Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick

HENRI WEIMERSKIRCH*, ANDRÉ ANCEL†, MICHEL CALOIN†, ALEXANDRE ZAHARIEV†, JÉRÔME SPAGIARI*, MARCEL KERSTEN*‡ and OLIVIER CHASTEL*

*Centre d’Etudes Biologiques de Chizé, CNRS/UPR 1934, 79360 Villiers en Bois, France; †Centre d’Ecologie et Physiologie Energétiques, CNRS/UPR 9010, 23 rue Becquerel, 67087 Strasbourg, France; ‡Zoological Laboratory, University of Groningen, the Netherlands

Summary

1. Foraging determines the intake of resources that are expended on fitness related activities, and allocation links foraging and life-history traits, but the extent to which individuals are able to adjust energy expenditure according to allocation decisions is still poorly studied.

2. To examine this, we studied for the first time the efficiency of foraging trips (defined as the ratio of energy gained over energy spent while foraging) in a pelagic seabird provisioning its chick by measuring simultaneously the energy flow to the chick, changes in adult body mass and foraging cost using doubly labelled water. The study was performed over two seasons.

3. Blue petrels (Halobaena caerulea) alternate between short foraging trips (average 1.9 days, range 1–4 days) where they maximize food delivery to the chick but lose mass, and long foraging trips (7.3 days, 5–10 days) where they increase in mass. They expend 1.5–2.2 times more energy per unit of time during short trips (2561 kJ day\(^{-1}\) kg\(^{-1}\), i.e. 3.2 times the resting metabolic rate) compared to long trips (1142–1676 kJ day\(^{-1}\) kg\(^{-1}\), i.e. 1.4–2.1 the resting metabolic rate).

4. The currency during long trips is therefore to maximize efficiency, whereas during short trips the currency is to maximize rate of energy delivery to the chick. Maximum efficiency peaks for 6-day trips, i.e. when adult mass gain is highest, foraging costs are lowest and efficiency was extremely low during short trips. A duration of 6 days is therefore the optimal duration of long foraging trips but trips of 7 days were more common.

5. Our study shows that self-feeding during long trips is crucial for the success of short trips because most of the energy used during short trips is probably derived from the energy stored during long trips. Self-feeding during short trips is probably negligible.

6. The study indicates that surprisingly long distance foraging may not always result in higher foraging costs compared to shorter movements. It highlights the predominant role of body store usage as a mechanism for this animal to adjust energy expenditure and energetic efficiency during foraging for allocation purposes.

Key-words: blue petrel, doubly labelled water, energetic yield, foraging decisions.

Introduction

For most animals, the only way to obtain resources is by expending energy while foraging. The ability of individuals to adjust energy expenditure while foraging is likely to influence fitness (Drent & Daan 1980; Stephens & Krebs 1986) because foraging determines the intake of resources that are expended on fitness related activities. However, individuals face many fitness trade-offs, so they must differentially allocate time and energy between competing life-history traits such as reproduction, survival or growth (Stearns 1992). Thus, allocation links foraging and life-history traits and foraging effort should be treated as the result of allocation (Boggs 1992). This implies that foraging individuals should...
be able to adjust their energy expenditure according to allocation decisions. This is generally overlooked because most studies that focus on allocation processes only consider the input of resources obtained from foraging on life history, mainly reproduction through provisioning, whereas measures of energy expenditure and especially of resource storage are not examined. Conversely, studies on foraging consider patterns of resource intake, but generally do not address resource use or effort. It is typically assumed that foraging animals always maximize efficiency, or the ratio of energy gained over energy spent while foraging (Ydenberg et al. 1992). In addition, the patterns of energy intake and expenditure observed may be interpreted as having been optimized by natural selection (Ricklefs 1996), but the extent to which individuals are able to adjust energy expenditure according to allocation decisions is poorly studied. Therefore, being able to measure energy expenditure of foraging individuals when allocation decisions differ is of particular interest, but often logistically difficult. Indeed measures of reproductive effort should be dynamic and they should include measures of the energy allocated and individual variation in activity and foraging efficiency (Stearns 1992).

Pelagic seabirds are long-lived animals that rely on a food that is often located at long distances from the breeding grounds, implying a high cost of foraging to reach distant food resources (Ricklefs 1990; Weimerskirch 1999). On the other hand, they have to feed the chick as frequently as possible to enhance the probability of producing an offspring in good condition. Several species solve this conflict by using a specific strategy whereby parents alternate between short foraging trips where they feed the chicks and loose mass and long foraging trips where parents restore their body reserves (Chaurand & Weimerskirch 1994a). Short trips allow parents to increase feeding frequency but have a negative yield. This strategy has been shown to occur in many species of petrels and albatrosses (Weimerskirch 1999), and even in penguins (Clarke et al. 1998) that rely on distant resources. In some species, it has been shown by tracking that during short trips, birds forage close to the colony over coastal waters, and during long trips far from the colony, birds forage over pelagic waters (Weimerskirch et al. 1997). This system has been viewed as a typical example of trade-offs of time and energy constraints on foraging, related to allocation decisions (Weimerskirch 1999). However, being able to understand how foragers adjust foraging effort, it is necessary to measure not only the rate of food delivery to the offspring and self-feeding, but to simultaneously measure energy expenditure. This has not yet been done.

The aim of this study is to explore the connections between foraging and allocation of resources and to examine to what extent foraging effort can be treated as a result of allocation. Here we examine simultaneously the foraging efficiency (defined as the ratio of energy gained over energy spent while foraging), foraging success, energy expenditure and resource storage in relation to investment in reproduction. Specifically, we estimate energy gain and energetic efficiency in a small pelagic seabird, the blue petrel (Halobaena caerulea Gmelin), which uses a two-fold strategy. This was done by measuring the flow of energy to the chick, the amount of self-feeding by adults, and field metabolic rates of foraging adults.

Materials and methods

STUDY AREA AND PROVISIONING
The study was carried out on Mayes Island, in Golfe du Morbihan, Kerguelen Islands (49° S, 70° E), South Indian Ocean. Prior to the experiment, in December 1998 and 1999, burrows were selected in a large colony of blue petrels. Adults were ringed when they were incubating and access to each nest chamber was achieved through a secondary hole that was dug above or to the side of the entrance. The study was carried out during the chick-rearing period on 22 burrows from 6 to 26 January 1999 and on another 16 burrows from 6 to 24 January 2000. At this time of the breeding season, adults arrived at the colony and fed their chick only during hours of darkness (22.00–02.00 local time). All chicks were weighed to the nearest 2 g with an electronic balance every evening at 19.00 and in the middle of night after most of the parents had visited the burrows (see Chaurand & Weimerskirch 1994a). Meal mass was deduced from the difference between these two weighings of the chick. The age of chicks was not known but because blue petrels hatch their chick synchronously within a few days, and because the study period was relatively short, we can be confident that the age of chick had no significant influence on provisioning parameters (see Chaurand & Weimerskirch 1994a). Each burrow entrance was fitted with a trap door that allowed adults to enter but precluded them from exiting after the chick had been fed. Burrow inspections lasted less than 1 h and were conducted 2–4 times per night. Adults were identified, weighed to the nearest 2 g with an electronic balance and immediately released back into their burrow with the trap door left opened. If both adults were present at nest during inspection, the meal mass received by the chick was excluded from the analysis because it was not possible to assign meal sizes to a particular parent. If adults and chick were weighed before the feeding was complete, there could be an overestimation of adult mass on return to the sea and an underestimation of meal size. However, because the duration of food delivery is very short in blue petrels (5–10 min) and the adults were not captured when begging calls of chicks were heard, weighing of adults or chicks before food delivery was completed was not likely to occur (Chaurand & Weimerskirch 1994a).

Inter-annual variations in breeding success were compared using demographic data obtained from the
long-term monitoring of about 200 nests in a separate colony located near the study colony (see Chastel, Weimerskirch & Jouventin 1995).

ENERGY EXPENDITURE DETERMINATION

Energy expenditure was determined using the DLW method (Lifson & McClintock 1966; Tatner & Bryant 1988). The principle of the DLW method is based on labelling the animal’s body water pool with the heavy isotopes (e.g. $^2$H and $^{18}$O), and the subsequent determination of their fractional turnover rates, $k_H$ and $k_O$, respectively (Lifson & McClintock 1966; Nagy 1980; Speakman 1997). Background blood samples were collected from a brachial vein before injecting the birds. Then each petrel received an intraperitoneal injection of DLW (0·1–0·2 mg per g of body mass, depending on the predicted duration of the next foraging trip, short or long, respectively). In 1999, the injectate was prepared by adding 3·9107 g of 99·9 atom percent excess (APE) deuterium (Isotec Inc., USA) to 7·9742 g of 94·4 APE $^{18}$O (Isotec Inc., USA) and in 2000, 4·0252 g of 99·9 APE deuterium was added to 8·1559 g of 94·4 APE $^{18}$O. The mass of the injected dose was measured to the nearest 0·1 mg by weighing the syringe before and after the injection. After labelling, birds were released in their burrow. One hour was allowed for distribution of the isotopes throughout the body water compartment (LeFebvre 1964; Williams 1985), after which time, the initial blood sample was collected from a brachial vein. The birds were then released outside of their burrow. During their next visit to the chick, they were captured again, weighed and a final blood sample collected. Bleeding sites were cleaned with ethanol before and after venipunctures. During each blood sampling, 3–6 capillary tubes were filled each with roughly 50 µL, immediately flame-sealed and stored at 5 °C until further analysis in our facility at Strasbourg (CEPE). Among the 18 blue petrels injected with DLW in 1999 and the 21 sampled in 2000 (accounting for a total of 18 and 29 foraging trips, respectively), 7 were not recaptured the following days (1 and 6, respectively); it was not possible to determine whether these individuals have deserted the colony or carried out exceptionally long trip. In January 2000, among the 21 blue petrels injected with DLW, one was injected three times and six other birds were injected 2 times. For both long and short trips, there was no difference between birds injected with DLW and other birds, in terms of foraging trip duration (two-way ANOVA on effect of injection, $F_{1,112} = 0·2$, $P = 0·803$), adult mass change ($F_{1,105} = 1·1$, $P = 0·298$), or meal size ($F_{1,115} = 0·5$, $P = 0·496$).

ISOTOPE ANALYSIS

Water was extracted from approximately 100 µL of blood by vacuum distillation (Wong, Lee & Klein 1987). Then from the distilled water the $^{18}$O/$^{16}$O ratio was determined by equilibration with CO$_2$, where water (15 µL) and CO$_2$ (0·04 mm) were introduced into an equilibration tube and placed for 48 h at 25 °C in a thermostatically controlled cabinet to allow exchange of oxygen atoms between the water and the CO$_2$. After equilibration, the CO$_2$ was separated by freezing the water to −80 °C and collecting the CO$_2$ with a liquid nitrogen trap. The $^{18}$O/$^{16}$O enrichment of the CO$_2$ was measured by isotope ratio mass spectrometry, and the enrichment for the water could be calculated from the enrichment of CO$_2$ and from the amount of water and CO$_2$ involved in the equilibration process (Wong, Lee & Klein 1987). Deuterium analysis was performed using the zinc-reduction method. An aliquot of 3 µL of the water sample was reduced with 100 mg of zinc (provided by the Geological Department, Indiana University, USA) in a furnace at 500 °C for 30 min. The $^{18}$O/$^{16}$O and $^{2}$H/$^{1}$H isotope ratios were measured in triplicate in our facility with a VG isotopic analyser mass spectrometer. All sets of measurements were calibrated using standards. For $^2$H, differences between replicates were 0·20 ± 0·14% (mean ± SD), 0·59 ± 0·39% and 0·17 ± 0·15% (background, initial and final isotope level, respectively, 16 short trips); 0·33 ± 0·39%, 0·36 ± 0·19% and 0·88 ± 0·33% (background, initial and final isotope level, respectively, 12 long trips). For $^{18}$O, differences between replicates were on average 0·03 ± 0·03%, 0·09 ± 0·08% and 0·05 ± 0·04% (background, initial and final isotope level, respectively, 16 short trips); 0·03 ± 0·03%, 0·12 ± 0·11% and 0·08 ± 0·04% (background, initial and final isotope level, respectively, 12 long trips).

The final isotopic enrichment of four birds after trips of long duration was too close to background abundance in 1999 and consequently, these results were discarded from the present analysis. For seven other samples it was not possible to estimate energy expenditure for technical reasons possibly related to injection of isotopes and to the ceiling of tubes and their conservation. Finally, we obtained 29 reliable sample sets, 11 in 1999 (4 short and 7 long trips) and 18 in 2000 (13 short and 5 long trips). Dilution spaces were calculated from the initial $^{18}$O and $^2$H enrichments. As is usually reported, the mean fractional body water content was greater for deuterium (53·7%) than for $^{18}$O (52·2%) because of the partial incorporation of $^2$H in substances other than water (Culebras & Moore 1977). In contrast, $^{18}$O is only slightly incorporated (Schoeller et al. 1980) and its dilution space represents a good determination of total body water. The mean dilution space ratios measured were close to those reported for humans and most animals including birds ($R_{dilut} = 1·03$, see Speakman 1997).

The rate of CO$_2$ production was calculated using the equation 7·17 proposed by Speakman (1997). Also we used an energy equivalent of 27·33 kJ per litre of CO$_2$ produced (Gessaman & Nagy 1988). A respiratory quotients of 0·72 was used to convert the rate of CO$_2$ production into units of energy expenditure. In
measuring the energy cost of foraging, one could expect a non-steady state of body composition, particularly with respect to water and fat. Following the first experiment using DLW (Lifson & McClintock 1966), many more publications reporting methodological refinements, validation tests and assumption evaluations have appeared (Nagy 1980, 1989; Speakman 1997). Initial validation studies indicated that error in the DLW method was approximately 8% but recent refinements and development of isotope-ratio mass spectrometer procedures reduced errors in studies of captive animals to approximately 2%. In birds, the validity of the flight energetic cost determined by the DLW method was dependent upon previous works collated by Speakman (1997). The accuracy of the DLW method has been examined by comparison with direct measurements of CO$_2$ production, or by comparison with indirect measurements such as energy budgets. To our knowledge, in total there have been 18 published validation studies on birds ranging in mass from 4 g to 4·2 kg: the average algebraic error was 0·2% (SD = 5·0%, individual range of errors from −7·1% to 13·8%, 18 studies, Speakman 1997). Even with the highest individual error (14%), the results of our comparison between 2 different foraging strategies stayed unchanged.

ENERGETIC YIELD, STATISTICAL ANALYSIS AND ETHICS

We have separated trips into short and long trips on the basis of previous studies showing that the distribution of the duration of trips is bimodal, with 4 and 5 days trips being very rare and absent some years, and that short trips (1–4 days) differ from long trips (5–10 days) in adult mass change and in diet (Chaurand & Weimerskirch 1994a; Cherel et al. 2002; Weimerskirch unpublished data). Estimation of average energy flow, energetic yield and foraging efficiency follow calculations of Chaurand & Weimerskirch (1994a) and Weimerskirch et al. (1997). Diet composition was based on data from Cherel et al. (2002) showing that diet differs in composition between short and long trips and thus in energy content. Results are reported as means with their standard deviations (± SD). Statistical analyses were performed with Systat 7·0 (Wilkinson 1996). When several values of one variable were available for the same individual, pseudo-replication problems were avoided by randomly selecting one sample per individual for short trips and one for long trips. Because for each individual we had two measurements of each variable one during a long trip and one during a short trip, we used repeated measure ANOVAs (except for energy expenditure where we used only one observation per individual).

The study was approved by the ethical committee of Institut Français pour la Recherche et la Technologie Polaires and followed the agreed measures for the conservation of Antarctic and sub-Antarctic fauna.

Results

PROVISIONING PARAMETERS AND BREEDING SUCCESS

The distribution of foraging trips during the two seasons was similar, showing a typical bimodal distribution, with short trips lasting 1–4 days, and long trips 5–10 days (Fig. 1a). Birds basically alternated a short trip with a long trip in 88·2% of the succession of trips, and rarely performed successive short trips (9·8%) or successive long trips (2%). Adults were heavier after long trips (184 ± 6 g) than when returning from a short trip (168 ± 7 g), and there was no difference between years (Table 1). On average, birds lost mass during short trips and gained mass during long trips, and there were significant differences in adult mass changes between years (Fig. 1b, Table 1). In 2000, birds gained more mass during a long trip than in 1999. The meal mass delivered to the chick was heavier after a long trip (61 ± 6 g) than after a short trip (46 ± 9 g), but there was no difference between years (Fig. 1c, Table 1). In 2000, birds gained more mass during a long trip than in 1999. The meal mass delivered to the chick was heavier after a long trip (61 ± 6 g) than after a short trip (46 ± 9 g), but there was no difference between years (Fig. 1c, Table 1).

The mass at fledging of chicks was similar between the two years ($t = 0·458$, d.f. = 114, $P = 0·648$). Fledging success was also similar between the two years ($\chi^2 = 2·75$, $P = 0·097$).
ENERGY EXPENDITURE

The daily mass specific energy expenditure was very different between short and long trips (Table 1). Blue petrels expended 2.2 times more energy during short trips than during long foraging trips (2561 vs. 1142 kJ day\(^{-1} \text{kg}^{-1}\)). There was no significant difference between years (Table 1).

Four samples obtained in 1999 after long trips had final isotopic enrichment that were close to background levels, suggesting that these birds could have expended energy fastest than the other birds during long trips. The samples have been discarded because it is not possible to estimate energy expenditure and this may result in an underestimate of the average costs of long trips. However even if the four birds had foraging costs as high as the highest cost measured during short trips, the difference between long and short trips would still be significant (2561 ± 284 vs. 1676 ± 1010 kJ day\(^{-1} \text{kg}^{-1}\), \(t = 3.3, P = 0.003\)), and represent 1.5 times more energy expended during short trips compared to long trips.

When comparing short and long foraging trips, shorter trips appeared to be more profitable because adult mass loss increased with the duration of short trips, and mass gain decreased with the duration of long trips (Fig. 1: \(r = -0.358, P = 0.022\) for short trips; \(r = -0.242, P = 0.037\) for long trips). The duration of foraging trips during either short trips or long trips did not affect meal sizes or energy expenditure (Fig. 1).

The simultaneous measurements of field metabolic rates (FMR), adult mass changes, and meal sizes delivered to the chick provide a unique opportunity to estimate how adults allocate energy between themselves and their chick, and therefore to estimate variations in foraging efficiency according to the duration of trips. The high costs of foraging incurred during short trips are covered in a large extent by the use of body reserves (as measured by the body mass loss) so that daily food requirements were only 15% higher during short trips compared to long trips (Table 2). Conversely, during short trips, the energy flow to the chick was twice that during long trips (Table 2). Thus overall, the daily mass of food required to cover energy requirements of both adults and chicks was 25% higher during short trips compared to long trips (Table 2).

Daily energy flow to chicks peaked for 1-day trips and declined progressively, whereas the daily energy equivalent for adult mass changes increased progressively up to 6 days, and then decreased. Daily energy expenditure declined from 1 to 6 days (Fig. 2). The total daily food requirement declined with the duration of foraging trip. The foraging efficiency, defined as the ratio of energy gained over energy spent while foraging was higher for short trips than for long trips, and peaked for trips of 6 days (Fig. 2).

### Discussion

Alternate foraging strategies are widespread among pelagic seabirds such as petrels and albatrosses (Chaurand & Weimerskirch 1994a; Weimerskirch et al. 1994, 1997, 1999; Granadeiro et al. 1998; Weimerskirch & Cherel 1998; Weimerskirch 1998, 1999), and also exist in other seabirds such as penguins (Clarke et al. 1998). This strategy is generally interpreted as having evolved in species relying on distant resources, where short trips are used to increase the energy flow to the

### Table 1. Statistical tests for comparisons of provisioning parameters and metabolic rates from data of Fig. 1

<table>
<thead>
<tr>
<th>Variable</th>
<th>Effect</th>
<th>d.f.</th>
<th>(F)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Repeated measure ANOVA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult body mass</td>
<td>Within subjects</td>
<td>Short vs. long trip</td>
<td>1</td>
<td>8.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Trip (\times) year</td>
<td>1</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>49</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Between subjects</td>
<td>Year</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>49</td>
<td></td>
</tr>
<tr>
<td>Adult mass change</td>
<td>Within subjects</td>
<td>Short vs. long trip</td>
<td>1</td>
<td>175.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Trip (\times) year</td>
<td>1</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>37</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Between subjects</td>
<td>Year</td>
<td>1</td>
<td>9.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>37</td>
<td></td>
</tr>
<tr>
<td>Meal size</td>
<td>Within subjects</td>
<td>Short vs. long trip</td>
<td>1</td>
<td>64.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Trip (\times) year</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Between subjects</td>
<td>Year</td>
<td>1</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td>Two-ways ANOVA</td>
<td>Energy expenditure</td>
<td>Trip</td>
<td>1</td>
<td>62.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Year</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Year (\times) trip</td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>24</td>
<td></td>
</tr>
</tbody>
</table>
chick (Weimerskirch 1999). However until this work, no study has been able to measure the foraging costs during short and long trips, thus limiting the possibility of comparing foraging effort of each type of trip. Indeed foraging effort can only be estimated by measuring energy allocated while taking into account foraging efficiency (Stearns 1992).

One of the major and unexpected result of this study is that energy expenditure of foraging blue petrels can differ extensively according to allocation decision of the adult. We clearly demonstrated that the metabolic cost of short foraging bouts is at least 1·5 times the energy expended during long bouts, and probably closer to 2·2. This result was unexpected because it is different from previous predictions on allocation, which assumed that foraging costs were similar between the two kinds of trips (e.g. Weimerskirch et al. 1997). The only study that has compared field metabolic rates during long and short foraging trips was carried out during two different periods, incubation (long trips) and brooding (short trips) in an albatross, and found only a 10% difference in foraging costs between long and short trips (Shaffer, Costa & Weimerskirch 2003). It is particularly surprising because one might expect that foraging in more distant areas would result in higher energy expenditure compared to foraging in nearby waters. Although foraging costs may not be so different between short and long foraging trips in other species during the chick-rearing period, at least in another species similar

| Table 2. Comparison of energy allocation during short and long trips of blue petrels |
|------------------------------------------|---------------------|---------------------|
| Duration of trips (days) | Short trip | Long trip |
| Adult mass (g) | 168·4 | 183·6 |
| Adult mass change (g) | −13·7 | 14·6 |
| Energy equivalent of mass change (kJ) | −306 | 433 |
| Energy expenditure (kJ) | 854 | 1450 |
| Daily energy expenditure (kJ day⁻¹) | 449 | 199 |
| Adult food requirement (kJ) | 548 | 1883 |
| Daily food requirement for activity (kJ day⁻¹) | 288 | 257 |
| Meal size (g) | 45·6 | 60·7 |
| Food energy content of meal (kJ) | 255 | 473 |
| Daily energy flow to chick (kJ day⁻¹) | 134 | 65 |
| Total food energy needed (kJ) | 803 | 2356 |
| Daily energy requirement (kJ) | 422 | 322 |
| Daily mass of prey required (g) | 86 | 65 |

Fig. 2. Estimated energy requirement, energy flow to chick and energy expenditure in relation to the duration of foraging trips, and measure of foraging efficiency in relation to the distribution of the duration of foraging trips.
differences exist. This study was preceded by a pilot study in 1997 undertaken on thin-billed prions (Pachyptila belcheri Mathews). Despite the very low number of individuals successfully studied (n = 2 for both groups), we obtained the same pattern as in blue petrels: short foraging trips are more expensive compared to long foraging trips, 3062 vs. 2197 kJ day$^{-1}$ kg$^{-1}$, respectively.

The much higher foraging cost of short trips has several consequences in terms of breeding effort and allocation decisions. First, it means that individual blue petrels are able to adjust foraging effort according to the allocation decision. This is the first time this has been demonstrated. Obviously, it was more costly for blue petrels to forage during short trips than during long trips. A priori this would not be expected because during short trips, blue petrels forage close to the islands over the shelf area, whereas during the long trips, birds forage at least 1000 km from their colonies where swarms of Antarctic krill Euphausia superba, one of their main prey during long trips, occur (Cherel et al. 2002). This means that during short trips, birds probably have completely different ways of foraging compared to long trips. During long trips birds commute to Antarctic waters, perhaps by using favourable wind conditions to lower flight costs, to search in highly productive waters. During short trips, birds catch a limited amount of prey and expend much more energy to do so. Furness & Bryant (1996) have shown that costs of foraging of an other petrel species can vary considerably in relation to wind conditions. Blue petrels may either use a different flight behaviour, not using winds optimally or taking off and landing more frequently, which can result in higher energetic costs (Weimerskirch et al. 2000; Shaffer, Costa & Weimerskirch 2001). Alternatively, petrels may make more dives (Chastel & Bried 1996), which is a costly activity for flying birds (Bevan et al. 1995). The cost of foraging during short trips is 3.2 times the energy expenditure during resting (800 kJ day$^{-1}$ kg$^{-1}$, Brown 1988), and during long trips only 1.4–2.1 times resting metabolic rate.

Foraging animals have to adjust their breeding effort in relation to time and energy constraints (Ydenberg et al. 1992). However, there are few empirical studies that have examined the currencies associated with foraging behaviour and reproduction, especially for animals relying on distant resources. Blue petrels basically forage in Antarctic waters and breed on sub-Antarctic islands. When time away from the nest is less of a constraint, such as during incubation, adults basically forage for trips of 9–18 days. At this time the yield decreases with the duration of trips, but increases as the season progresses to the summer (Chaurand & Weimerskirch 1994b). In summer, blue petrels rearing chicks are faced with a trade-off between foraging close to the breeding grounds to maximize food delivery to the chick, and foraging further from the colony where efficiency is higher (Fig. 2). Our results show that birds can make a compromise by alternating between short and long trips. The currency during long trips is to maximize efficiency, whereas during short trips the currency is to maximize rate of energy delivery to the chick. For blue petrels, maximum efficiency is achieved when adult mass gain is highest and foraging costs lowest, for trips lasting 6 days. Although 6 days is the optimal duration of foraging trips, the most frequent trip durations were 7 days.

Very few provisioning studies distinguish between self-feeding and delivery but this is probably crucial because allocation of food between self-feeding and delivery has an important influence on foraging decisions (Ydenberg et al. 1992). Our study shows that self-feeding during long trips is crucial for the success of short trips because most of the energy used during short trips was probably derived from the energy stored during long trips (Fig. 2). Thus, blue petrels are probably using two completely different decisions rules to determine the effort while foraging because of this ability to store energy during long trips which can then be used to supplement the higher costs of conducting short trips. Moreover, all food acquired during short trips is delivered to the chick.

The decision rules to allocate energy towards the offspring or for self-feeding are probably under the control of the body condition of adult birds (Weimerskirch 1998, 1999). Decisions to initiate a long trip are related to the proximity of a mass threshold, and blue petrels are the only species that almost always alternate short and long trips. They do not perform successive short trips before a long trip to increase the energy flow to the chick as do all other species of petrels and albatrosses (Weimerskirch 1999). The low adult body mass attained at the end of short foraging trips (168 g) is close to the mass threshold attained at egg desertion (164 g, Chaurand & Weimerskirch 1994b), but is nevertheless higher than the critical body mass of 160 g (Ancel, Petter & Groscolas 1998) when they start to use protein extensively instead of fat reserves, i.e. when mortality risks are increased.

There were no important differences in the provisioning and costs between 1999 and 2000. The distribution of foraging trips and provisioning parameters were also similar to data obtained in 1989 (Chaurand & Weimerskirch 1994a) and 1998 (Cherel et al. 2002; Weimerskirch unpublished data). This suggests that the foraging strategies of blue petrels are not as flexible as those of other petrel species which can adjust to a larger degree their foraging and provisioning effort by modifying the succession and number of short and long trips, or the duration of trips (Granadeiro et al. 1998; Weimerskirch, Fradet & Cherel 1999; Duriez, Weimerskirch & Fritz 2000). This reduced flexibility is probably related to the long distance between the colony and the feeding grounds, and to the efficiency of foraging. The small body size of blue petrels also means that it has a smaller safety margin of stored energy (Weimerskirch 1999).
Acknowledgements

Field work was financially and logistically supported by the Institut Français pour la Recherche et la Technologie Polaires, the Terres Australes et Antarctiques Françaises and by GDR 902 ‘Ecophysiologie des animaux antarctiques et subantarctiques’ from the CNRS. We thank R. Bersuder for valuable technical assistance with the isotopic analysis, O. Duriez for his contribution to the work on thin-billed prion and H. Visser for help with the DLW analysis. S.A. Shaffer also provided helpful comments on earlier drafts.

References


*Received 24 October 2002; accepted 24 February 2003*