SEX-SPECIFIC DIFFERENCES IN MOLT STRATEGY IN RELATION TO BREEDING IN THE WANDERING ALBATROSS[1]

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Abstract. The extent of molt of primary feathers was studied in relation to the status and to the duration of the interval between breeding attempts in the Wandering Albatross (*Diomedea exulans*). The replacement of primaries lasts for more than one season, birds showing a typical wave molt with one to three foci occurring on a wing. Molt never occurs on the breeding grounds. In breeding as in nonbreeding individuals, males invariably renew more feathers than females. Breeding males and females renewed each year an average of 8.3 and 7.3 primaries per wing, respectively. The extent of primary molt of breeders was directly related to the duration of the interbreeding period in females but not in males. Males and females breeding for the first time had fewer new feathers than did experienced birds. When they visited the nesting colonies, immature birds had fewer new feathers than did breeding birds of the same sex. In immature birds, the extent of molt was related to the body condition (mass) of males but not of females. The extent of molt was inversely related to mass gain from one season to the next in nonbreeding males. These results suggest that molting in the Wandering Albatross is probably an important constraint that could compete with breeding, particularly in females. Possible reasons for sex-specific differences in molt extent are discussed.

Key words: molt; Wandering Albatross; breeding; condition.

INTRODUCTION

In birds, molt and breeding are two major energy demanding functions and reproduction and molt are temporally separated in most species (Payne 1972). This separation of breeding and molt could result from a conflict in energy allocation between feather renewal and breeding (Pietiainen et al. 1984, Furness 1988). In albatrosses, the primary molt period never overlaps the breeding period and the replacement of flight feathers can last several years (Harris 1973, Furness 1988, Melville 1991). Birds show a "Staffelmauser" or "wave molt" (Streseman and Streseman 1966). The molt of primaries in albatrosses can be interrupted and several molt foci occur on the same group of primaries (Brooke 1981, Furness 1988). Thus, although primary molt takes place at sea outside the breeding season, its extent can be studied retrogressively on the breeding grounds by inspecting the number of freshly renewed feathers (see for example Furness 1988). In albatrosses, where some species breed annually and others breed every second year when successful in fledging a chick, the extent of molt necessary

to maintain flight efficiency could be in balance with the benefits of breeding in successive seasons (Furness 1988).

The Wandering Albatross (*Diomedea exulans*) is one of the most sexually dimorphic seabirds, with females only 80% of the mass of males. The breeding cycle lasts a complete year and pairs that are successful in fledging a chick breed in alternate years, while those failing during incubation or during the early stages of the chick-rearing period breed again the next year (Tickell 1968). The interval between breeding attempts is approximately 12 months for the successful breeders and between 5 to 11 months (according to the period when failure occurs) for the failed breeders. If energy or time for molting is limited, the extend of primary molt could depend on the length of the interbreeding season. In the Wandering Albatross sexual maturity is only acquired at an average age of 11–12 years and immature birds start visiting the colonies when they are 4–7 years old (Weimerskirch and Jouventin 1987). During this extended period of immaturity the plumage of both sexes becomes progressively whiter with age (Weimerskirch et al. 1989). Immatures have to attain a sufficient body condition for breeding and probably undergo several complete molts. Little information, however, is

TABLE 1. Differences in molt pattern between wings of the same bird in 25 males and 25 females.

Number of new feathers in both wings	Percent	
	Males	Females
Identical in both wings	48	56
Differs by one feather	40	24
Differs by two feathers	4	8
Differs by three feathers	0	4
Same number but different pattern	8	8

TABLE 3. Number of new primaries per wing in males and females (samples refer to the number of birds inspected).

	Males	Females
Nonbreeders	5.4 ± 2.5 (0–10, 116)	4.8 ± 2.1 (0–8, 125)
Breeders	8.3 ± 1.7 (2–10, 273)	7.3 ± 2.2 (0–10, 309)
Student's t test	$t = 8.8$, $P < 0.001$	$t = 9.1$, $P < 0.001$

available on the molt pattern during this period because the status and age of the birds inspected are not generally known (Melville 1990). In particular, nothing is known of the molt strategy of birds passing from immature to breeding status, when energy must be allocated for the first time between molting and breeding.

Using a population with birds of known age and breeding status, in this paper I examine the molt strategy of immature and breeding Wandering Albatrosses in relation to the length of time available between two successive breeding attempts and to the age, experience, and condition of the birds. Particular attention is paid to the differences between males and females in order to examine whether sex-specific differences in the extent of molt exist in this highly dimorphic species.

METHODS

The study was carried out on Possession Island, Crozet Islands (46°25′S, 51°45′E) in January–March 1989 and December 1989–January 1990. On Possession Island the entire population of Wandering Albatrosses has been banded since 1960 and sightings of banded birds have been carried out in every year since 1966 (Weimerskirch and Jouventin 1987). Consequently, the sex, age and previous breeding status of each bird is known (see Weimerskirch and Jouventin 1987).

The extent of primary molt was studied ret-

rospectively. Three generations of feathers are found in the wing of Wandering Albatrosses. I restricted my observations to the primaries that were classified as new, old and very old according to the criteria described in Furness (1988). New feathers have been renewed within the last 12 months, old ones 12–24 months earlier and very old ones 24–36 months earlier (Harris 1973, Furness 1988).

The breeding birds were weighed during incubation using the technique of Prince et al. (1981) that does not require restraining the breeder. Nonbreeders were weighed in a cotton sack. Weighings were performed with 10 and 20-kg spring balances accurate to 0.5 and 1% of capacity, respectively. During the period December–April, when they arrive at the colony from the sea, immature and breeding birds have empty stomachs and their mass is therefore basic body mass plus any body reserves. Immature birds were weighed when they visit the colonies in December–April to select their future mate (Pickering 1989). Values for the numbers of foci and of renewed primaries are given as the average ± one standard deviation, range and sample size.

RESULTS

Of 814 immature and adult birds inspected, none was found in active primary molt between December and April. The pattern of molt of pri-

TABLE 2. Number of foci per wing (samples refer to number of birds inspected, range for each category is 1–3).

	Males	Females	Students test	
			t	P
Nonbreeders	1.54 ± 0.55 (82)	1.62 ± 0.57 (90)	0.9	ns
Breeders	1.51 ± 0.61 (273)	1.63 ± 0.69 (310)	2.2	0.02

TABLE 4. Number of new primaries per wing in males and females with and without former breeding experience.

	Males	Females
First breeding attempt	6.7 ± 2.0 (1–10, 40)	6.2 ± 1.9 (1–10, 48)
Experienced breeders	8.6 ± 1.5 (3–10, 233)	7.5 ± 2.1 (1–10, 261)
Student's t test	$t = 5.6$, $P < 0.001$	$t = 4.1$, $P < 0.01$

TABLE 6. Influence of breeding experience of successful breeders on the number of primaries renewed when commencing breeding the next season.

	Number of renewed primaries after		Student's t test	
	First breeding	Several breedings	t	P
Males	8.3 ± 1.4 (5–10, 27)	8.9 ± 1.2 (5–10, 116)	2.1	0.05
Females	7.7 ± 2.1 (3–10, 31)	8.2 ± 1.5 (5–10, 132)	1.3	ns

maries was examined in 50 birds on both wings. It was symmetrical in 52% of birds. The number of renewed feathers was identical between wings in 52% of the birds, but could differ by one, two or three feathers (Table 1). The differences between the sexes were not significant. Because differences of this kind between wings in the number of feathers renewed was unlikely to be significant in terms of energy requirement, only one wing per individual was considered in the rest of the study. The number of foci per wing varied from 1–3. It was slightly higher in breeding females than in breeding males. In nonbreeders there was no difference in the number of foci between the sexes (Table 2).

Males had significantly more renewed primaries than did females (Table 3: nonbreeders, $t = 2.1$, $P < 0.035$; breeders $t = 6.2$, $P < 0.001$). In both sexes nonbreeders had significantly fewer new feathers than did breeding birds (Table 3). Males and females breeding for the first time had fewer new feathers than did birds that had bred at least once previously (Table 4). Females that

were successful in rearing a chick two years previously had a complete year between successive breeding attempts and they had more new primaries than did females that failed in breeding one year previously or than females that bred for the first time (Table 5). In males, previously failed and successful breeders had similar numbers of new primaries but more new feathers than did males attempting to breed for the first time (Table 5). Birds failing during incubation (January–February) had 10–11 months available for the molting between the successive breeding attempts whereas those failing during the first part of the chick-rearing period (March–July) had only 5–9 months between the successive breeding attempts. There was no significant difference in the number of renewed primaries between birds (males or females) failing during the incubation period and those failing during the first three months of the chick-rearing period.

On returning to breed after a successful breeding season males that had bred only once previously had fewer new primaries than did more

TABLE 5. Number of new primaries per wing in males and females with previous experience of breeding (the status indicated is that during the previous breeding cycle).

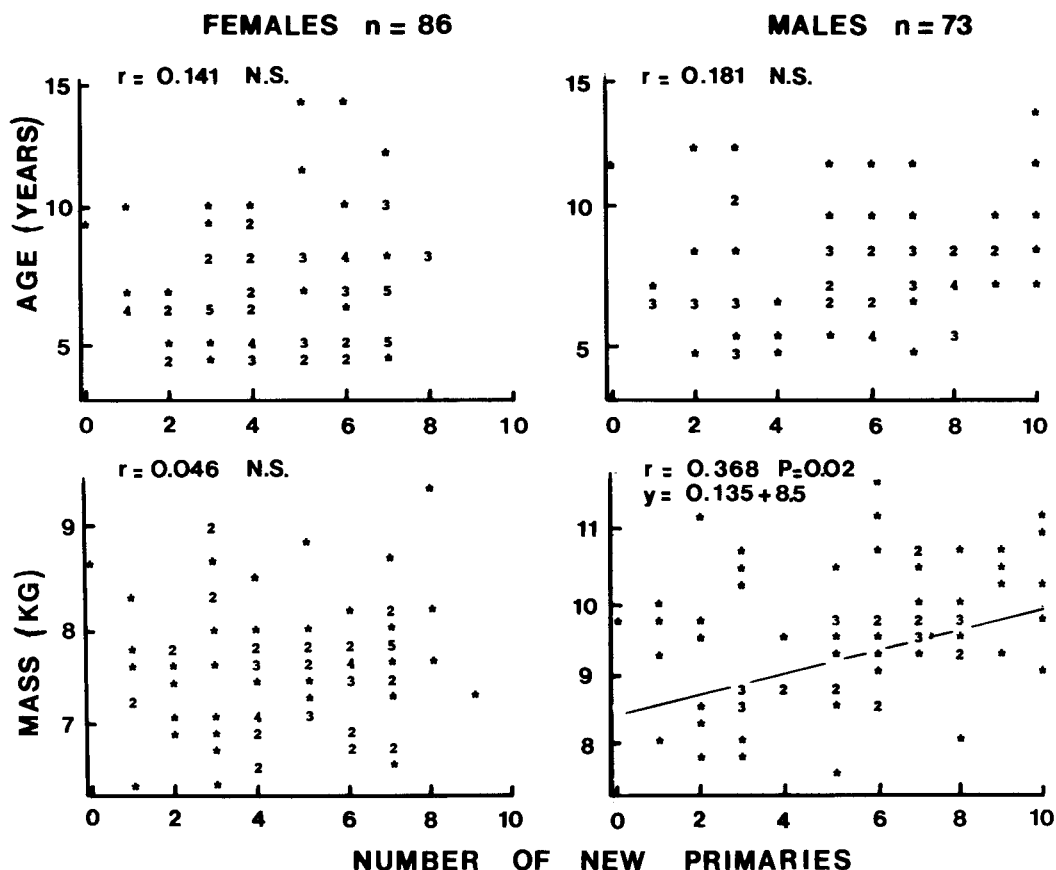|	Males	Females
Status (period available for molting)		
a) Successful breeders (12 months)	8.8 ± 1.2 (5–10, 142)	8.1 ± 1.6 (3–10, 162)
b) Failed breeders (5–10 months)	8.3 ± 1.9 (2–10, 53)	6.5 ± 2.2 (3–10, 57)
c) Failed during incubation (9–10 months)	7.9 ± 2.4 (2–10, 21)	6.8 ± 1.8 (3–10, 20)
d) Failed during chick-rearing (5–8 months)	8.6 ± 1.5 (5–10, 33)	6.4 ± 2.4 (0–10, 38)
Student's t tests:		
a)–b)	$t = 1.5$, ns	$t = 4.9$, $P < 0.001$
c)–d)	$t = 1.1$, ns	$t = 0.7$, ns

FIGURE 1.   Number of primaries renewed per wing in immature males and females in relation to age and body mass.

experienced breeders (Table 6). The difference in females, although it existed, was not significant (Table 6).

In nonbreeding males, the number of new primaries was significantly correlated with the mass of individual birds, but it was not related to the age of the birds (Fig. 1). In nonbreeding females, however, the number of renewed primaries was related neither to the age of birds nor to their mass (Fig. 1). When considering the number of new feathers and the mass of individual nonbreeding birds, during two consecutive years, the number of feathers renewed from one season to the next was inversely related to the relative mass gain from the first to the second season in males ($r = -0.45$, $n = 18$, $P < 0.05$) but not in females ($r = -0.07$, $n = 16$, ns). In breeding birds of either sex, there was no significant relationship between mass and extent of molt.

DISCUSSION

Since the identification of feathers is easiest with the primaries, the molt of birds is generally described by the molt pattern of primaries. This simplification appears reasonable because primary molt usually has a duration spanning the molt of all other feathers and requires a significant proportion of the total amount of energy necessary for the entire replacement of the plumage (Ginn and Melville 1983).

In the Wandering Albatross, as in other species of albatrosses studied (Harris 1973, Furness 1988), the replacement of primaries can extend over three successive seasons, with up to three molt foci occurring on a single wing. Males and females renewed an average of 8.3 and 7.3 primaries per wing, respectively, between successive breeding attempts. This figure is much high-

er than the number of feathers renewed each year by the small-sized Yellow-nosed Albatross (*D. chlororhynchos*) (2.1 kg) that molts on average 4.5 feathers each year (Furness 1988). It is however lower than the 3.3-kg Waved Albatross (*D. irrorata*) where breeders renew 9.4 feathers each year (Harris 1973). Thus, size probably has no influence on the extent of primary molt in albatrosses. Within each of the three species considered, but not in male Wandering Albatrosses, the extent of molt appears to increase with the time between two successive attempts (Fig. 2). However, interspecific comparisons indicated that the extent of molt is unrelated to time available for molting. Resource availability during the interbreeding season, which probably depends on the feeding zones visited for molting and on migration patterns, is more likely to have a major influence on the extent of molt of the different species, but more comparative data are needed.

In albatrosses the primary molting period is clearly separated from the breeding period. Very few albatrosses have been observed in active molt on the breeding grounds (Harris 1973, Furness 1988). In the Wandering Albatross, as well, molting occurs almost exclusively during the interbreeding period. However, some breeding birds start molting their primaries during the last months of the chick-rearing period (M. Salamolard, unpubl.). In breeders, the extent of molt could depend on the time available between two breeding attempts (Furness 1988). Wandering Albatrosses successful in fledging a chick have an entire year to recover from breeding, whereas birds that fail in their breeding before July have a shorter period (Tickell 1968). In males, the extent of primary molt is not significantly influenced by the length of the interbreeding period. In contrast, females renew more primaries after a successful breeding season than after failing to breed. Consequently, the extent of molt in females is related to the time available during the nonbreeding season. Failed and successful breeders from Crozet spend the interbreeding period at sea, in feeding zones that are different from those used during breeding period, particularly along the Australian coasts (Weimerskirch et al. 1985). In these oceanic zones, Wandering Albatrosses have to renew their feathers and, in addition, have to restore breeding condition for the next season. The replacement of feathers represents an increased energy requirement that could compete with the rebuilding of body re-
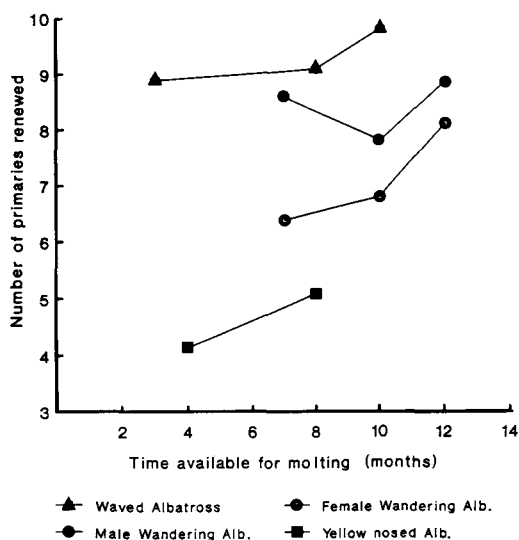

FIGURE 2. Number of primaries renewed per wing in relation to the length of the period between two breeding attempts (data for Yellow-nosed Albatross from Furne 1988 and for Waved Albatross from Harris 1973).

serves necessary for the next breeding season. This competition could occur in females where the extent of molt is dependent on the time available between two breeding attempts, but not in males. The difference between the sexes could result from the additional energy demand associated with egg formation. However, egg formation occurs in December in the Wandering Albatross, when the breeding females have already completed their molt. If energy is more limited for females than for males during the nonbreeding period, females could replace fewer feathers than do males in order to be able to breed the next season. However, molting may also increase the difficulty of obtaining food because of the reduced flight abilities incurred during the active replacement of flight feathers (Masman et al. 1988). Albatrosses are also subject to a higher mortality during the active renewal of flight feathers, being particularly vulnerable to storms (Kinsky 1968). Thus, in the life history of pelagic seabirds, molting could constitute an important constraint and very few relevant data on this topic are available on other species.

Immature birds have different constraints than do breeding birds. Although not concerned with breeding duties, they do visit their future breeding grounds regularly for pair formation (Pick-

ering 1989) and attain breeding condition and molt outside the breeding grounds. The smaller number of new primaries in immatures compared to breeding birds indicates that immatures probably have more difficulties in molting than do breeders. This difference probably results from a limitation in energy required for molting rather than in time available. Ultimately, the difference between immatures and adults results probably from young birds having not attained the same foraging skills than breeders (Burger 1988). When increasing their skills, immatures progressively increase their mass with age (Weimerskirch, unpubl. data), but not the number of renewed primaries. The significant relationship between the number of renewed primaries of nonbreeders and body mass observed in males, but not in females, indicates that body condition and molt could be more antagonistic in females than in males. In addition, molting during the period spent at sea and the ability to increase body mass from one season to another could be in conflict because at least in males the extent of molt is negatively related to the mass gain from one season to the next. The onset of breeding could be favored at the expense of molting in females because, when they start breeding, they are in the same body condition as are experienced birds (Weimerskirch, unpubl. data) but have fewer new feathers. During the period preceding their first nesting attempt, future breeders renewed more feathers than other immatures but less than did breeders. This indicates that, although they have a similar time available for molting, inexperienced birds breeding for the first time have not attained similar skills or met similar energy requirements as have experienced birds. After they have fledged a chick for the first time, males and females replace slightly fewer feathers than do successful experienced birds. This difference could result from the fact that during a first breeding attempt, inexperienced birds coordinate food provisioning to the chick much less effectively than do experienced birds (Lequette and Weimerskirch 1990). To recover from this first breeding season, consequently, they could have a higher energy requirement during the interbreeding season that could reduce the extent of molt.

Through this study, sex-specific differences in molting strategies have been highlighted. In Wandering Albatrosses, males and females differ significantly in several important aspects of their morphology, behavior, and life history. Females are 20–30% smaller in size and lighter than males. Males incubate slightly longer than do females (Fessanges du Bost and Segonzac 1976, Croxall and Ricketts 1983), and females probably take a smaller share than males in provisioning chicks towards the end of the chick-rearing period (Croxall and Prince 1990). The current study suggests that breeding and nonbreeding females have more difficulties in renewing their primaries than do males because they have invariably fewer new feathers. Each sex forages over different oceanic water masses (Weimerskirch and Jouventin 1987). Males favor the cold Antarctic waters whereas females are observed mostly over subantarctic and sub-tropical waters (Weimerskirch and Jouventin 1987). Food availability and weather conditions, particularly wind conditions that extensively influence foraging strategies in this species (Jouventin and Weimerskirch 1990), are very different between these two oceanic sectors. Consequently, differences in foraging zones are likely to be associated with sex-specific differences in foraging and food availability that inevitably affect the patterns of primary molt.

ACKNOWLEDGMENTS

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