

SOUTHERN FULMARS MOLT THEIR PRIMARY FEATHERS WHILE INCUBATING¹

CHRISTOPHE BARBRAUD AND OLIVIER CHASTEL

C. E. B. C./C. N. R. S., 79360 Villiers en Bois, France,

e-mail: petrel@cebc.cnrs.fr

Abstract. Molt-breeding overlap and the extent of molt of primary feathers were studied in the Southern Fulmar (*Fulmarus glacialisoides*) in relation to breeding status, sex, breeding experience, and age. Primary molt was observed among breeders and nonbreeders during the incubation period. Nonbreeders renew more feathers than breeders. In breeding individuals, males and females renew the same number of feathers. No difference in primary molt score was found between inexperienced and experienced breeders. However, the extent of primary molt was significantly related to age among breeders; older birds had less new feathers than younger birds. These results suggest that primary molt-breeding overlap in Southern Fulmars is a consequence of high food availability during the short summer and a reallocation of energy into molt during incubation. Possible reasons for differences in molt extent owing to age and breeding status are discussed.

Key words: breeding, *Fulmarus glacialisoides*, molt, Southern Fulmar.

Temporal overlap between molt and breeding is generally uncommon in bird species because of the great energy demands of each process (Payne 1972, Ricklefs 1974). However, overlap of breeding and molt has been found in several bird families, especially in the tropics (Payne 1969, Foster 1974). In seabirds, molt-breeding overlap is observed in Arctic/Antarctic species where resources are abundant for only a brief period (Carrick and Dunnet 1954, Furness 1988). Most of these studies indicate that body molt begins during incubation and that molt of the primary feathers in successful breeders does not commence until the young are near fledging, whereas in unsuccessful breeders primary molt may begin within a week of egg or chick loss.

Some authors suggest that the selective advantage of delayed primary molt in breeding birds is to retain maximum wing efficiency while feeding young (Beck 1970). In most seabirds of the order Procellariiformes, the primary molt period and the breeding period are separated (Stresemann and Stresemann 1966). For these species the molt-breeding overlap is narrow and birds usually do not shed their primaries until their chick is close to flying (Warham 1996), the only exception being the two species of Giant-Petrel (*Macronectes giganteus* and *M. hali*) in which wing molt starts before

or soon after the egg hatches (Hunter 1984). Warham (1962) also observed some Cape Petrels (*Daption capense*) losing their primaries in late incubation and during chick rearing, and more recently Monteiro and Furness (1996) found Cory's Shearwaters (*Calonectris diomedea*) molting their primaries during chick rearing.

Here, we report primary molt-breeding overlap in Southern Fulmars (*Fulmarus glacialisoides*) during incubation. Southern Fulmars breed during the brief austral summer in Antarctica and islands of the southern ocean. Laying occurs in early December, egg hatching lasts half of January, and departure occurs about mid-March to April (Prévost 1953). Birds breed annually and body molt begins during incubation in early January (Bierman and Voous 1950). These latter authors noted that outwards primaries molt from late December to early April, but gave no information concerning the status and age of birds inspected.

We document simultaneous breeding and primary molt in this fulmarine petrel, but also examine the wing molt in relation to the breeding status and age of the birds using a population of birds of known age and breeding status.

METHODS

The study was carried out at Pointe Géologie, Terre Adélie (66°20'S, 140°01'E) in January 1994. At Pointe Géologie, the entire population of Southern Fulmars (20 to 50 breeding pairs each year) has been banded since 1963, and thereafter captured every year (Weimerskirch 1990a). Thus, most birds were of known age and breeding experience. Birds were checked during the last part of the incubation period (1–10 January). Molt scores were collected from primary feathers on the right wing only as there is no apparent difference between both wings (Weimerskirch 1991). The scoring method used was that of Ashmole (1962) in which feather growth for each primary is estimated on a scale of 0 (old) to 5 (new). Scores for each primary are then summed to obtain an aggregate for the wing. We checked both breeders and nonbreeders. On average, 34% of experienced breeders skip breeding each year in Adélie Land (Chastel, unpubl. data). In this study, nonbreeders refer to birds known to have bred in a previous season. The extent of primary molt was studied in relation to breeding status and age. All statistical analyses were conducted using SYSTAT (1992). A significance level of $P < 0.05$ was used for all tests. Values are presented as mean \pm SD.

¹ Received 17 November 1997. Accepted 16 March 1998.

TABLE 1. The mean primary scores for Southern Fulmar breeders, nonbreeders, unsuccessful and successful breeders in January 1994 at Pointe Géologie (sample sizes in parentheses).

Breeding status	Primary scores	U^a	P
Nonbreeders	8.89 ± 3.41 (9)	54.5	<0.001
Breeders	3.37 ± 1.80 (49)		
Unsuccessful breeders	3.09 ± 0.54 (11)	207	ns
Successful breeders	3.45 ± 2.02 (38)		

^a Mann-Whitney U -test.

RESULTS

We inspected 58 birds and all were found in active primary molt in early January. There was a significant difference between breeders and nonbreeders in primary scores (Table 1). Nonbreeders had significantly more new primary feathers emerging or growing than breeders (G -test, $G_1 = 22.9$, $P < 0.001$). There was no significant difference between unsuccessful breeders and successful breeders in primary scores (Table 1). Considering breeding experience, first time breeders did not differ significantly from experienced breeders in their primary molt scores, although there was a tendency for inexperienced birds to exhibit lower scores (2.80 ± 0.84 , $n = 5$; 3.43 ± 1.87 , $n = 44$; respectively; $F_{1,48} = 0.5$). In breeding birds, the primary score was significantly correlated with the age of the birds, older birds having lower scores (Fig. 1). There was no significant difference in primary scores between males (3.53 ± 1.79 , $n = 17$) and females (3.44 ± 1.83 , $n = 27$; $F_{1,42} = 0.03$).

DISCUSSION

There is a clear primary molt-breeding overlap in the Southern Fulmar at Pointe Géologie, as primary molt was observed during the last part of the incubation period. Although for Procellariiformes the incubation period is less energy demanding than the brooding period (Ricklefs 1983), our result contrasts with previous studies on small fulmarine petrels indicating a delayed molt of the primary feathers until the young is near fledging (Carrick and Dunnet 1954, Brown 1966, Beck 1970). In the closely related Northern Fulmar (*Ful-*

marus glacialis) primary molt starts after departure from the breeding colony (late August) after successful nesting, earlier if failed (Cramp and Simmons 1977, Brown 1988). However, Carrick and Dunnet (1954) reported few birds molting their primaries while rearing a nestling. Molt-breeding overlap can occur only if energy and nutrients are available and adequate for both activities to occur simultaneously. Foster (1974) and King and Murphy (1985) proposed two hypotheses to account for this overlap: a dependence on nutrient reserves and a reduction or reallocation in energy or nutrient expenditure, or both. The absence of weight change at the beginning of shifts during incubation and the short time spent on foraging trips suggest that food availability is high and/or food is readily accessible to Southern Fulmars (Weimerskirch 1990b). Moreover, Weimerskirch suggested that during the incubation period the birds could have spent longer shifts on the nest, consequently losing more weight and consuming more energy. This result and ours suggest that Southern Fulmars might reduce or reallocate the energy or nutrient expenditure into primary molt during incubation.

The stage of molt was more advanced in nonbreeders than breeders, probably reflecting the trade-off between present reproductive effort and the timing of molt (Weimerskirch 1991). One possible explanation is that nonbreeders start molting primary feathers earlier than breeders. Because they do not invest energy into reproduction, nonbreeders could divert the energy not used for maintenance into the molting process. On the other hand, breeders and nonbreeders could initiate molting similarly, but breeders could delay their molt or molt at a slower rate than nonbreeders due to their high energy demand for reproduction. However, we did not study molting during the entire breeding cycle and cannot verify these hypotheses.

The stage of molt was identical between unsuccessful breeders and successful breeders during the study period. This result contrasts with previous studies on albatrosses indicating that failed breeders replaced more primaries than successful breeders and where primary molt and breeding do not overlap (Furness 1988, Weimerskirch 1991, Prince et al. 1993). When birds were inspected, unsuccessful breeders were birds which had lost their egg. Because primary molt usually begins within a week after egg loss (Warham 1990), the time interval was probably too short to detect differences in primary molt between unsuccessful and successful breeders at this stage of breeding.

Males and females had similar molt scores, probably indicating identical molting strategies for both sexes.

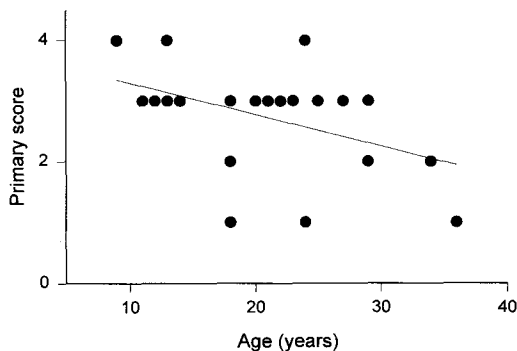


FIGURE 1. Primary scores in breeding male and female Southern Fulmars in relation to age ($r = -0.48$, $n = 31$, $P < 0.01$).

In Southern Fulmars, males and females do not differ significantly in weight losses during incubation and chick brooding, probably indicating similar energy expenditure for both sexes (Weimerskirch 1990b). It appears that sex-specific differences in molting strategies occur in species where males and females differ significantly in different aspects of their morphology, behavior, and life history (Payne 1972, Weimerskirch 1991), which could partly explain the absence of difference found in Southern Fulmars.

Studies conducted on albatrosses have shown that inexperienced breeders delayed primary molt compared to experienced birds (Furness 1988, Weimerskirch 1991). Although inexperienced Southern Fulmars tended to have lower scores than experienced birds, the difference was not significant. This might have been caused by the small sample size for inexperienced birds.

The stage of molt was clearly related to age of birds among breeders. Older birds molted less primary feathers than younger birds. Conversely, in albatrosses where primary molt and breeding do not overlap, first time breeders renewed less primaries than experienced and older birds (Weimerskirch 1991). One possible cause might be that among breeding fulmars, young birds started breeding later than old birds. Indeed, among Procellariiformes experienced and old birds usually lay earlier than inexperienced and young birds (Warham 1990). In Southern Fulmars, Weimerskirch (1990a) found that inexperienced birds hatched their eggs later than experienced birds. Consequently, young birds might have to start molting earlier than old birds to complete molt before the end of summer.

But why did not Southern Fulmars delay molting after breeding as apparently do other small fulmarine species? One possible cause might be that Southern Fulmars breed during a short summer season during which resource availability is high. Similarly, Hunter (1984) suggested that overlap between molt and breeding in Giant Petrels is a consequence of very abundant and easily available summer food supplies (mainly seal carrion from pupping fur seals). Indeed, the fact that both breeding and wing molt, which are high energy demanding processes, occur simultaneously could partly explain why Southern Fulmars lose weight at the highest daily rates known in Procellariiformes (Weimerskirch 1990b). Moreover, as fledging occurs in late March to early April when food availability decreases in Antarctic waters, molting might be too energy demanding at this time of the year. Molting and restoring body reserves after the breeding season might compete for energy, and this could have a negative influence on winter survival or future reproduction. Finally, as suggested for other petrel species (Hunter 1984, Chastel 1995), if Southern Fulmars delayed molt after breeding, timing also may be critical to both complete molt and restore body condition before the next breeding attempt.

This study was supported by the administration of Terres Australes et Antarctiques Françaises and the by the Institut Français pour la Recherche et la Technologie Polaires which provided the logistic and financial support. This study is a part of the programs on the ecology of birds and mammals of French southern ter-

ritories directed by P. Jouventin. We thank Peter Prince for suggestions and comments on an earlier version of this manuscript.

LITERATURE CITED

- ASHMOLE, N. P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 1. General biology. *Ibis* 103:235-273.
- BECK, J. R. 1970. Breeding seasons and molt in some smaller Antarctic petrels, p. 542-550. *In* M. W. Holdgate [ed.], Antarctic ecology. Vol. 1. Academic Press, London.
- BIERMAN, W. H., AND K. H. VOOUS. 1950. Birds observed and collected during the whaling expeditions of the 'Willem Barendsz' in the Antarctic, 1946-1947 and 1947-1948. Brill, Leiden, Netherlands.
- BROWN, D. A. 1966. Breeding biology of the Snow Petrel *Pagodroma nivea* (Forster). ANARE Sci. Rep. Ser. B.(1) Zool. Pub. 89:1-63.
- BROWN, R. G. B. 1988. The wing-moult of fulmars and shearwaters (*Procellariidae*) in Canadian Arctic waters. *Can. Field-Nat.* 102:203-208.
- CARRICK, R., AND G. M. DUNNET. 1954. Breeding of the fulmar *Fulmarus glacialis*. *Ibis* 96:356-370.
- CHASTEL, O. 1995. Influence of reproductive success on breeding frequency in four southern petrels. *Ibis* 137:360-363.
- CRAMP, S. 1977. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Vol. I. Oxford Univ. Press, Oxford.
- FOSTER, M. S. 1974. A model to explain molt-breeding overlap and clutch size in some tropical birds. *Evolution* 28:182-190.
- FURNESS, R. W. 1988. Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed Albatross *Diomedea chlororhynchus*. *J. Zool.* 215:719-727.
- HUNTER, S. 1984. Molt of the Giant Petrels *Macronectes halli* and *M. giganteus* at South Georgia. *Ibis* 126:119-132.
- KING, J. R., AND M. E. MURPHY. 1985. Periods of nutritional stress in the annual cycle of endotherms: fact or fiction. *Am. Zool.* 25:955-964.
- MONTEIRO, L. R., AND R. W. FURNESS. 1996. Molt of Cory's Shearwater during the breeding season. *Condor* 98:216-221.
- PAYNE, R. B. 1969. Overlap of breeding and molting schedules in a collection of African birds. *Condor* 71:140-145.
- PAYNE, R. B. 1972. Mechanism and control of molt, p. 103-155. *In* D. S. Farmer and J. R. King [eds.], Avian biology. Vol. 11. Academic Press, New York.
- PRÉVOST, J. 1953. Notes sur la reproduction du Fulmar Antarctique *Fulmarus glacialoides*. *Alauda* 21: 157-164.
- PRINCE, P. A., S. RODWELL, M. JONES, AND P. ROTHERY. 1993. Molt in Black-browed and Grey-headed Albatrosses *Diomedea melanophrys* and *D. chrysostoma*. *Ibis* 135:121-131.
- RICKLEFS, R. E. 1974. Energetics of reproduction in

- birds, p. 152–297. In R. A. Paynter [ed.], Avian energetics. Publ. Nuttall Ornithol. Club 15.
- RICKLEFS, R. E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Stud. Avian Biol.* 8:84–94.
- STRESEMAN, E., AND V. STRESEMAN. 1966. Die Mauser der Vogel. *J. Ornithol.* 107:1–445.
- SYSTAT. 1992. SYSTAT for windows: statistics. 5th ed. SYSTAT, Inc., Evanston, IL.
- WARHAM, J. 1962. The biology of the Giant Petrel *Macronectes giganteus*. *Auk* 79:139–160.
- WARHAM, J. 1990. The petrels: their ecology and breeding systems. Academic Press, London.
- WARHAM, J. 1996. The behaviour, population biology and physiology of the petrels. Academic Press, London.
- WEIMERSKIRCH, H. 1990a. The influence of age and experience on breeding performance of the Antarctic Fulmar *Fulmarus glacialis*. *J. Anim. Ecol.* 59:867–875.
- WEIMERSKIRCH, H. 1990b. Weight loss of Antarctic Fulmars *Fulmarus glacialis* during incubation and chick brooding. *Ibis* 131:68–77.
- WEIMERSKIRCH, H. 1991. Sex-specific differences in molt strategy in relation to breeding in the Wandering Albatross. *Condor* 93:731–737.

The Condor 100:566–568
© The Cooper Ornithological Society 1998

REJECTION OF ARTIFICIAL PARASITE EGGS BY GRAY KINGBIRDS IN THE BAHAMAS¹

MICHAEL E. BALTZ

*Division of Biological Sciences, University of Missouri, Columbia, MO 65211,
e-mail: c623359@showme.missouri.edu*

DIRK E. BURHANS

*North Central Research Station, 1-26 Agriculture Building, University of Missouri, Columbia, MO 65211,
e-mail: dburhans@raphael.snr.missouri.edu*

Abstract. We added artificial Shiny Cowbird (*Molothrus bonariensis*) eggs to Gray Kingbird (*Tyrannus dominicensis*) nests in the Bahamas, where Shiny Cowbirds were first recorded in 1993. Gray Kingbirds ejected 85% of artificial eggs within 48 hr of addition. Based upon the short time of contact between the two species, we suggest that egg ejection by Gray Kingbirds in the Bahamas is retention of ejection behavior from ancestral populations.

Key words: brood parasitism, egg ejection, Gray Kingbird, *Molothrus bonariensis*, Shiny Cowbird, *Tyrannus dominicensis*.

The Shiny Cowbird (*Molothrus bonariensis*) is a generalist brood parasite that has invaded the West Indies from South America during this century, recently arriving in North America (Post and Wiley 1977b, Post et al. 1993, Baltz 1995). The Shiny Cowbird parasitizes several host species in the West Indies region (Cruz et al. 1995), and some of these have been documented rejecting experimentally added cowbird eggs in Puerto Rico and St. Lucia (Cruz et al. 1985, Post et al. 1990). In many areas in the West Indies, Shiny Cowbirds have been in contact with host species for

over 90 years, enough time to have evolved egg ejection behavior (Rothstein 1975b). However, Shiny Cowbirds have only recently arrived in the Bahamas (Baltz 1995). Because Shiny Cowbirds have not been in prolonged contact with potential host species in the Bahamas, egg rejection behavior should not have had time to evolve in response to interspecific parasitism. We predicted that the Gray Kingbird (*Tyrannus dominicensis*), a known rejector of parasite eggs in Puerto Rico and St. Lucia (Cruz et al. 1985, Post et al. 1990), would not reject Shiny Cowbird eggs in the Bahamas. We tested this prediction by documenting the response of Gray Kingbirds in the Bahamas to artificial cowbird eggs added to their nests.

METHODS

The experiment was conducted from 3–14 July 1996, in the vicinity of Staniard Creek, North Andros Island, Bahamas. We generally followed Rothstein's (1975a) method of experimentally parasitizing nests. Artificial eggs were shaped by hand from Sculpey Modeling Clay (Polyform Products Inc., Elk Grove Village, Illinois), baked to harden, and painted with waterproof acrylic and enamel paints to resemble real Shiny Cowbird eggs: white ground color with "burnt umber" maculation. Real Shiny Cowbird eggs average 20.3 × 16.7 mm (Post and Wiley 1977a) and the artificial eggs averaged 20.8 × 16.4 mm ($n = 24$). Single artificial Shiny Cowbird eggs were added to 20 Gray Kingbird

¹ Received 15 December 1997. Accepted 16 April 1998.