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METHOD

Moulting patterns drive within-individual variations of stable isotopes and mercury in seabird body feathers: implications for monitoring of the marine environment

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Abstract One major limitation in the use of body feathers of seabirds as a monitoring tool of the trophic structure and contamination levels of marine ecosystems is the degree of heterogeneity in feather chemical composition within individuals. Here, we tested the hypothesis that moulting patterns drive body feather heterogeneity, with synchronous moult minimizing within-individual variations, in contrast to asynchronous feather growth. Chicks of white-chinned petrels *Procellaria aequinoctialis* (representative of bird chicks) and adults of king penguins *Aptenodytes patagonicus* (representative of adult penguins) that moult their body feathers synchronously showed very low within-individual variations in their feather $\delta^{13}C$ and $\delta^{15}N$ values and mercury (Hg) concentrations. By contrast, body feathers of adults of Antarctic prions *Pachyptila desolata* (representative of adult seabirds with asynchronous feather growth during a protracted moult) presented much higher within-individual variances for the three parameters. These findings have three important implications for birds presenting a synchronous body moult. (1) They suggest that all body feathers from the same individual have identical $\delta^{13}C$ and $\delta^{15}N$ values and Hg content. (2) They predict negligible within-individual variations in the body feather values of other useful stable isotopes, such as $\delta^{2}H$ and $\delta^{34}S$, as well as in the concentrations of other compounds that are deposited in the keratin structure. (3) Analysis of one or any number of pooled body feathers is equally representative of the individual. In conclusion, we recommend that long-term routine monitoring investigations focus on birds presenting synchronous rather than asynchronous moult of body feathers both in marine and terrestrial environments. This means targeting chicks rather than adults and, for seabirds, penguins rather than adults of flying species.

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Introduction

Feathers are used extensively in avian biology, chemoecology and toxicology because they can be easily collected and are metabolically inert after synthesis, thus preserving their chemical composition almost indefinitely. For instance, stable isotope analyses of feathers have provided insights into many aspects of avian ecology (Inger and Bearhop 2008; Hobson 2011), and feathers are considered as excellent non-destructive tools for monitoring contaminants, including heavy metals and persistent organic pollutants (Burger 1993; García-Fernández et al. 2013). More recently, the application of the stable isotope method to ecotoxicological studies has granted insight into patterns of contamination among sites, species and individuals (e.g. Ofukany et al. 2012; Ramos et al. 2013). Feathers from museum collections have been further used to depict historical changes in birds' foraging ecology and contaminant exposure (Vo et al. 2011; Jaeger and Cherel 2011).

Ideally, a monitoring tool must show little within- and between-individual variations in the levels of targeted compounds in order to facilitate the statistical description of spatio-temporal trends within a population. Indeed, a main limitation in the use of feathers is within-individual heterogeneity both between and within feather types. For

example, changes in foraging habitat or diet during moult lead to large variations in feather $\delta^{13}C$ and $\delta^{15}N$ values, respectively (Jaeger et al. 2010), and feathers that grow at different times present different mercury (Hg) concentrations, as the Hg body pool is progressively depleted during the moult (Furness et al. 1986; Braune and Gaskin 1987). For both scientific and ethical reasons, body feathers are generally considered as the best feather type to sample (Furness et al. 1986; Jaeger et al. 2009), but few investigations looked at their stable isotope values and contaminant levels of within-individual heterogeneity (Thompson et al. 1993; Bond and Diamond 2008; Jaeger et al. 2009, 2010; Brasso et al. 2013). Since body feathers grow asynchronously during the whole moulting period, a main recurrent problem is that the precise timing of synthesis of a given body feather remains unknown. However, the temporal drawback can be eluded in the case of synchronous or almost synchronous moult of body feathers. Indeed, assuming a constant growth rate for all body feathers, a synchronous growth theoretically means that all body feathers should have the same chemical composition and thus should show identical stable isotope values and contaminant levels.

Here, we tested this hypothesis by measuring $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations in four body feathers from the same individuals of three groups of marine birds showing different moulting patterns. Seabirds are useful organisms to biomonitor marine ecosystems, because they are long-lived animals that prey at the top of the marine food webs (Furness and Camphuysen 1997; Burger and Gochfeld 2004). Selected models were:

1. Chicks of white-chinned petrels *Procellaria aequinoctialis*. Chicks of this species were selected as representative of bird chicks, which present a complete moult with body feathers growing almost synchronously towards the end of the chick-rearing period. White-chinned petrel chicks have the advantage of showing significant between-individual variations in their feather stable isotope values (Jaeger et al. 2010), being thus a potentially good model to compare feather heterogeneity between and within individuals.
2. Adults of Antarctic prions *Pachyptila desolata*. Adults of this species were selected as representative of adults of flying seabirds that disperse after breeding and moult far away from their breeding grounds during the inter-nesting period. Moult is sequential and generally protracted over several weeks to months (Bridge 2006). Antarctic prions breed within the Southern Ocean and their feather $\delta^{13}C$ values indicate moulting primarily in northern warmer waters (Cherel et al. 2006).
3. Adults of king penguins *Aptenodytes patagonicus*. Adults of this species were selected as representative of penguins, which present a unique moulting pattern among birds. Penguins renew their whole plumage while fasting ashore, because transient reduction in thermal insulation during moult prevents them from going at sea. Consequently, all their body feathers grow simultaneously at the expense of energy reserves that are built up during the pre-moulting foraging period of hyperphagia at sea (Groscolas and Cherel 1992; Cherel et al. 1994).

As body feathers grow simultaneously in white-chinned petrel chicks and king penguin adults, but not in Antarctic prion adults, our driving hypothesis was that feather $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations would present lower within- than between-individual variations in the two former groups and would show an opposite pattern in the latter species. The main consequence of these moulting strategies is that chicks and penguins should be more suitable avian models than adults of flying species for long-term monitoring of the marine environment.

Materials and methods

Body feathers from white-chinned petrel chicks and king penguin adults were collected on Possession Island (46°30′S, 51°45′E), Crozet Archipelago in 2007 and 2005, respectively. King penguin adults were sampled during their annual moult, while well-feathered white-chinned petrel chicks were sampled at the end of the chick-rearing period. Antarctic prion adults were collected on the Kerguelen Islands (49°21′S, 70°18′E) during the 2011–2012 austral summer. Birds were found dead or dying after being trapped in the vegetation (*Acaena adscendens*); they were stored at −20 °C until dissection at the Centre d'Etudes Biologiques de Chizé, France. For all species, several whole body feathers per individual were pulled out from the lower back (dorsal tract) and stored dry in sealed plastic bags until analysis at the University of La Rochelle, France. Prior to chemical analysis, whole feathers were cleaned as described in Blévin et al. (2013) and then oven-dried for 48 h at 50 °C. Every whole feather was homogenized by cutting it with scissors into small fragments, and a subsample of ~0.3 mg was packed into tin containers for stable isotope analysis. The relative abundance of carbon and nitrogen isotopes was 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 relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors <0.15 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. The remaining homogenized subsample of every feather was then analysed

for total Hg in an Advanced Mercury Analyzer spectrophotometer (Altec AMA 254) following Blévin et al. (2013). Whenever possible, Hg analysis was repeated twice, and the relative standard deviation between runs calculated (<10 % for all samples). Accuracy was checked using a certified reference material (Tort-2 Lobster Hepatopancreas, NRC, Canada; certified Hg concentration: 0.27 ± 0.06 μg g^{-1} dry weight). Our measured values were 0.268 ± 0.022 μg g^{-1} dry weight ($n = 14$). Blanks were analysed at the beginning of each set of samples, and the detection limit of the method was 0.005 μg g^{-1} dry weight. Data of Hg concentrations are presented relative to the dry weight (dw).

Statistical analyses were performed using R 2.15.1 (R Core Team 2012). Linear mixed-effect models were used in order to test the repeatability of feather stable isotope values and Hg concentrations within individuals. Random effect models with the individual as a random intercept were constructed for the three groups of birds. The variance explained by the model (d), i.e. the between-individual variance, and the residual variance (σ) were used to calculate the intra-class correlation coefficient (ICC) as $d^2/(d^2 + \sigma^2)$, which is a measure of repeatability (Nakagawa and Schielzeth 2010). ICC ranges from 0 to 1, with values close to one meaning that most of the variance is explained by between-individual differences. Stable isotope values and Hg concentrations are mean ± standard deviation (SD).

Results

Feather stable isotope values and Hg concentrations were measured in four different body feathers from ten white-chinned petrel chicks, ten Antarctic prion adults and seven king penguin adults (Table 1; Fig. 1). Individual SD was very low and ICC very high for feather $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations of white-chinned petrel chicks and king penguin adults (Tables 1, 2). By contrast, Antarctic prion adults showed large within-individual variations, i.e. high SD and low ICC in feather $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations. In Antarctic prion adults, individual ranges of stable isotopes values were as large as 4.9 and 5.6 ‰ in feather $\delta^{13}C$ and $\delta^{15}N$ values, respectively. Noticeably, while feather Hg concentrations were within the same order of magnitude for the three groups of birds (overall individual range: 1.1–3.9 μg g^{-1} dw), CV was much lower in individual white-chinned petrel chicks (3–9 %) and king penguin adults (<1–8 %) than in Antarctic prion adults (15–60 %).

Discussion

To the best of our knowledge, this study is the first to compare the levels of heterogeneity in stable isotope values and contaminant concentrations of body feathers both within and between individuals in relation to different moulting patterns. The results verified the initial hypothesis stating that a synchronous moult leads to lower within- than between-individual variations in feather $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations, while asynchronous feather growth induces higher levels of feather heterogeneity within individual birds. Adult moult is potentially of variable duration according to sex, age, breeding status, species, phylogeny and environmental constraints. Hence, the synchronous/protracted moult hypothesis merits further investigations focusing on slow-moulting birds (e.g. albatrosses, Bridge 2006), species undergoing two moults per year (e.g. terns, Burger et al. 1992) and species with complex moulting patterns (e.g. alcids, Bridge 2004).

Feather $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations showed low variances and high ICC, thus indicating low levels of within-individual variations in white-chinned petrel chicks and king penguin adults. Noticeably, SD of $\delta^{13}C$ and $\delta^{15}N$ values was close to the accuracy of the isotopic method. These findings have three important implications.

1. They suggest that all body feathers that grow simultaneously have the same $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations.
2. When considering the overall feather chemical composition, they predict negligible within-individual variations in other useful stable isotope values of keratin, such as $\delta^{2}H$ and $\delta^{34}S$ (Hobson 2011; Ramos et al. 2013) and in the concentrations of other compounds that are deposited in the keratin structure, such as trace metals and metalloids, persistent organic pollutants and hormones (Burger 1993; Bortolotti et al. 2009; García-Fernández et al. 2013). This prediction is not verified for at least one group of molecules, the pigments, which can vary qualitatively and quantitatively from one body feather to the other (Stettenheim 2000). It also merits further investigations for those compounds that show a time-dependent deposition in feathers, such as steroid hormones (Bortolotti 2010).
3. Analysis of one to several pooled body feathers will provide identical stable isotope values and concentrations in various chemical compounds, meaning that any quantity of body feathers that grow simultaneously is equally representative of the individual. This is particularly relevant for studies including several elements and molecules, because some measurements necessitate only a single body feather (e.g. Hg, $\delta^{13}C$ and $\delta^{15}N$), but others require much more material, and hence several feathers (e.g. organic pollutants; García-Fernández et al. 2013).

Table 1 Feather $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations in white-chinned petrel chicks, Antarctic prion adults and king penguin adults

Id	$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)			Hg (μg g^{-1} dw)			
	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	CV (%)
White-chinned petrel chicks										
1	−21.7	−21.0	−21.3 ± 0.3	11.4	12.2	11.9 ± 0.3	1.22	1.51	1.35 ± 0.12	8.86
2	−20.7	−20.6	−20.6 ± 0.1	12.5	12.9	12.7 ± 0.2	2.06	2.20	2.11 ± 0.06	2.95
3	−23.0	−22.7	−22.8 ± 0.1	10.8	11.1	11.0 ± 0.1	1.01	1.22	1.09 ± 0.09	8.35
4	−20.6	−20.5	−20.6 ± 0.1	12.5	13.2	12.8 ± 0.3	1.93	2.33	2.18 ± 0.17	7.91
5	−22.3	−21.8	−22.0 ± 0.2	11.7	11.9	11.8 ± 0.1	2.47	2.93	2.72 ± 0.19	6.99
6	−21.5	−21.0	−21.2 ± 0.2	12.0	12.3	12.2 ± 0.1	1.47	1.74	1.59 ± 0.12	7.70
7	−20.3	−20.1	−20.2 ± 0.1	12.7	13.1	12.9 ± 0.2	2.85	3.42	3.11 ± 0.25	8.12
8	−21.6	−21.4	−21.5 ± 0.1	12.2	12.3	12.2 ± 0.1	1.61	1.81	1.74 ± 0.09	5.08
9	−22.1	−22.0	−22.1 ± 0.1	11.3	11.4	11.4 ± 0.1	1.28	1.40	1.34 ± 0.06	4.13
10	−21.1	−20.7	−20.9 ± 0.2	12.7	13.0	12.8 ± 0.1	2.40	2.73	2.59 ± 0.14	5.32
Antarctic prion adults										
1	−18.7	−18.4	−18.6 ± 0.2	8.8	9.4	9.1 ± 0.2	1.73	3.79	2.87 ± 1.07	37.3
2	−18.4	−16.9	−18.0 ± 0.7	9.7	15.2	11.7 ± 2.4	1.35	2.89	2.39 ± 0.71	29.7
3	−21.6	−16.7	−18.6 ± 2.1	9.0	13.0	10.9 ± 1.7	1.13	3.45	2.40 ± 0.96	39.9
4	−19.0	−17.9	−18.4 ± 0.5	8.5	10.8	9.2 ± 1.1	1.14	2.86	1.86 ± 0.78	42.0
5	−19.1	−18.6	−18.8 ± 0.2	8.2	9.4	8.6 ± 0.6	1.00	1.77	1.35 ± 0.40	29.8
6	−21.3	−18.3	−19.4 ± 1.3	8.3	9.9	9.3 ± 0.7	1.68	2.42	2.13 ± 0.36	15.3
7	−18.6	−16.4	−17.9 ± 1.0	8.4	14.0	10.0 ± 2.7	1.53	3.11	2.26 ± 0.84	37.3
8	−18.3	−17.8	−18.0 ± 0.2	9.1	10.1	9.7 ± 0.4	0.97	1.59	1.30 ± 0.25	19.6
9	−18.7	−16.3	−17.4 ± 1.2	9.1	11.3	10.4 ± 1.0	1.47	4.89	2.70 ± 1.61	59.8
10	−19.3	−17.8	−18.5 ± 0.6	8.6	10.8	9.4 ± 1.0	2.40	4.77	3.95 ± 1.08	27.3
King penguin adults										
1	−21.4	−21.0	−21.2 ± 0.2	10.7	11.1	11.0 ± 0.1	2.18	2.36	2.27 ± 0.08	3.52
2	−20.1	−19.8	−19.9 ± 0.1	11.3	11.7	11.5 ± 0.2	3.78	3.82	3.80 ± 0.02	0.54
3	−21.2	−21.0	−21.1 ± 0.1	11.3	11.5	11.4 ± 0.1	2.07	2.36	2.22 ± 0.14	6.38
4	−21.5	−21.2	−21.4 ± 0.1	10.7	11.1	10.8 ± 0.2	2.78	2.97	2.88 ± 0.08	2.79
5	−20.6	−20.3	−20.5 ± 0.1	11.0	11.1	11.1 ± 0.1	2.48	2.74	2.57 ± 0.12	4.69
6	−20.0	−19.8	−19.9 ± 0.1	12.1	12.3	12.2 ± 0.1	3.15	3.77	3.41 ± 0.28	8.20
7	−22.9	−22.1	−22.3 ± 0.4	11.1	11.6	11.4 ± 0.2	2.33	2.41	2.37 ± 0.04	1.84

Values are mean ± SD of four feathers per individual bird

CV coefficient of variation, *Id* individual

In contrast to white-chinned petrel chicks and king penguin adults, the amount of variability in feather $\delta^{13}C$ and $\delta^{15}N$ values and Hg concentrations within individuals was high in Antarctic prion adults. Such high levels of heterogeneity were previously found in the feather isotopic values of adults of light-mantled (*Phoebetria palpebrata*) and wandering (*Diomedea exulans*) albatrosses (Jaeger et al. 2009, 2010) and in body feather Hg concentrations of adults of Arctic (*Sterna paradisaea*) and common terns (*S. hirundo*) and of Leach's storm petrels (*Oceanodroma leucorhoa*) (Bond and Diamond 2008). The within-individual variation of adult flying birds likely results from body feathers being synthesized and replaced at different times during the moulting period (e.g. Battam et al. 2010). This heterogeneity reflects the birds' movements within different water masses and associated dietary shifts (Jaeger et al. 2010), together with changes in body burdens of Hg (Furness et al. 1986; Braune and Gaskin 1987) during the protracted moult. A positive aspect of feather variability is that measuring the isotopic values of several body feathers per individual can provide valuable information on the foraging strategies of adult birds during the moulting period (Jaeger et al. 2009, 2010). A negative aspect is that it complicates the use of body feathers as an effective monitoring tool because increasing variability can blur temporal and spatial trends. Hence, in a first step, within-individual heterogeneity must be accurately quantified, as well as the minimum number of body feathers to sample, as described for example by Jaeger et al. (2009) and Brasso et al. (2013). In a second step, body feathers of a given individual can be pooled in order to perform a unique measurement per bird. However, uncertainties in the biological interpretation of the data will remain, since, in most cases, practical reasons preclude determining the precise timing of synthesis

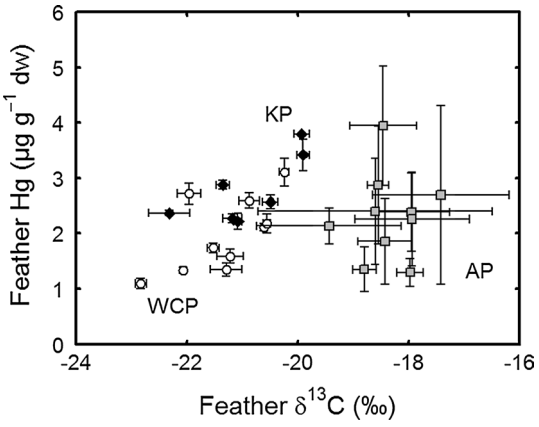

Fig. 1 Simultaneously moulting white-chinned petrel chicks (*WCP*; *white circles*) and king penguin adults (*KP*; *black diamonds*) show smaller SD in both feather $\delta^{13}C$ and Hg values than sequentially moulting Antarctic prion adults (*AP*; *grey squares*). Values are mean ± SD of four feathers per individual bird

of the sampled body feathers in relation to the food and feeding ecology of the individuals. Minimizing heterogeneity related to analytical procedure also requires thorough feather homogenisation.

We therefore recommend that long-term routine monitoring investigations on the trophic structure and contamination levels of ecosystems focus on birds presenting synchronous rather than asynchronous moult of body feathers. This means targeting chicks rather than adults (Blévin et al. 2013; this study), and, in the Southern Hemisphere, adult penguins rather than adult flying seabirds (Carravieri et al. 2013; this study). Chicks may present two disadvantages: (i) they may show low magnitude variation in feather $\delta^{15}N$ (not $\delta^{13}C$) in relation to varying chick growth rates (~0.6 ‰, Sears et al. 2009), and (ii) museum specimens include only a few well-feathered chicks, thus precluding determining historical changes. Nevertheless, chicks present several advantages over other age classes.

1. Most seabird chicks can be easily handled since they remain on land, while being fed exclusively by their parents. In addition, chick feathers can be sampled before fledging with minimum disturbance (e.g. during the annual ringing session in a long-term study colony).
2. The food of chicks and the foraging ecology of parent seabirds can be investigated by collecting stomach samples and using bio-logging. Hence, feather stable isotope values and contaminant levels can be related to the feeding ecology of the animals. Since adult seabirds are central place foragers when breeding, stable isotopes and contaminants in chick feathers likely represent primarily the local environment.
3. Chick moult is easy to study and the time window integrated by chick feathers is well-defined, because growth of body feathers takes place on land in the mid- to the second half of the chick-rearing period (Bost and Jouventin 1991; Phillips and Hamer 2000).
4. Working on chicks minimizes the temporal mismatch resulting from different integration times between feather stable isotopes and some contaminants, such as Hg (Bond 2010). Feather $\delta^{13}C$ and $\delta^{15}N$ values reflect the feeding ecology of the birds at the time of feather synthesis (Hobson and Clark 1992; Bearhop et al. 2002), while feathers integrate Hg accumulated in internal tissues during two successive moults (Furness et al. 1986). In chicks, this means the second part of the chick-rearing period (see above) versus a slightly longer period corresponding to the end of down growth (initial chick moult) to the beginning of body feather growth (Stewart et al. 1997), respectively.

In agreement with Stewart et al. (1997) and Burger and Gochfeld (2004), the present work provides new evidence showing that chick feathers are a useful avian tool for routine biomonitoring of the trophic structure and contaminant bioavailability in the marine environment. By targeting species with different breeding locations and chick-rearing periods (for example summer vs. winter breeders), different, but well-defined spatio-temporal scales of the marine environment can be investigated. The present work focuses on seabirds, but it can be generalized to water birds and terrestrial species, since a synchronous or almost synchronous moult of body feathers in chicks before fledging is a general pattern among avian species.

Table 2 Variance parameters and intra-class correlation coefficients (ICC) of linear mixed-effects models with the individual as a random intercept (random effects models) for white-chinned petrel chicks, Antarctic prion adults and king penguin adults

Species	$\delta^{13}C$			$\delta^{15}N$			Hg		
	d^2	σ^2	ICC	d^2	σ^2	ICC	d^2	σ^2	ICC
White-chinned petrel chicks ($n = 10$)	0.64	0.03	0.96	0.44	0.04	0.92	0.45	0.02	0.96
Antarctic prion adults ($n = 10$)	0.07	0.99	0.07	0.40	1.99	0.17	0.40	0.81	0.33
King penguin adults ($n = 7$)	0.72	0.03	0.96	0.21	0.02	0.91	0.37	0.02	0.95

d, variance explained by the model, here the between-individual variance; σ, residual variance

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