

FACTORS AFFECTING PRIMARY MOLT IN THE GRAY-HEADED ALBATROSS¹

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Abstract. The mean number of primaries molted by Gray-headed Albatrosses (*Diomedea chrysostoma*) varied with year and previous breeding experience independently, but was not related to individual reproductive success over a longer period. Within each category of breeding experience, birds renewed fewer primaries during the "poor" year of 1994, when subsequent reproductive success was only 27%, than in 1993 when subsequent reproductive success was 57%. Inspection of individual feathers indicated that the outer primaries were least likely to be renewed during the period of stress. Within each year, birds that failed in their breeding attempt during the previous year renewed fewer feathers than those which reared a chick two years previously, a difference which was probably partly related to the time available for molting. In 1994 only, the date of failure in the previous year was inversely related to the number of primaries molted by males. The arrival mass of males was positively correlated with the number of primaries molted in two out of four seasons. Males and females molted similar numbers of primaries.

Key words: arrival mass, breeding experience, *Diomedea chrysostoma*, Gray-headed Albatross, primary molt, South Georgia, year effects.

INTRODUCTION

As in most seabirds, the process of feather molt in albatrosses occurs during the pelagic phase of their life. The separation of breeding and molting has been interpreted as evidence for the avoidance of additional energetic demands which would be incompatible with chick rearing (Payne 1972). Albatrosses have evolved complex molt patterns (Prince et al. 1993, Langston and Rohwer 1995, Prince et al. 1997) that reflect the tradeoff between the frequent replacement of the remiges, necessary to maintain efficient flight, and the costs of feather replacement which include feather growth and flight efficiency during the molt. In addition, the long chick rearing periods of most species impose a time constraint on the molt schedules of birds which successfully rear a chick or fail late in the chick rearing period.

Studies of albatross molt have related previous breeding performance, age, experience, sex, mass, geographical race, and parasite load with the number of primaries replaced, although the balance of these factors varies according to species. In annual breeding species such as Waved Albatross *Diomedea irrorata*, Yellow-nosed Al-

batross *D. chlororhynchos*, and Black-browed Albatross *D. melanophris*, birds that successfully fledged a chick in the previous season retained significantly more old primaries than those which failed (Harris 1973, Furness 1988, Prince et al. 1993). In Wandering Albatross *D. exulans* and Gray-headed Albatross *D. chrysostoma*, which breed biennially following chick fledging (Tickell and Pinder 1967, Tickell 1968), successful breeders molted significantly more primaries than failed birds (Weimerskirch 1991, Prince et al. 1993), although in the Wandering Albatross this relationship was true only for females (Weimerskirch 1991). In Yellow-nosed, Gray-headed, and Black-browed Albatrosses there were no differences between the sexes in the numbers of primaries molted (Furness 1988, Prince et al. 1993). Wandering Albatrosses of both sexes breeding for the first time molted fewer primaries than experienced breeders, and males which had bred once successfully renewed fewer primaries than experienced males (Weimerskirch 1991, Prince et al. 1997). Laysan Albatrosses *D. immutabilis* that were infected with the nematode parasite *Seuratia* spp. molted fewer primaries than uninfected individuals (Langston and Hillgarth 1995).

During 1992/1993-1994/1995, we recorded data on the number and identity of primary feathers molted between breeding seasons in

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Gray-headed Albatrosses of known breeding experience and current breeding success as part of a study of breeding performance of these birds. In addition, these three years were characterized by considerable variation in overall breeding performance (expressed as % chicks reared from eggs laid) with 1992/1993 (57%) one of the best years and 1993/1994 (27%) and 1994/1995 (18%) two of the poorest years of the 21 years of continuous records from Bird Island (overall mean of 39%; Prince et al. 1994, Croxall et al., in press). There also was evidence of exceptional variation in environmental conditions. Whereas 1993 was apparently normal for food availability and weather during the breeding season, 1994 was normal for weather but there was greatly reduced availability of Antarctic krill *Euphausia superba*, and substantial changes in the abundance of other prey (Boyd et al. 1995, Brierley and Watkins 1996); 1995 was normal for prey but cold conditions prevailed during the arrival and incubation period of albatrosses, causing widespread breeding failure.

In this paper we examine relationships between primary replacement and (a) interannual variation in environmental conditions, (b) subsequent reproductive performance, including the utility of recent molt as a predictor of forthcoming reproductive performance, (c) individual bird quality, as measured by reproductive history, and (d) body condition as measured by mass on arrival at the breeding colony.

METHODS

The study was carried out at Bird Island, South Georgia (54°01'S, 38°03'W) during the 1993–1995 austral summers (each austral summer is referred to by the calendar year in which the chicks fledge, e.g., 1994 refers to the 1993–1994 season); some additional data on arrival mass were collected at the start of the 1996 season. Gray-headed Albatrosses have been monitored annually at Bird Island since 1976 and all birds in the study had either been ringed as chicks or breeding adults (Prince 1985, Prince et al. 1994). Birds were sexed by observations of copulation, behavior or size differences when both members of the pair were together (Prince et al. 1994). Some individuals were examined for primary replacement in successive years; to avoid problems of non-independence, these data only were used once in the main analysis, the year being chosen randomly.

We used two measures of breeding experience: (a) the outcome of the previous breeding attempt, comprising birds which either failed during the previous season, or successfully fledged a chick two seasons previously, and (b) an assessment of the quality of a bird, using breeding histories to assign birds to either "top" or "bottom" groups. To allocate individuals into a group, we included only birds with a minimum of five breeding attempts in which the outcome was known. If 70% or more of these attempts resulted in rearing a chick to fledging, birds were classified in the top group; conversely, birds with 70% or more failures were classified in the bottom group. Previous breeding attempt and group are not wholly independent, because the selection criteria we used to assign birds to a group include the last breeding outcome, so molt analyses were performed separately on each. Because of small sample size, birds breeding for the first time were excluded from the analyses as were their partners, regardless of their experience. During the last two weeks of September, the colony was checked each day and birds were normally weighed within 5 days of arrival (range 0–13 days, 67–100% within 5 days, $n = 50$), although in 1994 some were weighed later (range 0–16 days, 50% were weighed within 10 days, $n = 11$). Only birds which were in their first spell ashore were used in the arrival mass analyses, and those with an absence of more than a day were excluded. Because males arrive one week before females (Tickell and Pinder 1975) and females only remain at the colony for 1–2 days at this time (Asheimer et al. 1985), unsexed birds were assumed to be males. Of 27 known-sex birds that were weighed, only 2 (both captured in 1993) were females. In 1993, 1994, and 1996, birds were weighed using a bag and Pesola spring balance accurate to ± 100 g, and in 1995 using a fiberglass weighing platform incorporating a load cell, which fitted over the nest (Francis Scientific Instruments, 160 Caxton End, Bourne, Cambridge, UK). Arrival mass was corrected for the length of time the birds had spent ashore following Prince et al. (1981), using the formula:

$$W_t = W_0 e^{-kt}$$

where W_t is the mass (kg) at time t (days), W_0 is the mass (kg) at arrival, and k is the proportion of mass lost per day, which for Gray-headed

TABLE 1. Number of primaries renewed between successive breeding seasons in male, female, unsexed and all Gray-headed Albatrosses combined. Values are mean \pm SE, sample sizes in parentheses. Differences between sexes were not significant: 1993 $F_{1,44} = 0.1$; 1994 $F_{1,20} = 1.0$; 1995 $F_{1,57} = 0.4$.

Year	Males	Females	Unsexed	Combined
1993	5.6 \pm 0.46 (21)	5.6 \pm 0.36 (25)	6.1 \pm 0.28 (32)	5.8 \pm 0.20 (78)
1994	4.5 \pm 0.45 (16)	3.7 \pm 0.65 (6)	4.0 \pm 0.35 (27)	4.1 \pm 0.25 (49)
1995	5.5 \pm 0.37 (30)	5.1 \pm 0.45 (29)	5.6 \pm 0.36 (22)	5.4 \pm 0.23 (81)

Albatrosses was estimated to lie in the range 0.010–0.012 kg day⁻¹ (Prince et al. 1981); we used $k = 0.011$ kg day⁻¹, the midpoint of this range.

The number of new and 1-year-old primaries were determined on incubating birds using the methods and criteria of Prince et al. (1993). Primaries were numbered from inner (P1) to outer (P10), and as Prince et al. (1993) found no significant differences in molt patterns between wings, we only used data from the right wing. The distribution of new primaries was not significantly different from normal (Kolmogorov-Smirnov goodness-of-fit: $D = 0.11$, $n = 208$, $P > 0.05$) and parametric statistics were used in analyses of numbers of primaries renewed. The data were analyzed using SAS statistical software (SAS Institute 1990), and are presented as means \pm SE.

RESULTS

Male and female Gray-headed Albatrosses did not molt significantly different numbers of primaries in any year (Table 1). In 1994, there were significant differences within pairs in the mean number of primaries molted (paired t -test: $t_7 = 3.7$, $P < 0.01$), but not in 1993 or 1995. In subsequent analyses, the data for males, females, and unsexed birds were pooled.

Considering the effects of year, previous breeding outcome, and bird quality jointly, the number of primaries replaced was significantly related to year only ($F_{11,125} = 3.5$, $P < 0.001$), but there was appreciable, although not significant, interaction between bird quality effects and previous breeding outcome, probably arising because these two effects were not wholly independent as indicated above. When these effects were analyzed separately, the mean number of primaries that a bird renewed was significantly related to year ($F_{2,192} = 10.3$, $P < 0.001$) and

previous breeding outcome ($F_{1,192} = 13.3$, $P < 0.001$), and these effects were independent of each other (Fig. 1). Analysis of bird quality effects and year indicated that there were no significant effects of bird quality on the mean number of primaries renewed. As a further indication of the lack of a relationship between bird quality and primary replacement, 29 birds in which the assessment of bird quality was contrary to the previous breeding outcome (i.e., "top" birds which failed and "bottom" birds which fledged chicks), showed no significant relationship between the numbers of primaries replaced and bird quality ($F_{1,23} = 1.0$), but still showed between-year differences ($F_{2,23} = 3.4$, $P < 0.05$).

Considering the location of primary renewal among years, previously successful breeders renewed significantly fewer primaries at P5–7 and P10 in 1994 compared with the other two years (Fig. 2). Birds which had previously failed renewed significantly fewer feathers at P6–7 and P9–10 (Fig. 2). With respect to previous breeding outcome, in 1993 previously failed breeders renewed significantly fewer feathers at P4–5 than successful birds, in 1994 failed breeders renewed significantly fewer P4 but more P7, and in 1995 failed breeders renewed significantly fewer P1–3 and P6–7 (Fig. 2). Within years there were no significant differences between previously successful or failed breeders in the proportions of birds with new P8–10 (Fig. 2). However, comparing between years, a significantly lower proportion of birds renewed the outer three primaries in 1994 in both previously successful (P10) and failed breeders (P9–10) (Fig. 2).

The date of failure in the previous year was inversely related to the number of primaries renewed (i.e., the later birds failed the fewer primaries they renewed, combining egg and chick failures) in 1994 ($r_9 = -0.64$, $P < 0.05$; Fig. 3)

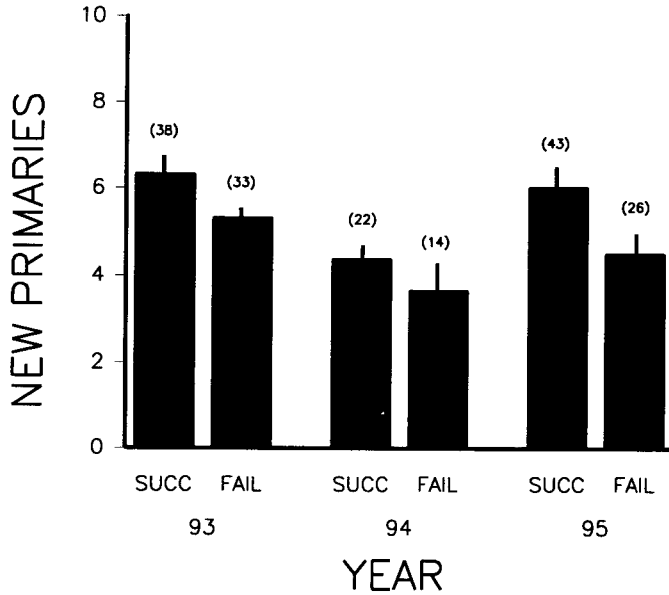


FIGURE 1. The effect of year and previous breeding outcome on the number of primaries renewed in Gray-headed Albatrosses. Values are means + SE, number of birds in parentheses, breeding outcome: succ = successful, fail = failed.

but not in the other years (1993: $r_{31} = 0.20$, $P > 0.20$; 1995: $r_{23} = -0.17$, $P > 0.20$). The stage at which the pair failed (egg or chick) did not significantly affect subsequent primary renewal (1993: no chick failure data available; 1994: egg $n = 4$, $\bar{x} = 3.8 \pm 1.1$, chick $n = 7$, $\bar{x} = 3.4 \pm 0.7$; 1995: egg $n = 17$, $\bar{x} = 4.4 \pm 0.6$, chick $n = 8$, $\bar{x} = 4.1 \pm 0.4$, all $P > 0.05$). Although there was a thirteen day spread of chick fledging in 1993, there was no relationship between the date of fledging a chick and the number of primaries replaced by 1995 ($r_{12} = 0.18$, $P > 0.50$).

There were significant positive relationships for males and unsexed birds combined between primary renewal and arrival mass in 1994 and 1995 (Fig. 4), but not in 1993 or 1996. For males only, none of the relationships were statistically significant, although again in 1994 and 1995, there was an appreciable correlation (1993: $r_2 = 0.17$, $P > 0.5$; 1994: $r_5 = 0.69$, $P > 0.05$; 1995: $r_7 = 0.64$, $P > 0.05$; 1995: $r_{17} = 0.03$, $P > 0.5$). There was significant variation in mean arrival mass between years ($F_{3,93} = 6.4$, $P = 0.001$), being highest in 1994 ($\bar{x} = 4.82 \pm 0.1$ kg, $n = 19$) and lowest in 1995 ($\bar{x} = 4.44 \pm 0.1$ kg, $n = 33$). The date of arrival was not significantly related to the number of primaries renewed, except in males during 1995 when

there was a significant inverse correlation ($r_{27} = -0.40$, $P < 0.05$), although the median date of male arrival (20 September: range 15–27 September) varied significantly between years (Kruskal-Wallis $H_3 = 20.1$, $P < 0.001$), being earliest in 1995. The overall breeding performance in the current year was not related to the number of primaries previously molted (Table 2), nor was there any significant relationship between the primary renewal and the subsequent date of failure (1993: $r_{12} = -0.17$, $P > 0.5$; 1994: $r_{25} = -0.18$, $P > 0.2$; 1995: $r_{58} = 0.0$, $P > 0.5$) or fledging (1993: $r_{57} = -0.16$, $P > 0.2$; 1994: $r_6 = -0.06$, $P > 0.5$; 1995: $r_{12} = 0.05$, $P > 0.5$) in any year. In pairs which failed, there was no significant relationship between primary renewal and the stage of failure (i.e., incubation or chick rearing) in any year.

A few individuals were molt scored in successive years after failure, or in 1993 and again in 1995 following successful breeding in 1993. For birds which bred successfully, there was no relationship between the number of new primaries in 1993 and the number renewed in the 1995 season ($r_7 = 0.0$, $P > 0.5$). Birds which failed in 1993 and returned in 1994 showed no relationship between the numbers of primaries renewed in either year ($r_6 = 0.23$, $P > 0.5$). How-

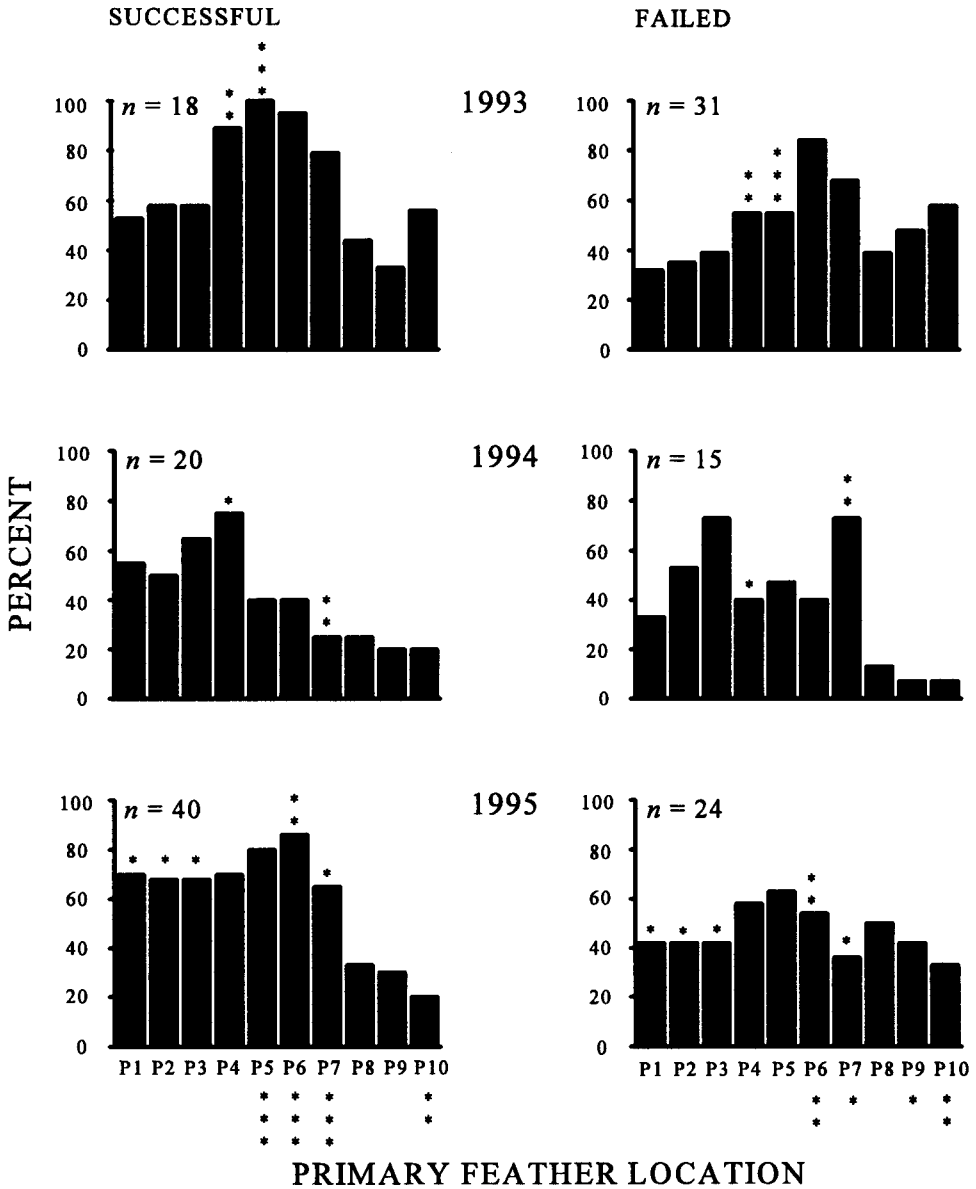


FIGURE 2. Percentage of new primaries at each feather location in relation to year and previous breeding outcome. Significant differences are starred: between years along x-axis; within each year on histograms. χ^2 test of proportion of new feathers at each primary location, significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n = number of birds.

ever, birds which failed in 1994 and returned in 1995 showed a significant inverse relationship between the number of primaries renewed in 1994 and in 1995, the more primaries replaced in 1994, the fewer replaced in the following year ($r_5 = -0.78$, $P < 0.05$).

DISCUSSION

The number of primaries renewed by breeding Gray-headed Albatrosses was dependent upon both the year of molt and the outcome of the previous breeding attempt. Because molt takes place outside the breeding season, when the

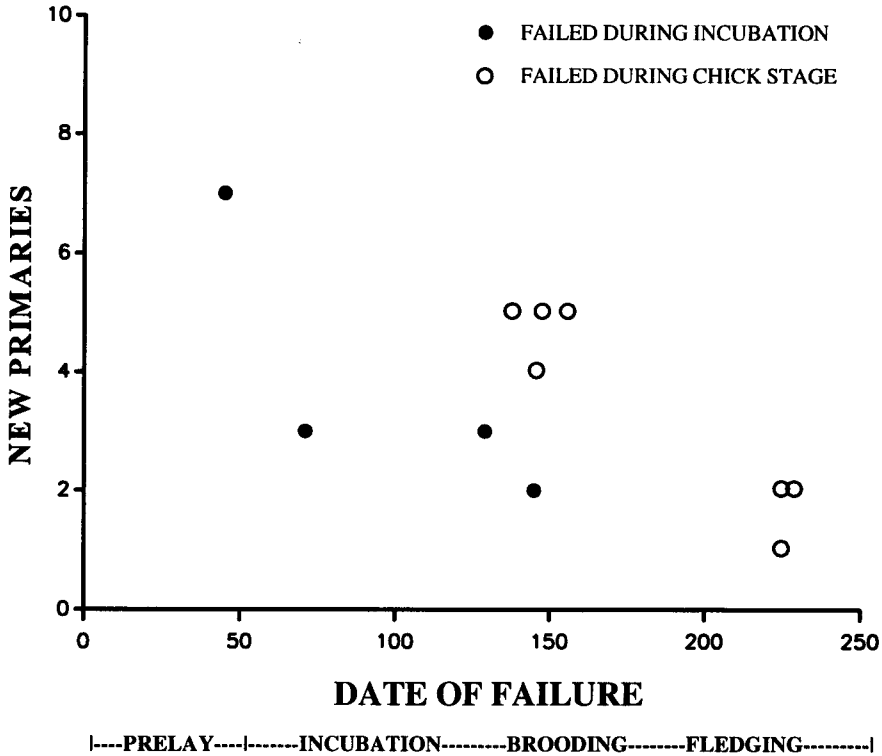


FIGURE 3. The effect of the date of failure in 1994 on the number of primaries renewed in 1995, day 1 = 01 September, $y = 6.6 - 0.02x$, $r_s = -0.64$, $P < 0.05$. Regression relates to the overall relationship. Stage of breeding cycle from Prince et al. (1994).

birds next return to the colonies the number of new feathers they possess will reflect the time available for molt and conditions they experienced during the preceding winter. Birds arriving at the colony at the start of the 1994 breeding season had molted up to two primaries fewer than in either of the other years, suggesting that during the 1993 winter birds experienced greater constraints. Paradoxically the mean arrival mass of males was highest at the start of the 1994 season. This may be because individuals which failed to attain some threshold mass prior to breeding simply did not return to the colonies and therefore could not be sampled. Additionally, birds that did return may have accumulated mass at the expense of molting more primaries. In 1994, there were significant differences within pairs, and in five pairs where the sexes were known, three males molted fewer primaries. In the Wandering Albatross, experienced breeders which did not breed during the current season had significantly lower masses than those which did (Weimerskirch 1992), and a similar effect

was found in Gray-headed Albatrosses although this was not statistically significant due to small sample sizes (Cobley et al., unpubl. data). Langston and Hillgarth (1995) have shown that primary replacement in Laysan Albatrosses is related to parasite load, more heavily parasitized individuals renewed fewer feathers than those with lower parasite loads. Although we have no information on the parasite loads of Gray-headed Albatrosses, the renewal of different numbers of primaries by the same individuals in 1994 and 1995 suggests that environmental conditions were more influential.

During the study period, there was substantial variation in marine productivity around South Georgia as evidenced by the reproductive performance of several higher predator species including Gray-headed and Black-browed Albatrosses, Gentoo Penguins (*Pygoscelis papua*), and Antarctic fur seals (*Arctocephalus gazella*) (Boyd et al. 1995, Veit and Prince, in press, British Antarctic Survey records), and acoustic target surveys of the surrounding shelf-break re-

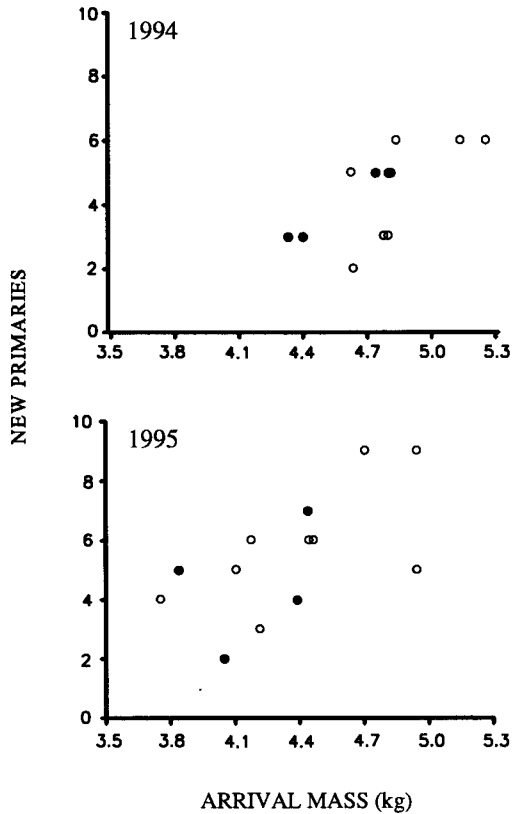


FIGURE 4. Relationship between mean number of primaries renewed and subsequent arrival mass for Gray-headed Albatrosses in 1994 and 1995. Males = solid circles, unsexed = open circles. 1994: $y = 3.92x - 14.3$, $r_{10} = 0.71$, $P = 0.01$; 1995: $y = 3.44x - 9.5$, $r_{11} = 0.62$, $P < 0.05$. Regressions relate to all birds combined.

gion (Brierley and Watkins 1996). In 1993, the breeding success of Gray-headed Albatrosses was 57%, one of the highest values recorded in 21 years of monitoring, whereas during 1994, it was only 27%, among the lowest recorded values (Prince et al. 1994, Croxall et al., in press.)

In these years the number of feathers replaced during the winter was related to subsequent breeding performance in that more extensive molt occurred during conditions which favored successful breeding.

The movements of adult Gray-headed Albatrosses outside the breeding season are poorly known, although the little evidence that exists suggests that birds from the South Georgia population are pelagic, remaining at higher latitudes, possibly around frontal systems (Tickell and Pinder 1967, Prince 1980, Prince et al., in press). This is consistent with food availability being a common underlying factor affecting both feather renewal and chick rearing, and suggests that primary molt could be a predictor of subsequent breeding success, where breeding success is primarily affected by biotic factors operating locally and/or regionally.

During the last year of the study, 1995, overall breeding success was again very low (18%), yet the level of feather renewal was more similar to the highly productive 1993 season. However, in 1995, heavy snowfall during September and October severely disrupted nest building and egg-laying, resulting in a high rate of loss of nests during early incubation. Those few pairs which managed to hatch chicks showed rates of fledging success similar to 1993 (1993: 75%, $n = 275$ chicks; 1995: 67%, $n = 84$ chicks), suggesting that food availability was comparable and adequate, at least during chick rearing. There is little information on interannual variation in molt in other seabirds, although in the tropical Black Noddy (*Anous tenuirostris*) the start of primary molt was delayed and the rate of feather renewal slower in one season when a reduction in food availability was suspected (Ashmole 1962). In the current study, the number of primaries an individual albatross replaced did not affect its breeding outcome in the fol-

TABLE 2. Mean number of primaries renewed by Gray-headed Albatrosses in relation to breeding performance during the current year. Values are mean \pm SE, n = number of observations, successful vs. failed: 1993 $F_{1,76} = 0.47$; 1994 $F_{1,41} = 0.91$; 1995 $F_{1,75} = 1.70$; all $P > 0.2$.

Current outcome	Year of Molt					
	1993		1994		1995	
	New primaries	n	New primaries	n	New primaries	n
Successful	5.7 \pm 0.21	61	4.8 \pm 0.64	9	5.9 \pm 0.60	15
Failed	6.1 \pm 0.55	17	4.1 \pm 0.30	34	5.2 \pm 0.25	62

lowing year, possibly because birds which fail to undertake adequate feather renewal and/or to acquire sufficient reserves for the breeding season do not attempt to breed in that year. Nevertheless there are indications that recording molt patterns in albatrosses could provide important data on potential resource availability in winter, complementing similar data inferred from breeding performance in the following summer. Whether feather renewal in winter will prove a realistic predictor of breeding performance will require additional data.

Within each year, Gray-headed Albatrosses that had bred successfully two years earlier renewed more primaries in the previous winter than those that had failed one year earlier. A similar effect of previous breeding success has been found in the biennially breeding Wandering Albatross where successful females (but not males) replaced more primaries than failed birds (Weimerskirch 1991). This contrasts with the situation in successful birds of annual breeding species, reflecting the reduced time available to them for molting (successful: 3–6 months; failed: 6–12 months) compared with the biennial breeders (successful: 12 and 16 months for Wandering and Gray-headed Albatross, respectively; failed: 6–12 months) (reviewed in Prince et al. 1993).

In our study, only feathers that were molted during the previous winter could be considered. Despite the equal time period, previously successful breeders replaced more feathers than previously failed breeders. If the rate at which individual feathers grow is constant, as in Laysan and Black-footed Albatrosses (Langston and Rohwer 1995), then successful breeders must be replacing more feathers simultaneously than failed breeders, suggesting that they are in better condition. Gray-headed Albatrosses which breed successfully are known to replace only three primaries (usually the innermost, shorter feathers) in the five months after fledging a chick and then replace eight primaries in the following year (including the outer, longest feathers), sometimes including feathers less than one year old (Prince et al. 1993).

Except in 1994, the number of primaries molted by failed breeders was similar to the average of 4.7 found by Prince et al. (1993), whereas successful breeders molted fewer than the 8.4 previously reported in the 1989–1990 study (Prince et al. 1993). This may be because in

winter 1989, birds renewed fewer primaries in the months immediately after chick rearing (and only 2 out of 30 had replaced any of the outer three feathers), deferring the bulk of feather renewal until the following year instead. During the 1989–1990 breeding season, the overall breeding success was only 29%, whereas the following year it was 50% (Prince et al. 1994); thus birds that had just fledged a chick in 1989 may have been responding to reduced food availability by waiting until the following year to molt more primaries.

The reduction in the number of primaries renewed in 1994 was not spread evenly across the wing. Primaries in the outer half of the wing were less likely to be renewed than other feathers (Fig. 2). Fewer outer primaries were renewed in 1995 also, especially among successful birds (i.e., from the 1993 season), which would have remained at sea throughout 1994. Because the outer primaries are the longest in the wing, their renewal requires more time than the shorter inner feathers; this is likely to be an important constraint on birds which fail late in the season. However, birds which had bred successfully two years previously also renewed fewer outer primaries during 1994 compared with 1993, suggesting that additional constraints were involved. The outermost primaries are subject to more wear than inner primaries and there is presumably a tradeoff between feather condition, resource availability, and the time available for renewal.

In the “poor” year of 1994, the timing of nest failure was significantly inversely related to the extent of primary renewal subsequently, again indicating that time constrained birds which failed late. In the other years, a weak effect was discernible among the latest failed breeders, and it may be that the relative abundance of late failures in 1994 compared to other years (Prince et al. 1994) highlighted the relationship. This also may explain the absence of a relationship between fail date and molt in other studies (Weimerskirch 1991, Prince et al. 1993); re-analysis of the Prince et al. (1993) data indicated a similar weak trend to those reported here.

The relationship between arrival mass and feather renewal indicated that individuals which had molted more feathers also returned to the colony at a higher mass. This suggests that some individuals were better able to combine feather renewal with acquiring reserves for the onset of

the next breeding season. This correlation was not merely a reflection of previous breeding status because heavy birds were not only those which had previously bred successfully.

The lack of a strong association of bird quality with molt suggests that individual condition, as measured by reproductive performance averaged over at least five years, has little direct influence relative to the conditions prevailing during the molting period. Indirect effects are more likely, because during the previous breeding attempt, birds in the top group tended to have been successful whereas those in the bottom group failed. The similarity in molt between the sexes is consistent with other mollymauk species.

In breeding Wandering Albatrosses, Weimerskirch (1991) found no relationship between the mass of incubating birds and the extent of primary molt, although it was not clear if mass was corrected for the time a bird spent ashore. We found that the association between molt and arrival mass was weaker if birds were weighed in subsequent periods ashore following arrival (Cobley, unpubl. data), probably because individual variation in attendance and foraging patterns obscures the relationship. By the start of incubation, individual variation in mass is likely to mask any relationship with molt, which may explain the absence of a correlation in breeding Wandering Albatrosses.

In addition to providing information on environmental conditions during the previous winter, data on primary molt at the start of the breeding season also may give an advance indication of the conditions likely to prevail subsequently and thereby be a valuable adjunct to data on breeding performance.

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LITERATURE CITED

- ASHMOLE, N. P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 1. General biology. *Ibis* 103:235–273.
- ASTHEIMER, L. B., P. A. PRINCE, AND C. R. GRAU. 1985. Egg formation and the pre-laying period of Black-

- browed and Grey-headed Albatrosses at Bird Island, South Georgia. *Ibis* 127:523–529.
- BOYD, I. L., J. P. CROXALL, N. J. LUNN, AND K. REID. 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *J. Anim. Ecol.* 64:505–518.
- BRIERLEY, A. S., AND J. L. WATKINS. 1996. Acoustic targets at South Georgia and the South Orkney Islands during a season of krill scarcity. *Mar. Ecol. Prog. Ser.* 138:51–61.
- CROXALL, J. P., P. A. PRINCE, P. ROTHERY, AND A. G. WOOD. In press. Population changes in albatrosses at South Georgia. In G. Robertson [ed.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, Australia.
- FURNESS, R. W. 1988. Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed Albatross *Diomedea chlororhynchos*. *J. Zool.* 215:719–727.
- HARRIS, M. P. 1973. The biology of the Waved Albatross *Diomedea irrorata* of Hood Island, Galapagos. *Ibis* 115:483–510.
- LANGSTON, N., AND N. HILLGARTH. 1995. Molt varies with parasites in Laysan Albatrosses. *Proc. R. Soc. Lond. B* 261:239–243.
- LANGSTON, N. E., AND S. ROHWER. 1995. Unusual patterns of incomplete primary molt in Laysan and Black-footed Albatrosses. *Condor* 97:1–19.
- PAYNE, R. B. 1972. Mechanisms and control of molt, p. 104–146. In D. S. Farner and J. R. King [eds.], *Avian biology*. Academic Press, New York.
- PRINCE, P. A. 1980. The food and feeding ecology of Grey-headed Albatross *Diomedea chrysostoma* and Black-browed Albatross *D. melanophris*. *Ibis* 122:476–488.
- PRINCE, P. A. 1985. Population and energetic aspects of the relationships between Black-browed and Gray-headed Albatrosses and the southern ocean marine environment, p. 473–477. In W. R. Siegfried, P. R. Condy, and R. M. Laws [eds.], *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin.
- PRINCE, P. A., J. P. CROXALL, P. N. TRATHAN, AND A. G. WOOD. In press. Foraging distribution of South Georgia albatrosses and relationships with fisheries. In G. Robertson [ed.], *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, Australia.
- PRINCE, P. A., C. RICKETTS, AND G. THOMAS. 1981. Weight loss in incubating albatrosses and its implications for their energy and food requirements. *Condor* 83:238–242.
- PRINCE, P. A., S. RODWELL, M. JONES, AND P. ROTHERY. 1993. Molt in Black-browed and Grey-headed Albatrosses *Diomedea melanophris* and *D. chrysostoma*. *Ibis* 135:121–131.
- PRINCE, P. A., P. ROTHERY, J. P. CROXALL, AND A. G. WOOD. 1994. Population dynamics of Black-browed and Grey-headed Albatrosses *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 136:50–71.
- PRINCE, P. A., H. WEIMERSKIRCH, N. HUIN, AND S. RODWELL. 1997. Molt, maturation of plumage and

- ageing in the Wandering Albatross. *Condor* 99: 58–72.
- SAS INSTITUTE. 1990. SAS/STAT user's guide. Version 6.10. SAS Institute, Inc., Cary, NC.
- TICKELL, W. L. N. 1968. The biology of the great Albatrosses, *Diomedea exulans* and *Diomedea epomophora*, p. 1–55. In O. L. Austin [ed.], Antarctic bird studies. Antarctic Research Series 12. Am. Geophysical Union, Washington, DC.
- TICKELL, W. L. N., AND R. PINDER. 1967. Breeding frequency in the albatrosses *Diomedea melanophris* and *D. chrysostoma*. *Nature* 213:315–316.
- TICKELL, W. L. N., AND R. PINDER. 1975. Breeding biology of the Black-browed Albatross *Diomedea melanophris* and the Grey-headed Albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 117:433–450.
- VEIT, R. R., AND P. A. PRINCE. 1997. Individual and population level dispersal of Black-browed and Gray-headed Albatrosses in response to Antarctic krill. *Ardea* 85:129–134.
- WEIMERSKIRCH, H. 1991. Sex-specific differences in molt strategy in relation to breeding in the Wandering Albatross. *Condor* 93:731–737.
- WEIMERSKIRCH, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos* 64:464–473.