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Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds

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Abstract Some procellariiform seabirds use a dual strategy for provisioning their chicks by alternating short (ST) and long (LT) foraging trips. Parent birds gain mass during LT but they lose mass while increasing the chick feeding frequency during ST. Self-feeding during LT is crucial for the success of ST because firstly most of the energy used during ST is likely to be derived from the energy stored during LT and secondly self-feeding during ST is presumed to be negligible. Self-feeding by adult procellariiforms is thus a key issue to understand allocation processes but it is still poorly known. We tested these predictions by using the stable isotope (δ^{15}N and δ^{13}C) technique on birds' plasma and prey with the short-tailed shearwater *Puffinus tenuirostris* breeding at Tasmania as a model. Parent shearwaters returning to the colony after a LT have an Antarctic/subantarctic δ^{13}C signature in their plasma (−23.8‰), thus indicating that they fed in cold waters, far away from their breeding colony, for their own maintenance. Parent birds returning to the colony after a ST also have a distant Antarctic/subantarctic δ^{13}C signature in their plasma (−24.3‰), thus verifying that self-feeding is negligible during ST and that birds fast at that time, using energy stores built up in cold waters. Plasma δ^{15}N values of adults (8.8‰) indicates they mainly prey upon zooplankton-eating organisms, probably mesopelagic myctophid fishes. A simple isotopic mixing model estimates that they consume by mass 87% myctophids and 13% subantarctic krill when self-feeding. Finally and as expected, the carbon isotopic signature of chick plasma (−22.2‰) was intermediate between those of high- and low-latitude marine organisms and is thus in agreement with chicks being fed with a large diversity of prey species caught by adult birds from Antarctic to Tasmanian waters. One main consequence of this system is that reproduction of a Tasmanian species is controlled by resources available at great distances from the breeding colony that drive allocation decisions of parent birds.

Keywords Short-tailed shearwater · Myctophid · Dual strategy · Antarctica

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Introduction

Within the framework of life-history theory, the concept of reproductive effort is based on the idea that trade-offs modulate parental investment between current reproduction and survival, with the assumption that resources are limited in the environment (Stearns 1992). Consequently, organisms continuously face allocation decisions during a reproductive event and evidence is accumulating that the role of the animal's physiological state, e.g. body condition, is important in these decisions (McNamara and Houston 1996). In long-lived species such as seabirds, the risk of increased mortality during a breeding attempt should be reduced because of their high residual reproductive value (Goodman 1974). In other words, seabirds should behave as prudent parents (Drent and Daan 1980), and their body condition could play a central role in their allocation decisions.

In agreement with this theory, the nutritional status of procellariiform seabirds, among the longest-lived avian species (Weimerskirch 2002), regulates their allocation decisions. Petrels and albatrosses work between a high body mass threshold that determines breeding decision and a lower mass threshold that determines foraging decisions and resource allocation (Weimerskirch 1999). During the chick-rearing period, several species have a dual strategy, performing alternately one or several short foraging trips (ST) with one

long trip (LT) (Weimerskirch et al. 1994). Parent birds gain mass during LT and lose mass during ST, indicating that LT are profitable for adults, probably through a build up of energy reserves and ST are profitable for chicks through an increase in their feeding frequency. The decision to perform a LT or a ST is controlled by individual body condition, which reflects the trade-off between current reproduction and survival (Chaurand and Weimerskirch 1994; Weimerskirch 1998; Weimerskirch et al. 1999). A recent energetic study showed that self-feeding during LT is crucial for the success of ST because most of the energy used during ST is likely to derive from the energy stored during LT. It was also hypothesized that self-feeding during ST is negligible (Weimerskirch et al. 2003).

Investigations on seabird diets are restricted by the general inability to determine bird feed over space and time. Self-feeding of adult birds is poorly known mainly because most of the available information on birds is restricted to the chick—not the adult—diet during the chick-rearing period, a time when parents bring food back to the colony to feed their offspring. This problem led to the use of indirect methods like lipid assays of adipose tissue and the stable isotopic signature of tissue protein as dietary tracers (Hobson 1993; Hobson et al. 1994; Raclot et al. 1998; Cherel et al. 2000). The basic assumption underlying the use of stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in ecology is that the isotopic signature of a consumer reflects that of its food. Indeed, $\delta^{13}C$ values of consumers usually are similar to those of their diets, while $\delta^{15}N$ values of consumers integrate both the signature at the base of the food web and the consumer trophic position, because consumer $\delta^{15}N$ values undergo a step-wise increase with trophic level (Kelly 2000; McCutchan et al. 2003; Vanderklift and Ponsard 2003). In seabird ecology, the stable isotopic technique was used to delineate bird feeding habitat within and outside the breeding season and their trophic relationships, including the diet of adult birds when they are self-feeding (Hobson 1993; Hobson et al. 1994; Cherel et al. 2000; Forero and Hobson 2003).

The food and feeding ecology of the short-tailed shearwater *Puffinus tenuirostris* and its dual foraging strategy during chick rearing were recently described (Weimerskirch and Cherel 1998; Klomp and Schultz 2000; Schultz and Klomp 2000). Birds alternate an average of two ST lasting 1–4 days before departing for a LT lasting 8–19 days. They travel from the Australian to the Antarctic waters during LT and remain close to their breeding colony during ST. While suggesting that the birds fed in cold waters during LT, the studies give no indication on the prey ingested when adult birds are self-feeding during LT, where prey are caught during LT and if shearwaters fed or not for themselves during ST. These pending questions are the key issues to be resolved to fully understand the two-fold foraging strategy of procellariiform seabirds, but they cannot be investigated using direct measurements and analysis.

The objective of this study was to investigate the connections between foraging and allocation of resources in parent procellariiforms by using the stable isotope technique to test the following predictions with the short-tailed shearwater breeding at Tasmania as a model.

1. Parent short-tailed shearwaters returning to the colony after a LT should have an Antarctic $\delta^{13}C$ signature in their plasma, thus indicating that they fed in cold waters for their own maintenance. The turnover of carbon in plasma is high with half-lives of about 3–4 days (Hobson and Clark 1993; Hilderbrand et al. 1996), a shorter period than the average duration of LT that was 12 days (Weimerskirch and Cherel 1998).
2. Parent birds returning to the colony after a ST should also have an Antarctic $\delta^{13}C$ signature in their plasma, thus indicating that self-feeding is negligible during ST, i.e that they fast at that time using energy stores built up in cold waters. Long-term fasting in birds is known to affect $\delta^{15}N$ values, not $\delta^{13}C$ values (Hobson et al. 1993).
3. Chicks were fed by their parents after both LT and ST and thus with different prey collected in different water masses (Weimerskirch and Cherel 1998). Since marine plankton $\delta^{13}C$ varies with latitude (Rau et al. 1982; Goericke and Fry 1994), the $\delta^{13}C$ signature of chick plasma should be different from that of the adults with a value intermediate between those of low- and high-latitude marine organisms.
4. Plasma $\delta^{15}N$ values should help with the determination of the prey targetted by adult birds when they are self-feeding. Since short-tailed shearwaters feed on swarming crustaceans and shoaling fish (Weimerskirch and Cherel 1998; Hunt et al. 2002) and pelagic fish prey upon zooplankton, a low $\delta^{15}N$ value would indicate feeding on crustaceans, a high value would indicate feeding on fish, and an intermediate value would indicate feeding on both.

Materials and methods

Field study

The study was carried out in March 1997 at the Neck Game Reserve, Bruny Island (43.3°S, 147.3°E), Tasmania. The methodology used is detailed in Weimerskirch and Cherel (1998). Briefly, individual burrows with marked adults were monitored during the night to determine attendance patterns of parent birds. If a visit was detected, the adult was caught, identified and weighed. The duration of individual foraging trips was defined as the time elapsed between two successive recoveries of the same bird. Food and blood samples were collected at the end of the study period to minimize disturbance of the experimental birds. Food samples

were obtained using the water off-loading technique or through spontaneous regurgitations of adult short-tailed shearwaters on arrival back at the colony after a foraging trip before they fed their chick. Blood was obtained from chicks and adult birds returning from ST and LT. A 1–2-ml blood sample was taken from a wing vein, centrifuged and the plasma stored—like food samples—at −20°C until analysis. Only a few food and blood samples were collected from adult birds returning after a ST, because poaching occurred at the end of March when most birds were performing LT, thus precluding the collection of more ST-samples. Since chicks were fed irregularly (Weimerskirch and Cherel 1998) and fasting can induce changes in tissue isotopic signature (Hobson et al. 1993), blood samples were collected from both fed and fasted chicks to investigate a potential fasting-effect on plasma δ^{15}N values.

Laboratory methods

Each food sample was thawed and drained by gravity to separate oil and water from the solid fraction. Fresh remains were divided into broad prey classes (mainly fish and crustaceans), which were weighed to estimate their proportions by fresh mass in the diet. Each different prey species was numbered and identified using published keys (Baker et al. 1990; Smale et al. 1995) and our own reference collection. Barely digested individuals of four species of crustaceans and of fish postlarvae were picked up from food samples and kept in 70% ethanol. Some individuals of each prey species were subsequently selected and pooled together species by species in order to measure their isotopic signature. Plasma samples were initially used for the determination of circulating hormones and metabolites (Weimerskirch and Cherel 1998). The remaining volumes of plasma samples were kept at −20°C until isotopic analysis.

Plasma and prey species were freeze-dried and powdered. Lipids were then removed from prey items and from a plasma subsample using a Soxhlet apparatus with chloroform solvent for 4–6 h. Since lipids are depleted in ^{13}C relative to whole tissues (Tieszen et al. 1983; Thompson et al. 2000), both whole- and lipid-free plasmas were analyzed to investigate a potential lipid-effect on the isotopic signature of plasma. Prey species differed in their C/N ratios, thus indicating that lipid removal was not complete (data not shown); consequently, δ^{13}C values of prey species were corrected according to Schmidt et al. (2003).

Stable-carbon and nitrogen isotope assays were performed on 1 mg subsamples of homogenized materials by loading into tin cups and combusting at 1,800°C in a Robo-Prep elemental analyzer. Resultant CO_2 and N_2 gases were then analyzed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS) with every five unknowns separated by two laboratory standards. Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000,$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N. The R_{standard} values were based on the PeeDee Belemnite (PDB) for ^{13}C and atmospheric N_2 (AIR) for ^{15}N. Replicate measurements of internal laboratory standards (albumen) indicate measurement errors of ±0.1‰ and ±0.3‰ for stable-carbon and nitrogen isotope measurements, respectively.

Statistics

Values are means ± SD. Data were statistically analysed using SYSTAT 9 for WINDOWS (Wilkinson 1999).

Results

Effect of lipid removal on δ^{15}N and δ^{13}C in plasma

Overall, lipid removal had no effect on plasma δ^{15}N values (paired t test, df = 22, $t = 0.36$, $P = 0.723$) (Table 1). It however significantly increased δ^{13}C values ($t = 15.70$, $P < 0.0001$), the increase being higher in chick plasma than in adult plasma (2.8 ± 0.6‰ versus 1.8 ± 0.3‰, respectively; two sample t test, df = 21, $t = 5.22$, $P < 0.0001$). The C/N ratio was higher in chick plasma than in adult plasma (two sample t test, df = 21, $t = 5.36$, $P < 0.0001$). Lipid removal induced an overall decrease in C/N values (paired t test, df = 22, $t = 9.52$, $P = < 0.0001$) (Table 1). This greatly reduced the difference between chick plasma and adult plasma, nevertheless C/N was significantly higher in chick plasma (two sample t test, df = 21, $t = 3.27$, $P = 0.004$) (Table 1). Due to these differences between chick and adult plasma, all the subsequent analysis on isotopic ratios have been done on lipid-free plasma to minimize the effect of lipids on δ^{13}C values between the two groups.

δ^{15}N and δ^{13}C in plasma of adults and chicks

The stable isotope signature of lipid-free plasma of adult shearwaters was identical after a ST and a LT (δ^{15}N: Mann–Whitney U test, $U = 20.0$, $P = 0.102$; δ^{13}C: $U = 5.0$, $P = 0.153$). In the same way, fasting in chicks induced a non-significant increase in δ^{15}N plasma values ($U = 22.0$, $P = 0.522$) and a non-significant decrease in δ^{13}C plasma values ($U = 8.0$, $P = 0.109$) (Table 1). Consequently, values from the two groups of adults and of the two groups of chicks were pooled together to compare the isotopic signature of adults with that of chicks. Plasma of chicks were significantly enriched in ^{15}N (two sample t test, df = 21, $t = 5.23$, $P < 0.0001$) and in ^{13}C ($t = 8.62$, $P < 0.0001$) when compared to the plasma of adult birds (Fig. 1).

Table 1 Stable carbon and nitrogen isotope values (means ± SD‰) of plasma of adults and chicks of short-tailed shearwaters breeding in Tasmania

	No. of birds	Whole plasma			Delipidated plasma		
		δ^{15}N	δ^{13}C	C/N	δ^{15}N	δ^{13}C	C/N
Adults							
Short trips	3	9.22 ± 0.71	−26.02 ± 0.26	4.80 ± 0.22	9.15 ± 0.41	−24.25 ± 0.26	3.78 ± 0.02
Long trips	8	8.61 ± 0.50	−25.57 ± 0.57	4.92 ± 0.17	8.69 ± 0.50	−23.80 ± 0.52	3.84 ± 0.05
All birds	11	8.78 ± 0.60	−25.69 ± 0.53	4.89 ± 0.18	8.82 ± 0.50	−23.92 ± 0.50	3.82 ± 0.05
Chicks							
Fed	6	10.60 ± 1.27	−24.65 ± 0.76	6.05 ± 0.71	10.67 ± 1.27	−21.97 ± 0.42	3.91 ± 0.06
Fasted	6	11.29 ± 1.10	−25.40 ± 0.85	6.51 ± 0.96	11.23 ± 1.30	−22.46 ± 0.36	3.98 ± 0.14
All birds	12	10.94 ± 1.19	−25.03 ± 0.86	6.28 ± 0.84	10.95 ± 1.26	−22.21 ± 0.45	3.95 ± 0.11

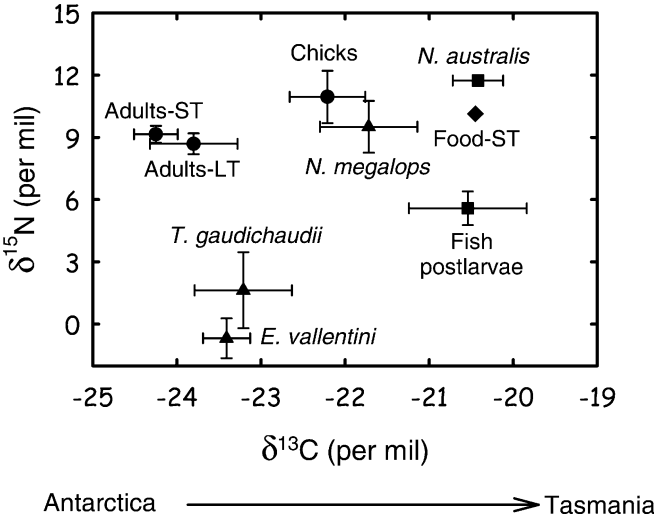

Fig. 1 Stable carbon and nitrogen isotope values of plasma of adults and chicks of short-tailed shearwaters (*circles*), of their prey caught during short trips (*squares*) and long trips (*triangles*), and of the chick diet during short trips (*diamond*). *ST* Short trips, *LT* long trips

δ^{15}N and δ^{13}C in prey

Food samples were mainly composed of fish and crustaceans, the former dominated after LT and the latter after ST (Table 2). ST samples included two main prey only: the euphausiid shrimp *Nyctiphanes australis* and fish postlarvae. Prey diversity was higher in LT samples, which included fish, mainly myctophids that dominated by mass, and various species of crustaceans that dominated by number. Interestingly, preys collected during ST have been found in LT samples, but in lesser amounts than in ST-samples (Table 2).

A large range of isotopic values was observed in the five prey collected in food samples (Fig. 1), which segregated by both their δ^{15}N and δ^{13}C values (Kruskall-Wallis test statistic = 24.15 and 20.02 for 27 cases, respectively; both $P < 0.0001$). δ^{15}N values ranged from −0.7 ± 1.0‰ (the euphausiid *Euphausia vallentini*) to 11.7 ± 0.3‰ (*N. australis*), with other prey species having intermediate values (the hyperiid amphipod *Themisto gaudichaudii*: 1.6 ± 1.8‰, fish postlarvae: 5.6 ± 0.8‰, and the euphausiid *Nematoscelis megalops*: 9.5 ± 1.2‰). δ^{13}C values ranged from −23.4 ± 0.3‰ (*E. vallentini*) to −20.4 ± 0.3‰ (*N. australis*), with other species having intermediate values (*T. gaudichaudii*: −23.2 ± 0.6‰, *N. megalops*: −21.7 ± 0.6‰ and fish postlarvae: −20.5 ± 0.7‰).

Since ST-samples were composed of two prey taxa in known proportions by mass and of known δ^{15}N and δ^{13}C values, we were able to calculate the isotopic signature of ST-food that averaged 10.1‰ and −20.5‰ for δ^{15}N and δ^{13}C, respectively (Fig. 1). Such estimation was not possible for food collected during LT, because first it was a mixture of different prey species in unknown percentages by mass, and second the very digested nature of the fish component precluded determination of its isotopic signature.

Table 2 Duration of foraging trips and food composition of stomach contents collected after short and long trips of adult short-tailed shearwaters breeding in Tasmania (from Weimerskirch and Cherel 1998)

	Short trips	Long trips
Duration (days)	1–3	8–17
Diet composition (% by fresh mass)		
Fish	26	82
Crustaceans	74	18
Main prey composition (% by number)		
Fish postlarvae	3.5	34.4
Themisto gaudichaudii	< 1	3.7
Euphausia vallentini	0	40.5
Nyctiphanes australis	95.8	19.4
Nematoscelis megalops	0	0.9

Discussion

Effect of lipid removal on δ^{15}N and δ^{13}C in plasma

Lipids present a particular problem in stable isotope analysis, because lipid composition of tissues can be quite variable and lipids are depleted in ^{13}C when compared to proteins, carbohydrates and to total organism (Tieszen et al. 1983; Thompson et al. 2000). For these reasons, lipids generally are removed from tissue samples. Only two previous works studied the effects of lipid extraction from whole blood on its isotope signature (Bearhop et al. 2000; Cherel et al. 2005) and, to our knowledge, the

present study is the first to investigate possible effects of lipid removal from plasma. Lipid-extracted plasma was consistently enriched in ^{13}C with no changes in ^{15}N when compared to whole plasma in both adults and chicks of short-tailed shearwaters. An increase in $\delta^{13}C$ values and almost no change in $\delta^{15}N$ values were expected since lipids are depleted in ^{13}C (Tieszen et al. 1983; Thompson et al. 2000) and lipid extraction does not greatly affect tissue $\delta^{15}N$ values (Pinnegar and Polunin 1999; Bearhop et al. 2000; Cherel et al. 2005).

Unexpectedly however, the decrease in $\delta^{13}C$ was larger in chick plasma than in adult plasma. This together with larger C/N ratios in chick plasma indicates a higher plasma lipid content in chicks than in adults. The present work thus indicates that plasma lipid content may vary with age, thus affecting interpretation of plasma $\delta^{13}C$ signature. Unlike previous studies suggesting that there is no need to extract lipids in avian blood (Bearhop et al. 2000; Cherel et al. 2005), we consequently propose to monitor the C/N ratio in avian plasma and, if C/N values are different among groups, to extract lipids to minimize their deleterious effect on isotopic comparison between groups.

Stable isotope signature of prey and latitudinal variation

Marine plankton $\delta^{13}C$ varies with latitude (Rau et al. 1982; Goericke and Fry 1994), and, in the Southern Ocean, the more south the latitude, the more depleted the particulate organic matter (POM) $\delta^{13}C$ value (François et al. 1993; Lourey et al. 2004). Since there is no or a slight increase in $\delta^{13}C$ with increasing trophic level (Kelly 2000; McCutchan et al. 2003), $\delta^{13}C$ values of prey of short-tailed shearwaters reflects the isotopic signature at the base of the food web (phytoplankton). Consequently, the wide range of $\delta^{13}C$ values indicates that preys were taken in different water masses. Figure 1 shows a gradient of prey taken from Antarctic to Tasmanian waters in the order: *E. vallentini*, *T. gaudichaudii*, *N. megalops*, fish postlarvae and *N. australis*. These results are in agreement with the known biogeography of the species. For example, the subantarctic krill *E. vallentini* is abundant between the Polar Front and the Subantarctic Front and *N. megalops* is found further north (Lomakina 1966; Terazaki and Wada 1986).

$\delta^{15}N$ values are generally linked to trophic levels of consumers (Kelly 2000; McCutchan et al. 2003; Vanderklift and Ponsard 2003). In the present work, prey $\delta^{15}N$ values span 12.4‰, corresponding to about four trophic levels. Such a difference between euphausiid species (*E. vallentini* and *N. australis*) is unrealistic from a trophic point of view and is more likely to result mainly from the species belonging to different ecosystems with different isotopic signatures at the base of their food web. Accordingly, $\delta^{15}N$ values of POM in oceanic waters—like $\delta^{13}C$ values—increase abruptly from south to north of the Subtropical Front (Altabet and François 1994), thus explaining, at least in part, the high ^{15}N content of *N. megalops* and *N. australis* (Fig. 1). The latter species has also a high $\delta^{13}C$ value that can be connected to its biogeography; *N. australis* is an endemic species of the Tasmanian shelf (Blackburn 1980) and $\delta^{13}C$ values are known to increase from offshore (oceanic) to inshore (neritic and costal) waters (Hobson 1993; Hobson et al. 1994). In the same way, the isotopic signature of fish postlarvae together with its importance in ST-food samples indicate their occurrence in neritic/coastal waters close to the breeding colony.

In summary, the isotopic signature of the prey has the potential to indicate where short-tailed shearwaters fed on them during LT and ST, i.e. from Antarctica to Tasmania and in oceanic versus neritic waters.

Adult shearwaters feed for themselves in cold waters

Plasma $\delta^{13}C$ values of adult short-tailed shearwaters sampled after LT were very negative. Such values are in the range of those from Antarctic procellariiforms (Hodum and Hobson 2000), and they are much lower than those of various albatrosses and petrels from the Southern Ocean (Thompson et al. 2000). Their $\delta^{13}C$ signatures thus indicate that short-tailed shearwaters fed for themselves in cold waters of the Southern Ocean, i.e. in Antarctic waters and/or in the vicinity of the Polar Front, which is in agreement with birds gaining weight (Weimerskirch and Cherel 1998) while reaching Antarctic waters during LT (Klomp and Schultz 2000). The ingestion of prey from lower latitudes when they were self-feeding was likely to be minimal since *N. megalops*, *N. australis* and fish postlarvae have much higher $\delta^{13}C$ values than plasma (Fig. 1).

The plasma isotopic signature of LT-birds likely represents food ingested during the previous LT that lasted 8–17 days, because turnover of plasma proteins is short with half-lives of about 3–4 days (Hobson and Clark 1993; Hilderbrand et al. 1996). On the other hand, since most ST lasted one day only and adults performed on average two consecutive ST before departing for a LT (Weimerskirch and Cherel 1998), the plasma isotopic signature of ST-birds cannot theoretically reflect food ingested during ST only, but is more likely to represent an average value between ST- and LT-food. However, ST-birds did not present higher $\delta^{13}C$ values than LT-birds and, instead, no differences in plasma isotope ratios were found between birds sampled after a LT and the few individuals collected after a ST (Table 1). This supports the hypothesis that self-feeding during ST is negligible and that adult birds use endogenous energy stores built up in cold waters at that time (Chaurand and Weimerskirch 1994; Weimerskirch 1998; Weimerskirch et al. 2003). A further argument is that plasma β-hydroxybutyrate was high and uric acid low in both ST- and LT-birds (Weimerskirch and Cherel 1998). Plasma β-hydroxybutyrate (a ketone body) and uric acid (the

main nitrogen excretory product in birds) are good indices of lipid and protein utilization, respectively (Cherel et al. 1988). Consequently, high plasma β-hydroxybutyrate levels and low uric acid indicate that adult shearwaters were fasting at the end of LT and during ST. This is a direct indication that they used their lipid reserves and spared their endogenous body proteins while carrying food to their chicks, suggesting that parent birds lowered or even stopped digestion at that time, an adaptation previously found in adult penguins (Cherel et al. 1994).

Adult shearwaters feed their chicks in both cold and warm waters

Shearwater chicks are unable to feed by themselves, depending exclusively for their nutrition on food brought back by their parents. Food analysis, prey biogeography (Weimerskirch and Cherel 1998) together with stable isotopic signature of the prey (this study) indicate that chicks were fed by adults with prey taken either in the vicinity of the colony during ST or a wider range of prey taken during LT. The latter includes species caught on their way back to the colony from distant foraging grounds (Fig. 1).

Stable isotopic signature of chick plasma was enriched in ^{15}N—but less than a trophic level—and was depleted in ^{13}C when compared to the calculated isotopic signature of ST-food (Fig. 1). The fact that the nitrogen isotopic signature of chick plasma was much closer to that of ST-food than that of subantarctic crustaceans reflects the lack of data in Fig. 1 about Antarctic/subantarctic myctophid fishes—the main component of the food after LT—that were too much digested to allow an accurate measurement of their isotopic signature. Indeed, the δ^{15}N value of the food of a specialist myctophid-eater from the Southern Ocean, the king penguin, is much higher (food of chicks in spring at Crozet Islands, δ^{15}N = 7.4‰; Cherel et al., unpublished data) than that of *E. vallentini* and *T. gaudichaudii*. The intermediary isotopic signature of chick plasma in both δ^{15}N and δ^{13}C therefore reflects the average of different isotopic values of different prey, because chicks integrate into their body proteins the various signatures of prey proteins received from their parents. Consequently, unlike adult birds, chicks depend for their nutrition on prey belonging to different ecosystems, from the pelagic oceanic Antarctic ecosystem in the South to the pelagic neritic Tasmanian ecosystem near the breeding colony in the north.

What is the main prey of adults when they feed for themselves?

Little is known about the food consumed by adult seabirds foraging for self-maintenance either during or outside the reproductive season. In procellariiforms, different diets between adults and chicks is likely to occur in species performing LT, because adults feed for themselves far away the breeding colony, but only a few very digested remains of these prey were found in food given to their chicks (Weimerskirch and Cherel 1998; Catard et al. 2000; Cherel et al. 2002a, 2002b). In short-tailed shearwaters, plasma δ^{13}C values indicate adults fed for themselves in cold waters and δ^{15}N values have the potential to shed new light on their trophic level and on their prey.

δ^{15}N values were much higher in the plasma of parent birds than in the two crustaceans that occur in cold waters, i.e. *T. gaudichaudii* and *E. vallentini* (Fig. 1). Other common oceanic pelagic swarming crustaceans in the Southern Ocean include the Antarctic krill *E. superba* and two species of the genus *Thysanoessa* that have also low δ^{15}N values (Wada et al. 1987; Rau et al. 1991; Schmidt et al. 2004). The difference in δ^{15}N values between shearwaters and crustaceans encompasses almost two trophic levels, indicating that the staple food of birds was not crustaceans but, instead, organisms feeding on crustaceans.

By far, the main available biomass of macrozooplankton-eating animals in the pelagic oceanic ecosystem of the Southern Ocean is shoaling fish of the family Myctophidae (Kock 1992; Pakhomov et al. 1996). There are several arguments indicating that myctophids were the main prey of adult shearwaters when they were self-feeding. First, the main component of LT-food was fish, including very digested remains of various myctophids (Weimerskirch and Cherel 1998). Second, the lipid-signature of Antarctic myctophids like *Electrona antarctica* or *Krefftichthys anderssoni* was found in stomach oil of LT-food samples (Connan et al. 2005). It is noticeable that the main fish found in LT-samples was also *K. anderssoni* (Weimerskirch and Cherel 1998), which is one of the most abundant myctophid species at and south of the Subantarctic Front (Sabourenkov 1991). Finally, the nitrogen isotopic signature of adult short-tailed shearwaters is close to that of the myctophid-eater king penguin (plasma of chicks in spring at Crozet Islands, $\delta^{15}N = 9.9$‰; Cherel et al., unpublished data).

As a last step, we used the following simple model on δ^{15}N values to estimate the proportions by mass of the main components of the diet of adults when they are self-feeding:

$$\delta^{15}N_{\mathrm{STS}} = x\delta^{15}N_{\mathrm{KP}} + y(\delta^{15}N_{\mathrm{vall}} + 2.7) \text{ and } \mathrm{x} + \mathrm{y} = 1,$$

where $\delta^{15}N_{STS}$, $\delta^{15}N_{KP}$, and $\delta^{15}N_{vall}$ are the δ^{15}N values for adult short-tailed shearwaters, king penguins and *E. vallentini* (the main crustacean prey from cold waters in LT-samples, Table 2), respectively; 2.7‰ is the mean enrichment factor between blood of a fish consumer and its diet (Cherel et al. 2005), and x and y represents the proportion by mass of myctophids and *E. vallentini* in adult food, respectively. The model calculates that the diet by mass of adult shearwaters includes about 87% myctophids and 13% *Euphausia vallentini*.

Conclusions

Using the short-tailed shearwater as a model and extending the previous investigation on that species (Weimerskirch and Cherel 1998), the present work highlights how oceanic procellariiform adults forage and allocate resources between themselves and their chicks. Data gathered with the stable isotopic technique complement the traditional methods of weighing birds and food analysis and the more recent satellite-tracking technology. δ^{15}N and δ^{13}C values of plasma verify the hypothesis that during the chick-rearing period adult short-tailed shearwaters feed for themselves far away from the breeding colony, in Antarctic/subantarctic waters, during which they mainly prey upon myctophid fish. The data also verify the hypothesis that self-feeding is negligible during ST and that, as expected, the carbon isotopic signature of chicks is intermediate between that of cold- and warm-water species. The study thus emphasizes the usefulness of the stable isotope method to shed new light on acquisition and allocation processes (Klaassen et al. 2001; Gauthier et al. 2003), a key issue in evolutionary ecology.

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