SEX DIFFERENCES IN PARENTAL INVESTMENT AND CHICK GROWTH IN WANDERING ALBATROSSES: FITNESS CONSEQUENCES

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Abstract. Parents should adjust expenditure on parental care so as to maximize fitness, but quantitative data are sparse, particularly for sexually dimorphic species. We use data from two breeding seasons to investigate the fitness consequences of variation in parent provisioning behavior and chick growth in a sexually dimorphic seabird, the Wandering Albatross (*Diomedea exulans*). Male parents brought more food to their single offspring than females did, and male chicks (sons) received more food than female chicks (daughters). The study of growth parameters indicates that sons had faster growth rates, reached higher asymptotic mass, and were heavier and larger at fledging than daughters. Male chicks that survived to adult age were larger than those that disappeared, whereas the females that survived were those in better condition at fledging, indicating that different factors affect survival of each sex during the first years of independence at sea. Survival to adult age seems to be influenced by the ability of parents to provision the offspring adequately, especially in the case of male chicks, whose costs appear to be higher. The age and experience of parents did not influence the amount of food delivered to the chick, but older birds rearing male chicks were more synchronized on a within-pair basis than younger parents, and consequently their sons grew faster, attaining both higher asymptotic mass and higher mass at fledging. Old adult males appeared to have a higher mortality rate than younger males when rearing a son. There was no such tendency for adult males rearing a daughter or for females rearing a son. Younger, less experienced pairs may tend to produce more sons than daughters when compared to older and more experienced pairs. If valid, this tendency for an age-related sex ratio could be the result of higher costs of raising the more expensive sex. These findings indicate that the optimal age-related investment by parents varies between males and females but also depends to a large degree on whether they are rearing a son or a daughter.

Key words: breeding effort, effect of age; Diomedea exulans; *fitness; parental investment; Procellariiformes; provisioning behavior; sex differences in chick growth; survival to adult age, influence of growth.*

INTRODUCTION

Both theoretical and empirical evidence suggest that the probability of survival to adult age is a major determinant of life history evolution (Charlesworth 1980), with survival explaining a large proportion of individual variance in lifetime reproductive success (Clutton-Brock 1988, Newton 1989). Environmental resources are typically limited, so parents are expected to adjust expenditure on parental care, balancing benefits to their offspring against costs to themselves so as to maximize fitness (Williams 1966, Winkler 1987). How much is invested in each offspring is therefore critical to parental fitness (Nur 1987), but adults must also base offspring allocation decisions on expected levels of resource availability in the environment (Lalonde 1991). Despite sizeable interest in this topic, the quantitative effects of parental investment on offspring fitness and adult survival are only poorly known (Fisher 1930, Charnov 1982, Clutton-Brock 1991). In species

where both parents share in the care, selection may favor differential investment in sons and daughters by male and female parents (Trivers 1972, Maynard-Smith 1980, Clutton-Brock 1991). Sex-biased investment should be particularly marked in species dimorphic in size where different parenting costs within pairs might affect the overall ability to provision offspring, and where differences in offspring size might result in more food being allocated to offspring of the larger sex (Stamps 1990). Where one sex is more expensive to rear, the costs of raising the more expensive sex may vary between parents, and these differences may favor sex ratio variation (Fisher 1930).

Relatively few studies have measured the energy expenditures on sons vs. daughters (Newton 1978, Howe 1979, Fiala and Congdon 1983, Roskaft and Slagsvold 1985, Stamps et al. 1987), and none has investigated the investment of parents in their offspring throughout the fledging period. Studies are needed on how parents treat sons and daughters in species where rearing costs vary according to offspring sex, while controlling for differences in behavior within the brood (Clutton-

Brock 1991). Furthermore, despite the obvious theoretical interest, relatively few studies have investigated the influence of parental investment in rearing offspring on survival to adult age or on the fate of offspring in relation to provisioning by adults, or to other factors relating to growth.

Procellariiformes (petrels and albatrosses) have several life history traits that simplify the study of sex differences in parental investment in male or female offspring. They lay a single egg clutch so offspring size and offspring number are not confounded, and no differences in offspring behavior (e.g., unequal begging) can exist within the brood. Both parents also perform similar parental roles (Warham 1990). The Wandering Albatross (*Diomedea exulans*) is one of the few Procellariiformes with a marked sexual dimorphism in size (Weimerskirch 1992), and this feature offers the additional opportunity to test hypotheses relative to parental sex-biased investment. Because distance to the food supply (and hence feeding frequency) has a major influence on the mode of development in seabirds (Ricklefs 1979), it is in wide-ranging species like albatrosses that constraints are likely to be most marked. The Wandering Albatross has the longest chick-rearing period of any bird (Tickell 1968), but obvious logistical problems previously precluded study of the relationship between the provisioning behavior of parents and growth of the chick throughout the rearing period.

During one prefledging period of 8.5 mo (in 1994) we used an automatic recording system to measure the attendance patterns of parent albatrosses, supplementing these records with data on meal sizes, and growth parameters of the chicks. During a different breeding season (1986) we had studied the growth parameters and survival to adult age of the chicks, together with the subsequent survival of parents. Here we combine these two data sets to investigate the fitness consequences for variations in provisioning behavior of a sexually dimorphic long-lived seabird, and to test the following predictions. (1) Being a long-lived species, investment in a given offspring is predicted to have little effect on adult survival, particularly when considering young parents with high residual reproductive values (Williams 1966, Goodman 1974). However, age-specific differences in provisioning behavior could be expected if resources for offspring production are limited. (2) The marked sexual size dimorphism suggests that male and female adults could have different provisioning abilities, due to differences in foraging abilities (e.g., Weimerskirch 1995, Weimerskirch et al. 1997b). (3) Sexual size dimorphism may already be evident prior to fledging, such that male and female chicks may have different needs during early growth, leading to differences in parental costs for rearing sons and daughters, and possibly to differences between factors affecting survival from fledging to adult age. (4) When differences in rearing costs between male and female offspring exist, parents should, on average, divide their total reproductive effort equally between the sexes so that the extra costs of rearing one sex should lead a numerical compensation so that the sex ratio at the end of the parental investment period is biased accordingly toward the less expensive sex (Fisher 1930). For the Wandering Albatross, one would expect older adult birds to produce more of the less expensive sex, presumably daughters.

MATERIALS AND METHODS

Field study

The study was carried out on Ile de la Possession, Iles Crozet (46°25′ S–51°50′ E), in the southwestern Indian Ocean, from 1 March to 24 December 1994 at the colony of Baie du Marin (see Weimerskirch and Jouventin 1987). Sex, age, and previous breeding experience of the parent birds were known from a long-term database (Weimerskirch et al. 1997a), each bird being banded with metal and plastic bands. Here we define ''inexperienced'' birds as those birds breeding for the first time, and ''experienced'' birds as those breeding for the second time or more (birds with a ''limited'' experience are those breeding for the second to the fifth time). The age and experience of each pair was expressed as the average of the age or experience of the male and female. For sex ratio and survival analyses, ''young'' birds are defined as birds <20 yr, and ''old'' birds ≥20 yr because survival and fecundity are known to decrease after the age of 20 years in Wandering Albatrosses (Weimerskirch 1992).

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 parents in the colony after their chick was left alone on the nest (which occurs ~31 d after hatching), 41 individuals (from 21 pairs) were fitted with VHF transmitters (model 1/2AA, ATS, Isanti, Minnesota, USA; 17 g, 55 pulses/min) clamped with cable ties, glued with araldite on the central rectrix, and protected by an adhesive white tape. Between 26 March and 4 April, during the brooding period, each parent was fitted with a transmitter of unique frequency. An automatic recording station, including a receiver, a data logger (R4000 and DCCII respectively, ATS, Isanti, Minnesota, USA), and a multidirectional antenna were installed in the middle of the colony. The 21 nests were monitored automatically (20 nests with two adults fitted with transmitters, one nest with a single adult fitted with a transmitter), and were well scattered within a 600 m diameter circle. The automatic recording station, powered by 12-V batteries that were regularly recharged, scanned the various frequencies continuously. Each frequency was scanned for a period of 10 s, so each frequency was scanned every 8 min. A total of 21 transmitters were lost during the course of the study (primarily because the feather was broken, but

also because some birds molted the feather fitted with the transmitter). The data were downloaded every 2 d during the brooding period and every 7–10 d thereafter onto a laptop computer.

To sample the size of meals delivered, the 21 chicks were weighed just after dawn and again one hour before dusk during each of the first 10 d of each month between May and October. The chicks were weighed with a Salter spring balance. To study the growth curve of the chicks, in addition to weighing twice daily during the first 10 d of each month, each chick was weighed and measured every 10 d from hatching to fledging. For each chick, the culmen, tarsus, and feet were measured to the nearest 0.1 mm with calipers, and the wing to the nearest 1 mm using a ruler.

To investigate the consequences, in terms of survival, of differential parental investment, and to study how the growth parameters of chicks affected their survival to adult age, additional data on the growth of 59 chicks were obtained during a study carried out between March and December 1986 in the same colony. The body mass and the lengths of culmen, tarsus, and wing were recorded every 4–8 d through the rearing period (Lequette and Weimerskirch 1990). The subsequent survival of chicks, and of the adults that fledged these chicks, was followed between 1988 and 1997 through the monitoring program carried out every year on Ile de la Possession as part of the long-term population study of Wandering Albatrosses (Weimerskirch and Jouventin 1987, Weimerskirch et al. 1997a).

Data analysis

The information downloaded from the automatic recording station provides a list of frequencies each representing an individual for a particular time, with a number of pulses. The number of visits was calculated from these data. As the series of pulses were not continuously recorded, probably due to the movement of the bird from the landing area to the nest, and crossing areas out of the monitoring antenna's purview, and to interference, we defined a foraging trip, on the basis of observations, as being represented by a period greater than 1 h (Weimerskirch et al. 1997b). 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 attributed signal loss to some local problem), corresponding to one visit. To determine, from twice daily weighings, the mass of food delivered to a chick during a visit, it was necessary to take into account losses of mass due to respiration and defecation. As we knew when the visit occurred, and therefore when the meal was delivered (from the telemetry record), 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 estimated as the difference between the mass estimated before and after the meal was delivered.

The amount of food delivered by individual male and female parents to male and female chicks was estimated using the total number of visits recorded multiplied by each individual's average meal mass.

Growth data

Throughout the fledging period, changes in the chick's mass were characterized by long periods of gradual decrease (corresponding to the assimilation of food ingested) punctuated by steep increases (corresponding to meals). Overall, procellariiform chicks have a typical growth curve for mass, with a period of rapid increase up to a peak, which occurs in Wandering Albatrosses at ~28 wk, 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 $M = A/(1 + \lambda \exp[-K(t - Ti)])^{1/\lambda}$ where A is the asymptotic or maximum mass, K is the growth rate, and Ti 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 (i.e., the logistic, von Bertalanffy, and Gompertz curves, which have been used to describe the growth of birds [Ricklefs 1968, 1983]). A growth curve was fitted to the body mass data for each individual chick, using a weighted least squares 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 the Gompertz curve for all individuals (similar to Ricketts and Prince 1984; see also Warham 1990:364–365) and calculated the growth rate, K_G, and the asymptotic mass, A_G. Because this procedure does not yield the age at peak mass, we also modeled the data for each individual using a third degree polynomial equation, and calculated the age and mass for the asymptote of the polynomial curve. To allow for comparison with data from the literature, we also calculated the growth rate of chicks during the linear portion of the growth curve, by computing growth over the time taken to grow from 10 to 90% of asymptotic mass ($K t_{10}–t_{90}$, see Ricklefs 1973).

Sex, body size, and condition 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 that were subsequently sexed on their return to the colonies as adults. At this time they could be sexed reliably according to well-established size and plumage dimorphism criteria (Weimerskirch et al. 1989, Weimerskirch 1992; H. Weimerskirch, *unpublished data*). Thirty-one chicks fledged in 1986 were observed by fieldworkers as adults between 1990 and 1997: 13 females, 11 males, and seven that were not sexed. The growth parameters and measurements at fledging of the 24 sexed chicks

HENRI WEIMERSKIRCH ET AL.

TABLE 1. Growth parameters and measurements at fledging of chicks reared in 1986 and 1994 (mean $\pm$ 1 SD).

Parameter	1986 Combined ($n = 59$)	1994 Combined ($n = 28$)	Comparison 1986/1994 P	1986			1986
				Male ($n = 33$)	Female ($n = 26$)	Comparison M/F, P	Male survived ($n = 14$)
Hatching date (March)	17.8 $\pm$ 5.9	15.1 $\pm$ 5.8	0.045	17.7 $\pm$ 5.4	18.0 $\pm$ 6.7	0.867	17.3 $\pm$ 6
Mass at hatching (g)	341.7 $\pm$ 48.7	357.9 $\pm$ 43.5	0.304	344.3 $\pm$ 60.5	338.0 $\pm$ 32.0	0.836	352.5 $\pm$ 12.6
Age when left alone (d)	33.1 $\pm$ 4.2	32.8 $\pm$ 4.6	0.752	31.5 $\pm$ 3.8	35.1 $\pm$ 4.0	0.001	30.9 $\pm$ 3.6
Growth rate Kt_{10-90} (g/d)	76 $\pm$ 9.9	74.5 $\pm$ 9.2	0.509	81.4 $\pm$ 8.8	69.2 $\pm$ 6.4	<0.0001	83.3 $\pm$ 5.7
K_G, growth rate	0.026 $\pm$ 0	0.025 $\pm$ 0	0.250	0.026 $\pm$ 0.004	0.026 $\pm$ 0.005	0.856	0.027 $\pm$ 0
A_G, asymptotic mass (g)	11 757 $\pm$ 1273	11 783 $\pm$ 1073	0.927	12 498 $\pm$ 1010	10 817 $\pm$ 900	<0.0001	12 396 $\pm$ 690
Max. absolute mass (g)	13 386 $\pm$ 1108	13 471 $\pm$ 1281	0.620	14 142 $\pm$ 694	12 426 $\pm$ 723	<0.0001	14 283 $\pm$ 685
Age at max. pol. mass (d)	197.9 $\pm$ 13.9	197.8 $\pm$ 13.5	0.975	195.0 $\pm$ 13.6	201.7 $\pm$ 13.6	0.065	192.8 $\pm$ 7.5
Max. pol. mass (g)	12 200 $\pm$ 1217	11 761 $\pm$ 1098	0.109	12 956 $\pm$ 964	11 241 $\pm$ 733	<0.0001	13 155 $\pm$ 699
Duration of decrease (d)	62.2 $\pm$ 10.7	65 $\pm$ 11.4	0.259	63.9 $\pm$ 9.6	60.0 $\pm$ 11.8	0.165	66.9 $\pm$ 7.5
Rate of decrease (g/d)	-36 ± 11.9	-27.3 ± 12.7	0.003	-38.5 ± 11.7	-32.8 ± 11.6	0.064	-38.8 ± 5.8
Age at fledging (d)	260.1 $\pm$ 9.4	262.9 $\pm$ 11.2	0.233	258.9 $\pm$ 10.2	261.7 $\pm$ 8.1	0.261	259.7 $\pm$ 10.8
Date of fledging (Nov.)	32.5 $\pm$ 11.7	32.9 $\pm$ 13.1	0.861	30.6 $\pm$ 12.5	34.9 $\pm$ 10.4	0.163	29.8 $\pm$ 14.2
Mass at fledging (g)	9995 $\pm$ 1099	9992 $\pm$ 1108	0.992	10 542 $\pm$ 1033	9301 $\pm$ 736	<0.0001	10 558 $\pm$ 635
Culmen at fledging (mm)	164.9 $\pm$ 5.8	165.5 $\pm$ 7.9	0.705	166.8 $\pm$ 5.3	162.5 $\pm$ 5.7	0.003	168.9 $\pm$ 4.5
Wing at fledging (mm)	683.1 $\pm$ 15.3	682.7 $\pm$ 24	0.927	685.9 $\pm$ 15.3	679.5 $\pm$ 14.8	0.112	690.8 $\pm$ 12.7
Foot at fledging (mm)	292.2 $\pm$ 10.5	292.3 $\pm$ 5.7	0.961	297.4 $\pm$ 10.0	285.7 $\pm$ 7.1	<0.0001	301.7 $\pm$ 9.1
Body size	-0.01 ± 0.98	0.022 $\pm$ 1.06	0.891	-0.039 ± 1.51	-0.077 ± 1.34	0.003	0.798 $\pm$ 0.74
Body condition	-5.8 ± 643	12.4 $\pm$ 734	0.906	-11.8 ± 706.9	10.7 $\pm$ 571.5	0.927	-317.3 ± 456

Notes: Male and female chicks together make up the ''Combined'' category; n = number of chicks. ''Survived'' (S) and ''Died'' (D) refer to the fate of 1986 chicks. ''Max. pol. mass'' = maximum polynomial mass.

were incorporated in a discriminant function analysis to sex the 28 additional chicks reared in 1994, plus the 1986 chicks that survived but were not sexed, and those that were never recaptured. 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 three parameters selected (wing length at fledging, age at maximum polynomial mass, and absolute maximum mass) explained 100% of the variance with the first component. With only these three parameters, the sexes of 96% of the chicks were assigned correctly. A jackknife classification, which uses the same discriminant function for all the chicks except the case being classified, assigned 92% of individuals as correctly classified, a value very close to 96%, suggesting that the number of predictors is sufficiently small (Wilkinson 1996).

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. To give an overall measure of body size of the chicks at fledging, we took the factor score computed from the first principal component of the culmen, foot, and wing lengths using a Principal Component Analysis for each sex (Freeman and Jackson 1990). The body condition at fledging was estimated as the residual of the linear regression of the mass at fledging on body size, performed for males and females separately. The proportions of variance explained by the first component were 69.6% for males and 72.5% for females.

Statistical analysis

Analyses were carried out using SYSTAT 6.0 (Wilkinson 1996) and SAS, Statistical Analysis System (SAS Institute 1987). Pearson correlations were used when data were normally distributed and Spearman rank correlations were used otherwise. Average values are given with ± 1 SD, unless stated differently.

RESULTS

Sex ratio, chick growth, and survival to adult age

Sex ratio.—The sex ratio of the 87 chicks reared in 1986 and 1994 was not biased (40 females and 47 males, ($\chi_1^2 = 0.280$, $P = 0.597$). There was a tendency, although not significant, for the sex ratio of progeny of young parents to be biased toward males, in comparison with that of the progeny of old parents ($\chi_1^2 = 3.44$, $P = 0.063$; statistical power $1 - \beta = 0.73$). Similarly, the progeny sex ratio of parents with a ''limited'' breeding experience (2–5 yr) was biased toward sons ($\chi_2^2 = 6.17$, $P = 0.039$).

Chick growth.—The mass growth of chicks was typical of Procellariiformes, with a period of rapid increase followed by a period of slow decline before fledging (Fig. 1). The growth parameters and measurements at fledging of all chicks were similar in 1986 and 1994 (Table 1). When the sex of the chick was considered, the growth parameters and measurements at fledging were similar within each sex for both years (Table 1). Males were left unbrooded earlier than females, had faster growth rates, reached a higher absolute, asymptotic, and maximum polynomial mass, and were heavier

TABLE 1. Extended.

1986		1986			1994			Comparison	
Male died (n = 19)	Comparison S/D, P	Female survived (n = 17)	Female died (n = 9)	Comparison S/D, P	Male (n = 14)	Female (n = 14)	Comparison M/F, P	Male 1986/ 1994, P	Female 1986/ 1994, P
18 ± 5	0.711	16.6 ± 4.7	20.6 ± 9.2	0.157	17 ± 5.2	13.1 ± 5.6	0.071	0.683	0.028
333.3 ± 102	0.717	350 ± 20	290 ± 50	0.152	373.6 ± 49.3	342.1 ± 30.9	0.054	0.248	0.802
32 ± 3.9	0.428	35.1 ± 3.6	35 ± 4.9	0.944	31 ± 4.3	34.6 ± 4.3	0.038	0.665	0.712
80 ± 10.4	0.291	69.5 ± 7.5	68.4 ± 3.5	0.684	80.3 ± 6.5	68.8 ± 7.7	<0.0001	0.665	0.881
0.024 ± 0	0.028	0.026 ± 0.01	0.025 ± 0	0.730	0.025 ± 0.003	0.024 ± 0.003	0.364	0.605	0.318
12 573 ± 1207	0.627	10 906 ± 1074	10 649 ± 419	0.499	12 476 ± 856	11 089 ± 788	<0.0001	0.943	0.347
14 038 ± 700	0.325	12 404 ± 831	12 470 ± 495	0.830	14 342 ± 986	12 600 ± 896	<0.0001	0.431	0.511
196.5 ± 16.7	0.445	202.1 ± 16.2	200.9 ± 7.2	0.838	195.4 ± 13.9	200.2 ± 13	0.356	0.874	0.313
12 809 ± 1116	0.317	11 385 ± 824	10 970 ± 435	0.175	12 481 ± 881	1104 ± 1782	<0.0001	0.121	0.426
61.7 ± 10.5	0.132	58.4 ± 13.3	62.9 ± 8.3	0.363	66.2 ± 10.8	63.9 ± 12.3	0.605	0.478	0.333
−38.3 ± 14.7	0.899	−34.1 ± 13.3	−30.3 ± 7	0.438	−26.7 ± 13.6	−27.9 ± 12.1	0.802	0.004	0.224
258.3 ± 10	0.704	260.5 ± 7.6	263 ± 9.1	0.326	261.6 ± 11.1	264.1 ± 11.6	0.565	0.418	0.439
31.1 ± 11.4	0.760	32.5 ± 9.2	39.3 ± 11.8	0.116	33.6 ± 13.6	32.3 ± 12.9	0.789	0.457	0.495
10 530 ± 1268	0.939	9428 ± 774	9061 ± 628	0.233	10 642 ± 905	9342 ± 905	0.001	0.753	0.877
165.3 ± 5.3	0.048	162.1 ± 6.2	163.2 ± 5	0.644	167.9 ± 4.8	163.1 ± 9.6	0.104	0.517	0.809
682.2 ± 16.3	0.110	677.1 ± 14.9	684 ± 14.3	0.267	691.1 ± 24.8	674.3 ± 20.7	0.063	0.385	0.362
294.2 ± 9.6	0.030	285.2 ± 7.6	286.8 ± 5.2	0.594	295.1 ± 4.1	289.6 ± 5.8	0.007	0.421	0.090
0.08 ± 0.93	0.024	−0.605 ± 0.84	−0.334 ± 0.81	0.433	0.459 ± 0.823	−0.416 ± 1.1	0.026	0.795	0.760
211.7 ± 775	0.030	178.8 ± 552	−329 ± 450	0.028	30.1 ± 761	−5.3 ± 735	0.901	0.853	0.969

and larger at fledging (Fig. 1, Table 1). Whereas parental age or experience could not be shown to influence the growth parameters of female chicks ($P > 0.1$ for all cases using Pearson and Spearman rank correlation), both factors (averaged by pair) were significantly related to several growth parameters of male chicks. Specifically, the following growth parameters of 47 male chicks increased with the age of the parents; growth rate (Pearson $r = 0.521$, $P < 0.0001$), mass at fledging (Spearman $r_s = 0.395$, $P = 0.007$), and condition at fledging (Pearson $r = 0.290$, $P = 0.05$).

At fledging, both male and female chicks were heavier than adult birds (Tables 1 and 2; $t = 5.8$, df = 192, $P < 0.001$ and $t = 10.4$, df = 173, $P < 0.001$, respectively), and had longer wings ($t = 7.1$, df = 142, $P < 0.001$ and $t = 12.0$, df = 144, $P < 0.001$, respectively). The culmen length was similar in chicks and adults of the same sex ($t = 0.79$, df = 219, $P = 0.430$ and $t = 1.13$, df = 202, $P = 0.260$, respectively).

Growth and survival to adult age.—Out of 59 chicks fledged in 1986, 26 were females and 33 males, a sex ratio not different from 1:1 ($\chi^2_1 = 0.412$, $P = 0.521$), and 31 were recaptured as adults between 1990 and 1997 on Ile de la Possession. For the chicks fledged in 1986, the growth parameters of birds surviving and of birds disappearing were similar within each sex, except that the surviving males had a larger body size (foot and culmen lengths) at fledging and had been in poorer body condition than those that disappeared, while the females surviving had been in better body condition than those disappearing (Table 1).

To investigate which parameters during the growth of the chick and prior to fledging were responsible for

large size in male chicks and a good body condition in female chicks, we used a stepwise multiple regression. We found that for males, large size at fledging was explained ($R^2 = 0.742$) by a high maximum polynomial mass ($F_{1,46} = 15.6$, $P < 0.0001$), a high absolute maximum mass ($F_{1,46} = 15.6$, $P = 0.0003$), and a high rate of mass decrease ($F_{1,46} = 12.0$, $P = 0.012$). For females, good body condition at fledging was explained ($R^2 = 0.527$) by high asymptotic mass ($F_{1,41} = 18.8$, $P < 0.0001$), high rate of mass decrease ($F_{1,41} = 25.5$, $P < 0.0001$), and a short period of mass loss ($F_{1,41} = 8.35$, $P = 0.006$).

Male chicks that disappeared had shorter culmens than adult birds (Tables 1 and 2; $t = 2.39$, df = 191, $P = 0.0178$), whereas those surviving had similar culmen lengths to those of adults ($t = 0.96$, df = 186, $P = 0.343$). For females, there was no difference in culmen length between adult birds and chicks that either survived ($t = 0.659$, df = 179, $P = 0.511$) or disappeared ($t = 1.233$, df = 171, $P = 0.219$).

Provisioning

Between the beginning of May, when all chicks have been left alone on the nest, and the time when chicks attain the peak (or asymptotic mass) in September, male parents delivered more meals than females (i.e., they were at sea for shorter foraging trips) irrespective of the sex of the chick (Fig. 2a), but male chicks received larger meals than female chicks, irrespective of the sex of the parent (Table 3, Fig. 2b). During this period the total amount of food delivered varied according to both the sex of the chick and of the parent, male chicks receiving more food than female chicks and adult males
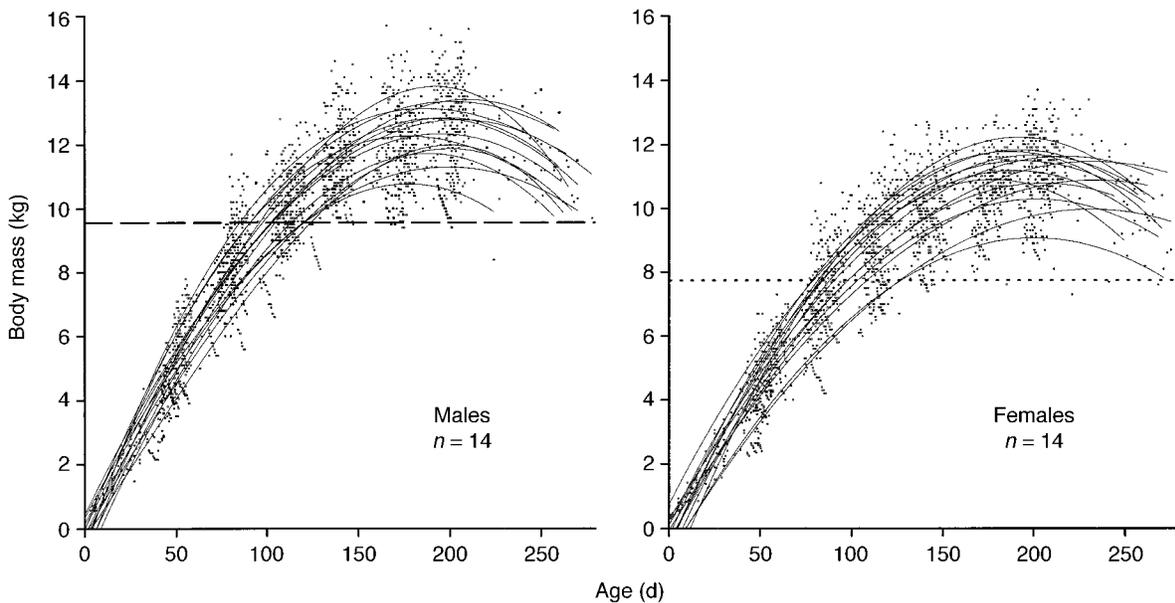
Fig. 1.   Change in mass of male and female chicks throughout the 1994 chick-rearing period, with polynomial growth curve for each individual. Dashed and dotted lines indicate average mass of adult birds.

delivering more food than females (Table 3, Fig. 2c). The overall amount of food received by individual chicks (the sum of food brought by the male and the female parent) was 139.9 ± 13.4 kg ($n = 3$) for male chicks, and 104.3 ± 18.9 kg ($n = 3$) for female chicks ($t = 2.93$, $P = 0.032$).

Between May and fledging in November/December, sample sizes were smaller because of the loss of transmitters. The total amount of food delivered during this period varied according to the sex of the adult, males delivering more food than females, but not to the sex of the chick (Table 3; Fig. 2d). The overall amount of food received by the chick was 165.4 kg for one female chick, and 170.6 and 184.2 kg for two male chicks.

There was no significant relationship between the amount of food delivered, the number of meals delivered, the average size of meals, and the age or the experience of the birds ($P > 0.1$ for all cases using Pearson or Spearman rank correlation).

Relationship between the growth of chicks and the provisioning parameters of the parent

We found no relationship between the total number of meals or the total amount of food delivered by the two parents up to peak mass, and during the whole fledging period, and the growth parameters (all parameters of Table 1) of their chick ($P > 0.1$ for all cases using Pearson and Spearman rank correlation). The regularity with which meals are delivered by each parent, by the two parents, and the time elapsed between deliveries by the two parents may influence the growth of the chick. We investigated whether these parameters were related to the growth parameters of the chick.

There was no relationship between the average duration of fasting periods of the chick and its growth parameters up to the peak mass ($P > 0.1$ for all cases using Pearson and Spearman rank correlation). We found a significant relationship between the coefficient of variation (CV) of the time elapsed between two meals received by the chick and the growth rate and maximum polynomial mass of the male chicks ($r_s = -0.648$, $P = 0.034$, $r_s = -0.661$, $P = 0.025$), indicating that growth rates and maximum polynomial masses are higher when the two parents synchronize the delivery of meals so that the duration of fast is the least variable. There was no such relationship for female chicks ($r_s = 0.430$, $P = 0.200$, $r_s = -0.236$, $P = 0.502$).

Because of the small sample size for the provisioning parameters after the chick attained peak mass, we were only able to investigate the relationship between the experience of adults and their provisioning parameters until the male and female chicks attained peak mass. We found no influence of age or experience of both parents on the number of meals and amount of food delivered up to peak mass ($P > 0.1$ for all cases using Pearson and Spearman rank correlation). More experienced or older pairs tended to provision a male chick more regularly than less experienced or younger pairs during the first part of the period of mass increase ($r_s = -0.742$, $P = 0.020$ and $r_s = -0.735$, $P = 0.025$ respectively).

Survival of adult parents

In 1986, only 1 of the 26 adult males rearing a female chick disappeared whereas 5 of the 33 rearing a male chick disappeared (Fisher's exact test, $P = 0.215$). Old

TABLE 2. Body mass and measurements (mean ± 1 SD) of male and female parents (sample sizes in parentheses).

Measure	Males	Females
Body mass (kg)	9.6 ± 1.0 (146)	7.8 ± 0.8 (134)
Wing length (mm)	672.1 ± 16.5 (96)	648.8 ± 18.7 (105)
Culmen length (mm)	167.8 ± 4.2 (173)	161.3 ± 4.4 (163)

males were more likely to die than were young males after rearing a son ($P = 0.047$), but not after they fledged a female chick ($P = 0.385$). Two of 26 adult females rearing daughters disappeared compared with 1 of 33 rearing sons (Fisher's exact test, $P = 0.577$) and there were no differences between the survival of old vs. young mothers after they fledged a son ($P = 0.364$) or a daughter ($P = 1.00$).

DISCUSSION

Sex differences in chick growth and parent provisioning abilities

The period of mass increase to the asymptote and the period of mass decline, typical of the growth of Procellariiformes (Warham 1990), were similar for male and female chicks. Growth rates were higher for male chicks than for females, whereas the development period was similar in duration for both. Male chicks received more food than female chicks, with male parents delivering more food than females. A male parent rearing a male chick thus delivered almost twice as much food as a female parent rearing a female chick. These results show that the four permutations of feeding relationship from father–son to mother–daughter involve different amounts of resources. Male and female chicks have a similar proportionate rate of mass loss (H. Weimerskirch, *unpublished data*), suggesting that there are no differences in energy requirement per unit of body mass. The four levels of provisioning are probably the result of different energy requirements for chick growth and of different energetic constraints for adults, rather than the result of any differential selective pressure related to sexual selection (Trivers 1972). Male chicks therefore appear more costly to rear for parents of both sexes than female chicks, as they receive more food overall.

Males provisioned their chick more often than females by performing more frequent visits. The less frequent visits by females may be due to the parents different feeding zones, males concentrate on the continental shelf edge and females move farther off in oceanic waters bordering the shelf edge (Weimerskirch et al. 1993, 1997b). In addition to the slightly longer commuting distances, females may also have lower rates of prey capture (Weimerskirch 1995). The sex-specific differences may indicate that females have greater difficulties than males in provisioning their chick.

Parameters influencing survival to adult age

At Crozet, long-term studies of 16 cohorts of banded chicks indicate that there is no sex difference in survival from fledging to adult age in Wandering Albatrosses (Weimerskirch et al. 1997a), as seen in our sample of chicks fledged in 1986. In our study, the number of individuals banded as chicks and subsequently recaptured between 1990 and 1997 is likely to closely represent the real proportion of birds surviving from the sample, because Crozet Wandering Albatrosses are very faithful to their birthplace. Thus in 1997, when birds were 11 yr old, all birds from the cohort are likely to have been recaptured at least once in our study colonies (Weimerskirch et al. 1997a).

The probability of survival to adult age is a major determinant of life history evolution (Charlesworth 1980), but very few studies have examined the role of provisioning and growth factors on the subsequent survival to adult age (Richner 1989), especially for long-lived animals such as seabirds. At fledging, Wandering Albatross chicks of both sexes had similar culmen lengths in comparison to adult birds, but longer wings than adults. This difference is not surprising per se, because wing length may change with each molt, but
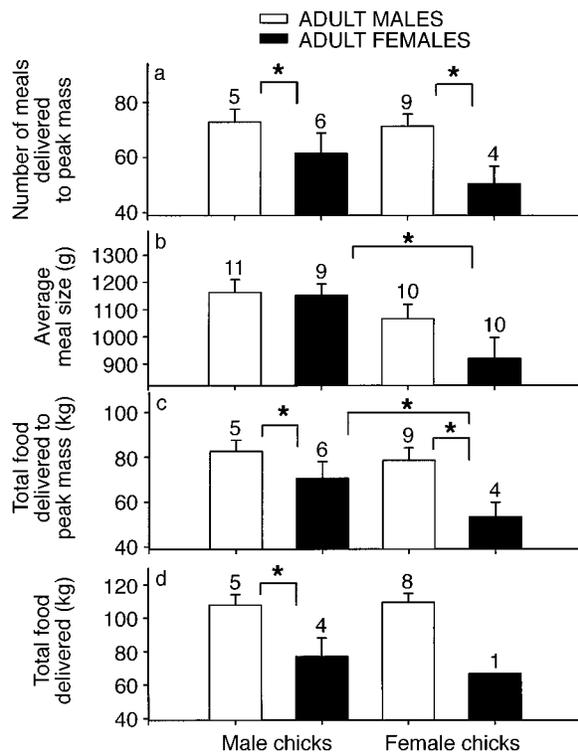

FIG. 2. Mean (+1 SE) number of meals (a), meal size (b), and total amount of food (c) delivered up to peak mass by male and female parents to male and female chicks; and (d) mean (+1 SE) total amount of food delivered by male and female parents to male and female chicks. Numbers above bars indicate sample sizes. * Significantly different at $P < 0.05$.

TABLE 3. Results of two-way ANOVA on provisioning parameters of parents as a function of sex of parents and of sex of their chick (data are presented in Fig. 2).

Parameter	Source	df	Mean square	F	P
Number of meals delivered up to peak mass	Sex of adult	1	736.1	6.90	0.0145
	Sex of chick	1	26.4	0.25	0.6232
	Sex of adult × sex of chick	1	2.7	0.02	0.8756
	Error	25			
Average meal mass delivered up to peak mass	Sex of adult	1	61 950.1	2.04	0.1616
	Sex of chick	1	269 655.1	8.89	0.0051
	Sex of adult × sex of chick	1	45 754.1	1.51	0.2273
	Error	36			
Food delivered up to peak mass	Sex of adult	1	1396.9	10.00	0.0043
	Sex of chick	1	804.1	5.75	0.0249
	Sex of adult × sex of chick	1	124.6	0.89	0.3546
	Error	23			
Total food delivered	Sex of adult	1	3356.3	12.09	0.0037
	Sex of chick	1	58.1	0.21	0.6544
	Sex of adult × sex of chick	1	102.6	0.37	0.5530
	Error	14			

for most bird species chicks fledge with shorter wings than adults (e.g., Warham 1990 for petrels). The magnitude of this difference (>20 mm) indicates that it is not the result of wear of adult wing feathers, but rather that long wing length may confer an advantage to young birds. Chicks at fledging are also heavier than adult birds, suggesting that they probably leave the colony with an accumulation of body reserves.

Chick survival to adult age seems to be related to different characteristics at fledging. Female chicks surviving to adulthood were in better condition than those disappearing. This result is consistent with the hypothesis that energy reserves stored before fledging are important across many avian taxa in allowing the birds to survive the critical first weeks of independent feeding (see review in Magrath 1991). For males, large individuals in poor body condition appeared to survive better than smaller birds, as surviving chicks had larger structural dimensions (culmen and foot lengths) than those disappearing. These differences in the factors influencing survival to adult age suggest that extra energy reserves are advantageous for females while large size is advantageous for males. Male Wandering Albatrosses are larger than females. This, and their whiter plumage at adult age, are believed to make them dominant to females in competitive situations (Bretagnolle 1993). For the subordinate sex, i.e., for female Wandering Albatrosses, there should be an advantage in storing extra energy reserves, and an advantage of a large size for the dominant sex, namely males (Sullivan 1989, Stamps 1990). In the context of limited resources, especially for male chicks, body condition is likely to be traded off against size as indicated by the observation that larger chicks are in poorer condition. Another factor that may lead to sex differences in the relationship between body condition and size is related to the problem of wing loading. During their first year at sea, juvenile Wandering Albatrosses move north of the foraging range of adults into subtropical waters (Weimerskirch and Jouventin 1987) where they encounter calmer wind conditions than exist in the waters where adults forage. Adults have the ability to exploit strong winds to minimize energy costs of flight (Salamolard and Weimerskirch 1993). In subtropical waters a low wing loading (large size with a low mass) would therefore be probably more advantageous than a higher loading (Pennycuick 1989). The observation that both male and female chicks fledge with longer wings than adults also suggests that low wing loading is probably advantageous during the first years that young birds spend in subtropical waters.

Optimal provisioning strategy in relation to the survival of the chick and of the parent

To maximize the chance of chick survival to adult age it appears that for both sexes a high asymptotic or maximum polynomial mass is advantageous for the chick. Good body condition at fledging that allows female chicks to survive better to adult age is related to a high asymptotic mass followed by a short period of rapid mass loss. A large body size and low body condition that allows male chicks to survive better is also related to a high asymptotic mass followed by a rapid mass loss. To attain this high asymptotic mass, high rates of mass increase are necessary. These are not attained through high total amounts of food being delivered as might be expected. This is probably because the energy needed for growth is only a small part of the total energy requirement. 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). 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.

Maximum growth rates during the first period of growth are made possible by the adults delivering food regularly to the chick, i.e., with a low variance in the interval between meals delivered by the two parents. Such a provisioning strategy has the advantage of avoiding erratic and irregular feeding. Because Wandering Albatrosses are able to transport meals ranging to almost three times the size of the overall meal mass, the optimal provisioning strategy appears to be delivering small meals regularly, rather than larger meals at variable intervals. Several studies have shown that in the case of intermittent feeding, fewer shorter fasting periods would indeed optimize chick growth (Pinchasov et al. 1985, Schaffner 1990). For food deliveries to be regular, the two parents must have a certain degree of synchrony. How can this be achieved while seabird parents are believed to feed independently from one another? The nutritional status of the chick may convey some information to the parent through begging behavior (but see Ricklefs 1992) or through its swallowing capacity (Weimerskirch et al. 1997*c*). Because older pairs appear to be more synchronized than younger ones, at least when raising a son, and because this species pairs for life (Warham 1990), with no divorce (H. Weimerskirch, *unpublished data*), synchrony between the members of a pair may be attained progressively over the long pair bonding period.

The additional effort invested in rearing male chicks has no detectable effect on subsequent survival of young or old female parents as would be expected in a long-lived animal (Williams 1966) like the Wandering Albatross (Weimerskirch 1992). However, old males rearing the more costly male chicks appear to have a higher subsequent mortality rate than do young males. Because old males have a lower residual reproductive value than younger ones, life history theory predicts that old birds would be more likely to be affected by high costs of reproduction than young birds (Charlesworth 1980). The risk connected with increased breeding effort is either the result of old birds being less efficient (e.g., because of senescence), older birds investing more effort (Williams 1966, Pugesek and Diem 1990), or both. Whether being more synchronized when getting older involves greater effort is not known. Young birds make fewer visits than old birds, suggesting a reduced foraging efficiency by young birds rather than a greater effort by old birds. It is also difficult to ascertain why rearing a male chick could be more costly for old male parents than for female parents. Male parents make many more foraging trips and contribute much more to the care of the chick, irrespective of their larger size, and this difference could eventually account for the higher mortality.

The age and experience of parents influenced the growth rate and mass at fledging of male but not of female chicks. This was made possible because older and more experienced pairs were more synchronized during the first part of the growth of the male chicks

than younger and less synchronized pairs. This probably was not the case for female chicks because they require much less energy so that synchronized behavior of parents is not necessary for maximum growth rate and asymptotic mass.

Because the costs of raising the more expensive sex should vary between parents, differences may favor sex ratio variation (Clutton-Brock 1991). The tendency for an age-related sex ratio variation observed in our study could be the result of such selection. Our data show higher rearing costs for male than for female chicks, and higher investment for male than for female Wandering Albatross parents. According to Fisher's (1930) theory on sex differences in rearing costs of male and female offspring, one should expect older adult birds to produce more females than younger adults, on average. The sex ratio produced by younger, less experienced parents (male biased) is consistent with Fisher's prediction. Furthermore, the increased risk of mortality of older male parents raising sons should favor female offspring production in older males. However, results suggest that older parents are more synchronized and adequately provision male chicks with a higher chance of survival until adult age than younger parents. Consequently, when male parents get older, the higher chance of producing good male chicks may be balanced by increased mortality risk. Rearing a female chick leads to completely different strategies in terms of age-related breeding effort as the age of birds has no significant influence on the provisioning behavior of parents or on the quality of the chick produced. Therefore, in the Wandering Albatross, predictions about the optimal age-related investment by male and female parents (Charlesworth 1980) depend on whether adults are rearing a male or a female offspring. These observations lead to the theoretical prediction that fitness optimization for male parents would be reached by first producing females until their level of experience is high enough to produce male offspring with a high chance of survival, and by producing females when old, to minimize chances of mortality due to a high investment in male offspring. Further studies should be undertaken to test these predictions.

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