers, or ii) scoring error resulting from difficulty in differentiating old and new feathers. These difficulties may also have affected scoring in immatures sampled in the non-breeding period that had all primaries ($n = 4$) and rectrices ($n = 3$) scored as old. Difficulties in differentiating old and new feathers may explain birds with all rectrices scored as new in moult states 'a' ($n = 7$) and 'c' ($n = 4$) (Table II).

The great shearwater winters in the north-west Atlantic Ocean, mostly north of 45°N. Brown (1988) suggested that adult breeders start primary moult when they reach wintering grounds in May–June, and primary moult lasts around 40 days, with up to six inner primaries replaced simultaneously. A few documented cases of birds moulting in the south Atlantic Ocean have been interpreted as immatures because most long-distance migrant Procellariiformes breeding in high latitudes do not overlap breeding and moult, and postpone moult until arrival in wintering grounds. Great shearwaters

moulting inner primaries and primary coverts were recorded in Tierra del Fuego in January (Watson 1971). One moulting bird was seen offshore west Africa in December (Bourne 1963). Three birds collected in North Carolina, USA, in June were completing moult of the outermost primaries and tail (Watson 1970). These results suggest that the south-west Atlantic Ocean holds important numbers of great shearwaters moulting primaries and tail, which may include immatures and failed breeders, as well as breeding birds starting moult at the end of the breeding period, as occurs in Cory's shearwaters (Alonso *et al.* 2009). In our sample, birds without active primary moult in February ($n = 9$) may have included breeding birds on long foraging trips as well as non-breeding birds that had not yet started primary moult. If so, birds without active primary moult sampled in April and June ($n = 13$) probably included mostly breeding birds, which may start primary moult in the north Atlantic wintering grounds. Similarly, the short-tailed shearwater (*Puffinus tenuirostris* Temminck), also a high-latitude, trans-equatorial migrant, moults head and body feathers in breeding grounds after breeding and delays primary and tail moult until June–July when they reach north Pacific wintering grounds (Marshall & Serventy 1956). On the other hand, Cory's shearwater, which migrates shorter distances within the north Atlantic Ocean, can start wing moult during breeding and probably completes moult in wintering grounds (Alonso *et al.* 2009). Our data suggest that great shearwaters could start moult in the Southern Hemisphere, halting moult for migration, and finishing moult in the north Atlantic, a situation distinct from that proposed by Brown (1988).

Moult patterns across species

The onset of primary moult in the spectacled petrel and great shearwater was during chick-rearing, similar to that observed in the sooty shearwater (*Puffinus griseus* Gmelin) and the northern fulmar (Allard *et al.* 2008), with nearly simultaneous shedding of the inner primaries (although information on age and breeding status is not available). While great shearwaters synchronize primary and tail moult, spectacled petrels and Atlantic yellow-nosed albatrosses had no moult synchronization in these feather tracts.

Prince *et al.* (1993) reported that black-browed albatross and grey-headed albatross (*Thalassarche chrysostoma* (Forster)) replaced rectrices from the outermost to the innermost pair so that the central pair was the last one to moult. Our data suggest that Atlantic yellow-nosed albatross, along with the spectacled petrel, replace rectrices alternately and apparently without a fixed sequence. Great shearwaters moulted rectrices outward, starting at the central pair.

Tail moult started well after the onset of primary moult in the spectacled petrel and the great shearwater (unknown age and breeding status). Breeding and non-breeding birds may have different timing of onset of primary and tail moult. Delay of the onset of tail moult in these species until completion of inner primary moult may prevent simultaneous growing of a relatively large number of inner primaries and rectrices or simultaneous gaps in wings and tail. The lack of progress in moult scores of primaries and rectrices of spectacled petrel with Julian day (despite a trend shown in Fig. 2) suggests that our sample included birds of different age and breeding status.

The synchronization in moult differed among species. Male and female great shearwaters synchronized primary and tail moult, while spectacled petrels and Atlantic yellow-nosed albatross did not. This difference could be explained by the long-distance migration of great shearwaters constraining the time available for moult, a situation not faced by the other two species. Some moult states with active tail moult and inactive primary moult seemed to represent advanced moult where primary moult was already complete and tail and body moult either started later or extended for a longer period of time, as found in immature Atlantic yellow-nosed albatross during non-breeding. Primary moult may represent a substantial proportion of the cost of the moult in some species. However, extensive overlap of moult in different feather tracts suggests that metabolic costs of primary moult may not be overly restrictive. For example, body feathers account for 75–80% of total feather weight in cape petrels (*Daption capense* (L.)) (Beck 1969) and may contribute to a significant part of the cost of replacing all feathers.

Around 50% of the Procellariiformes species overlap moult of different feather tracts (tail and body, sometimes primaries) with breeding (Bridge 2006). The metabolic and nutritional ability to afford simultaneous moult of different feather tracts supports the idea that impaired flight performance caused by wing moult is a strong factor driving no overlap of primary moult and breeding (Edwards 2008). Impaired flight performance caused by primary moult could explain why albatrosses undertaking long foraging trips do not moult primaries during breeding, while similarly-sized giant petrels (*Macronectes* spp.), which feed on carrion near breeding colonies, start primary moult during egg laying or early chick provisioning (Hunter 1984). When the requirement for extremely high flight efficiency is loosened (for example by abundant food resources close to breeding colonies), a variable degree of overlap between primary moult and breeding may be observed.

A broad understanding of moult ecology requires information on all components of the population, age and breeding status, multiple feather tracts, breeding performance and other biological data in successive years.

Moult sampling at sea may yield samples that represent the population in an incomplete manner depending on the spatial and temporal distribution of age classes, breeding and non-breeding birds, males and females. However, strategic spatial and temporal allocation of offshore sampling effort when birds are in active moult has great potential to complement moult studies conducted at breeding colonies.

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Author contribution

L. Bugoni: contributed with study delineation, field sampling, data analysis, writing and revision. L.C. Naves: contributed with data analysis, writing and revision. R.W. Furness: contributed with study delineation, writing and revision.

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