The Condor 101:360–368

WING AND PRIMARY GROWTH OF THE WANDERING ALBATROSS[1]

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Abstract. We investigated the relationship between body mass and the rate and pattern of feather growth of the four outermost primaries of Wandering Albatross (*Diomedea exulans*) chicks. Maximum growth rates were similar (4.5 mm day^{-1}) for all feathers and between sexes, although primaries of males were significantly longer than those of females. There was a distinctive pattern to primary growth with p10 grown last, reaching its asymptote just prior to fledging. Primaries growing did so at different maximum rates; thus p7 reached its asymptote at an earlier age than p8 or p9, but maximum growth rates were the same for all primaries. Maximum growth rates of p7 and p8 were significantly correlated with chick mass at the start of the period of primary growth, and chick mass also was correlated with age at fledging. The heavier the chick, the earlier it grew its primaries and the younger it fledged. Fledging periods for Wandering Albatross chicks may be constrained by the time required to grow a full set of primaries. We suggest that the observed pattern of feather growth is a mechanism to minimize potential wear of the outer primaries prior to fledging.

Key words: Diomedea exulans, *growth rates, primaries, Wandering Albatross, wing growth.*

INTRODUCTION

For adult seabirds, molt is probably one of the most significant activities outside the breeding season (Prince et al. 1993, 1997, Langston and Rohwer 1996). In annually breeding albatrosses, the time available for molt may be as little as 100 days, so feather replacement is spread over two or more years (Prince et al. 1993, Langston and Rohwer 1995). Breeding status and body condition also influence the extent of annual molt (Weimerskirch 1991, Langston and Hillgarth 1995, Cobley and Prince 1998), and such are the potential interactions between breeding and molt that some species of albatross may need to skip a year of breeding to replace accumulated worn primaries (Langston and Rohwer 1996).

Chicks face potentially even more substantial challenges. They need to grow all their flight feathers within one-half of their complete fledging period (Ricketts and Prince 1981). For biennial breeding species such as the Gray-headed (*Diomedea chrysostoma*) and Wandering Albatrosses (*D. exulans*), chicks must grow twice the number of primaries in half the time available to adults. Existing studies suggest that completion of wing growth, as measured by length of longest primary, by petrels (Procellariiformes) prior to fledging is accorded high priority. Harris (1966) showed that both light and heavy Manx Shearwaters (*Puffinus puffinus*) had similarly developed wings on fledging, demonstrating that there was a premium on being able to fly even if poorly fed during development. Development of albatross chicks also suggests that wing growth is largely independent of body mass. Wing growth in Gray-headed and Black-browed Albatrosses (*D. melanophris*) was less affected by body mass than growth of internal organs (Reid et al., in press), and also was less susceptible to changes in diet quality (Prince and Ricketts 1981). Lequette and Weimerskirch (1990) showed that despite differences in growth and provisioning rates, all Wandering Albatross chicks, of both sexes, have similar sized wings on fledging.

Petrels are amongst the most pelagic of all seabirds, covering vast areas of ocean in search of food (Warham 1996), so fully developed wings are important to forage successfully. After fledging, at the start of the austral summer after a chick rearing period of around 277 days, Wandering Albatross chicks do not start to replace flight feathers until their second winter, and it may be five years for males and six years for females before all juvenile primaries are re-

[1] Received 21 June 1998. Accepted 4 January 1999.

placed for the first time (Prince et al. 1997). Thus, the feathers they fledge with must sustain them through the critical period after fledging.

In this study we examine the rate and pattern of growth of individual primaries in the Wandering Albatross. We also investigate the interaction between the rate of feather growth and the fledging period and mass change over this period.

METHODS

This study was carried out at Bird Island, South Georgia (54°01′S, 38°03′W) during the 1996 austral winter. Wing length from carpal joint to the tip of the flattened, straightened wing (Spencer 1984) was measured, using a stopped rule (one which had a raised perpendicular end to which the carpal could be abutted), every 15 days, from when the chick was 10 days old until it fledged. The study nests were visited every day throughout chick rearing, and hatching and fledging dates recorded to the nearest day. A record was kept when wings were measured of when emerging primaries were first observed. Each of the four outer primaries (p 7–10) was measured from the tip to the carpal joint, to the nearest mm, every 5 days from 205 days of age until fledging. Overall wing length is defined as the length of the bent wing using the carpel bend to the tip of the longest primary. To provide a potential index of body condition, chicks were weighed at 145 and 250 days of age using an electronic weighing platform accurate to ± 10 g. Chicks were sexed by discriminant function analysis, using bill length (mm) and bill depth (mm) at 260 days old, with the regression: 0.205 length + 0.609 depth − 54.610. If the result was positive, the sex was male, if negative, female. This regression gave 100% discrimination as verified by all birds returning to breed on the study ridge (Huin, unpubl. data, $n > 500$). Of the 64 chicks in the study, 29 were male and 31 female; 4 were of unknown sex as they had fledged before bill dimensions were measured.

GROWTH MODELS

Various growth models from the Richards family of growth models (Brown and Rothery 1993) were fitted to the data on feather growth from individual chicks. Gompertz and von Bertalanffy growth models fitted the data fairly well, accounting for over 90% of the variance. However, these curves gave unrealistic estimates of maximum primary length because the growth of p10 and to a lesser extent p9 right up to fledging meant that, for some chicks, asymptotic growth was not attained within the time span of the observations. We obtained better results using the generalized model of Schnute (1981) which includes the Richards family, the Gompertz and the von Bertalanffy as special cases. This model is non-negative and a non-decreasing function of length, y, with time, t, and is given by:

$$y = (y_1{}^b + (y_2{}^b - y_1{}^b))\left[\frac{1 - e^{-a^{t-t_1}}}{1 - e^{-a^{t_2-t_1}}}\right]^{1/b}$$

where t_1 = 205 days, t_2 = age at last measurement, y_1 = fitted feather length at t_1, y_2 = fitted feather length at t_2, and a and b are parameters which describe the shape of the curve and are estimated by maximum likelihood from the data. This model fitted the primary growth data better than any of the alternatives we explored, accounting for more than 98% of variance for all feathers. For these wing growth data the fitted curves all had parameter estimates where $a > 0$ and $b < 0$, implying that the model approximates to a Richards curve (Keen 1993).

Wing length was measured from 205 days of age which corresponded to a period of rapid, approximately linear growth (Fig. 1) from an initial length of around 75% of the final wing length. However, there was large variation between individual chicks in their position along the growth curve at this age, with some of the more advanced chicks having already reached asymptotic lengths for primaries 7 and 8. In order to model the pattern of feather growth more accurately, a subsample of 28 chicks was selected (13 males, 15 females) whose growth curves were measured sufficiently early to include the period of rapid linear growth. These chicks did not differ significantly in mass at 145 or 250 days of age from those chicks omitted from this subsample (two-sample *t*-tests, t_{19-24} = 1.50–0.27, $P > 0.10$) and therefore we consider them to be representative of the sampled population.

Growth models and correlation analyses were carried out using the statistical package GENSTAT, and all means are presented ± SE unless otherwise stated. All *t*-tests were two-tailed, and a Mann-Whitney *U*-test was used on nonparametric data. Two-way ANOVAs were used to test for differences between sexes.

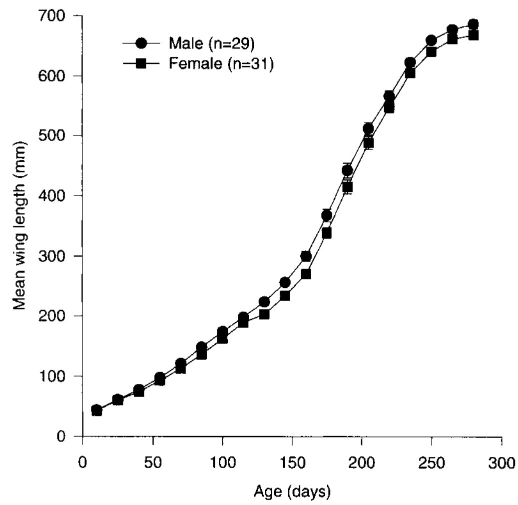

FIGURE 1. Growth of Wandering Albatross wing from 10 days of age to fledging.

RESULTS

WING GROWTH AND EMERGENCE OF PRIMARIES

Wings grew slowly during the first 145 days at a mean rate of 1.4 mm day^{-1}, increasing to 3.9 mm day^{-1} between 145 and 250 days of age, after which the growth rate declined to 0.9 mm day^{-1} to fledging at around 280 days (Fig. 1). Primaries first emerged at 127 days, and there was no significant difference between male and female chicks (Mann-Whitney U-test, $U = 789$, $P > 0.7$) (Table 1). There was a wide range in age at fledging, with an average of 277 days. Male chicks fledged at 277 days old and female chicks at 281 days (Table 1), but these differences were not significant (Mann-Whitney U-test, $U = 779$, $P = 0.10$). The average time from emergence of primaries to fledging was very similar between sexes (Table 1). Age at emergence of primaries is only accurate to within 15 days. Fifteen of the 62 chicks monitored (24%) grew their full set of wings in under 150 days from the start of primary growth, but only 1 chick in under 135 days.

GROWTH RATES OF PRIMARIES

Primaries were already increasing rapidly in length when measurements began; later growth rate declined and feathers eventually reached their maximum length (Fig. 2). The asymptote was reached first by p7 and was reached progressively later by each primary with p10 continuing to grow right up to fledging. At fledging, p10 was the longest primary followed by p9, then p8, and finally p7 which reached around 83% of the asymptotic length of p10 (Fig. 2A and 2B).

The age at which the maximum growth rate was attained increased from p7 to p10, indicating that feathers were not all growing at their maximum rate simultaneously (Table 2). There was no significant difference in the age that

TABLE 1. Mean ± SD (range) age in days at first emergence of primaries and at fledging for male and female Wandering Albatross chicks.

	Males	n	Females	n	All	n
Age when emergence first recorded ± 15 days	126.7 ± 13.5 (115–160)	27	128.1 ± 16.1 (115–175)	31	126.6 ± 14.9 (115–175)	62
Age at fledging ± 1 day	276.8 ± 12.4 (262–301)	29	280.7 ± 11.1 (265–309)	31	277.6 ± 12.0 (255–309)	64
Time for primary growth (days)	150.8 ± 14.5 (129–186)	27	152.6 ± 11.7 (133–185)	31	151.3 ± 11.8 (129–186)	62

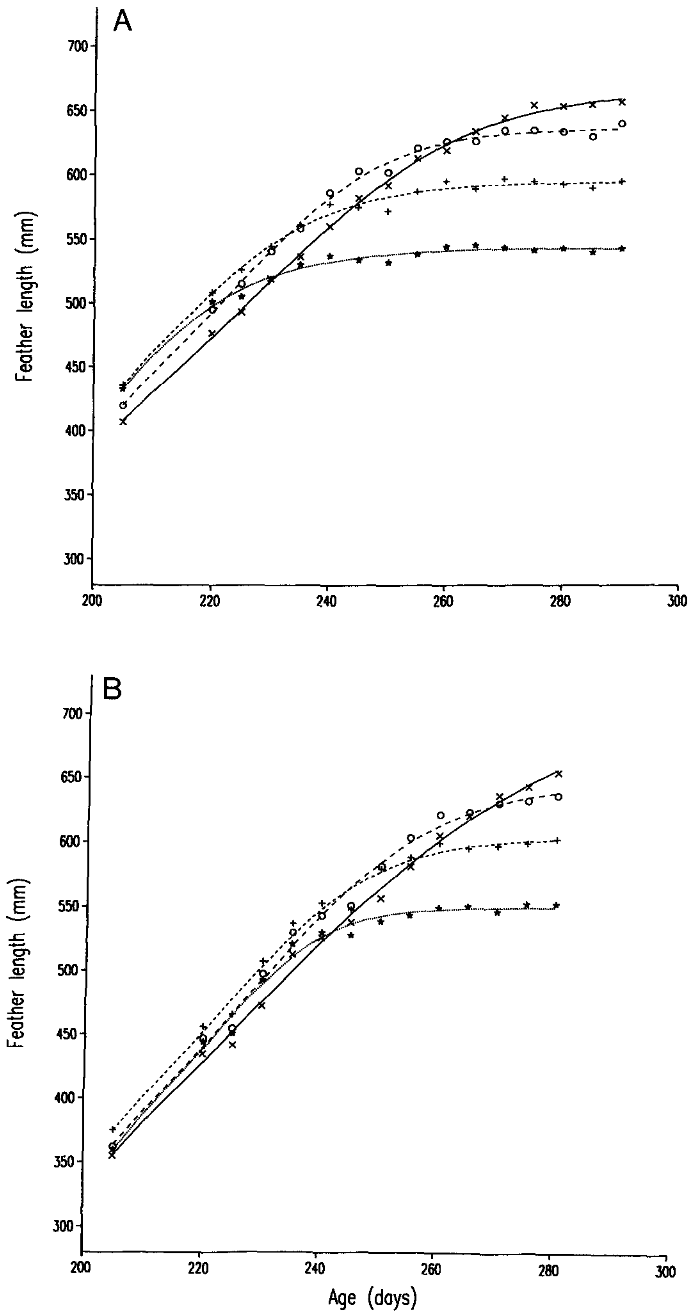

FIGURE 2. Typical feather growth curves for (A) male (B) female Wandering Albatross chicks using the Schnute model. (x = p10, o = p9, + = p8, * = p7).

maximum growth rate was attained, maximum growth rate or relative growth rate between each adjacent primary for either sex (male: $F_{3,9}$ = 0.21–1.67, female: $F_{3,11}$ = 0.21–1.45, $P > 0.05$), nor between sexes ($F_{1,26}$ = 0.45–0.98, $P > 0.20$). Primary nine had the greatest maximum growth rate of any feather (4.7–4.8 mm day^{-1}), which may be explained by its relatively long length at

TABLE 2. Mean ± SD age at maximum growth (days), maximum growth rates (mm day^{-1}), and relative growth rate (day^{-1}) for primaries 7–10 of Wandering Albatross chicks using the Schnute growth model. Relative growth rate is the fractional change in size per unit time.

Parameter	Sex	p10	p9	p8	p7
Age at maximum growth rate	Male	230 ± 10	225 ± 5	213 ± 10	213 ± 8
	Female	228 ± 7	224 ± 5	214 ± 9	213 ± 8
Maximum growth rate	Male	4.54 ± 0.27	4.71 ± 0.41	4.40 ± 0.69	3.87 ± 1.32
	Female	4.61 ± 0.34	4.83 ± 0.45	4.57 ± 0.64	4.02 ± 1.09
Relative growth rate	Male	0.0091 ± 0.0014	0.0093 ± 0.0016	0.0094 ± 0.0026	0.0082 ± 0.0034
	Female	0.0100 ± 0.0021	0.0103 ± 0.0019	0.0099 ± 0.0021	0.0097 ± 0.0033

fledging (96% of p10) but the shorter time during which this feather is growing. The maximum growth rate of p7 may have been greater prior to the beginning of the measurements as p7 was closer to its asymptotic value than the other primaries when measurements began (Fig. 2A and 2B). Relative growth rate was consistent across primaries (males: 0.009 day^{-1}, females: 0.010 day^{-1}) and the differences between sexes were not significant (Fig. 3; Table 3). Primary 10 was the longest primary on fledging and was still growing at 0.5 mm day^{-1} with a relative growth of 0.0008 day^{-1}. Primaries seven and eight had stopped growing and p9 was growing slowly at 0.1 mm day^{-1}. Each primary was significantly smaller ($F_{1,26}$ = 5.08–7.60 $P < 0.05$) for female chicks on fledging when compared to male chicks, but growth rates ($F_{1,26}$ = 0.01–0.76, $P >$ 0.30) and relative growth rates ($F_{1,26}$ = 0.02–0.69, $P > 0.40$) were not.

PATTERN OF GROWTH

The pattern of growth of primaries 7–10 is shown in Figure 4. For each age, measurements were categorized according to the length of each primary. There is a clear trend in the pattern of growth of primaries from 8 > 7 > 9 > 10 (35% of birds) or 8 > 9 > 7 > 10 (29%) at 205 days of age through 9 > 8 > 10 > 7 (34%) or 9 > 10 > 8 > 7 (37%) at around 245 days of age before reaching 10 > 9 > 8 > 7 at least 10 days before fledging (Fig. 4). There was some variation between individual chicks in how this pattern was attained, but for 61 of the 64 chicks the growth followed the sequence: 7 > 8 > 9 > 10 to 8 > 7 > 9 > 10 to 8 > 9 > 7 > 10, then predominately either 9 > 8 > 7 > 10 (25%) or 8 > 9 > 10 > 7 (34%), all chicks then continuing 9 > 8 > 10 > 7 to 9 > 10 > 8 > 7 and finally 10 > 9 > 8 > 7. From this two main growth patterns are apparent: (1) p9 > p8 before p10 > p7 or (2) p10 > p7 before p9 > p8.

MASS OF CHICKS AND GROWTH OF PRIMARIES

Correlations between the linear scaling measure, cube root of chick mass at 145 days and 250 days, and growth rates and timing were calculated and corrected for multiple comparisons using the Bonferroni method (Sokal and Rohlf 1995). There was a significant correlation between mass at 145 days and maximum growth rate for p7 ($r^2 = 0.27$, $P < 0.01$) but not for p8,

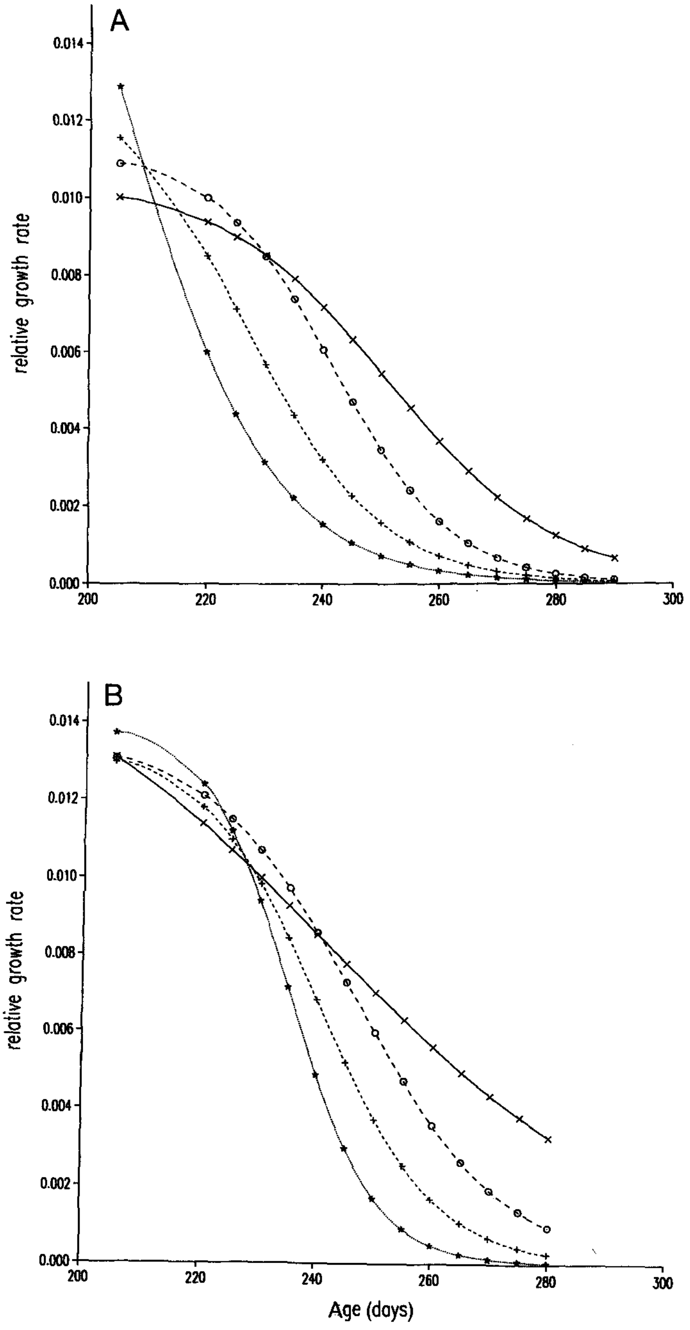

FIGURE 3. Typical relative growth rates (day $^{-1}$) for primaries p7–p10 for (A) male and (B) female Wandering Albatross chicks. (x = p10, o = p9, + = p8, * = p7).

TABLE 3. Mean ± SD asymptotic length (Y_2; mm), growth rate (mm day^{-1}), and relative growth rate × 10^3 (day^{-1}) of primaries at fledging for male (n = 13) and female (n = 15) Wandering Albatross chicks.

Parameter	Sex	p10	p9	p8	p7
Y_2	Male	692.2 ± 16.7	668.0 ± 15.5	627.0 ± 14.4	575.9 ± 12.7
	Female	677.5 ± 17.7	653.5 ± 14.2	612.9 ± 14.4	561.8 ± 14.2
Growth rate	Male	0.52 ± 0.54	0.10 ± 0.12	0.02 ± 0.02	0.009 ± 0.010
	Female	0.59 ± 0.60	0.11 ± 0.12	0.02 ± 0.03	0.006 ± 0.010
Relative growth rate	Male	0.76 ± 0.79	0.15 ± 0.18	0.03 ± 0.03	0.016 ± 0.000
	Female	0.87 ± 0.89	0.16 ± 0.19	0.03 ± 0.05	0.011 ± 0.000

p9, or p10. There was no such correlation between mass and relative growth rate or for any other parameter and mass at 250 days of age. There also was a significant correlation between chick mass at 145 days and age at fledging (r^2 = 0.19, $P < 0.01$) but not between mass at 250 days old and age at fledging (r^2 = 0.03, $P >$ 0.05). Maximum growth rates of p7 and p8 also were significantly correlated to mass at 145 days, but not p9 or p10. As p7 and p8 reach maximum growth rates at a younger age than p9 and p10, the mass at 145 days is more likely to influence these rates compared with primaries which grow later. The heavier the chick at 145 days old, the younger the chick will tend to fledge. The correlation between age at which primaries emerged and mass at 145 days also was significant (r^2 = 0.19, $P < 0.01$), with primaries emerging at a younger age in heavier chicks.

DISCUSSION

There was considerable variation in the age, between 115 and 175 days old, when primaries first emerged, which was correlated with the mass of the chick at the start of this period. Once primaries started to grow, it took an average of 151–153 days for full development, around one half of the chick rearing period, and chicks did not fledge until the growth of p10 had reached its asymptote. Lighter chicks, whose primaries emerged later than heavier chicks, fledged proportionately later, but not before completing the full period required for wing and primary growth. Feather emergence data were collected only every 15 days and only one bird fledged less than 150 ± 15 days after emergence of primaries. The actual date of fledging will depend on a number of other factors such as wind conditions and body mass, but most chicks fledged as soon as their wings were fully developed, suggesting this may have been an important limiting factor. There was, however, no significant difference in fledging age between male and female chicks, although the maximum length of female primaries was significantly smaller than males. Feathers emerged at the same age, and growth rates were similar. If time needed to fully

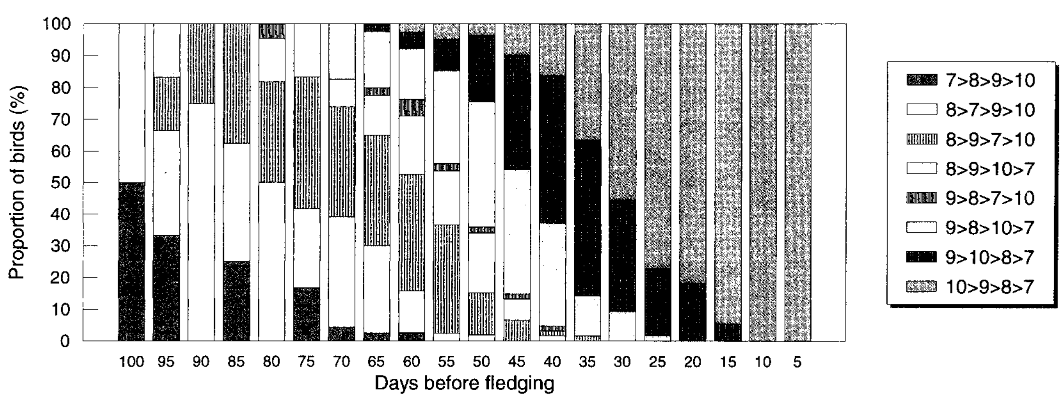

FIGURE 4. Pattern of primary growth of Wandering Albatross chicks. (7 > 8 > 9 means p7 is longer than p8, which is longer than p9).

develop wing feathers limits the age at which chicks can fledge, we would have expected female chicks to fledge around 4 days younger (using mean wing length and maximum growth rates) than males as they have less feather to grow. In fact, they fledged when 4 days older. Growth curves were similar for both sexes, which suggests that other factors, operating differentially on each sex, may influence fledging date.

GROWTH RATES

Wing and primary growth in albatross chicks followed a sigmoid curve, typical of logistic-type growth curves (Brown and Rothery 1993). The rate of wing growth was slow at the beginning of chick development reaching a linear increase about half way (145 days) through the chick rearing period (~ 280 days). Reid et al. (in press) suggested that this is when albatross chicks preferentially allocate incoming resources to growing flight feathers. Procellariiformes have relatively long wings and flight feathers for birds (Adams et al. 1996), but Wandering Albatross growth rates (4.4–4.8 mm day^{-1} for a wing of overall length 655–718 mm) are relatively low compared to birds of comparable size, for example: Mute Swan (*Cygnus olor*) with a wing length of 535–628 mm have growth rates 8.3–9.0 mm day^{-1}; Siberian Crane (*Grus leucogeranus*) wing length 538–625 mm, growth rate 9.0 mm day^{-1}; Lammergeier (*Gypaetus barbatus*) wing length 695–756 mm, growth rate 6.6 mm day^{-1}; Wattled Crane (*Bugeranus carunculatus*) wing length 613—717 mm, growth rate 9.0–13.0 mm day^{-1} (Prevost 1983). The relatively low growth rates for Wandering Albatrosses are most likely due to chicks receiving only infrequent meals (about one every 3 days, with occasional fasts of 10 or more days; Tickell 1968) of squid and some fish (Rodhouse et al. 1987, Croxall et al. 1988) which are of relatively low energy content.

There was no difference in the maximum growth rate of each primary which grew at around 4.5 mm day^{-1}. This rate falls in the middle of the ranges presented by Prevost (1983) who reviewed growth rates in a variety of species. Species with long wings rarely had growth rates much above 10 mm day^{-1}, whereas small species such as the White Wagtail (*Motacilla alba*) have growth rates of between 4 and 5 mm day^{-1}. Langston and Rohwer (1996) consistently recorded growth rates in molting adult Laysan Albatrosses (*Diomedea immutabilis*) of around 5 mm day^{-1} which, in their opinion, suggested that feather growth was limited physiologically. This conclusion was based on the examination of growth bands laid down in growing feathers, with the assumption that two light-dark bands were laid down each 24-hr period. Growth rates reported here are consistent with their findings, as maximum growth rates of all four primaries measured were similar despite differences in asymptotic feather length. Feather growth rates of developing albatross chicks also are of the same magnitude as molting adults, which further suggests physiological limitations and supports the assumptions of Langston and Rohwer (1996) regarding growth bands.

Wandering Albatrosses have 10 primaries and 32 secondaries in each wing. Using mean feather lengths presented here and assuming lengths of 500 mm for the six inner primaries and 150 mm for secondaries, chicks have to grow around 20.6 m of feathers before fledging. This growth is completed in about 150 days. Thus albatross chicks are growing between 137 mm and 138 mm of flight feathers per day during the second half of development.

PATTERN OF GROWTH

This study shows that primaries do not all grow at the same rate at the same time. They start growing in a particular sequence, have overlapping periods of linear growth, and eventually reach their asymptote at different times. The innermost primaries grow first, while the outermost continue to grow right up to fledging. The pattern of growth is very consistent and on fledging all feather lengths were in the order 10 > 9 > 8 > 7. In some cases, this order was not achieved until 10 days before fledging, and around 50% of birds were only 30 days off fledging before p10 became the longest primary. Wandering Albatrosses, unlike the smaller albatross species which stay in their nest throughout development, are highly mobile at an early age, an adaptation to breeding during the winter in order to avoid drifting snow which may cover their nests (Tickell and Pinder 1972). Young albatrosses also spend considerable time exercising their wings to develop their pectoral muscles prior to their first flight. During these periods of travel and pre-fledging exercise, chicks may abrade their wing feathers on contact with the ground. The outermost primaries receive more wear than other flight feathers (Langston and Rohwer 1995) and all albatrosses so far studied prioritize the replacement of the outermost primaries (Harris 1973, Furness 1988, Prince et al. 1993). Given that Wandering Albatrosses retain their three outer primaries for 3 years and the other primaries for 4 years after fledging (Prince et al. 1997), the observed pattern of growth seems likely to be an adaptation to protect these outermost primaries from damage prior to fledging.

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