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## Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick

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**Abstract** Procellariiform seabirds have a number of extreme life-history characteristics in common, in particular low reproductive rates and slow postnatal development, which are generally assumed to reflect the difficulty in acquiring energy in the marine environment. The wandering albatross (*Diomedea exulans*) is a sexually dimorphic species with the longest postnatal growth found in any bird, suggesting severe constraints on provisioning and possible sex-specific strategies of provisioning. We studied the provisioning behaviour and mass changes of male and female parent wandering albatross throughout the 9-months rearing period to examine how each sex adjusts its foraging effort in relation to the needs of the chicks and the seasonal changes in food availability. The study was carried out on the Crozet Islands, using an automated system recording continuously the attendance pattern of parents between March and December 1994. During the brooding period when energy requirements are highest, parents only perform trips of short duration to sea, and their body condition deteriorates. When the chick is old enough to be left alone, the parents mix short and long foraging trips. The proportion of short trips is very high until July, allowing high rate of food delivery and rapid growth, and at the same time the body condition of adults improves. From August this proportion declines until fledging in December. As a result, the feeding rate decreases from August and adult condition declines, suggesting that feeding conditions at sea are better during the first part of the chick-rearing period, i.e. in autumn and winter. Male parents perform more short trips of shorter duration and provide larger meals than females, delivering an estimated total after brooding of 110 kg of food, compared to 70–80 kg delivered by

females. Meal size is inversely related to the body condition of male chicks but not to that of female chicks, suggesting that food delivery is regulated by the adults in response to the condition of the male chick. Male chicks received larger meals and more food every month than female chicks, and overall it was estimated that they receive, after brooding, 195 kg of food compared to 180 kg for the female. As a result, male chicks have a higher growth rate, attain a higher asymptotic mass, and are larger and heavier at fledging than female chicks. However, the differences are relatively small between the chicks of each sex and suggest that energy may be used differently between the sexes to maximise fitness. The results of the study suggest that provisioning effort of wandering albatrosses is adjusted by parents in relation to the availability of food, to the energetic needs of the chick and to the sex of the chick. The adult body mass is likely to play an important role in the long term for the regulation of provisioning, deficits in body mass probably providing the buffer in high power-requirement periods.

### Introduction

The period of growth from hatching till independence of the offspring from its parents is crucial for the fitness of birds. When they leave their nest and become independent from their parents, the chicks have attained a size close to that of adults and their body condition at this time will have a significant influence on the survival till breeding. A significant rate of mortality occurs soon after fledging and it has often been found that heavier or larger fledglings survive better (see review in Magrath 1991). The patterns of growth are directly influenced by the rate of resource provisioning by the parents and are generally assumed to be adapted to the specific environmental conditions (Lack 1968). Food supply is likely to be the major factor influencing growth patterns; poor food conditions result in slower growth and poor-quality

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fledglings (Bryant 1978; Konarzewski and Taylor 1989; Becker and Specht 1991). Because resources are likely to be limited in the environment, parents probably have to allocate the resources available in the environment between the provisioning of the young and their own needs (Stearns 1992). To measure allocation it is consequently of interest not only to measure provisioning, but also to be able to measure the condition of adults. This is, however, rarely done in provisioning studies because it is generally assumed for simplicity that adults balance their energetic income and expenditure during the chick-rearing period. However, it is more likely that adults accept energy deficits for periods of high power requirements (Ricklefs 1983).

The extent to which parents care for their young varies widely among birds and of course has a profound effect on the growth of the chicks. The growth of the offspring will also depend on the role of each parent, and its ability to find and collect food. Procellariiformes (petrels and albatrosses) are particular among birds: they lay a single egg and the parents perform similar parental roles (Warham 1990). The chick is semialtricial and its growth is known to be particularly slow in these seabirds (Starck and Ricklefs 1998). Since growth rates are generally interpreted as an adaptation to ecological factors, especially food supply, it has been suggested that the slow growth of petrels and albatrosses results from the difficulty of parents to find food or to the long distance to feeding zones (Lack 1968; Ashmole 1971; Ricklefs 1990). One advantage of slow growth is to reduce the probability of starvation by reducing metabolic requirements of the nestling (Ricklefs 1973). The major disadvantage of slow growth, the prolonged exposure to predation of chicks, is not a problem for Procellariiformes that breed on islands free of terrestrial predators. As distance to the food supply and hence feeding frequency have a major influence on the mode of development in seabirds (Ricklefs 1979), it is in long-ranging species that constraints are likely to be most marked. Recent studies have indeed shown that they forage at extensive distances from the nest (Weimerskirch 1998a). Until now no study has examined the relationship between the growth of the chick and the provisioning behaviour of parents throughout the chick-rearing period, because of the obvious logistical problems related to the duration of the study and the difficulty in monitoring the behaviour of parents.

The wandering albatross (*Diomedea exulans*) is the largest Procellariiformes and one of the largest flying birds. It has the longest chick-rearing period and slowest growth rate among birds (Starck and Ricklefs 1998). Chick rearing occurs in winter when food availability is presumably the lowest. Breeding birds are foraging at extensive distances (Weimerskirch et al. 1993) and parents deliver food relatively infrequently to their chick (Weimerskirch et al. 1997a). Furthermore, it is one of the few Procellariiformes with a marked sexual size dimorphism, males being 20% larger than females. Males and females are known to have different foraging

strategies at sea when rearing chicks (Weimerskirch et al. 1993, 1997a) and, consequently, differences in provisioning behaviour are expected. With its extreme and particular life-history traits, especially long foraging, long period of growth and high sexual dimorphism, the wandering albatross appears therefore to be a good model to investigate several hypotheses related to the evolution of chick growth, provisioning behaviour and sex-biased parental investment.

During the pre fledging period of 9 months, we used an automatic recording system to measure the attendance patterns of adult wandering albatrosses, supplementing these records with data on meal sizes, adult body mass and growth parameters of the chicks. Here we examine: (1) how the provisioning behaviour and adult mass change throughout the chick-rearing period in relation to seasonal changes (from autumn through winter and spring) and energy requirements of the offspring, (2) whether sex-specific differences in provisioning behaviour occur, and (3) whether adults provision their offspring differently according to the sex of the chick.

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## Materials and methods

### Field study

The study was carried out on Possession Island, Crozet Islands (46°25'S 51°50'E) from 1 March to 24 December 1994 at the colony of Baie du Marin (see Weimerskirch and Jouventin 1987). The sex of the parent birds was known from a long-term database (Weimerskirch et al. 1997b), each bird being banded with metal and plastic bands. All nests at Baie du Marin were checked daily from early March to determine the dates of hatching and the nest attendance by male and female parents. To monitor the presence or absence of adult birds in the colony after the chick was left alone on the nest (which occurs ca. 31 days posthatching), 41 individuals (from 21 pairs) were fitted with VHF transmitters (model 1/2AA, ATS, Isanti, Minn.; 17 g, 55 pulses per min) clamped with cable ties, glued with Araldite on the central rectrice feather and protected by an adhesive white tape. Between 26 March and 4 April, during the brooding period, each parent was fitted with a transmitter with unique frequency. An automatic recording station, comprising a receiver, a data logger (R4000 and DCCII, respectively, ATS, Isanti, Minn.) and a multidirectional antenna, was installed in the middle of the colony. The 21 nests monitored automatically (20 nests with 2 adults fitted, 1 with only 1 adult) were spread in a 600-m-diameter circle. The automatic recording station, powered by 12-V batteries recharged regularly, scanned the different frequencies continuously. Each frequency was searched during 10 s, so each frequency was searched every 8 min. In total, 21 transmitters were lost during the course of the study (mainly because the feather was broken, but some birds moulted the feather fitted with the transmitter). The data were downloaded every 2 days during the brooding period and every 7–10 days afterwards, to a laptop computer.

To measure the size of meals delivered, the 21 chicks were weighed just after dawn and again 1 h before dusk during the first 10 days of each month between May and October. The chicks were weighed to 0.5% with a Salter spring balance. A sample of 4–17 adult parents of each sex was weighed each month between March and October in other colonies on Possession Island using a Salter spring balance accurate to 1%. Adult birds were captured by hand and weighed in a bag after they had fed the chick and were about to leave the nest. Each adult was weighed only once during the study

period. To study the growth curve of the chicks, in addition to the weighings during the first 10 days of each month, each chick was weighed and measured every 10 days from hatching to fledging. For each chick, the lengths of culmen and tarsus were measured to the nearest 0.1 mm with a calliper, and the wing to the nearest 1 mm with a ruler.

#### Data analysis

The information downloaded from the automatic recording station gives a list of frequencies, each representing an individual for a particular time, with a number of pulses. From these data, the durations of the stay on land and of the stay at sea were calculated. The stay on land was calculated as the period between the first and last series of pulses. As the series of pulses were not continuously recorded, probably due to the bird either moving from the landing area to the nest or crossing areas out of the monitoring antenna's purview, we defined (on the basis of previous observations; Weimerskirch et al. 1997a) a foraging trip as represented by a period greater than 1 h. When the period between two series of pulses was less than 1 h, the bird was considered to have remained on land (i.e. we assumed signal loss to some local problem).

To determine from twice-daily weighings the mass of food delivered to a chick, it was necessary to take into account losses of mass due to respiration and defecation. As we knew from the telemetry record when the feed was delivered, we were able to calculate the mass of the chick before and just after being fed by regression on a log scale, since the rate of mass loss is linear (Ricketts and Prince 1984). The meal mass was calculated as the difference between the mass estimated before and after the meal was delivered.

To estimate the proportion of time during each month spent in foraging trips of short or long duration, we selected only birds tracked during at least 15 days during that month. For birds that had lost their transmitters, we used the last contact with the receiving station to determine the duration of the last recorded foraging trip. To examine whether provisioning parameters of adults were related to the short-term nutritional status of the chick, we defined body condition as the residual from the linear regression of body mass upon age for each period when the chick was weighed daily.

#### Growth data

Throughout the fledging period, changes in the mass of chicks show long periods of decrease, corresponding to the assimilation of food, with steep increases corresponding to meals. Overall, Procellariiformes chicks have a typical growth curve for mass, with a period of rapid increase up to a peak followed by a period of slow decrease until fledging (Warham 1990). The period of mass increase up to peak mass belongs to the family of sigmoid growth curves best described by the Richards (1959) equation  $M = A / \{1 + \lambda \exp[-K(t - T_i)]\}^{1/\lambda}$  where  $A$  is the asymptotic or maximum weight,  $K$  is the growth rate and  $T_i$  is the time of inflection of the growth curve or time of maximum growth rate (see Ricketts and Prince 1984). This family of curves includes special cases, namely the logistic, von Bertalanffy and Gompertz curves that have been used to describe the growth of birds (Ricklefs 1983). A growth curve was fitted to the data of each individual using a weighted least-square technique from the procedure NLIN (SAS Institute 1987). Proportions of chicks following each type of growth curve were Gompertz (47.1%), von Bertalanffy (40.2%) and logistic (12.6%). To compare growth parameters we used for all individuals the Gompertz curve (similarly to Ricketts and Prince 1984; see also Warham 1990), and calculated the growth rate  $K_G$  and the asymptotic mass  $A_G$ . Because this procedure does not yield the age at peak weight, we also modelled the data of each individual by a third-degree polynomial equation and calculated the age and mass for the asymptote of the polynomial curve. To allow comparison with data from the literature, we also calculated the

growth rate of chicks for the linear portion of the growth curve, by computing growth over the time taken to grow from 10 to 90% of asymptotic weight ( $Kt_{10-t_{90}}$ , see Ricklefs 1973).

To estimate the rate of mass loss of chicks during their periods of fast, we used the rate of mass loss during the linear phase of the mass decrease, thus excluding the exponential phase just after the feed (Ricketts and Prince 1984). To do this, we calculated a rate of decrease for all periods of mass decline, with log-transformed mass data. The rate of mass decline plotted against the time since the last meal was delivered indicated that, for wandering albatrosses chicks, from 2 days the mass decrease was linear. We have therefore corrected the rate of mass loss for fasts longer than 2 days by the mass of the chick at different ages.

#### Sex of chicks at fledging

To determine the sex of chicks from their growth parameters and measurements at fledging, we used the parameters of chicks fledged in 1986 (see Lequette and Weimerskirch 1990) and subsequently sexed on their return to the colonies as adults (see Weimerskirch et al. 2000a). Twenty-four chicks fledged in 1986 were observed and sexed as adults between 1990 and 1997: 13 females, 11 males. The growth parameters and measurements at fledging of the 24 sexed chicks were used in a discriminant analysis to sex the 28 chicks reared in 1994. To select the growth characteristics that best discriminate the sexes, we entered all the parameters shown in Table 1 into a backward stepwise discriminant analysis. The parameters selected were the wing length at fledging, the age at maximum polynomial mass and the absolute maximum mass, and explained 100% of the variance with the first component. With only these three parameters, the sex of 96% of the chicks was assigned correctly. A jackknife classification, which uses the same discriminant function for all the chicks except the case being classified, classified 92% of individuals correctly, a value very close to 96%, suggesting that the number of predictors is small enough (Wilkinson 1996).

The measurements and mass of adult birds used to compare with chick data were taken from Weimerskirch et al. (2000a).

#### Statistical analysis

Analyses were carried out using SYSTAT 6.0 (Wilkinson 1996) and Statistical Analysis System (SAS Institute 1987). To avoid duplicate data for the same individual for the same categorical variables, we used average values. To avoid the problem of artificially inflated  $F$ -values when applying Analysis of Variance to repeated measures (when measuring the same parameters for the same individual over several months), we used the analysis of variance (ANOVA for Repeated Measure Analysis). We investigated with the Repeated Measure ANOVAs the effects of the sex of the adult and of the chick on foraging trip duration, proportion of time spent in trips of different duration, number of meals delivered and meal mass over successive months. Since all parents were not measured in all months, especially the later months when transmitters had been lost, we performed in some cases Repeated Measure ANOVAs with a reduced number of months so that the sample sizes were large enough for every month.

## Results

### Growth of chick

Males hatched at similar dates as females and were slightly (although not significantly) heavier than females at hatching (Table 1). They were left unbrooded earlier

**Table 1** Growth parameters and measurements at fledging of chicks (average  $\pm$  1 standard deviation)

Sample size	Combined 28	Male 14	Female 14	Difference between M/F ( <i>t</i> -test) <i>P</i>
Hatching date (March)	15.1 $\pm$ 5.8	17 $\pm$ 5.2	13.1 $\pm$ 5.6	0.071
Mass at hatching (g)	357.9 $\pm$ 43.5	373.6 $\pm$ 49.3	342.1 $\pm$ 30.9	0.054
Age when left alone (days)	32.8 $\pm$ 4.6	31 $\pm$ 4.3	34.6 $\pm$ 4.3	0.038
Growth rate $K_{t_{10-90}}$ (g/day)	74.5 $\pm$ 9.2	80.3 $\pm$ 6.5	68.8 $\pm$ 7.7	< 0.0001
$K_G$ Growth rate	0.025 $\pm$ 0	0.025 $\pm$ 0.003	0.024 $\pm$ 0.003	0.364
$A_G$ Asymptotic mass (g)	11783 $\pm$ 1073	12476 $\pm$ 856	11089 $\pm$ 788	< 0.0001
Max. absolute mass (g)	13471 $\pm$ 1281	14342 $\pm$ 986	12600 $\pm$ 896	< 0.0001
Age at max. pol. mass (days)	197.8 $\pm$ 13.5	195.4 $\pm$ 13.9	200.2 $\pm$ 13	0.356
Maxi. Polynom. Mass (g)	11761 $\pm$ 1098	12481 $\pm$ 881	1104 $\pm$ 1782	< 0.0001
Duration of decrease (days)	65 $\pm$ 11.4	66.2 $\pm$ 10.8	63.9 $\pm$ 12.3	0.605
Rate of decrease (g/days)	-27.3 $\pm$ 12.7	-26.7 $\pm$ 13.6	-27.9 $\pm$ 12.1	0.802
Age at fledging (days)	262.9 $\pm$ 11.2	261.6 $\pm$ 11.1	264.1 $\pm$ 11.6	0.565
Date of fledging (November)	32.9 $\pm$ 13.1	33.6 $\pm$ 13.6	32.3 $\pm$ 12.9	0.789
Mass at fledging (g)	9992 $\pm$ 1108	10642 $\pm$ 905	9342 $\pm$ 905	0.001
Culmen at fledging (mm)	165.5 $\pm$ 7.9	167.9 $\pm$ 4.8	163.1 $\pm$ 9.6	0.104
Wing at fledging (mm)	682.7 $\pm$ 24	691.1 $\pm$ 24.8	674.3 $\pm$ 20.7	0.063
Tarsus at fledging (mm)	151.4 $\pm$ 5.7	154.2 $\pm$ 4.1	148.7 $\pm$ 5.8	0.007

than females (Table 1). The age at fledging and dates of fledging were similar for both sexes (Table 1).

#### *Growth in mass and rate of mass loss*

The overall mass growth curve of chicks was typical of Procellariiformes with a period of rapid increase, followed by a period of slow decline before fledging (Fig. 1a). Males had faster growth rates, reached a higher absolute, asymptotic, and maximum polynomial mass, and were heavier and larger at fledging than females (Fig. 1a; Table 1). At fledging, both male and female chicks were heavier than adult birds (Fig. 1a, Table 1 and Weimerskirch et al. 2000a for data on adults; values averaged for the whole breeding season  $t = 5.8$ ,  $df = 159$ ,  $P < 0.001$  and  $t = 10.4$ ,  $df = 147$ ,  $P < 0.001$ , respectively).

The mass growth of chicks is described by a series of mass increases (as parents deliver meals), followed by periods of mass loss as the chick fasts. The relative rate of mass loss during the periods of fasts differed between months (Repeated Measures ANOVA  $F_{5,40} = 3.8$ ,  $P = 0.007$ ) but did not differ between male and female chicks ( $F_{1,8} = 1.0$ ,  $P = 0.336$ ). It decreased from 0.042 g/kg in May to 0.013 g/kg in August, remaining steady thereafter.

#### *Culmen, tarsus, and wing growth*

The growth curves of culmen, wing and tarsus show typical shapes for birds (Fig. 1b–d). Tarsus length reached an asymptotic value at the age of ca. 150 days, and culmen length later, at the age of 200 days (Fig. 1b, d). The culmen length and tarsus length were similar for chicks at fledging and for adults of the same

sex (Fig. 1;  $t = 0.79$ ,  $df = 186$ ,  $P = 0.430$  and  $t = 1.13$ ,  $df = 176$ ,  $P = 0.260$ , respectively). The length of the wing was reaching an asymptotic value at the time of fledging (Fig. 1c) but both male and female chicks had longer wings than adult birds ( $t = 7.1$ ,  $df = 109$ ,  $P < 0.001$  and  $t = 12.0$ ,  $df = 118$ ,  $P < 0.001$ , respectively).

#### *Provisioning parameters*

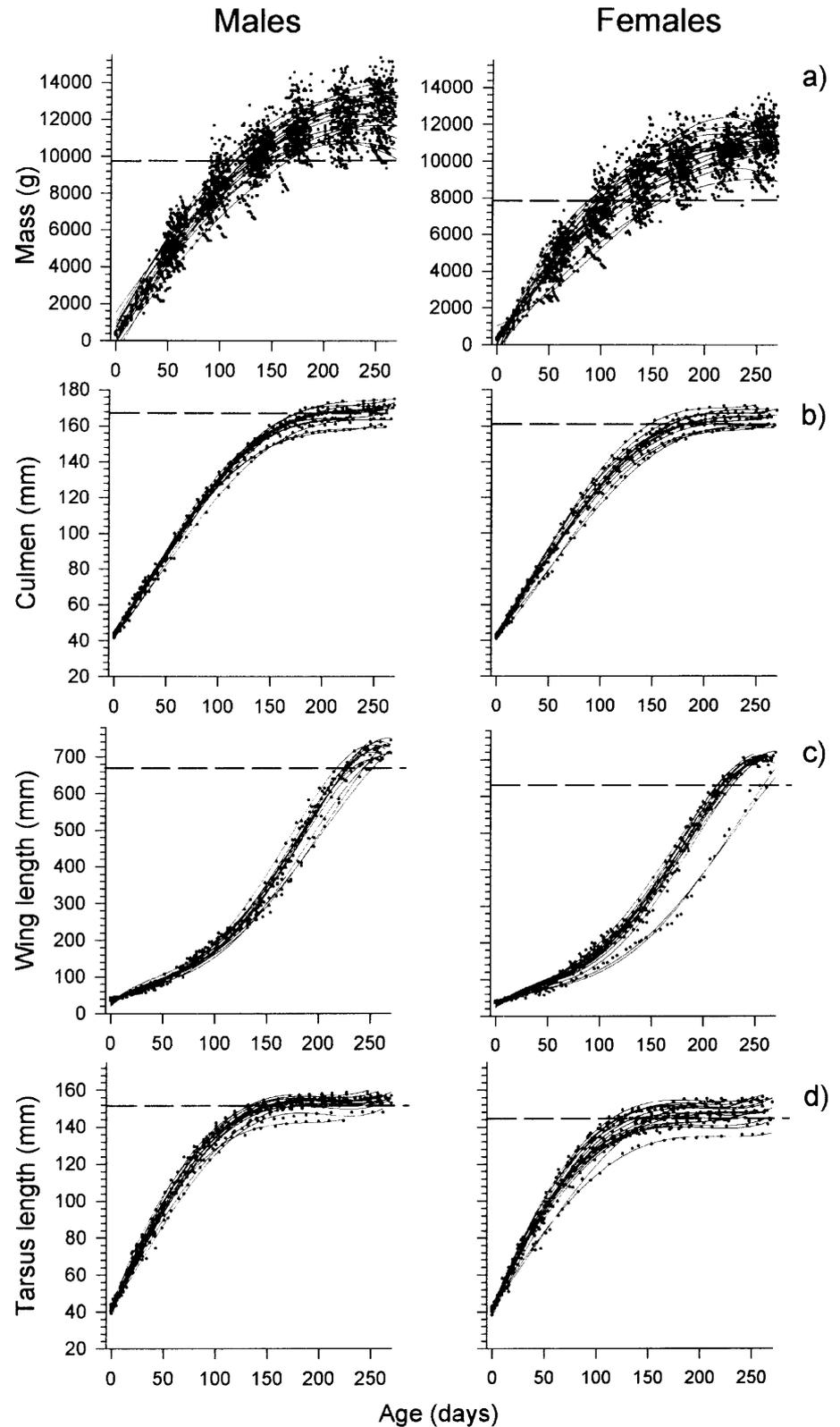
##### *Timing and duration of visits to the nest*

Males and females returned to the nest throughout the period of day-time, with few visits during the night (Fig. 2). When they provisioned the chick, adults spent between 8 min and 1.87 days (average  $4.9 \pm 6.0$  h,  $n = 436$ ) in the colony. The duration of stays on land with the chick differed between months (Repeated Measures ANOVA,  $F_{6,126} = 15.7$ ,  $P < 0.001$ ) but there was no influence of the sex of the adult ( $F_{1,21} = 1$ ,  $P = 0.338$ ) or of the sex of the chick ( $F_{1,21} = 2.45$ ,  $P = 0.133$ ). The time spent with the chick by the adult was particularly long in April just after brooding ( $11.4 \pm 8.1$  h,  $n = 39$ ) and decreased regularly from June ( $6.3 \pm 4.0$  h,  $n = 36$ ) to September ( $2.1 \pm 1.3$  h,  $n = 27$ ).

##### *Duration of foraging trips*

During the brooding period, foraging trips lasted between 12 h and 6 days (Fig. 3). The overall distribution of foraging trips was different for males and females, with male parents making shorter foraging trips ( $2.46 \pm 0.63$  days) than females ( $3.27 \pm 0.72$  days;  $F_{1,40} = 14.1$ ,  $P = 0.0006$ ).

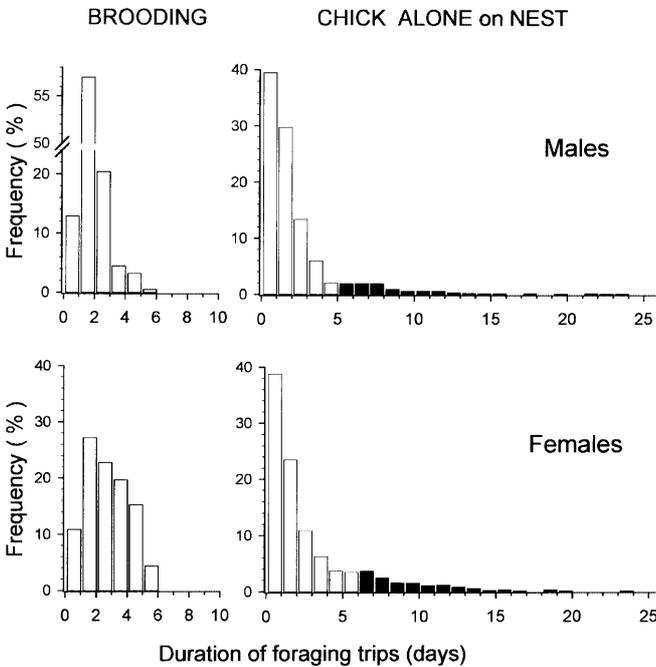
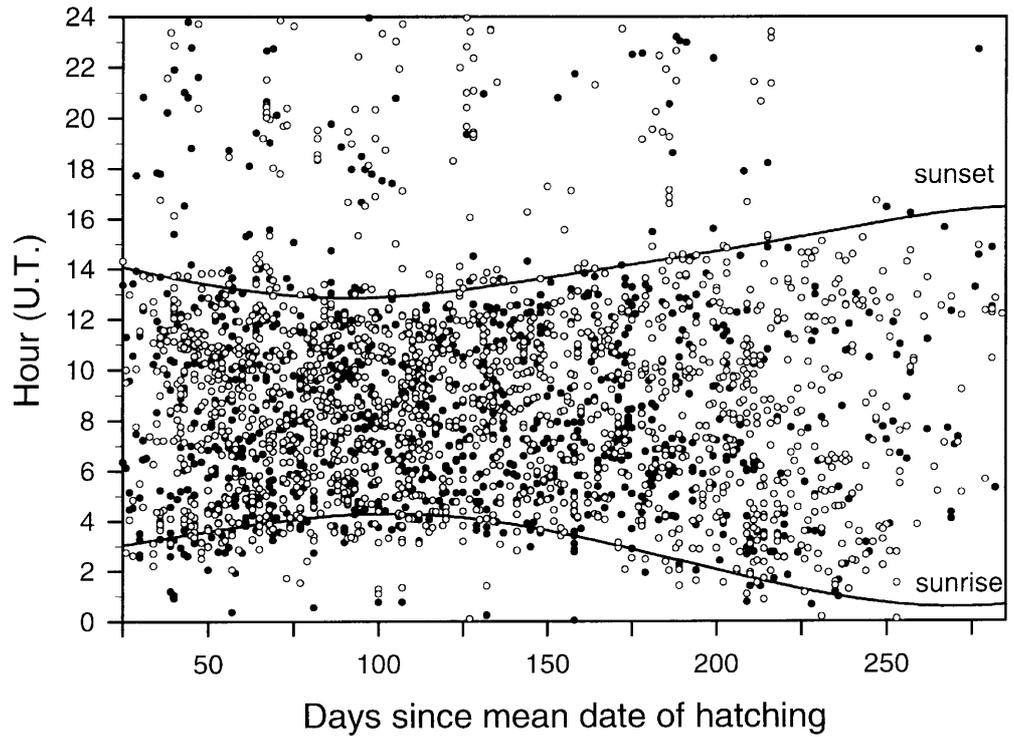
**Fig. 1** Growth curves of male and female wandering albatross chicks for: **a** mass (with polynomial growth curve for each individual), **b** culmen length, **c** wing length, and **d** tarsus length. *Dotted lines* indicate average values of adult birds



After the chick had been left alone on the nest, foraging trips lasted anywhere from 6 h to 24 days (Fig. 3). Based on studies using satellite telemetry (Weimerskirch et al. 1993, 1997a), we separated trips into short trips

(ST) and long trips (LT). ST (shorter than 5 days for males, and 6 days for females) are close to the nesting colony in neritic waters, and they are similar in duration (see Fig. 3) and location (see Weimerskirch et al. 1993)

**Fig. 2** Time of adult arrival (Universal Time) to the colony relative to time of sunset and time of sunrise throughout the chick-rearing period. Males in white; females in black



**Fig. 3** Distribution of the duration of foraging trips by male and female adults during the brooding period ( $n = 92$  and  $99$  foraging trips, respectively) and after the chick was left alone on the nest ( $n = 1597$  and  $1042$ ). White columns indicate short trips; black columns indicate long trips

to the trips of the brooding period. LT are performed in pelagic waters only after the brooding period (Fig. 3). Each individual adult bird generally mixes several

successive ST with one LT. The duration of LT did not vary according to the month and was not affected by the sex of parent or the sex of chick (Fig. 4, Table 2; Repeated Measures ANOVA  $F_{6,30} = 0.9$ ,  $P = 0.493$ ; Sex of Adult  $F_{1,8} = 0.3$ ,  $P = 0.578$ ; Sex of Chick  $F_{1,8} = 0.1$ ,  $P = 0.727$ ). For ST, there was a significant increase in the duration of trips with time (Repeated Measures ANOVA  $F_{7,112} = 3.5$ ,  $P = 0.002$ ), with males tending to make shorter ST than females ( $F_{1,16} = 3.8$ ,  $P = 0.068$ ). There was no effect of the sex of the chick on the duration of ST ( $F_{1,16} = 0.543$ ,  $P = 0.472$ ).

*Proportion of time spent in ST and LT*

For each month and each individual, we calculated the proportion of time spent foraging in ST. The proportion of time spent in ST was different between months, with males spending more time in ST than females, but there was no effect of the sex of the chick (Repeated Measures ANOVA  $F_{6,90} = 4.5$ ,  $P < 0.001$ ; Sex of Adult  $F_{1,15} = 4.5$ ,  $P = 0.050$ ; Sex of Chick  $F_{1,15} = 0.3$ ,  $P = 0.601$ ). After increasing from April to July, the proportion of time spent in ST declined for both sexes from July until December and males spent more time foraging in ST than females (Fig. 5a).

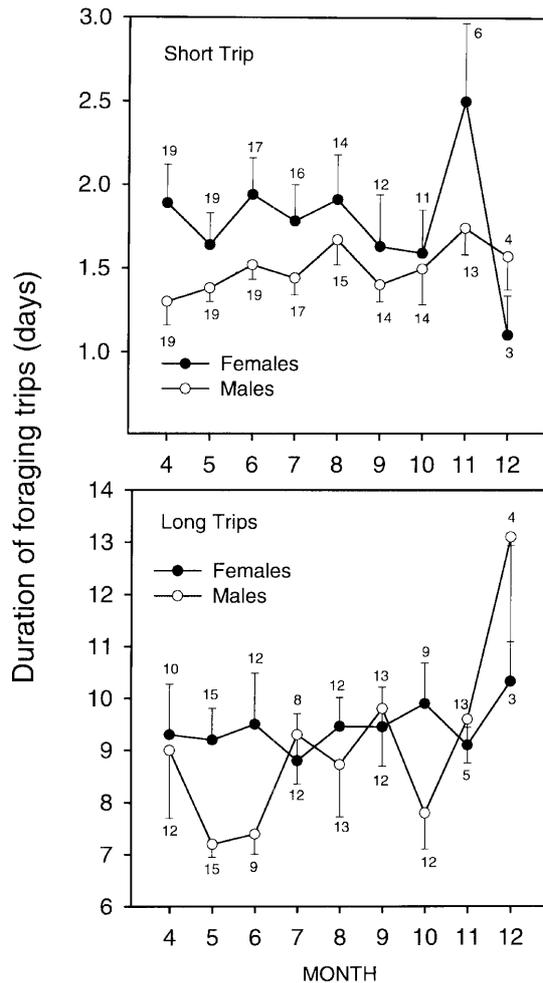
*Number of meals delivered*

There was a continuous decline in the number of meals delivered through the chick-rearing period, with males

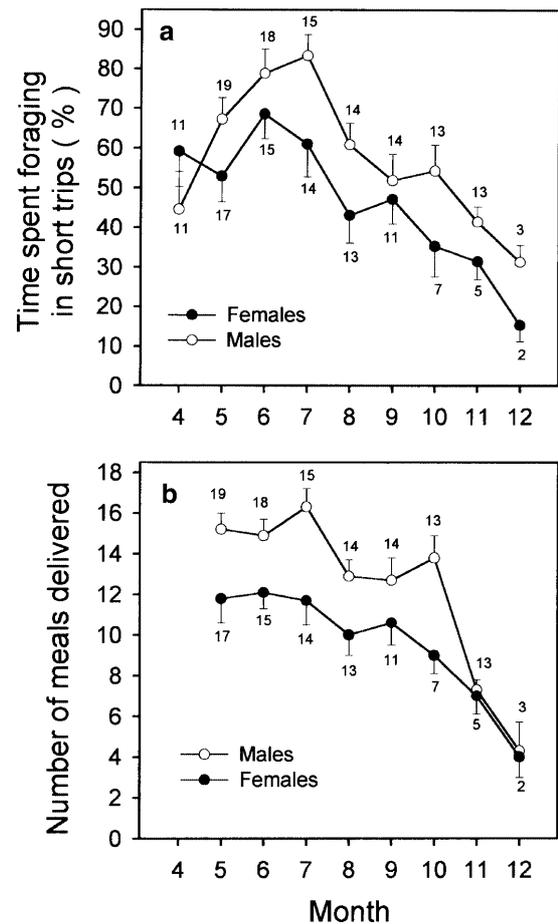
delivering more meals than females (Fig. 5b), but the sex of the chick had no influence on the number of meals delivered (Repeated Measures ANOVA  $F_{5,85} = 2.5$ ,  $P = 0.038$ ; Sex of Adult  $F_{1,21} = 6.8$ ,  $P = 0.017$ ; Sex of Chick  $F_{1,21} = 0.7$ ,  $P = 0.410$ ). In summary, chicks received on average 27 meals per month between May and July, 18–22 between August and October, and only 14 in November and 5 in December.

### Meal mass

Because sample sizes were small in some months (Fig. 6), we grouped the months in pairs. The meal size delivered to chicks did not vary over the season (Fig. 6) but varied according to the sex of the parent (males delivered larger meals to the chicks than females) and to the sex of the chick, male chicks receiving larger meals



**Fig. 4** Changes throughout the chick-rearing period in the duration of short trips and long trips for male and female parents. Data were sorted and averaged by individual parent. *Error bars* indicate standard errors and *numbers* indicate sample sizes (number of individuals)

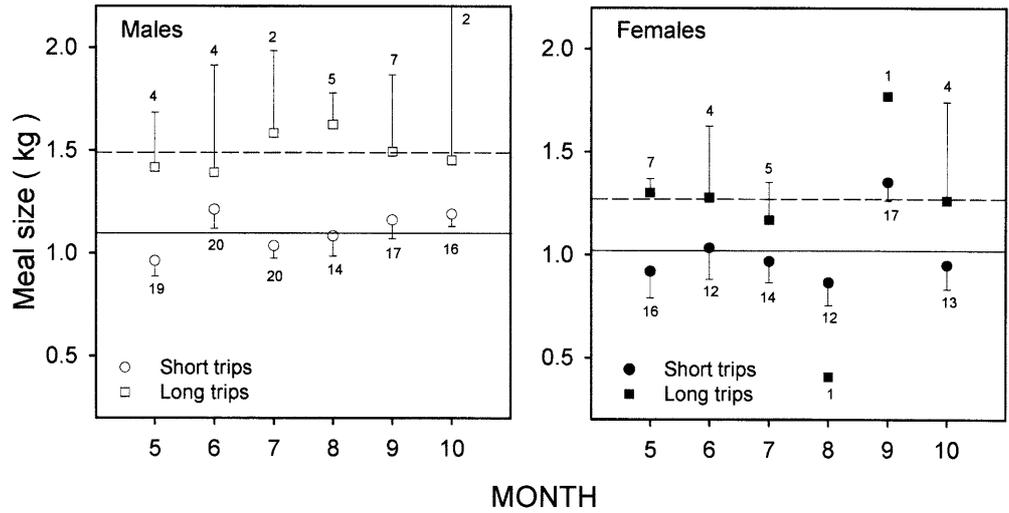


**Fig. 5** Changes throughout the chick-rearing period, **a** in the average proportion of time spent in ST by male and female parents per month, and **b** in the average number of meals delivered by male and female parents per month. Data were sorted and averaged by individual parent. *Error bars* indicate standard errors and *numbers* indicate sample sizes (number of individuals)

**Table 2** Duration of foraging and size of meals after short trips (ST) and long trips (LT) by male and female adults rearing male and female chicks (average  $\pm$  1 SD, sample size in parentheses). Data were sorted and averaged by parent

		Male adult		Female adult	
		Male chick	Female chick	Male chick	Female chick
Foraging trip (days)	ST	1.39 $\pm$ 0.33 (57)	1.55 $\pm$ 0.62 (77)	1.61 $\pm$ 0.68 (82)	2.25 $\pm$ 1.2 (35)
	LT	8.9 $\pm$ 3.34 (41)	8.69 $\pm$ 3.4 (58)	9.33 $\pm$ 2.65 (70)	9.43 $\pm$ 2.67 (20)
Meal size (kg)	ST	1.16 $\pm$ 0.34 (56)	1.04 $\pm$ 0.33 (50)	1.12 $\pm$ 0.45 (48)	0.91 $\pm$ 0.44 (36)
	LT	1.63 $\pm$ 0.84 (9)	1.41 $\pm$ 0.78 (15)	1.21 $\pm$ 0.57 (16)	1.33 $\pm$ 0.49 (6)

**Fig. 6** Changes throughout the chick-rearing period in the size of meals delivered by male and female parents during short and long trips. Data were sorted and averaged by individual parent. *Error bars* indicate standard errors and *numbers* indicate sample sizes (number of individuals). *Solid lines* indicate average values for short trips and *dashed lines* average values for long trips



than female chicks (Table 2; Repeated Measures ANOVA  $F_{2,56} = 0.2, P = 0.807$ ; Sex of Adult  $F_{1,28} = 4.9, P = 0.034$ ; Sex of Chick  $F_{1,28} = 5.9, P = 0.025$ ).

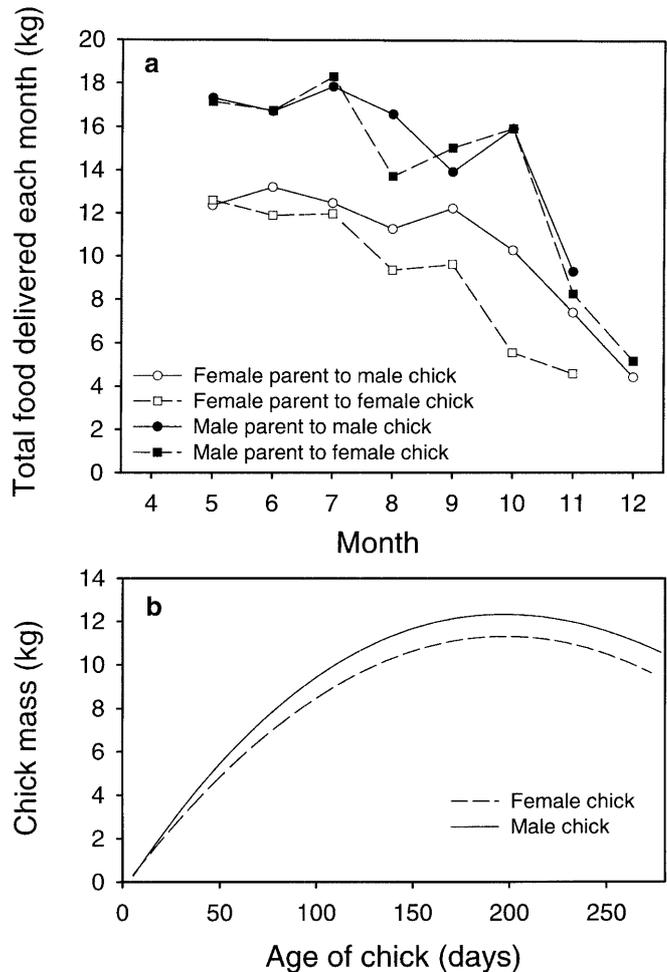
For male chicks, the mass of the meal delivered by either male or female parents was inversely related to the body condition of the chick (male parents  $r = -0.518, n = 185, P < 0.0001$ ; female parents  $r = -0.488, n = 126, P < 0.0001$ ), chicks in poor condition receiving larger meals. For female chicks, the relationship was weaker, and only involved the meals delivered by adult males (male parents  $r = -0.196, n = 187, P = 0.0076$ ; female parents  $r = -0.212, n = 75, P > 0.05$ ).

*Mass flow to chick*

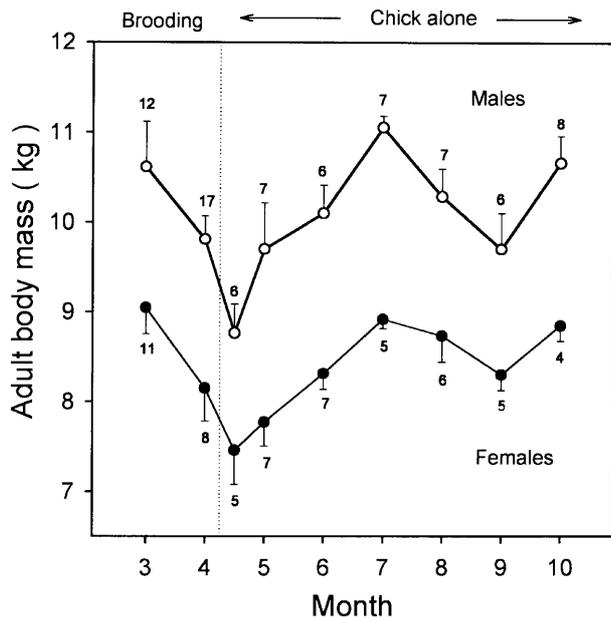
The amount of food delivered by male and female parents to male and female chicks each month was estimated using the average values of the above provisioning parameters, i.e. average meal size, five average number of meals delivered. It was stable between May and July, and declined after this period, especially after October (Fig. 7a). Males delivered similar amounts of food monthly to male and female chicks, whereas female adults delivered more food to male chicks (Fig. 7a). It followed a parallel pattern for male and female chicks, with consistently larger amounts brought by males than by females throughout (Fig. 7a).

Adult mass

The mass of adult parents varied significantly over the chick-rearing period ( $F_{8,125} = 4.92, P < 0.0001$ ) and males were always heavier than females ( $F_{1,125} = 99.63, P < 0.0001$ ). The mass of males and females followed the same trends throughout the period. It reached its lowest values after the end of the brooding period at the end of April and increased thereafter until July, to decrease in August and September (Fig. 8).



**Fig. 7** Changes throughout the rearing period **a** in the average total amount of food delivered per month by male and female adults to male and female chicks, and **b** in the average body mass of male and female chicks modelled using a polynomial function. The time scales in month and in age are synchronous



**Fig. 8** Changes in the average body mass of adult male and female birds between March and October. Data were sorted and averaged by individual parent. Error bars indicate standard deviations and numbers indicate sample sizes (number of individuals)

## Discussion

Changes in the provisioning strategy throughout the fledging season

The 260-days fledging period of wandering albatrosses, from mid-March till early December, is the longest of any bird and the growth rate is the slowest (Starck and Ricklefs 1998). Compared to birds of similar size but of other orders, the slow growth of wandering albatrosses is related generally to the inability of adult parents to provision their chick regularly due to limitation in food availability or the distance to feeding zones (Lack 1968). The chick-rearing period of this species is centred on the winter when, for adults, feeding conditions at sea are generally believed to be unfavourable and when, for the chick, temperatures on the colonies are the lowest. Moreover, the short day-time in winter, not only reduces foraging time of wandering albatrosses that are known to forage mainly during daylight (Weimerskirch and Wilson 1992), but also reduces the feeding opportunities since our results show that adults visit the colonies only during the day-time.

The provisioning strategy was much different before and after the chick was left alone on the nest. In pelagic species, but also in other seabirds, generally the most constraining period in terms of energy requirement is probably the brooding period (Ricklefs 1983; Salamolard and Weimerskirch 1993; Wendeln and Becker 1996) when our results show that the body condition of adults declines to its lowest values. The low mass of adults at the end of the brooding period confirms the suggestion

of Ricklefs (1983) that seabirds may accept energy deficits for short periods of high power requirements, particularly the chick-brooding period. At this time, adults perform only ST when they forage close to the colony on the edge of the Crozet shelf (Weimerskirch et al. 1993). When the chick is left alone, energy requirements become lower (Ricklefs 1983) and wandering albatrosses use a twofold foraging strategy, mixing ST similar to those of the brooding period with LT far from the breeding colony, at more than 1000 km away. ST allow adult birds to increase the provisioning rate, but they tend to lose mass. When body mass is low, they initiate LT during which they restore their body condition. Thus, ST allow allocation to the production of the offspring, whereas LT allow energy storage and restoration of adult body reserves (Weimerskirch et al. 1997a). The period from May until July appears particularly favourable since adult wandering albatrosses are able to bring the highest quantities of food to their chick with high feeding frequencies, and at the same time they are able to improve their body condition. This occurs when day length, and therefore foraging time, is the shortest. Feeding frequency increases because adults increase the time spent in short trips. The time spent in long trips that enable adult birds to restore their body reserves decreases but, nevertheless, adults are able to increase their body mass in the longer term. Therefore, at the start of winter, feeding conditions are likely to be particularly favourable for wandering albatrosses and allow adults to maximise the energy flow to the chick. Satellite tracking indicates that birds feed close to the breeding grounds on the edge of the shelf during short trips (Weimerskirch et al. 1993), suggesting that squids, the major prey of this species (Cooper et al. 1992; Weimerskirch et al. 1997a) are available there in large quantities at this time of the year. Wandering albatrosses from Crozet feed mainly on onychoteuthid squids (Ridoux 1994; Weimerskirch et al. 1997a). Between June and early August 1994, the major species caught was the onychoteuthid squid *Kondakovia longimana* (Cherel and Weimerskirch 1999), the squid species most abundant in the diet of wandering albatrosses in southern breeding localities (Imber 1992). This squid species was, therefore, probably very abundant in the vicinity of the colonies at this time, allowing birds to perform mainly short trips to the shelf edge.

From August, food availability probably deteriorates since while the needs of the chicks are still high, adults feed the chick less frequently, performing more long trips and their body condition deteriorates. Although we have no information on the diet from September, it is highly likely that the availability of *K. longimana* declined then, since Clarke (1980) indicated that in the Southern Ocean adult *K. longimana* are abundant until July and start to disappear afterwards. The breeding cycle of wandering albatrosses could be synchronised so that the first part of chick growth occurs when onychoteuthid squids are the most abundant. Wandering albatrosses would therefore adjust their allocation

decisions according to resource availability (see, for example, Lalonde 1991).

From October, adults further reduce the energy flow to the chick by performing mainly long trips, but improve their body condition. This suggests that during the period of declining chick mass between October and December (Fig. 7b), adults reduce their input to the chick in order to improve their own body condition, whereas in August/September they maximise the energy flow to the chick at the expense of their condition. The changes in body mass throughout the chick-rearing period indicate that adults do not continuously balance their energy income and expenditures. Periods of mass decrease indicate periods of high power requirement during the season, such as during the brooding period, or after July when food availability possibly decreases. Periods of mass increase suggest that incomes exceed expenditures. The body mass of adult has, therefore, a functional role and is a convenient indicator of energy balance and stress. It probably plays an important regulating role in the long term for the regulation of provisioning.

#### Seasonal change in provisioning rate and growth of chicks

The mass growth curve is typical of Procellariiformes, with a rapid increase in mass to an asymptotic mass higher than the mass of adults, followed by a decline (Fig. 7b). The period of mass increase to the asymptote is when energy flow to the chick is highest, probably when food is the most abundant in the vicinity of the breeding grounds. To attain this high asymptotic mass, high rates of mass increase are necessary. The energy needed for growth is only a small part of the total requirement, particularly as the total reaches its maximum (Ricklefs 1979) in July. In slow growing seabirds the daily requirement peaks early in the growth period, probably as soon as the first third of the growth period (Ricklefs 1979). In the wandering albatross, maximum food delivery occurs at this time and it declines thereafter (Fig. 7a). The increases in the requirement for maintenance only are believed to be matched by decreases in growth rate (Ricklefs 1979), i.e. in wandering albatrosses when growth rates start to decline before asymptotic mass is reached (Fig. 7b). The period of mass decline, typical of the mass growth curve of Procellariiformes (Warham 1990), appears to be the result of the energy flow being halved.

The culmen and tarsus attain adult size well ahead of fledging, as soon as 200 and 150 days of age, respectively, at the same time when the asymptotic mass is reached. This asymptotic mass is 2 kg heavier than the mass at fledging and the adult mass. This suggests that chicks probably attain their adult structural size as soon as they have reached the asymptotic mass and stored large amounts of food. At this time a new process is taking place, the replacement of the down by feathers.

Feathers start to appear at this time, at the start of spring, and at fledging all body feathers are fully grown, with the flight feathers reaching an asymptote (see also Berrow et al. 1999). During this period of mass decrease, when energy flow is much reduced, part of the energy used for maintenance and growth is likely to be derived from the fat reserves accumulated during the period of rapid growth.

#### Differences between male and female parents

Overall, males bring much more food to the offspring of either sex than female parents. When summing the average amount of food brought monthly after the brooding period, it appears that male parents deliver a total of ca.110 kg to either male or female chicks, compared to about 70–80 kg delivered by females to female and male chicks, respectively. The difference of about 30% between the two parents is larger than the 20% difference in size between the two sexes. Males brought larger amounts overall because they provision their chick more often than females by doing shorter short trips more often and by bringing larger meals. The differences in meal size are probably related to males being 20% larger than females and thus able to carry more food. The longer duration of short trips by females is probably related to the separation of feeding zones between the two sexes, males concentrating on the shelf edge and females farther off in oceanic waters bordering the shelf edge (Weimerskirch et al. 1993, 1997a). Females might spend longer foraging in short trips not only because of the slightly longer commuting distances but also because they could have lower rates of prey capture (Weimerskirch 1995). The sex-specific differences appear to be consistently parallel throughout the fledging period, indicating that females have greater difficulties than males in provisioning their chick but that the changes in resource availability are similar for the two sexes. This is confirmed by the parallel changes in body condition of the two sexes.

The period of mass decline of the chick until it fledges is the result of decreasing energy flow during October/December, mainly because adults visit their offspring less often. This is particularly true for female parents and is probably the reason why several studies have assumed that from October a significant proportion of the females stop rearing their chick (Croxall and Prince 1990; Weimerskirch et al. 1997a). Our study indicates that, in fact, females visit their chick sporadically but do not desert them before fledging.

#### Differences between the growth of male and female chicks

In total, from the period when chicks were left alone on the nest until they fledged, it can be estimated that male chicks received on average 195 kg of food and female

chicks 180 kg, to produce fledglings weighing, respectively, 10 and 9 kg. Mass growth rates during the rapid phase of growth are higher for male chicks than for females whereas the development period is similar in duration for both. Male and female chicks have similar proportionate rates of mass loss, suggesting that there are no differences in energy requirement per unit of body mass. Male chicks received overall only slightly more food than females, with male parents delivering more food than females. However, male parents delivered similar amounts monthly to male and female chicks whereas female parents delivered more food to male chicks than to female chicks. The slightly larger total amount of food received by male chicks may therefore come from a differential effort by the female, not by the male. Male chicks could be more costly to rear for the female parents than female chicks as they receive more food overall. For male chicks, both parents regulate the food provisioning by delivering smaller meals when the chick is in good condition and larger meals when the chick is in poor condition. This observation, together with the shorter duration of foraging trips observed in male and female parents rearing male chicks, suggests that adults rearing males are able to regulate their provisioning behaviour in relation to the needs of the chick. There has been a considerable amount of controversy over the possibility that Procellariiformes parents may be able to regulate provisioning according to the needs of the chick. Differences probably exist between species (see most recent reviews in Hamer and Thompson 1997; Hamer et al. 2000; Weimerskirch et al. 2000b). However, those studies where the individual behaviour of parents has been studied all suggest that parents are able to regulate provisioning according to the chick need, often to a small extent only (review in Weimerskirch et al. 2000b), underlining the importance of studying individual behaviour (see also Granadeiro et al. 1999). Our results indicate that the ability to regulate provisioning differs according to the sex of the parents and the sex of the chick. Finally, the mass of adults is likely to play a fundamental role in provisioning decisions (Weimerskirch et al. 1994; Weimerskirch 1998b), and long-term mass changes by adults as shown in our study are probably related to the short-term regulation of provisioning according to the mass of the parent (Weimerskirch et al. 1997a).

The differences in the total amount of food delivered to male chicks compared to female chicks are relatively small, but we have been able to detect differences in growth rates and asymptotic mass between the two sexes. The asymptotic mass, although different, is attained at similar ages. These results suggest that energy received may be used differently between the two sexes, and may confer different fitness values. Indeed, heavier females survive better till breeding, whereas for males the body condition has no influence on the survival till breeding: it is the size of the adult at fledging that is important, larger males surviving better than small males (Weimerskirch et al. 2000a). This may be

due to the fact that females fledging from the colony have been able to store energy reserves prior to fledging, because energetic needs are limited due to their smaller size. Conversely, for larger males the energetic needs are more important, and the energy has been mainly used to produce a large size (Weimerskirch et al. 2000a).

Chicks are fledged at the beginning of summer, when feeding conditions are probably the most favourable in the environment. The chick-rearing period of the wandering albatross appears to be adjusted so that adults can provide their chick with a relatively abundant food resource available close to the colony when growth rates have to be the highest, but also so that chicks fledge during the most favourable period.

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## References

- Ashmole NP (1971) Seabird ecology and the marine environment. In: Farner DS, King JR (eds) Avian biology. Academic Press, New York, pp 223–286
- Becker PH, Specht R (1991) Body mass fluctuations and mortality in common tern *Sterna hirundo* chicks dependent on weather and tide in the Wadden sea. *Ardea* 78: 45–55
- Berrow SD, Huin N, Humpidge R, Murray AWA, Prince PA (1999) Wing and primary growth of the wandering albatross. *Condor* 101: 360–368
- Bryant DM (1978) Environmental influences on growth and survival of nestling house martins *Delichon urbica*. *Ibis* 120: 271–283
- Cherel Y, Weimerskirch H (1999) The spawning cycle of Onychoteuthid squids in the southern Indian Ocean: new information from seabirds predators. *Mar Ecol Prog Ser* 188: 93–104
- Clarke MR (1980) Cephalopoda in the diet of the sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Rep* XXXVII: 1–324
- Cooper J, Henley SR, Klages NTW (1992) The diet of the wandering albatross *Diomedea exulans* at sub-Antarctic Marion Island. *Polar Biol* 12: 477–484
- Croxall JP, Prince PA (1990) Recoveries of wandering albatrosses *Diomedea exulans* ringed at South Georgia 1958–1986. *Ringing Migration* 11: 43–51
- Granadeiro JP, Burns MD, Furness RW (1999) Food provisioning to nestling shearwaters: why parental behaviour should be monitored? *Anim Behav* 57: 663–671
- Hamer KC, Thompson DR (1997) Provisioning and growth of nestling fulmars *Fulmarus glacialis*: stochastic variation or regulation? *Ibis* 139: 31–39
- Hamer KC, Hill JK, Bradley JS, Wooller RD (2000) Contrasting patterns of nestling obesity and food provisioning in three species of *Puffinus* shearwaters: the role of predictability. *Ibis* 142: 146–150
- Imber MJ (1992) Cephalopods eaten by wandering albatrosses (*Diomedea exulans* L.) breeding at six circum-polar localities. *J R Soc NZ* 22: 243–263
- Konarzewski M, Taylor JRE (1989) The influence of weather conditions on the growth of little auk *Alle alle* chicks. *Ornis Scand* 20: 112–116
- Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

- Lalonde RG (1991) Optimal offspring provisioning when resources are not predictable. *Am Nat* 138: 680–686
- Lequette B, Weimerskirch H (1990) Influence of parental experience on the growth of wandering albatross chicks. *Condor* 92: 726–731
- Magrath RD (1991) Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *J Anim Ecol* 60: 335–351
- Richards FJ (1959) A flexible growth function for empirical use. *J Exp Bot* 10: 290–300
- Ricketts C, Prince PA (1984) Estimation by use of field weighings of metabolic rate and food conversion efficiency in albatrosses chicks. *Auk* 101: 790–795
- Ricklefs RE (1973) Pattern of growth in birds. II. Growth rate and mode of development. *Ibis* 115: 177–201
- Ricklefs RE (1979) Adaptation, constraint, and compromise in avian postnatal development. *Biol Rev* 54: 269–290
- Ricklefs RE (1983) Some considerations on the reproductive energetics of pelagic seabirds. *Stud Avian Biol* 8: 84–94
- Ricklefs RE (1990) Seabird life histories and the marine environment: some speculations. *Colon Waterbirds* 13: 1–6
- Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet islands. *Mar Ornithol* 22: 1–192
- Salamolard M, Weimerskirch H (1993) Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Funct Ecol* 7: 643–652
- SAS Institute (1987) SAS/STAT user's guide. Release 6.30 edn. SAS Institute, Cary, NC
- Starck JM, Ricklefs RE (1998) Avian growth and development. Oxford University Press, New York
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Warham J (1990) The petrels. Their ecology and breeding systems. Academic Press, London
- Weimerskirch H (1995) Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* 102: 37–43
- Weimerskirch H (1998a) Foraging strategies of southern albatrosses and their relationship with fisheries. In: Robertson G, Gales R (eds) Albatross biology and conservation. Surrey Beatty, Sydney, pp 168–179
- Weimerskirch H (1998b) How can a pelagic seabird provision its chick when relying on a distant resource? Cyclic attendance, foraging decision and body condition in sooty shearwaters. *J Anim Ecol* 67: 99–109
- Weimerskirch H, Jouventin P (1987) Population dynamics of the wandering albatross of the Crozet islands: causes and consequences of the population decline. *Oikos* 64: 464–473
- Weimerskirch H, Wilson RP (1992) When do wandering albatrosses *Diomedea exulans* forage? *Mar Ecol Prog Ser* 86: 297–300
- Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110: 325–342
- Weimerskirch H, Chastel O, Chaurand T, Ackerman L, Hindermeier X, Judas J (1994) Alternate long and short foraging trips in pelagic seabird parent. *Anim Behav* 47: 472–476
- Weimerskirch H, Cherel Y, Cuenot Chaillet F, Ridoux V (1997a) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* 78: 2051–2063
- Weimerskirch H, Brothers N, Jouventin P (1997b) Population dynamics of wandering albatrosses *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with longline fisheries: conservation implications. *Biol Conserv* 79: 257–270
- Weimerskirch H, Barbraud C, Lys P (2000a) Sex differences in parental investment and chick growth in wandering albatross: fitness consequences. *Ecology* 81: 309–318
- Weimerskirch H, Prince PA, Zimmermann L (2000b) Chick provisioning by the yellow-nosed albatross: response of foraging effort to experimentally increased costs and demands. *Ibis* 142: 103–110
- Wendeln H, Becker PH (1996) Body mass change in common terns (*Sterna hirundo*). *Bird Study* 43: 85–95
- Wilkinson L (1996) SYSTAT 6.0 for Windows: Statistics. SPSS, Chicago, Ill