

How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters

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Summary

1. Sooty shearwaters are abundant in waters too distant from their colonies to account for the observed average frequency with which the chicks are fed. This, and the unexplained cyclic pattern of attendance at their colonies, have led to contradictory interpretations related to evolution of the extreme life histories of pelagic seabirds and their relationship with the marine environment.

2. Study of the provisioning behaviour of individual parent sooty shearwaters indicates that they can rely on productive distant waters, probably 1550 km away, to build up their body reserves and to provision their chick. These long foraging trips on average last 11 days and account for 84% of the foraging time.

3. Birds use this stored energy to cover the costs of performing several successive foraging trips of short duration in nearby less productive waters. These brief trips double the energy flow to the chick and take only 16% of the foraging time but are at the expense of adult body condition, i.e. there is a net energy loss. Foraging successively with short and long trips allows parents to increase by 20% the energy flow to the chick over what it would get if foraging was exclusively in distant waters.

4. The results suggest that maximal fitness in this pelagic seabird is not achieved by maximization of foraging efficiency but is the result of a trade-off system whereby at some stages birds forage with net energy losses. The decision to feed close to or far from the colonies, i.e. to allocate to the chick or to store body reserves, is not related to any endogenous rhythm, nor to the nutritional status of the chick, nor to the length of the previous foraging trip. Rather, it is under the sole control of adult body condition, with the possible existence of a threshold body mass around 750 g. Thus, adult body mass plays a central role in foraging decisions, linking foraging and allocation.

5. The synchronized return of foraging birds every 2 weeks is not due to environmental factors. By modelling attendance patterns with an increasing variance in the foraging routine, it is shown that the periodicity of feeding times is retained throughout the chick rearing period, with a cyclicity of 14 days. This result indicates that cyclic attendance at the level of the whole colony is an emergent property of the two-fold foraging strategy of individual adults.

6. One main consequence of this system appears to be a reduction in competition close to the breeding grounds and this may help explain the existence of huge populations of sooty and short-tailed shearwaters that rely on distant food resources.

Key-words: allocation, energy gain, foraging efficiency, chick growth, Antarctica.

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Introduction

The costs and benefits of foraging behaviour are generally expressed in terms of a common currency that

is assumed to be linked to fitness (Stephens & Krebs 1986). It is generally considered that maximization of fitness is achieved by maximizing the efficiency of foraging behaviour, i.e. the ratio of energy gained over

energy spent while foraging, rather than maximizing rate of acquisition of food (e.g. Kacelnik *et al.* 1986). When considering animals that forage in order to provision offspring, measures of efficiency must discriminate between provisioning and self-feeding (e.g. Ydenberg *et al.* 1994): provisioning is generally measured by the energy flow to the offspring, self-feeding by short-term changes in the body mass of the provisioner. In the short-term organization of foraging, changes in adult mass can play an important role (Norberg 1981), but there can be longer-term implications because of the mortality risks associated with some foraging decisions (Houston *et al.* 1988). Evidence is accumulating about the role of the animal physiological state, e.g. body condition, in allocation decision (MacNamara & Houston 1996). Thus, foraging and the allocation of resources during reproduction should be considered under the conceptual framework of life-history theory (Stearns 1992), and foraging effort could be regarded as the result of an allocation decision (Boggs 1992).

Petrels are notable for their extreme life-history traits (low mortality, low fecundity) and are potentially interesting examples of central place foragers in that they provision their single chick only infrequently (Lack 1968). This low rate of provisioning is attributed to the unpredictability of their food resources (Ashmole 1971) and to the costs of travelling long distances between their feeding and breeding sites (Lack 1968). As the efficiency of energy transfer is expected to decrease as distance to feeding zones increases (e.g. Houston 1993), possibly because of the energy required for commuting to distant feeding grounds (Houston 1995), the energy flow to the chick is weak. The growth of petrel chicks is slow as a result, and this and the inability of adults of several species to increase their provisioning rate when the food demand of the chick is experimentally increased (e.g. Rice & Kenyon 1962; Harris 1966; Ricklefs 1987) have suggested that the adult is gathering food at the maximum possible rate, under the constraint of foraging success (Ricklefs & Schew 1994). One prediction would be that adults provision their chicks with an endogenous rhythm (Ricklefs *et al.* 1985), and not according to the needs of the chick. Recent studies (Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994, 1997) and models (Ricklefs & Schew 1994) have suggested, moreover, that the foraging behaviour of adult petrels could be related to the energy reserves of the adult and not to the nutritional state of the chick. In this context the enormous fat stores of petrel chicks are interpreted as an insurance against long periods of starvation (Lack 1968) or as a result of individual variation in foraging success due to external factors (Ricklefs & Schew 1994). Indeed, environmental factors such as the phase of the moon (Watanuki 1986; Oka *et al.* 1987; Klomp & Furness 1992) or wind strength (Dunn 1975) are likely to play an important role in the pattern of food provisioning. Such factors

may also be responsible for the tendency of several pelagic Procellariiformes to visit their chick cyclically (Richdale 1963; Oka *et al.* 1987) but there is no definite explanation yet for these cycles (Warham 1996). No study has, so far, separated the influences of adult condition, chick nutritional state, environmental factors and, potential endogenous rhythms on the provisioning behaviour of petrels.

The sooty shearwater *Puffinus griseus* (Gmelin) is often taken to exemplify the low feeding frequency and cyclic colony attendance of parent petrels: data obtained by Richdale (1963) have been reanalysed several times to this end (e.g. Lack 1968; Ricklefs *et al.* 1985; Oka *et al.* 1987; Hamer & Hill 1993). These birds feed their chicks infrequently. The average feeding interval is 2.8 days but chicks can fast on their nest for periods lasting more than 15 days (Richdale 1963). Although birds are observed feeding in the vicinity of the breeding grounds (Fenwick 1978), the only concentrations of feeding birds that are in proportion with the huge breeding populations are in Antarctic waters, 1500–2000 km from nesting sites (Warham 1996), a minimum foraging trip of at least 6 days. Their visits follow cycles of abundance of 13–15 days whose significance has never been clearly elucidated (see Richdale 1963; Oka *et al.* 1987).

The aim of this study is to examine the possible influence of adult condition, chick condition, environmental factors or endogenous cycle on the provisioning behaviour and colony attendance of individual sooty shearwaters. Particular attention is paid to the influence of these factors on the decision of adult birds to return to feed the chick, or to remain at sea and follow a particular pattern of foraging behaviour.

Methods

The study was carried out on North-east Island, Snares Island, south of New Zealand, where there is an estimated breeding population of 2.7 million pairs of sooty shearwaters (Warham & Wilson 1982). Between 26 February and 16 March 1995, 30 burrows were fitted with trap doors at the entrance, and if access to the nest chamber was not possible through the burrow entrance, a hatch was installed over the nest. The function of the trap door was to retain the adult in the burrow. Sticks were placed at the mouth of the burrow and kept the door open, so that a visit by an adult could be detected by the displacement of the sticks and closure of the door. When closed, the swinging door still allows the entrance of other birds but prevent birds from leaving the burrow. Burrows were inspected during five 1-hour systematic round tours just after dusk at 20.30 h, at 23.00 h and at 05.30 h just before dawn, and during the day at 09.00 h and 17.00 h. During the day visits chicks were weighed to the nearest 10 g with a Salter spring balance. During the night, if a visit was detected the adult was caught

when chick begging had ceased, i.e. when feeding had stopped and the adult was returning to sea, otherwise a repeat visit was made to the burrow at the end of the round tour. When first caught, the parent was ringed and at every capture thereafter identified by its ring and weighed to the nearest 10 g. The chick was weighed each time that an adult had visited the nest. Adults start to return to land at dusk, the peak of returns occurring during the first hour after dusk (42.7% of the visits, $n = 155$). The rest of the visits were distributed through the night. Birds returning during the first part of the night stayed with the chick for only 1 hour and then left. Adults visiting the chick after midnight, after delivering the meal, stay at the entrance of the burrow and leave the colony en masse at dawn. This second group of parents was thus easily recaptured at the entrance of the burrow during the 05.30 h visit.

The duration of individual foraging trips was defined as the time elapsed between two successive recoveries of the same bird. As 14% of the birds escaped from the recaptures, all trips of uncertain duration were excluded from the analysis. Feed mass was calculated as the difference in mass between the 17.00 h weighing and the mass recorded after a visit, added to the estimated mass loss since the 17.00 h weighing. Indeed, as the chick mass decreases asymptotically with time following the last feed (Ricketts & Prince 1981), rate of mass loss was calculated for the first and second day after a feed, and for more than 2 days after a feed. The hourly mass loss was 2.4 ± 1.1 g h⁻¹ ($n = 58$) 1 day after a meal, 1.6 ± 0.8 g h⁻¹ ($n = 39$) 2 days after, 1.4 ± 0.5 g h⁻¹ ($n = 32$) 3 days after, and 0.9 ± 0.4 g h⁻¹ ($n = 87$) more than 3 days after. When two parents had fed the chick between two burrow inspections, the mass increase corresponding to the double feed was not used in the calculations of meal mass. The body condition of each individual chick was defined as the residual from the linear regression of mass on time. Laying and hatching are highly synchronized in sooty shearwaters on the Snares Islands, each within a period of 10 days and at similar dates from one year to the next (Richdale 1963; Warham *et al.* 1982). Using the average hatching date obtained from previous studies (13 January), the average age of chicks on 26 February when the study started was estimated to be 43 days. Thus, when the study started chicks were close to peak weight that is attained at the age of 55 days (Richdale 1963).

In sooty shearwaters the two sexes are very similar, but males tend to be larger than females (Marchant & Higgins 1990). I have therefore assumed that males were heavier than females as it is the case for all other shearwater species where sex has been discriminated (Marchant & Higgins 1990). In this study the sex of the parent is determined on the basis of the male of a pair being heavier than the female. The study encompassed a complete half lunar cycle from no moon (1 March) to full moon (17 March). Data on weather

conditions were provided by the meteorological station of Invercargill, 220 km north from the Snares Islands. To study the influence of meteorological factors on the number of birds visiting the colony each night, we used average and maximum wind speeds over the 12 h preceding the first arrival on the colonies at 19.00 h, barometric pressure at 12.00 h before the first arrival.

To study whether the factors adult body mass, chick body condition, meal size, time since last meal and duration of the previous foraging trip influence the decision to make either a short or a long trip (see results) I used PROC CATMOD with maximum-likelihood estimators in Statistical Analysis System (SAS Inst. 1987).

Energy flow and energetic yield of foraging trips were estimated following Chaurand & Weimerskirch (1994). The energy flow is the average quantity of energy received by the chick per unit of time, i.e. twice (two parents) the mass of the meal multiplied by its calorific value per unit of time. The energetic yield is calculated as the energy delivered to the chick added to the energy stored or lost by the adult after a foraging trip, assuming that in the long term the adult is keeping its body mass stable. The calorific value of meals is the energy equivalent of each component, with value of 4.35 kJ g⁻¹ for crustacean (Croxall *et al.* 1985) and 7.0 for myctophid fish (Cherel & Ridoux 1992). The energetic equivalent of change in adult mass is 19.8 kJ g⁻¹ assuming that the material lost is lipid (Groscolas *et al.* 1991). The energy expenditure at sea for sooty shearwaters was estimated using a regression of log body mass against field metabolic rates estimated for petrels and albatrosses, excluding storm petrels and diving petrels which have a different flight type, and hence mass specific energy expenditure (Pennycuik 1989). Values used are summarized by Birt-Friesen *et al.* (1989) and give for a sooty shearwater with a mass of 850 g an energy expenditure of 1.2 kJ day⁻¹ g⁻¹.

To model the change in numbers of birds visiting their chick each day over the whole period of chick rearing, I used the mean, variance and range of hatching dates, and the duration of the brood guard period (5 days) measured on the Snares Island sooty shearwaters (Warham *et al.* 1982) to simulate the distribution of days when a theoretical sample of 100 birds would first start their foraging routine after the chick has been left alone on the nest. To this sample of birds is then attributed randomly a routine of foraging trips with an increasing variability, within the range of the values observed in the study. The periodicity of the cycle was estimated by measuring the time elapsed between two successive low values.

The position of the Antarctic Polar Front in early March 1995 was estimated using sea surface temperatures provided by the IGOSS (International Global Ocean Service System) weekly sea surface temperatures (Reynolds & Smith 1994).

Results

CHICK GROWTH AND COLONY ATTENDANCE

For each of the 30 burrows monitored, both parents were ringed and weight data were gathered for the chicks. The average body mass of chicks tended to decrease during the first part of the study period and to increase thereafter (Fig. 1a). A total of 155 visits were made by adults. The number of adult birds visiting their chick varied significantly from one day to the next over the study period ($\chi^2_{17} = 30.7$, $P = 0.022$, Fig. 1b), ranging from 6 to 31% of the adults visiting their chick each day (Fig. 1b). The proportion of parents visiting their chick on a particular day was not related to lunar phase ($r = 0.3892$, $n = 18$, $P > 0.1$), average wind speed ($r = -0.197$, $P > 0.1$), maximum wind speed ($r = -0.145$, $P > 0.1$) nor wind direction ($r = -0.004$, $P > 0.1$). Over the study period, the average number of feeds received per day was 0.35 ± 0.14 (range 0.11–0.54), i.e. on average a chick received a meal every 2.86 days, suggesting that the average foraging trip of each parent was 5.7 days.

FORAGING TRIPS

Of the 155 foraging trips, 76% were foraging trips of short duration (1, 2 or 3 days), and the others lasted from 5 to 15 days with no trip of 4 days (Fig. 2a). In this study, foraging trips lasting 1–3 days are denoted Short Trips (ST), and those of 5–15 days or more, Long Trips (LT). For ST, females tended to make more 1-day trips and males more 2-day foraging trips (68.6% of 1-day trips for females against 37.6% for

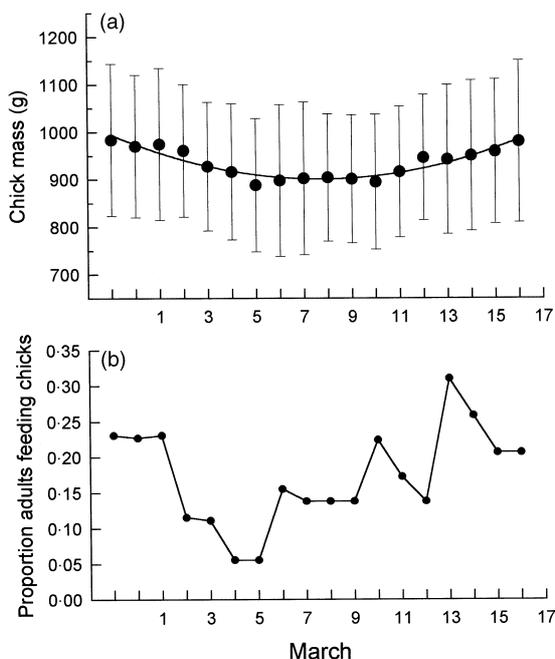


Fig. 1. Changes between 27 February and 16 March 1995 (a) in the average mass (± 1 SD) of chicks, and (b) in the proportion of adult parents visiting their chicks.

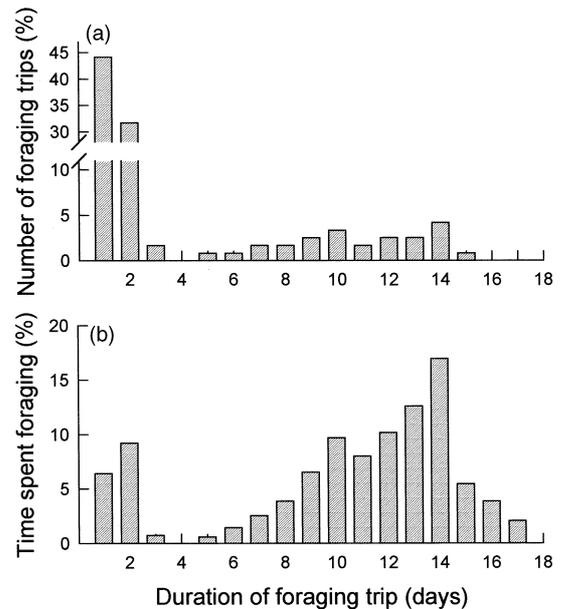


Fig. 2. Distribution of (a) foraging trips of different lengths considering all adult birds, and (b) time spent foraging by adult birds among foraging trips of different duration.

males; $\chi^2_1 = 6.03$, $P = 0.014$). There was no sex-specific difference in the distribution of long trips (G -test, $G = 9.2$, $P = 0.513$). LT may have been underestimated for the longer trips because of the relatively short study period. The maximum range is likely to have been slightly underestimated as two foraging trips were longer than 15 and 16 days. On average, 56 birds studied spent $83.7 \pm 10.5\%$ (range 46.7–100) of their foraging time in LT, so it is possible to calculate the extent of the underestimate and estimate the proportion of foraging trips and of time spent for each duration, assuming that foraging trips of 16 and 17 are rare as suggested by the low occurrence of trips longer than 15 days (Fig. 2b). In all, 60.4% of the foraging trips were ST.

Males and females were making ST and LT in a similar proportion ($\chi^2_1 = 0.165$, $P = 0.685$) and there was no tendency for individual birds to make only ST or only LT (for 17 males, $G = 3.97$, $P = 0.999$, for 21 females $G = 6.19$, $P = 0.997$). The succession of foraging trips was not random. When birds returned from a LT, they tended to start a ST more often than would be expected from the distribution of ST vs. LT ($\chi^2_1 = 5.67$, $P = 0.017$). After the first ST following a LT, they started a ST in a proportion similar to that expected from the theoretical distribution ($\chi^2_1 = 0.0$, $P = 1.00$), but after the second or third ST following a LT, they tended to start a LT in a higher proportion than would be expected (G -test, $G = 3.62$, $P = 0.057$). The typical succession of foraging trips was to make on average a LT followed by 2 ST, then another LT (Table 2). In total the succession of ST and LT was ST–LT 31.5%, ST–ST 28.5%, LT–LT 6.9% and LT–ST 33.1%.

MEAL SIZE

The average mass of feeds delivered to the chick was 132.3 ± 66.2 g (range 10–340, $n = 172$). Meals delivered after LT were significantly heavier than after ST (Table 1). The mass of meals was similar for ST of 1 and 2 days (92.2 ± 47.4 , $n = 55$, range 10–230 and 102.9 ± 48.5 , $n = 39$, range 10–240, respectively, $P = 0.285$). For LT there was no significant relationship between the duration of the foraging trip and the meal size ($r = -0.179$, $n = 26$, $P > 0.1$). The mass of the meal delivered after a ST was not influenced by whether it was the first, second or third ST ($F_{2,75} = 1.87$, $P = 0.1599$).

The time elapsed since the last meal had no influence on the mass of a meal delivered after a LT ($r = 0.1476$, $n = 55$, $P > 0.05$) nor on the duration of the next foraging trip ($r = -0.057$, $P > 0.5$). The condition of the chick did not influence the mass of the meal delivered after a ST ($r = -0.167$, $n = 94$, $P > 0.1$). For LT adults tended to deliver smaller meals to chicks in good condition ($r = -0.291$, $n = 53$, $P = 0.038$). The condition of the chick had no influence on the duration of the next foraging trip after a ST ($r = 0.100$, $n = 52$, $P > 0.1$) or after a LT ($r_s = 0.2$, $n = 60$, $P > 0.1$).

ADULT MASS

After delivery of a meal, body mass of adult birds was significantly higher after a LT than after a ST (Table 1). Adult mass changed from one trip to the next, although not as the result of a long-term change in adult mass, as there was no relationship between the mass of adult and the date ($r = 0.134$, $n = 95$, $P > 0.1$). Changes in adult mass were negative after ST and positive after LT (Table 1), indicating that, taking account of the meal delivered, parents gain mass during a LT and lose mass during a ST. The extent of mass loss was similar for foraging trips of 1 and 2 days (-27.3 ± 28.0 g, range -70 to 30, $n = 11$ and -42.5 ± 23.6 , -90 to 10, $n = 20$, respectively, $P = 0.118$), and after a first and a second ST (-36.3 ± 28.5 g, range -90 to 30, $n = 19$ and -35.5 ± 19.4 , -65 to -10, $n = 9$, respectively, $P = 0.943$).

Birds starting a LT were significantly lighter weight than birds starting a ST, irrespective of the nature of the preceding trip (Table 2). Conversely, the mass of birds starting a ST or starting a LT was similar whether after a LT or after the first, second or third ST (Table 2). The only factor to influence the duration of the next trip was the body mass of the adult (Table 3), a ST being more likely when body mass was high (Fig. 3a). Birds lighter than 750 g always started a LT, suggesting the existence of a threshold (Fig. 3b).

ENERGY FLOWS AND FORAGING EFFICIENCY

There were two types of meals delivered to chicks during the study period, some of fresh crustacean (mainly *Nyctiphanes australis* G.O. Sars, but also *Themisto gaudichaudii* Guérin), others of digested myctophid fish. Energy flow to chicks was estimated assuming that crustaceans were delivered after ST, because large numbers of sooty shearwaters feed on crustaceans (especially *N. australis*) in the vicinity of the Snares (Fenwick 1978), and myctophids during LT. This assumption is supported by results obtained on the closely related short-tailed shearwater *Puffinus tenuirostris* Temminck (Weimerskirch & Cherel, unpublished). The energy delivered to the chick was calculated as 417 kJ after a ST and 1351 kJ after a LT, giving an energy flow to chick of 6.38 W ($J s^{-1}$) for ST and 3.27 W for LT. The net energy flow, giving that birds made on average 2.5 ST for 1 LT is consequently 3.9 W. Energy expended by the adult during the average ST (mass-specific daily energy expenditure \times body mass \times duration of trip) was calculated as 1479 kJ and for LT, 10914 kJ. The increase in body mass after the average LT was equivalent to 1554 kJ, and the decrease after the average ST, to -742 kJ. Combining these values gives values for energetic yield of -4.38 W for ST and $+3.57$ W for LT.

CYCLIC ATTENDANCE PATTERN

The pattern of colony attendance observed during the study period resembles part of a cycle (Fig. 1b) reminiscent of the cyclic colony attendance observed by Richdale (1963) over the entire chick rearing

Table 1. Provisioning parameters of foraging trips of short and long duration [average \pm 1 SD (sample size), range]

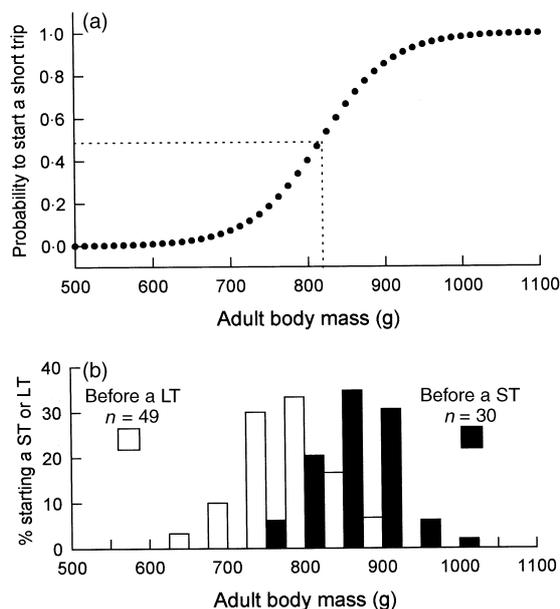
	Short trips	Long trips	<i>P</i>
Duration of foraging trips (days)	0.45 ± 0.54 (95) 1–3	10.74 ± 2.78 (27) 5–15	
Meal size (g)	96.2 ± 47.5 (96) 10–240	193.0 ± 49.6 (55) 100–340	< 0.0001
Adult mass (g)	837.0 ± 53.3 (46) 730–990	869.1 ± 68.4 (35) 680–1020	$= 0.0196$
Change in adult mass (g)	-37.5 ± 25.5 (32) -90–30	78.5 ± 52.5 (10) 15–165	< 0.0001

Table 2. Body mass (average mass \pm 1 SD) and percentage of birds classified according to the type of trip just completed, and to the type of trip then commenced (sample size in parentheses)

	Start ST		Start LT		Comparison between masses
	%	Mass (g)	%	Mass (g)	
After a LT	82.7% (52)	897.1 \pm 49.7 (24)	17.3% (7)	794.3 \pm 74.8 (7)	$t = 4.28, P < 0.0001$
After a first ST	62.9% (35)	862.7 \pm 54.8 (15)	37.1% (12)	820.8 \pm 44.6 (12)	$t = 2.14, P = 0.042$
After a second ST	27.8% (18)	863.3 \pm 56.8 (3)	72.2% (6)	793.3 \pm 28.0 (6)	$t = 2.57, P = 0.037$
After a third ST	0.0% (3)		100% (1)	850.0 (1)	
Comparison between masses after ST	$F_{2,39} = 2.24, P = 0.120$		$F_{2,22} = 1.02, P = 0.376$		

Table 3. Maximum likelihood analyses of categorical variables associated with the decision to start a ST or a LT

Source of variation	d.f.	χ^2	P
Adult mass	1	9.27	0.0023
Meal size	1	0.13	0.7228
Previous foraging trip	1	0.48	0.4904
Chick condition	1	0.82	0.3656
Time since last meal received by chick	1	1.55	0.2425
Adult mass \times previous foraging trip	1	0.67	0.4138

**Fig. 3.** Changes in (a) the probability of starting a short trip according to the adult body mass estimated from a logistic regression ($y = [\text{Exp}(-17.76 + 0.0217 \times \text{adult mass})] / [1 + \text{Exp}(-17.76 + 0.0217 \times \text{Adult mass})]$), and (b) the observed proportion of adult starting a short or a long trip according to the body mass of the adult.

modelling the number of birds attending the colony each day. The model starts with 100 adult parents hatching their chick between 7 and 18 January (average 13 January, from Warham *et al.* 1982) and starting a two-fold provisioning 5 days later when the chick is left alone in the nest (Warham *et al.* 1982). Four successive simulations (Fig. 4a–d), where the variance and range in the duration of the foraging trips and the variability in their routine have been increased, were performed and result each in a succession of eight cycles over the entire chick-rearing period. When using first the average values of one LT of 11 days followed by two ST of 1 and 2 days and considering that all birds have the same routine, the number of parents visiting the colony follows a cyclic pattern with a periodicity of 14 days (Fig. 4a). Thereafter, we have considered that each bird displayed a particular routine. With a regular alternation of one LT ranging between 9 and 14 days (average 11.1 ± 1.5 days, $n = 22$ birds with a different routine) followed by 2–3 ST lasting between 1 or 2 days, the number of birds followed a cyclic pattern with a periodicity of 13.8 ± 2.5 days (range 10–18 days, Fig. 4b). By increasing the variability of trip duration, with LT ranging from 5 to 16 days (average 10.9 ± 2.2 days) followed by 2 or 3 ST lasting 1–3 days a cyclic pattern of 14.0 ± 2.7 days (range 11–15) still occurs (Fig. 4c). Using the same duration of LT and ST but considering that the birds do not follow the same routine throughout the breeding season as it was considered in the three previous cases, a cyclic pattern of 14.3 ± 3.1 days (range 10–20) is still apparent (Fig. 4d). The duration of cycles was similar for the four models, and was also similar to the values observed in the colonies (average 14.4 ± 2.07 days, range 12–17, $n = 5$; Richdale 1963) in 1952 and 1953 ($F_{4,29} = 0.05, P = 0.994$).

Discussion

This study has clarified several aspects of the foraging ecology of sooty shearwaters that have been discussed

period. I have investigated whether the strategy of alternating several successive ST with a LT could be responsible for the cyclic pattern of attendance by

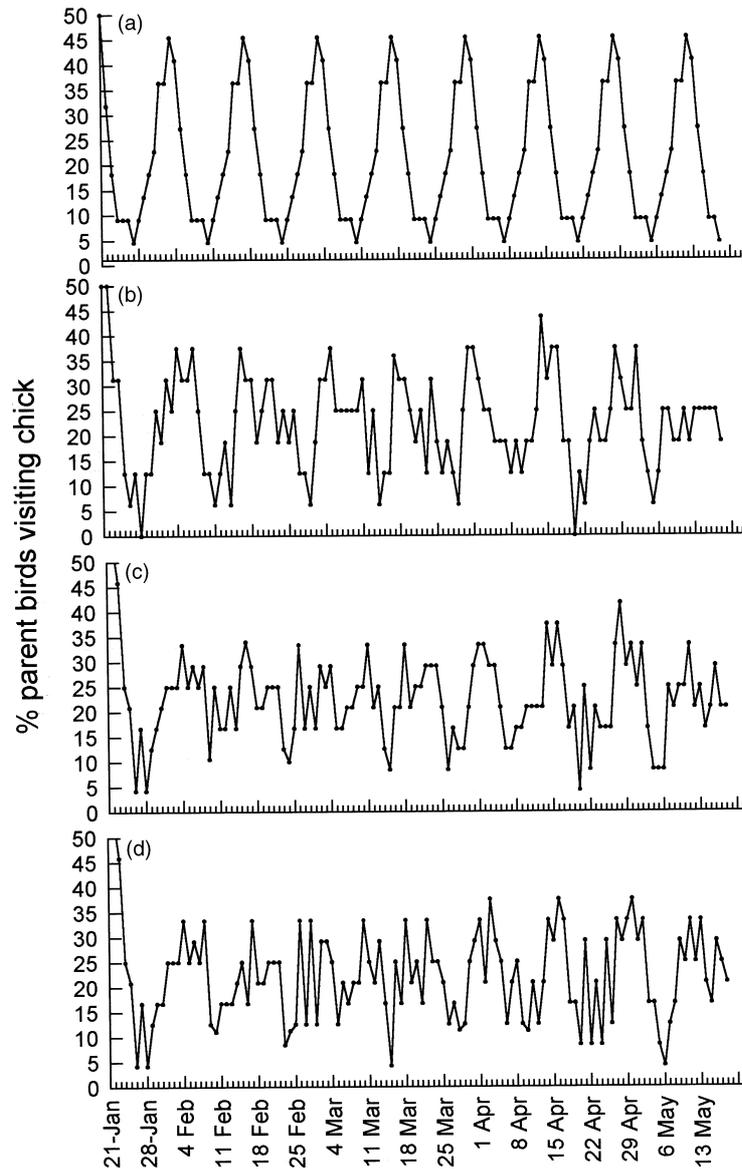


Fig. 4. Attendance pattern of the colony by adult parents feeding their chick modelled throughout the chick-rearing period with increasing variance in the duration of the foraging trips and their succession.

for some decades, particularly (i) how sooty shearwaters breeding in New Zealand can rely on food resources located in Antarctic waters, and (ii) why they visit the colonies with temporal cyclicality. The clue to these two paradoxes lies in the understanding of their specialized provisioning strategy. To answer these questions it has been necessary to measure simultaneously the provisioning behaviour of individuals and the energy flows, distinguishing self-feeding from storing energy. The meal mass, feeding frequency and cyclic attendance pattern measured in this study are very similar to the results obtained by studies in 1952 and 1953 at a similar stage of the chick-rearing period (Richdale 1963). The chicks were heavier, at a similar age, in our study than in the study of Richdale (1963). These observations suggest that the repeated capture of the adult birds had no influence on their provisioning behaviour. The occurrence of two types of

foraging trips of short and long duration is similar to what has been found in other species of Procellariiformes (Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994, 1997). However, this study is the first that demonstrates that body mass can influence foraging decisions.

FORAGING EFFICIENCY, FORAGING DECISION AND ADULT BODY MASS

Very few provisioning studies have been able to separate self-feeding and delivery because the individual behaviour and mass of adults were not monitored. However, self-feeding and delivery have to be taken into account because the allocation of food between them may be very important in foraging decisions (Ydenberg *et al.* 1994). Models generally assume that provisioners maximize the amount of energy delivered

and that provisioners are self-feeding and provisioning at each foraging trip. I have shown here that this is not the case in sooty shearwaters. During ST the energy necessary to cover the costs of foraging is 1479 kJ whereas the use of body reserves, measured by the energetic equivalent of adult mass loss, would cover only half this cost. The discrepancy between the energy equivalent of mass loss and foraging costs means that in order to cover foraging costs, birds self-feed, but that they also have to use body reserves. It can be estimated that birds gain an energy equivalent of 795 kJ day⁻¹ during ST and 1146 kJ day⁻¹ during LT. This suggests that birds probably forage in two distinct water masses with different profitabilities. They are known to dive to different depths according to the duration of foraging trips (Weimerskirch & Sagar 1996), suggesting they do not catch the same prey. The value of 1146 kJ day⁻¹ concerns the entire foraging trip, but birds are likely to commute to rich foraging zones, and thus not to feed during the commuting part of the foraging trip. Estimating a minimum commuting time of 4 days suggest a foraging success of 1830 kJ day⁻¹ caught in the distant feeding zone.

The foraging strategy of sooty shearwaters appears to be the result of a trade-off between two opposing provisioning strategies and is probably the one that would maximize fitness in species relying on distant food resources. Foraging only close to the colony, i.e. performing only ST would not be possible as with a daily rate of prey capture of 795 kJ day⁻¹, birds would not be able to cover their foraging costs (1020 kJ day⁻¹) and provision the chick, and their body mass would fall. Foraging only in distant waters results in an energy flow that is 20% lower than that resulting from a dual strategy. However, if birds only foraged in distant waters they would not have to store body reserves to cover foraging costs during ST and could thus deliver more energy to the chick. But meals represent already 22.2% of the body mass of the adult bird and have a much lower energetic density than fat stores; an additional food load for the chick would increase travelling costs for a bird of this size (Pennycook 1989; unpublished). Also large amount of food brought irregularly are less profitable for the growth of the chick than small amounts brought more frequently (Schaffner 1990). The calculations presented here are based on the assumption that the diet is different between LT and ST, and more energetic for LT than for ST. The second assumption is not only the result of the first, but also because some stomach oil, rich in energy, is likely to occur in meals from LT (see Weimerskirch *et al.* 1997; Weimerskirch & Chérel, unpublished).

The net rate of energy gain (energy gained – energy expended) is negative during ST and positive during LT, suggesting that to maximize efficiency, as would be predicted by foraging theory (Stephens & Krebs 1986), bird should only do LT. As pointed out by

Houston (1995), it is important to take into account the energy expenditure during periods when birds are commuting but not feeding. I have shown that despite the long time that may be spent commuting, LTs give a positive net rate of energy gain because food availability is much higher in distant than in close waters. This is mainly due to the observed difference in adult mass change, and only in a small extent to the difference in diet composition. Furthermore, the positive net rate of energy gain of LT is likely to be underestimated as meals delivered after LT probably contain stomach oil with a higher energy content than solid food (Weimerskirch *et al.* 1997; unpublished). Models of foraging efficiency have not yet considered the possibility that birds could forage accepting a negative net rate of energy gain in order to increase the provisioning rate to the offspring. The present study shows that measures of foraging efficiency cannot be separated from the allocation processes and thus must be considered under the conceptual framework of the life-history theory (Stearns 1992). Maximization of fitness can only be achieved under a currency that considers maximization of foraging efficiency as a result of a trade-off between present and future reproduction. Adult body mass plays a central role in foraging decision and thus in linking foraging and allocation.

Sooty shearwaters have to make a choice after feeding their chick: they can either start a ST to provision the chick at a high rate but not to feed for themselves, or they can feed for themselves and provision the chick at a lower rate. The switch from one pattern to another appears to be controlled only by the adult mass, and not by the nutritional status of the chick, the duration of the previous foraging trip, nor any endogenous rhythm. The decision to start a LT probably depends on the attainment of a threshold mass. Using a body condition index that would account for the structural size of the birds would probably prove the existence of a threshold value for this behavioural decision. In this study the size of the birds was not measured but when their masses are lower than 750 g birds always start a LT, indicating that they will not allow their condition to deteriorate further when visiting the chick. This probably reduces the risk of increased adult mortality, by allowing birds to reach productive feeding zones where they will regain condition. However, birds do not make more than three successive ST, even if their condition continues to be good, which would be a consequence of successful foraging.

As a result of the two-fold strategy, if the two parent birds within a pair are doing their long foraging trips simultaneously, the chick is likely to fast for periods of up to 15 days, the extreme measured by Richdale (1963). This value of 15 days was thereafter used by many author (starting with Lack 1968) to show that the large fat deposits of petrels provide insurance against periods of poor feeding conditions. The large

fat deposits of sooty shearwaters chicks are indeed likely to be used during their extended periods of fasting. They probably do not provide insurance against stochastic variation in food provisioning as suggested by Ricklefs & Schew (1994) because in sooty shearwaters provisioning of food, although infrequent, appears predictable as indicated by the regular alternation of foraging trips and cyclic attendance. However, as pointed out by Ricklefs & Schew (1994), other species of petrels are fed much more regularly than sooty shearwaters, and therefore in these species the probability of undernutrition is very low compared to sooty shearwaters. Thus, it would be interesting to test whether sooty shearwater chicks accumulate more lipid reserves than similar sized petrels feeding their chicks more regularly.

DISTANT FOOD RESOURCES AND COMPETITION

In the South Pacific, sooty shearwaters are extremely abundant in the Polar Front area when they rear their chick (Ainley *et al.* 1984; Pakhomov & McQuaid 1996). The Polar front area was located at least 1550 km south of the Snares Islands. The Polar Front area is well known to be a zone of increased productivity (Laubscher *et al.* 1993). Birds observed feeding there were assumed to be non-breeders because the average time between chick feeds, based on a feeding frequency of 2.8 days, would be insufficient for the parents to commute to the Polar Front and forage (see Warham 1996). With a flight speed of 30 km h⁻¹ (calculated from Pennycuik 1989) it would take between 2 and 3 days (with or without a stop at night, respectively) to reach the Polar Front. My study indicates that during long trips of an average duration of 11 days, birds would have ample time to commute and forage in this area with 5 days, the shorter LT, being the minimum time necessary to reach the Polar Front area, spend 1 day there and return to the nest. With LT lasting on average 10.7 days, 5–7 days would be spent to forage in this area to restore body reserves and gather food for the chick before returning to the nest.

With a population of 2.7 million pairs breeding on the Snares (Warham & Wilson 1982) and a foraging radius of 400 km during ST of 1.5 days, the density of birds would be extremely high if birds were performing only ST. In fact, at any stage of the fledging period, only 17% of the birds rearing chicks are within this radius, the others probably commuting to or from, or foraging in the Polar front area. The increase in foraging radius decreases the rate of provisioning but not the net rate as foraging far from the colony could be more profitable than foraging nearby, either because of higher prey availability far from the nest, but also perhaps because of decreased competition close to the colony. Thus, the use of this distant pro-

ductive zone could help to sustain the huge populations of sooty and short-tailed shearwaters.

CYCLIC COLONY ATTENDANCE

The general pattern of ST and LT being in the proportion of 2:1 results in an apparent endogenous cycle for each bird, probably because of the predictability of foraging success. The cycle is not endogenous because decisions to forage in one particular area, to self-feed or to forage only for the chick are only under the control of the adult mass and are not related to the duration of the previous foraging trip. However, no more than three ST were performed in succession. As a result of the regular succession of several ST and one LT, the return of parents appears synchronized, with a periodicity of 14 days corresponding to the average figure of a LT of 11 days followed by 2 ST of 1.5 days each. One consequence of the cyclic attendance of parents is the decrease in the average mass of the chick when few parents are visiting the colonies and the increase thereafter when the number of adults peaks. Interestingly, the closely related short-tailed shearwater visit the colony with a cyclic pattern during the chick-rearing period and it was noted that the average mass of chicks exhibited a regular alternation of increase and decrease throughout the fledging period (Oka *et al.* 1987). As indicated by our model, the synchronous return of birds every 14 days is observed in the longer term and it remains apparent throughout the fledging period. The periodicity is similar for the four simulations and to the data obtained by Richdale (1963). This is surprising because it would be expected that at the end of 4 months chick rearing period, i.e. after seven cycles of succession of ST and LT feeding bouts, the increase in the variance of a mean cycle should obscure the periodicity of feeding times. As the variability in the duration of foraging trips and in the regularity of the alternance increases, the peak numbers of birds visiting the colony decreases and spread out but the periodicity of the visits still occurs at the end of the breeding season (Fig. 4) The retention of cycles is probably favoured because hatching is very synchronized (Warham *et al.* 1982). Also, cyclicality is probably favoured because the strategy of regular alternation is likely to be kept constant throughout the fledging period, as suggested by the observation that the same individual tends to perform ST of similar duration from one cycle to the next. Thus, cyclic attendance at the level of the whole colony appears as an emergent property of the foraging strategy of individual adults. Because the duration of cycles is similar to the duration of half a lunar phase, Oka *et al.* (1987) suggested that in sooty and short-tailed shearwaters the moon synchronizes the bird's return to the colony, because the waxing moon could increase accessibility of prey close to the breeding grounds. In fact, the correlation with the half moon phase was probably fortuitous during the year of their study,

and could not explain our results and those of Richdale (1963). Cyclic visits in short-tailed shearwaters are more likely to be the result of a two-fold strategy similar to that of sooty shearwaters. This is strongly suggested by the fact that birds feed their chick partly with Antarctic prey species (Skira 1986) available at a minimum distance of 1700 km from the colonies in Tasmania. Short-tailed and sooty shearwaters thus probably both rely on Antarctic food resources while rearing a chick in Tasmania or to the south of New Zealand. The use of a two-fold strategy is probably a general rule in pelagic Procellariiformes, and possibly in penguins such as the Adélie penguin (Kerry *et al.* 1995), but its manifestation is extreme in the two shearwaters because of the extreme separation between nesting and feeding zones.

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