

MOLT, MATURATION OF PLUMAGE AND AGEING IN THE WANDERING ALBATROSS¹

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Abstract. We compare the pattern and rate of molt and plumage maturation in Wandering Albatrosses (*Diomedea exulans chionoptera*) using prebreeding and breeding birds from South Georgia (S. Atlantic Ocean) and Crozet Islands (S. Indian Ocean). Immatures from both sites have a molt cycle which basically alternates molt of outer primaries in one year and inner primaries in the next year. This is similar to, but in its details more complex and flexible than, the molt of the smaller, sympatric Black-browed and Gray-headed Albatrosses (*D. melanophris* and *D. chrysostoma*). It differs from the wrap-around molt characteristic of Laysan and Black-footed Albatrosses (*D. immutabilis* and *D. nigripes*). Juvenile Wandering Albatrosses have most new primaries when 5-year-olds but even at this age some birds have retained primary 1 since they fledged. Males, but not females, from South Georgia replace more primaries than do Crozet birds. Adults breeding for the first time molt fewer primaries than birds breeding 7-11 months after a failed breeding attempt; these adults molt on average 6 primaries, similar to successful or failed Black-browed Albatrosses. Successful Wandering Albatrosses, in the 12 months before breeding again, only molt 7-8 primaries on average, in contrast to the 11 primaries molted by biennial Gray-headed Albatrosses in their 16 month breeding interval. The duration of the interval between successive breeding attempts is probably the main constraint on the amount of primary molt that can be accomplished. Failed, but not successful, Wandering Albatrosses breeding at Crozet molt more primaries than similar birds at South Georgia. At both sites, the plumage of birds of both sexes gets whiter until about 20 years old. However, South Georgia males are already whiter than Crozet birds at 5 years old (presumably reflecting the faster molt rate of South Georgia birds) and they maintain this difference for the next decade. In contrast, females from both sites mature at similar molt rates until age 10 years (median age of first breeding) when South Georgia birds become and stay whiter than Crozet birds. Plumage maturation rate is much slower in birds from Macquarie Island, but these may not belong to the same subspecies. Conventional (Gibson) plumage scores do not provide a reliable means of estimating age of Wandering Albatrosses, except in very general ($\pm 3-5$ year) categories. The pattern and extent of molt, however, can age most immature birds of *D. e. chionoptera* to within one year; we provide a key for doing this.

Key words: *Diomedea exulans chionoptera*, Wandering Albatross, primary molt, secondary molt, plumage maturation, ageing, subantarctic.

INTRODUCTION

Molt is well recognized as an important element in the annual cycle of birds. Despite the energetic, physiological and behavioral costs of

molting, most birds undertake at least one complete molt each year. For birds which have very large wings and great reliance on flight (e.g., seabirds, birds of prey), there is presumably a premium in maintaining flight performance at high efficiency; nevertheless annual replacement of all flight feathers is rarely possible. Therefore, how such birds organize the pattern

¹ Received 4 March 1996. Accepted 22 October 1996.

and rate of molt is of particular interest. However, very few critical studies of this topic have been undertaken.

Recent studies of albatrosses indicate that they have some of the most complex and unusual molt patterns yet described for birds. Prince et al. (1993) showed that prebreeding and breeding Black-browed Albatrosses (*Diomedea melanophris*) and prebreeding and failed breeding Gray-headed Albatrosses (*D. chrysostoma*) have biennial primary molt, replacing half their primaries ("descendantly") in the first year and the other half ("ascendantly") in the following year. However, successful Gray-headed Albatrosses, which have 16 months between their chick fledging and starting a new breeding attempt (molt being suspended during breeding), are able to replace all primaries in this period. Yellow-nosed Albatrosses (*D. chlororhynchos*) have a broadly similar pattern, replacing about half the primaries each year, using a descendant wave molt (Furness 1988). These species all belong to *Diomedea* subgenus *Thalassarche* group of smaller species often known collectively as mollymawks. In contrast, Laysan and Black-footed Albatrosses (*D. immutabilis* and *D. nigripes*), which belong to *Diomedea* subgenus *Phoebastria*, appear to molt all or most of the outermost five primaries descendantly every year (Langston and Rohwer 1995). The innermost primaries are molted every second or third year and in such a way that the molt in the following year starts with the primary next due to be molted in the ascendant sequence (termed wrap-around molt by Langston and Rohwer 1995).

Molt patterns for the sooty albatrosses (genus *Phoebastria*) and for the larger (great) albatrosses (*Diomedea* subgenus *Diomedea*) remain unknown, except for the work of Weimerskirch (1991), which was concerned with factors influencing rate of primary renewal rather than with the molt patterns themselves. In addition to their size, the great albatrosses also differ from mollymawks in the duration and timing of their breeding season (laying in mid-summer and fledging a chick nearly one year later), thereby influencing the time, and time of year, at which molt can take place in a different way from the smaller species.

In this paper, we describe the basic pattern of primary and secondary molt of the Wandering Albatross. We use data from two sites (South

Georgia and Crozet Islands), to make the first assessment of plumage and primary molt variation between different populations within one subspecies (*D. exulans chionoptera*). We also compare data between sites on plumage maturation, a phenomenon unique to *D. exulans* amongst albatrosses, whereby adult plumage becomes progressively whiter with age. Finally, we investigate the extent to which molt pattern can be used to age immature Wandering Albatrosses.

METHODS

PHENOLOGY

Breeding Wandering Albatrosses arrive at the colony in the second half of November (mean arrival dates are 25 November for males and 4 December for females). Laying takes place in December (mean 22 December, range 8 December to 9 January) and the parents alternately incubate the egg until it hatches in March (mean 11 March, range 27 February to 26 March). The successful chicks leave the island the following December (mean 19 December, range 14 November to 27 January) (Tickell 1968, Huin, unpubl. data). Birds failing before mid-July are able to breed again the next season. Successful birds or birds that failed after July do not breed again until the season after next. Immature birds do not return to the breeding grounds before they are 3 years old; most return when 5 to 7 years old. The peak of activity of immature birds is between mid-December to mid-March, the oldest birds returning earliest and staying ashore longest (Pickering 1989). Modal age of first breeding is 10 years (Croxall et al. 1990). Wing molt occurs solely during the austral winter when birds are away from the breeding grounds.

MOLT SCORE

At South Georgia, data on molt as deduced by flight-feathers condition were collected from 146 nonbreeders and 703 breeders on Bird Island (54°00'S, 38°00'W) in December 1989–February 1990 and in January–March 1993, 1994 and 1995. At Crozet Islands, similar data (from 260 nonbreeders and 526 breeders) come from Possession Island (46°25'S, 51°45'E) in January–March 1989 and December 1989–January 1990. At both locations all birds examined were of known age and/or known breeding status. Birds were originally classified as: (a) nonbreeders (birds with no previous history

of breeding but of known age), (b) first-time breeders, (c) failed during incubation in the previous season, (d) failed the previous season during chick-rearing, (e) failed two seasons previously during chick-rearing, and (f) bred successfully two seasons previously. At South Georgia, three categories of feathers were distinguished in the same way as by Prince and Rodwell (1994), who provide detailed descriptions. These categories were: new feathers (unabraded and fresh in appearance), feathers between one and two years old (abraded at the tips and lacking the waxy, fresh appearance of a new feather), and feathers two or more years old (very abraded and brownish in color; referred to in the text as third generation feathers). At the Crozet Islands, feathers were classified as new or old. At both sites data were recorded from one wing only.

MOLT AND FEATHER TERMINOLOGY

The feathers scored were the 10 primaries (p1 being the innermost, p10 the outermost) and for nonbreeders at South Georgia the 34 secondaries (s1 is closest to primary 1, s34 is closest to the body). When mentioned in the text, the term "outer primaries" refers to primaries p8 to p10, "mid-inners" to p6 and p7 and "inners" to p1 to p5. We were unable to define "molt series" because this requires knowledge of the precise rules by which a single set of feathers is molted (Langston and Rohwer 1995). As we studied only the results of the molt process, we were unable to determine the direction in which feathers were molted. We use the term "ascendant primary molt" when feathers are molted towards the body (e.g., from p6 to p1) and "descendant primary molt" when feathers are molted towards the wing tips (e.g., from p8 to p10). We use the term "phase" to describe only the status of the primary feathers during the nonmolting period of the year (Prince et al. 1993); it is not equivalent to "molt series." We believe it helps in distinguishing the two main categories of birds: those which have the outer primaries new and the mid-inner primaries old (phase 1) and those which have the outer primaries old and the mid-inner primaries new (phase 2).

PLUMAGE MATURATION

Plumages of nonbreeding and breeding birds were scored according to the plumage code de-

vised by Gibson (1967), excluding the tail score. At Crozet, birds ($n = 366$ males, 355 females) were scored in the field (Weimerskirch et al. 1989). At South Georgia, birds ($n = 291$ males, 258 females) were held with one wing completely extended and photographed to show the dorsal pattern; plumage was scored later from the photographs.

Statistical treatment of the data followed Sokal and Rohlf (1981) and Fowler and Cohen (1993). After testing for homogeneity of variances (F -test), we used t -tests or Z -tests to compare data, depending on the sample sizes.

RESULTS

PRIMARY MOLT IN NONBREEDING BIRDS

Chicks fledge from their breeding sites in November at the start of the austral summer. We have examined only one first-year (unsexed) bird caught in May, six months after fledging from South Georgia, by a longline vessel fishing for tuna in the Indian Ocean. It had started body molt but showed no signs of primary molt. At South Georgia the three sexed 3-year-old birds each had three new outer primaries (Table 1), whereas the rest were all abraded and bleached, indicating that they were two or more years old. At Crozet Island, one 3-year-old of each sex was examined (Table 1). The male had molted the outer three primaries (8–10) and the female the outer four primaries (7–10); it is unknown whether the inner primaries of either bird were one, or more than one, year old. At both sites, 4-year-old birds molt their mid-inner and inner primaries (especially primaries 1, 2, 5, 6, and 7) and at 5 years old switch back to molting their outer primaries and some combination of inner primaries, especially primaries 2–5. There is thus good evidence that the pattern of molt is based on molting the outer and mid-inner primaries in alternating years and that this persists until birds eventually breed.

The general pattern of molt is very similar between sexes and populations studied. The main difference between the sexes is in the number of primaries molted (Table 1). At both sites males generally molt more primaries than females, except for birds aged 3 and 4 years at Crozet Islands. At Crozet Islands, between the ages of 3 and 9 years, males replaced an average total of 31.3 primaries compared with females replacing a total of 29.9 primaries. At

TABLE 1. Average number of primaries replaced by nonbreeding Wandering Albatrosses of different age and sex at South Georgia and Crozet Islands.

Age (years)	Mean number of new primaries (10 maximum)							
	South Georgia				Crozet Islands			
	<i>n</i>	Male	<i>n</i>	Female	<i>n</i>	Male	<i>n</i>	Female
3	2	3.0	1	3.0	1	3.0	1	4.0
4	16	5.1	16	5.0	7	3.6	17	4.6
5	10	5.0	23	5.7	17	5.9	21	5.5
6	11	3.5	19	2.1	25	2.9	24	2.3
7	14	5.7	15	4.9	39	5.8	40	4.9
8	3	5.7	8	3.6	27	5.3	19	4.8
9	6	6.7	2	3.5	14	4.7	8	3.6
Total	62	34.6	84	27.8	130	31.3	130	29.9
Mean ± SE		5.0 ± 0.3		4.3 ± 0.2		4.9 ± 0.2		4.4 ± 0.2

South Georgia males replaced 34.6 primaries and females 27.8 primaries, respectively. The average number of primaries replaced annually by males at South Georgia is not significantly different from males at Crozet ($Z = 0.36, P > 0.05$). There were no significant differences between females from the two islands ($Z = 0.28, P > 0.1$) nor between Crozet males and females ($Z = 1.78, P > 0.05$), but South Georgia males

replaced more primaries than females ($Z = 2.13, P < 0.05$).

In nonbreeding birds, the effect of the alternating pattern of molt, combined with often fewer than half the primaries being molted in any one year, results in some feathers that are not replaced for two or more years. In Figure 1 and Table 2a the frequency of new, 1-year-old and 2 (or more)-year-old (third generation)

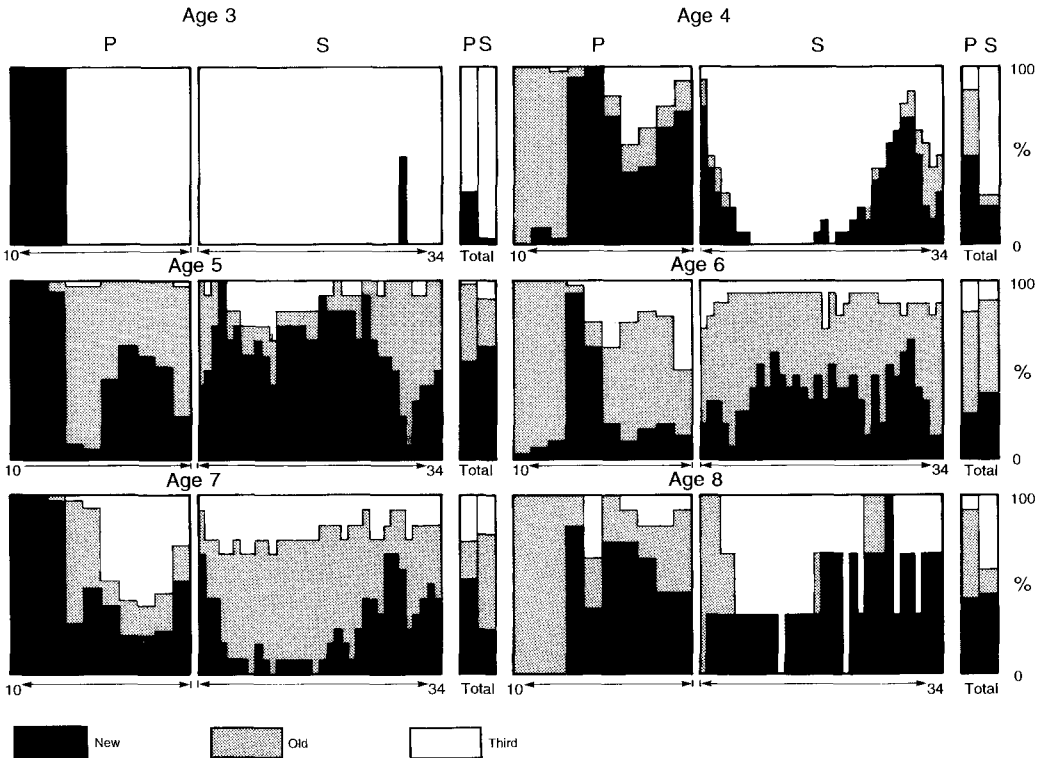


FIGURE 1. Percent of new, old and third generation feathers at each primary and secondary location for nonbreeding Wandering Albatrosses (sexes combined) at South Georgia.

TABLE 2. Mean number of new primaries (a) and secondaries (b) and percentage of new, old and third generation primaries (a) and secondaries (b) for each sex and age of nonbreeding Wandering Albatross from South Georgia.

(a): Primaries (10 maximum)										
Age	Male					Female				
	<i>n</i>	Mean new	Percentage of:			<i>n</i>	Mean new	Percentage of:		
			New	Old	Third			New	Old	Third
3	2	3.0	30.0	0.0	70.0	1	3.0	30.0	0.0	70.0
4	16	5.1	50.6	39.4	10.0	16	5.0	50.0	34.4	15.6
5	10	5.0	50.0	50.0	0.0	23	5.7	57.4	41.3	1.3
6	11	3.5	34.5	52.7	12.7	19	2.1	20.5	59.5	20.0
7	14	5.7	57.1	20.0	22.9	15	4.9	48.7	22.0	29.3
8	3	5.7	56.7	40.0	3.3	8	3.6	36.3	52.5	11.3
9	6	6.7	66.7	23.3	10.0	2	3.5	35.0	60.0	5.0
3-9	62	34.6	49.4	32.2	18.4	84	27.8	39.7	38.5	21.8

(b): Secondaries (34 maximum)										
Age	Male					Female				
	<i>n</i>	Mean new	Percentage of:			<i>n</i>	Mean new	Percentage of:		
			New	Old	Third			New	Old	Third
3	1	0.0	0.0	0.0	100.0	1	1.0	2.9	0.0	97.1
4	6	10.0	29.4	4.9	65.7	8	5.6	16.5	5.9	77.6
5	5	24.8	72.9	26.5	0.6	7	19.0	55.9	27.3	16.8
6	5	16.8	49.4	47.7	2.9	10	10.6	31.2	53.2	15.6
7	7	11.6	34.0	58.4	7.6	5	4.4	12.9	45.3	41.8
8	1	16.0	47.0	11.8	41.2	2	14.5	42.6	14.8	42.6
9	1	18.0	52.9	26.5	20.6	0	—	—	—	—
3-8	25	79.2	38.8	24.9	36.3	33	55.1	27.0	24.4	48.6

feathers at each primary location is shown for both sexes combined for birds at South Georgia (similar data are not available for Crozet birds). The pattern of molt is clearly visible, with birds alternating between molting outer and mid-inner primaries. Although we have handled only three 3-year-old birds, we can further deduce the pattern of primary molt for 3-year-old birds by examining the distribution of old feathers in 4-year-old birds. Thus on average, 4-year-old birds when age three years molted 3.7 primaries, which included all three outer primaries. As 4-year-old birds, they still had 13% of primaries unmolted since fledging. Of these unmolted primaries, 34% were primary 4, a further 56% was divided between primaries 2, 3 and 5. As 5-year-olds virtually all primaries present are either new or one year old; approximately 1% of primaries are third generation, but it is not known if these are original primaries retained since fledging or primaries grown later as 3-year-olds. At this age, birds have, on average, the best set of flight feathers at any time during their nonbreeding years (Fig. 1 and Table 2a); not until they breed successfully will they have a wing with more new and

fewer old and third generation primaries. As 6- and 7-year-olds they have a high proportion of primaries (mainly between locations 1 and 6) that are 1 and 2 or more years old. A similar but less extreme situation is shown in nonbreeding birds aged 8 and 9 years. Nonbreeding birds do not normally have primaries more than one year old at any of the three outermost primary locations (8-10).

SECONDARY MOLT IN NONBREEDING BIRDS

The average number of secondaries molted by male and female Wandering Albatrosses is shown in Table 2b. In 3-year-olds, from the small sample (two birds, one of each sex), the male had not molted any secondaries while the female had molted a single outer secondary (location 29). Secondary molt in 4-year-olds is more extensive with males molting 10 (29.4%) secondaries and females molting 5.6 (16.5%) secondaries. As 5-year-olds both sexes molt more secondaries at this age (range 3-9) than at any other time prior to breeding. Males molted an average 24.8 secondaries (72.9%) and females 19.0 secondaries (55.9%). As 6-year-olds males molted 16.8 (49.4%) second-

aries and females 10.6 (31.2%). However, as 7-year-olds males molt only 11.6 (34%) secondaries and females molt only 4.4 (12.9%) secondaries. Thereafter, it appears that the number of secondaries molted annually increases up to a maximum at age 5 years and decreases thereafter. The number of secondaries molted from fledging until 9 years of age is significantly greater in males ($t_{56} = 2.22, P < 0.05$) than in females.

The secondaries also have at least three generations of feathers: new, 1-, 2- or more year-old, or even older. Table 2b shows the percentage of new, old and third generation primaries and secondaries and Figure 1 shows the pattern of molt of these flight feathers. What is immediately apparent is the extent of third generation feathers still present in 4-year-old birds. For 3-year-olds, virtually all the secondaries in both sexes are the original secondaries that they fledged with. As 4-year-olds, males still have 65.7% of these secondaries while females have over 77%. Most of these third generation secondaries are distributed centrally with the newer feathers in two blocks at either end of the secondary row. As 5-year-olds, males have molted almost all remaining third generation secondaries while females still have 16.8% remaining. As 6-year-olds, males have almost 3% third generation secondaries while females have 15.5%. However, in the case of males, these third generation feathers are almost certainly secondaries that were new in their fourth year, but in females they are probably a combination of the original secondaries (dating back to when they fledged) and genuine two-year-old secondaries. From the age of 6 years onwards, the number of third generation secondaries increases in both sexes as they undertake a more even pattern of molt along the entire wing. However, males at all ages always molt more secondaries in any year than females, and as a consequence females always have more third generation secondaries than males.

PRIMARY MOLT IN BREEDING BIRDS

In both sexes at South Georgia there was no difference in the number of primaries molted between birds that failed the previous year with an egg or with a chick (males $Z = 0.59$; females $Z = 1.57$). There also was no difference between birds that failed with a chick two seasons previously and successful breeding birds

from two years previously (males $Z = 0.62$; females $Z = 1.42$). Therefore, we combined original categories C plus D, and E plus F into new categories: failed breeders last year and breeders two years ago, respectively.

Birds breeding for the first time molted fewer primaries (mean \pm SD; males 6.7 ± 2.4 , females 4.5 ± 2.2) compared with established breeders (Table 3), whether these were failed birds of the previous season breeding 7–11 months later (males 7.2 ± 2.4 , females 5.2 ± 2.4) or breeders from two years ago breeding again at least 12 months later (males 8.6 ± 1.4 , females 7.1 ± 7.7). The difference between males and females that bred two years previously was significant ($Z = 8.73, P < 0.01$) as it was between the previous season's failed males and females ($Z = 6.41, P < 0.01$) and between first time breeding males and females ($Z = 4.16, P < 0.01$).

Comparison with data from the Crozet Islands (Weimerskirch 1991), reveals several differences. At the Crozet Islands, birds breeding for the first time molted on average 6.4 primaries (males 6.7 ± 2.0 , females 6.2 ± 1.9), significantly more than South Georgia females ($Z = 3.99, P < 0.01$) but not males ($Z = 0.05, P > 0.05$). As for birds that failed the previous year, Crozet birds molted 7.4 primaries (males 8.3 ± 1.9 , females 6.5 ± 2.2), which for both sexes is significantly different (males $Z = 3.05, P < 0.01$, females $Z = 3.63, P < 0.01$) from South Georgia birds. Birds that last bred two years ago at Crozet, however, renewed 8.4 primaries (males 8.8 ± 1.2 , females 8.1 ± 1.6), significantly more than South Georgia females ($Z = 5.60, P < 0.01$) but not males ($Z = 1.64, P > 0.05$).

For South Georgia birds we can examine the distribution of molt scores for each sex of the three status categories of breeding birds (Fig. 2 and Table 3). For birds of both sexes that bred two seasons previously, priority was given to molting their outer primaries although they also molted a high proportion of all primaries. In birds that failed the previous season, where only half (females) or almost three quarters (males) of all primaries had been molted, priority was given to molting outer primaries at the expense of inner primaries. This is particularly evident in comparison with the number of inner primaries molted by first time breeders. First time breeders of both sexes not only have fewer pri-

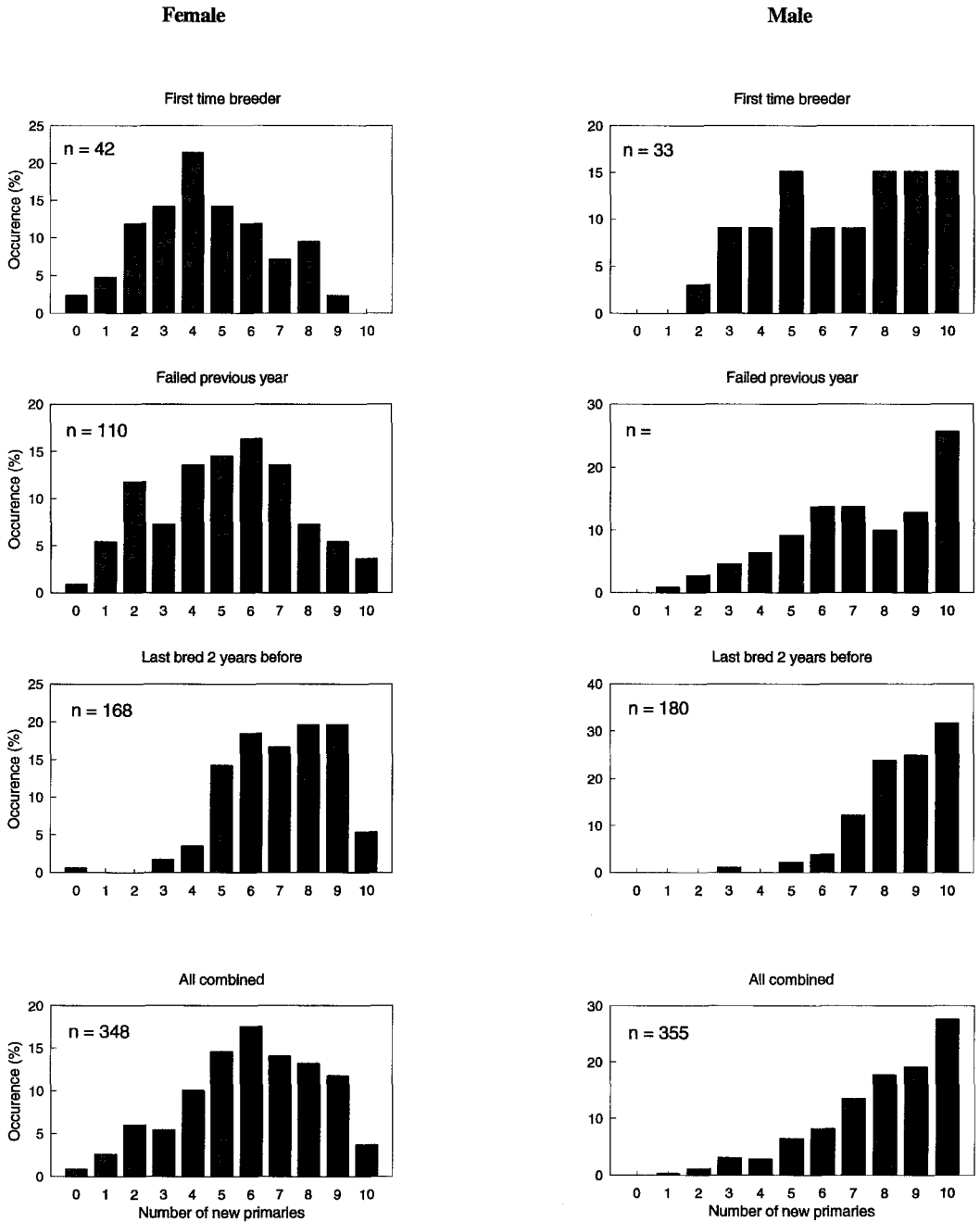


FIGURE 2. Frequency distribution of new primaries for each sex and status of breeding Wandering Albatrosses at South Georgia.

primaries molted than in the two previous categories, but the distribution of primaries molted is more even.

First-time breeders molt their primaries in the

winter prior to breeding. Thus we would expect them to be alternating between the two phases of molting their mid-inner or outer primaries. According to the age of the birds breeding for

the first time in our sample we would expect 21 females to be in phase 1 molt and 20 in phase 2, whereas for males we would expect 16 birds in phase 1 and 17 in phase 2. However we found that 20% of females (2 birds in phase 1, 3 in phase 2) and 65% of males (1 in phase 1, 10 in phase 2) did not conform to predictions. Regardless of the phase of molt, males molt more primaries than females (phase 1: $t_{28} = 2.19$, $P < 0.005$, phase 2: $t_{31} = 3.84$, $P < 0.001$), but only females molt more primaries in phase 1 than in phase 2 (female: $t_{38} = 2.55$, $P < 0.02$, male: $t_{30} = 0.62$, $P > 0.5$). However, if we exclude the males in the opposite phase to that predicted, then the number of primaries molted in phase 1 is significantly lower than in phase 2 ($t_{21} = 2.55$, $P < 0.02$). Similarly, these males and females in phase 2 and breeding for the first time molt significantly fewer primaries than birds that failed in the previous season (female: $t_{29} = 2.99$, $P < 0.01$, male: $t_{21} = 3.07$, $P < 0.001$).

DEVELOPMENT AND MATURATION OF PLUMAGE

Fledgling Wandering Albatrosses have a dark gray-brown plumage except for a white face mask and white underwing. As Weimerskirch et al. (1989) for the Crozet Islands and plumage scores for South Georgia (Fig. 3) show, when birds return to their natal colonies (not before three years of age and usually at four to six years of age) their plumage is considerably whiter and males are already very much whiter than females. This process of whitening continues with age and each molt, and the disparity between the sexes is maintained to the median age of breeding (10 years) and beyond. However, after about age 15 years the rate of whitening is much reduced in both sexes, males at South Georgia having already reached their maximum score. Males at South Georgia are already whiter than Crozet birds at age 5 years and this difference is maintained until about age 20 years (Fig. 4). However, this is not the case with females from the two sites whose plumage scores prior to commencing breeding are indistinguishable, indicating similar rates of maturation of plumage at both localities. From about 10 years of age onwards, however, female breeding birds at South Georgia are consistently whiter in plumage than those from Crozet.

TABLE 3. Comparison of the number and location of new primaries between males and females that breed for the first time, that last bred last year or two years ago. Data from Wandering Albatrosses at South Georgia.

Sex	Breeding history	n	Percentage of new feather at primary number:										Overall average ¹
			1	2	3	4	5	6	7	8	9	10	
Male	First time breeders	33	64	45	64	67	67	64	76	79	76	73	67.3 ^a
	Failed last year	109	60	58	60	72	69	74	80	88	86	78	72.4 ^b
	Bred two years ago	180	87	74	65	65	84	88	96	99	99	99	85.6 ^{a,b}
Female	First time breeders	42	26	33	33	40	40	48	55	64	55	52	44.9 ^a
	Failed last year	110	39	37	33	35	54	59	65	66	65	62	51.5 ^b
	Bred two years ago	168	51	48	48	50	63	67	86	98	98	82	70.6 ^{a,b}

¹ Means sharing the same letter within each sex are significantly different, $P < 0.01$, Z-test.

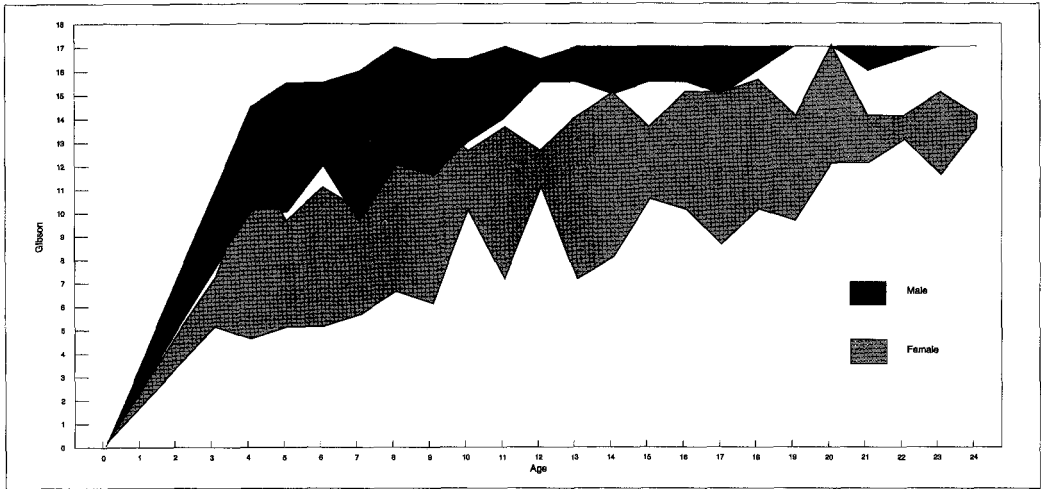


FIGURE 3. Distribution of plumage scores of known-age Wandering Albatrosses at South Georgia. Scores were made following the Gibson (1967) method, excluding the tail (see text for further details).

DISCUSSION

PRIMARY MOLT IN NONBREEDING BIRDS

The pattern of primary molt in nonbreeding Wandering Albatrosses is similar to that described in Prince et al. (1993) for the smaller Black-browed and Gray-headed Albatrosses. These species also have a molt cycle with birds switching between molting their outer primaries (phase 1 molt) and some combination of the in-

nermost primaries in one year and molting their mid-inner primaries and innermost (phase 2 molt) primaries in the next year. In the two molymawk species, Prince et al. (1993) found that the molt cycle starts with molt of the outer three and some innermost primaries descendantly; in the next year the inner primaries are molted ascendantly, starting at primary 7. Thereafter, there is a general progression to molting equal numbers of primaries in each half of the cycle, but the switch from molting the outer three primaries in one cycle to molting primaries 6 and 7 in the following cycle is a consistent feature of their molt pattern. It is unknown whether the Wandering Albatross has an alternating sequence of ascendant and descendant molt. However, it is very probable, and if so, then their pattern differs only in that there does not seem to be as strict an adherence to molting just the outer three primaries or primaries 6 and 7 in successive cycles.

Results for the 3-year-old South Georgia birds, with three new outer primaries and the other primaries two or more years old, suggest that the onset of primary molt did not occur until their second winter. Of the two 3-year-old Crozet birds, the female had molted four and the male three outer primaries (the age of the inner primaries was not determined), a pattern entirely consistent with that of the South Georgia birds. Thus birds fledging in November/December at the start of an austral summer only undergo body molt during their first winter, but

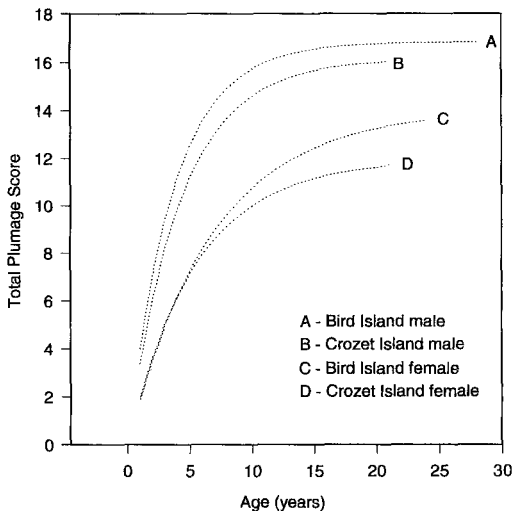


FIGURE 4. Mean plumage scores of known-age Wandering Albatrosses from South Georgia and Crozet Islands (data from Weimerskirch et al. 1989). Curves fitted by eye.

in their second winter, 15 to 16 months after fledging, the process of flight feather replacement begins starting with the outer primaries.

At a more detailed level, however, some differences are apparent between the sexes, especially for younger birds. The most obvious difference between the sexes is that males generally have more new primaries and fewer third generation primaries than do females. It is not clear whether this reflects differences in foraging distribution, or that males, which are significantly larger in mass than females (Weimerskirch 1991), have an advantage over females in foraging interactions.

SECONDARY MOLT IN NONBREEDING BIRDS

Not until males are at least 5 years old and females 6 years of age have all the secondaries present at fledging been molted. This extraordinary length of time taken to molt some of the secondaries possibly reflects the energetic costs of replacing so many flight feathers, and the priority both sexes give to molting their primaries, especially the outer five primaries. The main difference between sexes in age composition of secondaries is between 3 and 8 years of age, when males have about 12% more new and 12% fewer third-generation secondaries than do females.

PRIMARY MOLT IN BREEDING BIRDS

In general the Wandering Albatross follows the biennial molt pattern already established for Black-browed and Gray-headed Albatrosses (Prince et al. 1993). That is, it molts approximately seven primaries between successive breeding attempts. However, at South Georgia, failed birds that breed 7–11 months later are only just able to renew 6 primaries, thereby resembling the annual breeding Black-browed Albatross, which molts 4–5 primaries per year, whether successful or failed (Prince et al. 1993). In contrast, successful Wandering Albatrosses, which have one complete year off, molt 8 primaries on average. In this they resemble the other biennially breeding species at South Georgia, the Gray-headed Albatross. However, the Gray-headed Albatross has a much shorter breeding season, with a 16 month interval between breeding attempts when successful. It is able to molt 3 primaries during the winter after its chick fledges and another 8 primaries in the rest of the year before it breeds again (Prince

et al. 1993). Unlike the Wandering Albatross, it is able to renew all the primaries in the wing. Therefore, despite affecting an economical alternation of breeding and molt such that the complete wing is renewed every 2 years, the lengthy breeding period and the relatively reduced interbreeding interval constrain the amount of molt that can be achieved by Wandering Albatrosses much more so than Gray-headed Albatrosses, despite both having biennial breeding cycles. In general, the duration of the interval between successive breeding attempts seems to be the main constraint on the amount of molt that can be undertaken.

Birds breeding for the first time molt fewer primaries than birds with previous breeding experience. However, when first-time breeders of both sexes are compared with birds that failed the previous year, the number of primaries molted by first-time breeders was not significantly fewer. Throughout the nonbreeding years, birds are alternating their molt between inner and outer primary feathers with variable extents of molt of inner primary feathers. In the winter prior to their first breeding attempt, both sexes, but especially males (60%) in phase 2 molt, switch to molting their outer primaries and as many other primaries as possible. Presumably this reflects the need to have the best possible flight feathers during the year of their first breeding attempt. Males can readily achieve this, which is consistent with their ability to molt more primaries than females at all stages of their life history. Furthermore, any birds that breed successfully at their first attempt and have old outer primaries will, by the end of the year, have outer primaries more than two-years-old. This is probably the only time in their life that the outer three primaries will be of the third generation.

The reason for the difference between Crozet and South Georgia birds in the number of primaries molted by failed breeders, i.e., one primary more for each sex at Crozet, is uncertain. At Crozet, females breeding for the first time molt nearly two more primaries than females breeding for the first time at South Georgia. Similarly, females at Crozet, which last bred two years previously molted one more primary than South Georgia females. It seems possible that the inter-site differences relate to different feeding areas and/or to different distances birds travel to reach their principal wintering grounds

which, for both populations, includes the Indian Ocean and the east coast of Australia. To reach these two areas, South Georgia birds must travel nearly twice as far as Crozet birds; the extra cost that this entails may be sufficient to delay either the onset or the rate of molt in the relatively short period before they need to return to breeding condition. Birds that bred two years previously however, have a whole year to undertake molt and regain breeding condition, so a difference of a couple of weeks in transit to and from the wintering grounds may be less critical—which may be why it is not reflected in different molt rates at the two sites.

COMPARISON WITH OTHER ALBATROSS SPECIES

There are detailed studies of molt and feather replacement in only four other species of albatross. In adult Laysan and Black-footed Albatrosses, the 10 primaries are divided at their mid-point into two series, each with an independent set of rules for replacement (Langston and Rohwer 1995). The primaries of the two series are replaced in opposite directions, with molt proceeding descendantly towards the wing tip in the outer series and ascendantly towards the body in the inner series. The outermost three primaries are replaced every year without fail and the time available for molt seems to determine what proportion of primaries 6 and 7 are molted; older birds molt more of these two primaries than immatures birds. In the inner series, feather replacement occurs only every second or third year and is normally incomplete. It proceeds in an ascendant wraparound pattern which ensures that the oldest and most worn primaries are always molted.

Prince et al. (1993) also noted the priority that Grey-headed and Black-browed Albatrosses gave to molting their outer five primaries. Immature nonbreeding birds of both species molt their primaries biennially. In the first year of a cycle the outer three and some inner primaries are molted; in the next year the inner primaries are molted starting at primary 7. There is a general progression to molting equal numbers of primaries in each year of the cycle by the time breeding starts at about 10 years of age. Breeding Black-browed Albatrosses continue the molt pattern established as immatures whether they fail or not, as do Grey-headed Albatrosses which fail while breeding. Successful Grey-

headed Albatrosses, which next breed 16 months later, molt some of the innermost primaries in the remainder of the current year after breeding finishes. Then, after a period when molt is interrupted, they renew the remaining primaries the following year. This ensures that at the next breeding attempt they have the maximum possible number of new primaries. Similarly, breeding Laysan and Black-footed Albatrosses have new outer primaries at each annual breeding attempt. In contrast, the Black-browed Albatross, which breeds annually but molts biennially, breeds with old outer primaries in alternate years.

Langston and Rohwer (1995) described Laysan and Black-footed Albatrosses as showing a bidirectional pattern of incomplete primary molt. They defined a molt series as an adjacent set of flight feathers that are molted according to a single set of rules. In Laysan and Black-footed Albatross the primaries are organized into two molt series. The outer series is replaced in sequence from primary 6 to primary 10 (descendant); the inner series is replaced in the opposite direction, from primary 5 to primary 1 (ascendant). In Black-browed Albatross the outer three primaries are molted every other year; in the year that these primaries are not molted priority is given to molting primaries 6, 7 and, less frequently, primary 5. Of the innermost four primaries (1–4), some are molted each year (Prince et al. 1993). Brooke and Furness (1982) provided evidence for an ascending molt in this species. In Grey-headed Albatrosses, 28 out of 30 birds examined one year after a successful breeding season were actively molting their inner primaries ascendantly (Prince et al. 1993).

These two studies on four species of albatrosses highlight the flexible nature of molt, presumably relating to the different balance of constraints facing species with different breeding cycles and environments. The Wandering Albatross is extreme amongst albatrosses, being the largest of the group, with a breeding season that lasts over a full year, after which it takes a complete year off from breeding. We have no information on its direction of molt because we have not examined any birds in active molt. For immature birds the pattern of molt shows that birds molt their outer primaries and mid-inner primaries in alternate years, together with some of the innermost primaries each year. In this respect

their molt resembles that of Black-browed and Grey-headed Albatrosses. For breeding birds that fail in their attempt and return to breed the following year, the alternating pattern of molt continues. If successful in their breeding attempt, meaning that no molt will have taken place for at least one year, birds will molt most of their primaries (the proportion depending on sex) in their year off before their next breeding attempt. How this molt is conducted, in terms of series and direction, we do not know because these birds are at sea during this stage of their cycle. However, it is clear that the Wandering Albatross molt pattern, whether as failed or successful breeders, does not resemble that of the more tropical albatross species. There is no evidence of a wave molt and the presence of feathers left unmolted over several cycles clearly indicates that in Wandering Albatrosses molt does not recommence at the "next" primary after the previous molt sequence, that is, there is no evidence of "wrap around" molt as there is in Laysan and Black-footed Albatrosses (Langston and Rohwer 1995).

PLUMAGE MATURATION

The overall pattern of plumage maturation is broadly similar, and the differences between sexes equally marked, at both South Georgia and Crozet. However, there are some interesting site-specific differences. Thus, until about age 20 years, South Georgia males are consistently whiter than Crozet ones. In contrast, up to age 10 years, females are indistinguishable; after age 10 however, South Georgia females become and remain whiter than Crozet females.

The sex-specific patterns at the two sites over the first 10 years of life are entirely consistent with the different rates of primary renewal. Thus South Georgia males consistently replace more primaries than Crozet ones but no difference exists between females. It is not surprising that, by age 20 years, plumage of males at the two sites have become similar because by then the bulk of the plumage maturation is complete. However, the reasons for the apparent sudden divergence in plumage scores of females at the two sites at around the age of first breeding at about 10 years is unknown. It could relate to differences in food availability in the different foraging areas (South Atlantic and South India Oceans) to which breeding birds are much more restricted than nonbreeding birds.

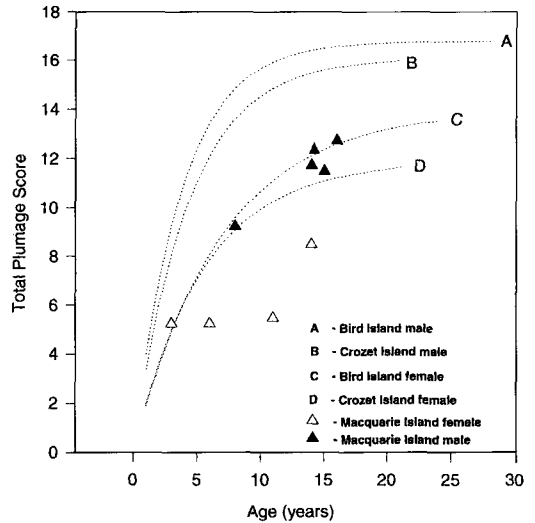


FIGURE 5. Plumage scores of known-age Wandering Albatrosses from Macquarie Island in comparison with similar data taken from Figure 4 for South Georgia and Crozet Islands.

Despite the basic similarities in pattern of plumage maturation at Crozet and South Georgia, this should not be regarded as necessarily characteristic of the species as a whole, because at least some of the other races of *D. exulans* have rather different plumages. Thus, *D. e. chionoptera*, the race breeding at the highest latitudes and with a circumpolar at-sea distribution, is the largest and whitest; *D. e. antipodensis* and *D. e. gibsoni* breed in the New Zealand area, are thought to be restricted to the Pacific Ocean (Robertson and Warham 1992), and are smaller and darker. *D. e. dabbenena* of Tristan da Cunha and Gough Islands, which may be confined at sea to the South Atlantic Ocean, also is small but intermediate in plumage.

Unfortunately no data on plumage maturation are available for these other races and there are few data available for *D. e. chionoptera* from other breeding sites with which to assess the nature of site and subspecies-specific variation. Plumage scores for a small number of birds from Macquarie Island (Tomkins 1984) suggest substantial differences from Crozet and South Georgia (Fig. 5). These data indicate that both sexes are darker in plumage at equivalent ages; thus Macquarie males have a maturation pattern similar to South Georgia and Crozet females, whereas Macquarie females are darker still. However, although birds from Macquarie are

TABLE 4. Key for ageing nonbreeding Wandering Albatross *Diomedea exulans chionoptera* using molt patterns of primaries and secondaries. Data from South Georgia.

	Outer primaries (8, 9 and 10)				Inner primaries (1 to 7)				Secondaries				Gibson	Age	
	New		Old		New		Old		New		Old				Third
	n	%	n	%	n	%	n	%	n	%	n	%			
Sex															
Male	→		→		→		→		→	→		→	→	→	→
Female	→		→		→		→		→	→		→	→	→	→
New (Phase 1)	0		5		0		0		0		0		0		0
Old (Phase 1)	2		2		5		9		9		25		0.2		34
New (Phase 2)	3		2		2		35		20		60		2		5
Old (Phase 2)	4		2		2		55		9		25		7		20
New (Phase 1)	5		1		1		30		2		5		22		65
Old (Phase 1)	4		2		2		50		16		50		1		few
New (Phase 2)	6		1		1		50		4		10		14		40
Old (Phase 2)	0		0		0		0		0		0		34		100
New (Phase 1)	3		4		4		60		9		25		6		15
Old (Phase 1)	2		2		2		15		16		45		14		40
New (Phase 2)	few		few		few		—		—		—		—		—
Old (Phase 2)	5		few		few		15		2		5		26		80
New (Phase 1)	2		3		3		30		18		50		5		20
Old (Phase 1)	2		2		2		40		5		20		14.5		40
New (Phase 2)	4		2		2		40		5		20		14.5		40
Old (Phase 2)	4		2		2		40		5		20		14.5		40

Key should be used as follows:
 1—separate by sex
 2—separate by state of outer primaries (all new or all old)
 3—separate by combination of molt of inner primaries and of secondaries,
 Gibson values might help between nonconsecutive ages and
 to distinguish between breeding and nonbreeding birds.

Note: 1: New refers to feathers freshly molted.
 Old refers to feathers molted 1 year before.
 Third refers to feathers molted at least 2 years before (third generation feathers).
 Gibson values do not include tail score.
 2: Values for inner primaries (actual number) and secondaries (number and percentage of all 34 secondaries) are means from the whole sample size; allowance should be made for individual variation.

usually assigned to *D. e. chionoptera* (Marchant and Higgins 1990, De la Mare and Kerry 1994), Tomkins (1984) noted that few taxonomic data are available to assess the status of the population. Indeed, if biometric data from Tomkins (1984) are compared with those from South Georgia (Tickell 1968), the Macquarie birds, except for a couple of prominent outliers, are significantly smaller in culmen measurements ($P < 0.05$ for both length and depth). This, combined with the plumage score data, suggests that Macquarie birds might not necessarily be *D. e. chionoptera*. Even if Macquarie was originally populated by *D. e. chionoptera* the near-extirmination of the species by visiting sailors and sealers in the 19th century may have given opportunities for re-colonization by another race (e.g., *D. e. gibsoni* from the nearby Auckland Island group), rather than from another population of *D. e. chionoptera*. It is possible, therefore, that the current population represents introgression between individuals of more than one origin. Re-examination of the remains of 65 or more birds found cached in a cave on Macquarie (Gillham 1967) might shed more light on this hypothesis. Whatever the situation at Macquarie, we have no means of knowing at present whether the differences in plumage maturation between South Georgia and Crozet birds reflect a genetic difference between these relatively isolated populations or responses to different environmental conditions.

AGEING WANDERING ALBATROSSES BY PLUMAGE AND MOLT

Gibson (1967) developed a system of plumage scoring of Wandering Albatrosses that enabled field workers to describe the approximate age of birds based on the correct premise that birds become whiter with age. This method has been widely used ever since, especially at breeding locations (Tickell 1968, Tomkins 1984, Weimerskirch et al. 1989). Seabird observers frequently allocate their observations of Wandering Albatrosses to a particular plumage stage, implying that the bird under observation is of an age that can be determined. The data in Figure 3 indicate the problems associated with trying to do this. The range in plumage variation for age-cohorts is so great that if a bird has been incorrectly sexed, a 5-year-old male could be mistaken for a 20-year-old female. Even when sexed correctly, the variation in plumage spans

a range of 5–10 years. In addition, most at-sea observations take little account of the subspecies of *Diomedea exulans* under observation; as indicated above these vary greatly in plumage characteristics (see also Robertson and Warham 1992). To assist field workers (but not, as yet, at-sea observers) working with populations of unknown age and especially scientists researching threats to Wandering Albatrosses from mortality in longline fisheries, we provide information based on molt patterns that should enable most individuals of *Diomedea exulans chionoptera* to be aged correctly to within one year (Table 4).

ACKNOWLEDGMENTS

We thank the New South Wales Albatross Study Group for providing unpublished data, Nigel Brothers for facilitating examination of albatrosses killed on longline vessels in Australian waters, John Croxall for assistance with the manuscript, and Julie Leland for typing the various drafts.

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