Polar Biol
DOI 10.1007/s00300-013-1309-5

ORIGINAL PAPER

Differences in the timing and extent of annual moult of black-browed albatrosses *Thalassarche melanophris* living in contrasting environments

Paulo Catry · Maud Poisbleau · Miguel Lecoq · Richard A. Phillips

Received: 15 November 2012 / Revised: 5 February 2013 / Accepted: 16 February 2013

Abstract Moult entails costs related to the acquisition of energy and nutrients necessary for feather synthesis, as well as the impact of reduced flight performance induced by gaps in the wing plumage. Variation in moult strategies within and between populations may convey valuable information on energetic trade-offs and other responses to differing environmental constraints. We studied the moult strategies of two populations of a pelagic seabird, the black-browed albatross *Thalassarche melanophris*, nesting in contrasting environments. According to conventional wisdom, it is exceptional for albatrosses (Diomedeidae) to moult while breeding. Here we show that black-browed albatrosses breeding on the Falklands regularly moult primaries, tail and body feathers during chick-rearing, and the majority of those at South Georgia show some body feather moult in late chick-rearing. The greater moult-breeding overlap at the Falklands allows the birds to annually renew more primary feathers than their counterparts at South Georgia. The results of the present paper, pooled with other evidence, suggest that black-browed albatrosses from South Georgia face a more challenging environment during reproduction. They also serve to warn against the uncritical acceptance of conventional ideas about moult patterns when using feathers to study the ecology of seabirds and other migrants for which there is scant information at particular stages of the annual cycle.

Keywords Feathers · South Georgia · Falkland Islands · Moult-breeding overlap · Stable isotopes

Introduction

Fully grown feathers are inert structures that suffer relatively rapid deterioration due to physical abrasion and ultraviolet radiation. As such, most feathers need to be replaced annually or, at most, every 2 (exceptionally more) years (Rohwer et al. 2009). The growing of new feathers is costly because of increased demands in energy and nutrients; the moult of flight feathers is even more so, because the gaps created after old feathers are lost impair flight performance until replacements are fully grown (Hedenström and Sunada 1999). As a result of such increased costs, most bird species organise their annual cycle in such a way that moult does not overlap with either reproduction or migration (Bridge 2006; Newton 2008).

Due to fundamental limits on the rate of feather growth, larger birds often have a protracted moult period due to the time required to grow their relatively long feathers (Rohwer et al. 2009). Large birds also tend to have long breeding seasons, and this is particularly true in many pelagic seabirds. As a result, large birds have developed specific moult strategies that often include, amongst other adaptations, the retention of some flight feathers for 2–3 years, in contrast to

P. Catry (✉) · M. Lecoq
Eco-Ethology Research Unit, ISPA, Rua Jardim do Tabaco 34, 1149-041 Lisbon, Portugal
e-mail: paulo.catry@gmail.com

P. Catry · M. Lecoq
Museu Nacional História Natural e da Ciência, Universidade de Lisboa, Rua da Escola Politécnica 58, 1250-102 Lisbon, Portugal

M. Poisbleau
Department Biology, Ethology, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Antwerp, Wilrijk, Belgium

R. A. Phillips
British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

the annual moult of the complete plumage which is characteristic of smaller species (Rohwer et al. 2009). Despite this, large birds with long breeding seasons, such as albatrosses, still face difficulties in finding sufficient time during the non-breeding period to replace enough feathers, and in at least one genus *Phoebastria,* the accumulation of old feathers eventually forces birds to skip breeding seasons in order to renew their plumage (Langston and Rohwer 1996; Rohwer et al. 2011).

Moult strategies may show some flexibility within species in response to changing states of individuals (e.g. from active breeding to non-breeding), as well as to environmental variation (Langston and Hillgarth 1995; Hemborg et al. 2001; Borras et al. 2004; Alonso et al. 2009). As such, their study can be highly informative about responses of birds to environmental constraints. In addition, results from the chemical analysis of feathers (mostly studies of stable isotopes, trace elements and pollutants) are used increasingly to infer trends in the spatial and trophic ecology of many species, as well as to determine levels of environmental contamination (Stewart et al. 1999; Hobson and Wassenaar 2008; Inger and Bearhop 2008). In such studies, obtaining reliable information on timing of moult of different feather types is not only critical for validating results, but may also allow further inferences about variation among individuals, for example in migration strategies (González-Solís et al. 2011).

According to conventional wisdom, albatrosses (Diomedeidae) suspend moult during the entire breeding season, with rare exceptions in a small minority of species where occasional, largely aberrant individuals have been recorded moulting (Harris 1973; Berruti 1979; Melville 1991; Weimerskirch 1991; Prince et al. 1993; Langston and Rohwer 1996; Cobley and Prince 1998; Edwards 2008). The only study reporting the regular moult of flight feathers during breeding involved yellow-nosed albatrosses *Thalassarche chlororhynchos* and found less than 10 % of the individuals still growing the last of the moulted primaries (>90 % growth completed) at the start of the incubation (Furness 1988). The chemical analysis of albatross feathers is therefore used regularly to obtain information believed to pertain to the non-breeding period (Cherel et al. 2000, 2013; Phillips et al. 2009, 2011). During a long-term demographic and ecological study of black-browed albatrosses *Thalassarche melanophris* in the Falkland Islands (Catry et al. 2010, 2011; Granadeiro et al. 2011), we noted the occurrence of moult of feathers of different types in the breeding colony. There are no published data on moult patterns of black-browed albatrosses at the Falklands, and previous studies of conspecifics ca. 1,500 km away at South Georgia are inconclusive as to whether some individuals might moult feathers during breeding, as birds were not checked in the late season (Tickell and Pinder 1975; Prince et al. 1993).

Black-browed albatrosses nesting on the Falkland Islands forage north of the Antarctic Convergence, over rich waters of the Patagonian Shelf, while those nesting at South Georgia forage predominantly south of the Antarctic Convergence and mostly over deep oceanic waters (e.g. Wakefield et al. 2011). Birds from the Falklands are relatively sedentary, wintering on the Patagonian shelf and shelf-break (Grémillet et al. 2000), while those from South Georgia are long-distance migrants, mostly wintering off southern Africa (Phillips et al. 2005). Black-browed albatrosses from the Falklands generally enjoy a higher breeding success and a lower incidence of breeding deferral by experienced breeders (skipping breeding in 1 year) than their counterparts from South Georgia (Arnold et al. 2006; Nevoux et al. 2010; Catry et al. 2011). If this indicates a more benign environment, presumably with greater food availability, we could predict a higher moult-breeding overlap in the Falklands, as in these conditions individual birds would be in a better position to simultaneously invest in offspring and self-maintenance (Alonso et al. 2009). Furthermore, as birds do not usually moult during migration, sedentary albatrosses from the Falklands may have more time to carry out a more extensive moult than those from South Georgia.

The purpose of this study was therefore to carry out a systematic comparison of moult strategies of black-browed albatrosses at the two sites, with particular attention to the existence of a moult-breeding overlap.

Methods

This study took place on New Island (51°43′S, 61°18′W), West Falklands and on Bird Island (54°00′S, 38°03′W), South Georgia. The Falklands are located on the Patagonian Shelf ca. 600 km north of the Antarctic polar convergence, whereas South Georgia emerges from deep oceanic waters and is ca. 300 km south of the Antarctic polar convergence; consequently, the two archipelagos have contrasting climates (the weather is generally colder, wetter and windier around South Georgia), and the surrounding waters are distinct in terms of the dominant oceanographic characteristics.

Checking of overwinter moult patterns in birds that had returned relatively recently to the colony was carried out in early to mid-incubation, mostly in October–November, on New Island, annually from 2005 to 2011. This was done with minimal disturbance, as follows. Without ever restraining the bird, the egg was gently removed from the nest. Then, the observer held the tip of one of the wings, while the albatross remained sitting or standing above the nest, rapidly stretched the wing and examined the moult pattern. This procedure took only a few seconds during which time most albatrosses remained on the nest pedestal (the few that stepped off, returned immediately), and the egg was then returned. As all the individuals inspected were ringed breeders in the long-term monitoring colony, we had information on their previous breeding success. Each of the 10 primary feathers was classified, based on colour and wear (see Prince et al. 1993), as "new" (moulted since last breeding attempt), "old" (moulted the year before the last attempt) or "very old" (moulted 2 years before).

To check for moult-breeding overlap, birds were also examined in late chick-rearing. On New Island, this took place between 24 and 31 March 2012, ca. 2–6 weeks before fledging, and on Bird Island between 20 and 28 April 2012, when chicks were roughly at the same stage of development as when we performed the checks on New Island (laying is ca. 3 weeks later at South Georgia). On both sites, adults were captured by hand just after they had finished feeding their chick. To keep handling times to a minimum, we checked each primary of one wing only, looking for missing, actively growing or recently grown feathers, and did not attempt to determine the age of the old feathers. Each feather was scored as: 0 = old feather; 1 = feather missing or in pin; 2 = new feather emerging from the sheath, grown to up to one third of its maximum length; 3 = grown between one-third and two-thirds; 4 = between two-thirds to full grown and with remains of waxy sheath or blood in calamus; 5 = fully developed new feather (Ashmole 1962). We also recorded the number of actively growing secondary and tail feathers. Finally, by gently blowing on the back, neck and wing of the birds, we looked for evidence of active moult of wing-coverts and body feathers. Besides the checks of actively breeding birds, we also were able to capture 4 failed breeders that were present at the colony on New Island and examined moult on those as well.

In this paper, we follow Prince et al. (1993) in recognising two main types of moult of primaries. Individuals in *Phase* 1 *moult* had moulted the 3 outer primaries over the previous winter and a variable number of inner primaries, whereas individuals in *Phase* 2 *moult* had not moulted the outer 3 primaries, but had moulted primaries 6–7 and some combination of the 5 inner primaries. The vast majority of moult patterns could be categorised in this scheme, although there were occasional exceptions (see results, and Catry et al. unpubl. data).

We used General Linear Models (GLM) to assess the influence of previous breeding success (0 or 1 chick raised), moult phase (contrasting *Phase* 1 and *Phase* 2) and year on the number of primaries moulted overwinter on New Island. We used t tests to compare the number of primaries moulted overwinter by birds nesting on New Island with the published values from Bird Island, South Georgia (Prince et al. 1993). We used Fisher's Exact Test to compare the number of actively breeding individuals moulting on New Island and on Bird Island.

Results

Number of primaries moulted overwinter

We tested whether the number of fresh primaries in albatrosses inspected during incubation on New Island differed according to previous breeding success, moult phase and year. Moult phase was not significant and was removed from the model. The final model suggests that there are year differences which interact with previous nesting success (Table 1). This is because the difference in the number of primaries moulted per year by previously successful and by unsuccessful breeders was inconsistent, and variability between years appeared to be fairly low in previously unsuccessful birds (Table 2). Table 2 also shows that there is no consistent tendency for previously failed breeders to moult more primaries than previously successful breeders.

Across years, unsuccessful breeders from New Island moulted 4.95 ± 1.23 ($n = 370$) primaries per annum, which compares to 4.57 ± 1.42 ($n = 35$) reported by Prince et al. (1993) at South Georgia ($t_{403} = 3.11$, $P < 0.10$). For previously successful breeders, if data from the year with fewest primaries moulted on New Island (2005, 4.50 ± 0.97 primaries, $n = 66$) are compared with the published value for South Georgia (3.66 ± 0.74, $n = 15$), the difference is highly significant ($t_{79} = 3.11$, $P < 0.01$). The same comparison for each year from 2006 to 2011 (data in Table 2) similarly yields significant (and larger) differences, which clearly show that birds from New Island moult more feathers between breeding attempts than those from Bird Island. The mean difference in number of primaries moulted per year between New Island and South Georgia is 0.4 and 1.2 for unsuccessful and successful breeders, respectively.

Table 1 GLM with significant predictors of number of primaries moulted overwinter on New Island

	df	Mean square	*F*	*P*
Intercept	1	18,539.5	13,095.2	<0.001
Year	6	3.69	2.61	0.016
Previous success	1	0.05	0.04	0.851
Year × previous success	6	3.09	2.18	0.043
Error	864			

Table 2 Number (±SD) of primary feathers moulted per year in relation to previous breeding success on New Island

Years	Previously unsuccessful	Previously successful
2005	5.05 ± 1.33 ($n = 84$)	4.50 ± 0.97 ($n = 66$)
2006	5.14 ± 1.22 ($n = 36$)	5.17 ± 1.15 ($n = 71$)
2007	4.74 ± 0.98 ($n = 46$)	4.75 ± 1.04 ($n = 67$)
2008	4.93 ± 1.11 ($n = 59$)	4.97 ± 1.10 ($n = 116$)
2009	4.96 ± 1.14 ($n = 71$)	5.47 ± 1.22 ($n = 32$)
2010	4.90 ± 1.43 ($n = 40$)	4.63 ± 1.12 ($n = 79$)
2011	4.82 ± 1.45 ($n = 34$)	4.94 ± 1.47 ($n = 77$)
Annual comparison	$F_{6,369} = 0.53$, $P = 0.79$	$F_{6,507} = 4.21$, $P < 0.001$

Moult-breeding overlap

Of 32 breeders examined in late chick-rearing on New Island, 26 (81 %) had at least 1 primary missing or growing, 12 (38 %) had either 1 or 2 rectrices growing and 1 (3 %) had 1 secondary growing. The number of primaries in active moult (or recently grown) per individual was 1.7 ± 1.1.

At least 9 (28 %) of the active breeders had wing-coverts growing and at least 7 (22 %) had body feathers growing. Note, however, that these latter values are underestimates of the real-proportion moulting, given that birds were only rapidly and superficially checked for wing-covert and body feather moult in order to minimise disturbance. All four failed birds checked at this time were moulting primaries (2–3 primaries growing; 2 of them had one primary fully grown, including one case of an individual with a new P8 fully grown that must have started moult several weeks earlier).

On Bird Island (South Georgia), none of 18 active breeders checked in late chick-rearing were moulting primaries, secondaries or rectrices. Comparing with New Island, the difference is statistically significant for primaries (Fisher's Exact Test: $P < 0.001$) and for rectrices ($P = 0.002$). On Bird Island, at least 10 (56 %) out of 18 individuals were growing some body feathers. We refrain from comparing this figure to the one obtained on New Island, as checks of body feathers are not necessarily comprehensive given the large skin area and high feather density, and we could not fully standardise the method between islands.

Moult progression

At New Island, primary moult did not follow straightforward rules, such as a simple scheme with *Phase* 1 *moult* progressing descendently from P8 to P10, and *Phase* 2 *moult* starting at P7 and progressing ascendently. Of 13 individuals engaged in active *Phase* 1 *moult*, P8 was the first primary to be shed and regrown in 6 birds, whereas P9 was the first in the other 7 birds. Of 17 birds engaged in *Phase* 2 *moult*, 16 had started at P7 and 1 at P6. Note, however, that for most birds where moult appeared to start at P7, P6 was at a similar stage of growth, and hence, P7 and P6 were moulted almost simultaneously. Furthermore, there was an individual simultaneously growing P6 and P9 (and no other primaries), hence entirely outside the simple *Phase* 1 or *Phase* 2 classification system.

Total moult score for active breeders in late chick-rearing at New Island was 5.2 ± 3.8 (range: 0–11), while for failed birds, it was 9.0 ± 4.2 (range: 4–13), a difference that approaches significance, despite the small sample of only 4 failed individuals ($F_{1,35} = 3.56$, $P = 0.068$).

Discussion

The present study documents, for the first time in an albatross species, an extensive and presumably regular moult-breeding overlap. It also shows that the progression of primary moult is not fixed, but highly variable and, at present, largely unpredictable. These findings have implications for the use of data on the chemical composition of feathers to infer distribution, habitat use, trophic level, environmental concentrations of heavy metals, other pollutants, etc. experienced by birds in the non-breeding season. They also imply that black-browed albatrosses from the Falklands and South Georgia are exposed to challenges imposed by the environment that differ considerably in their intensity and perhaps seasonality.

Black-browed albatrosses from South Georgia annually engage in long-distance migrations predominantly to the Benguela Upwelling region, around the southern tip of the African continent (Phillips et al. 2005), while most albatrosses from the Falklands are largely sedentary, showing an extensive overlap between breeding and non-breeding ranges (Grémillet et al. 2000, Catry et al. unpubl. data). Such difference in migratory strategies may well explain, at least in part, the differences in moult patterns described here. In a review of moult strategies of seabirds, Bridge (2006) reported that moult-breeding overlap is more common in species or populations that are relatively sedentary, as opposed to migratory. Nevertheless, (primary) moult-breeding overlap does occur in petrels that are long-distance migrants (e.g. Alonso et al. 2009), as birds have the option of starting moult while still breeding, and then suspending it until after they reach the winter quarters (Ramos et al. 2009). This allows them to migrate without the need to allocate energy and nutrients to feather synthesis, as well as avoid costs related to gaps in the wing plumage at a time when efficiency during long-distance flight is paramount. Hence, if foraging conditions were sufficiently good at South Georgia, we might have expected moult-breeding overlap to have arisen as a viable strategy to allow a more extensive replacement of flight feathers.

Black-browed albatrosses from the Falklands and South Georgia do not seem merely to be following different strategies to obtain a similar result. Not only does the timing of primary and tail feather moult differ, but so too does the extent. This suggests that albatrosses from South Georgia face more difficult conditions throughout their annual cycle, because moulting fewer feathers is thought to have consequences for fitness (Rohwer et al. 2011). We note, however, that the available data for South Georgia comes from one single year, and given that there is considerable annual variation in the number of moulted feathers, more data would be desirable. Other lines of evidence point similarly to the conclusion that black-browed albatrosses nesting in South Georgia face a more challenging environment, not only when breeding, but perhaps throughout the annual cycle. The probability of breeding deferral for experienced individuals is much higher on South Georgia than on the Falklands (Arnold et al. 2006; Nevoux et al. 2010; Catry et al. 2011). Furthermore, breeding success is considerably lower and more variable at South Georgia (Arnold et al. 2006; Nevoux et al. 2010; Catry et al. 2011, own unpubl. data). Adult survival rates are also likely to differ, but they are less informative of the natural environment that the two populations face, given that much mortality is believed to be directly human induced, occurring when birds attend fishing vessels.

The annual variation in extent of primary moult reported here for the Falklands can be understood in a context where birds respond in a flexible way to fluctuations in environmental conditions. Similar variation has been reported for grey-headed albatrosses *Thalassarche chrysostoma* from South Georgia (Cobley and Prince 1998). Interestingly, we only found significant annual differences for successful breeders, which may indicate that failed breeders have more time to complete the moult of an optimal number of primaries and hence greater scope to compensate for any hardships imposed by the environment in less favourable seasons. However, successful breeders did not consistently moult fewer feathers than failed breeders, which somewhat challenges the idea that there might be an allocation trade-off between caring of offspring and plumage self-maintenance.

The results presented here warn investigators against the uncritical acceptance of established conventions. The general conclusion that can be taken from the bibliography that albatrosses do not moult during breeding (e.g. Cherel et al. 2013) does not apply to the two populations of black-browed albatrosses studied here. In the Falklands, moulting of primaries, tail feathers and body feathers during the breeding season is common. Even in South Georgia, despite previous very valuable research on moult patterns (Prince et al. 1993), closer investigation late in the season revealed that body feathers can be grown during breeding. If sampled, such feathers would not convey information on conditions in the wintering grounds. It is this far uncertain whether these two populations are exceptional, or whether a closer examination of both active and failed breeders of other species and populations towards the end of chick-rearing would also reveal the presence of birds in active moult.

More work is needed to fully understand the moult strategies of albatrosses and other taxa. Basic investigations such as checking moult progression in samples of birds at different stages of the annual cycle are a necessity in order to ensure that inferences about their lives and environments from feather analyses are robust. Otherwise, the number of examples in the literature where inappropriate assumptions have led to major errors of interpretation (e.g. Norris et al. 2004; Reudink et al. 2008) will be set to increase.

Acknowledgments We are grateful to the many fieldworkers who assisted with the study, particularly Rafael Matias (who first noted the moult-breeding overlap on New Island), Ana Almeida, José Pedro Granadeiro, Ruth Brown and Jennifer James. The New Island Conservation Trust supported field studies on their New Island reserve. This study was financed by Fundação para a Ciência e a Tecnologia (FCT-Portugal) through Project PTDC/MAR/099366/2008 and project PEst-OE/MAR/UI0331/2011. Formal permits and further financial support were received from the Falkland Islands Government. Ian, Maria and Georgina Strange provided important support in the field and in Stanley.

References

Alonso H, Matias R, Granadeiro JP, Catry P (2009) Moult strategies of Cory's shearwaters *Calonectris diomedea borealis*: the influence of colony location, sex and individual breeding status. J Ornithol 150:329–337

Arnold JM, Brault S, Croxall JP (2006) Albatross populations in peril: a population trajectory for black-browed albatrosses at South Georgia. Ecol Appl 16:419–432

Ashmole NP (1962) The black noddy *Anous tenuirostris* on Ascension Island. Part 1. General biology. Ibis 103:235–273

Berruti A (1979) The breeding biologies of the sooty albatrosses *Phoebetria fusca* and *P. palpebrata*. Emu 79:161–175

Borras A, Cabrera T, Cabrera J, Senar JC (2004) Interlocality variation in the speed of moult in the citril finch *Serinus citrinella*. Ibis 146:14–17. doi:10.1111/j.1474-919X.2004.00199.x

Bridge ES (2006) Influences of morphology and behavior on wing-moult strategies in seabirds. Mar Ornithol 34:7–19

Catry P, Phillips RA, Forster IP, Matias R, Lecoq M, Granadeiro JP, Strange IJ (2010) Brood-guarding duration in black-browed albatrosses: temporal, geographical and individual variation. J Avian Biol 41:460–469

Catry P, Forcada J, Almeida A (2011) Demographic parameters of black-browed albatrosses *Thalassarche melanophris* from the

Falkland Islands. Polar Biol 34:1221–1229. doi:10.1007/s00300-011-0984-3

Cherel Y, Hobson KA, Weimerskirch H (2000) Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122:155–162

Cherel Y, Jaeger A, Alderman R, Jaquenet S, Richard P, Wanless RM, Phillips RA, Thompson DR (2013) A comprehensive isotopic investigation of habitat preferences in nonbreeding albatrosses from the Southern Ocean. Ecography. doi:10.1111/j.1600-0587.2012.07466.x

Cobley ND, Prince PA (1998) Factors affecting primary moult in the grey-headed albatross. Condor 100:8–17

Edwards AE (2008) Large-scale variation in flight feather moult as a mechanism enabling biennial breeding in albatrosses. J Avian Biol 39:144–151

Furness RW (1988) Influences of status and recent breeding experience on the moult strategy of the yellow-nosed albatross *Diomedea chlororhynchos*. J Zool (Lond) 215:719–727

González-Solís J, Smyrli M, Militão T, Gremillet D, Tveraa T, Phillips RA, Boulinier T (2011) Combining stable isotope analyses and geolocation to reveal kittiwake migration. Mar Ecol Prog Ser 435:251–261

Granadeiro JP, Phillips RA, Brickle P, Catry P (2011) Albatrosses following fishing vessels. How badly hooked are they on an easy meal? PLoS ONE 6:e17467

Grémillet D, Wilson RP, Wanless S, Chater T (2000) Black-browed albatrosses, international fisheries and the Patagonian Shelf. Mar Ecol Prog Ser 195:269–280

Harris MP (1973) The biology of the waved albatross *Diomedea irrorata* of Hood Island, Galapagos. Ibis 115:483–510

Hedenström A, Sunada S (1999) On the aerodynamics of moult gaps in birds. J Exp Biol 202:67–76

Hemborg C, Sanz JJ, Lundberg A (2001) Effects of latitude on the trade-off between reproduction and moult: a long-term study with pied flycatcher. Oecologia 129:206–212. doi:10.1007/s004420100710

Hobson KA, Wassenaar LI (2008) Tracking animal migration with stable isotopes. Academic Press, London

Inger R, Bearhop S (2008) Applications of stable isotope analyses to avian ecology. Ibis 150:447–461

Langston NE, Hillgarth N (1995) Moult varies with parasites in Laysan albatrosses. Proc R Soc Lond B 261:239–243

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

Melville DS (1991) Primary moult in black-browed and shy mollymawks. Notornis 38:51–59

Nevoux M, Forcada J, Barbraud C, Croxall J, Weimerskirch H (2010) Bet-hedging response to environmental variability, an intraspecific comparison. Ecology 91:2416–2427

Newton I (2008) The migration ecology of birds. Academic Press, London

Norris DR, Marra PP, Montgomerie R, Kyser TK, Ratcliffe LM (2004) Reproductive effort, moulting latitude, and feather colour in a migratory songbird. Science 306:2249–2250

Phillips R, Silk J, Croxall J, Afanasyev V, Bennett V (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. Ecology 86:2386–2396. doi:10.1890/04-1885

Phillips RA, Bearhop S, McGill RA, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. Oecologia 160:795–806. doi:10.1007/s00442-009-1342-9

Phillips RA, McGill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. Mar Biol 158:2199–2208

Prince PA, Rodwell S, Jones M, Rothery P (1993) Moult in black-browed and grey-headed albatrosses *Diomedea melanophris* and *D. chrysostoma*. Ibis 135:121–131

Ramos R, Militão T, González-Solís J, Ruiz X (2009) Moulting strategies of a long-distance migratory seabird: the Mediterranean Cory's shearwater. Ibis 151:151–159

Reudink MW, Marra PP, Langin KM, Studds CE, Kyser TK, Ratcliffe LM (2008) Moult-migration in the American redstart (*Setophaga ruticilla*) revisited: explaining variation in feather δD signatures. Auk 125:744–748

Rohwer S, Ricklefs RE, Rohwer VG, le Copp MM (2009) Allometry of the duration of flight feather molt in birds. PLoS Biol 7:e1000132

Rohwer S, Viggiano A, Marzluff JM (2011) Reciprocal tradeoffs between moult and breeding in albatrosses. Condor 113:61–70

Stewart FM, Phillips RA, Bartle JA, Craig J, Shooter D (1999) Influence of phylogeny, diet, moult schedule and sex on heavy metal concentrations in New Zealand Procellariiformes. Mar Ecol Prog Ser 178:295–305

Tickell WNL, Pinder R (1975) Breeding biology of the black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at Bird Island, South Georgia. Ibis 117:433–451

Wakefield ED, Phillips RA, Trathan PN, Arata J, Gales R, Huin N, Robertson G, Waugh SM, Weimerskirch H, Matthiopoulos J (2011) Habitat preference, accessibility and competition limit the global distribution of breeding black-browed albatrosses. Ecol Monogr 81:141–167

Weimerskirch H (1991) Sex-specific differences in moult strategy in relation to breeding in the wandering albatross. Condor 93:731–737