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MOLT OF CORY'S SHEARWATER DURING THE BREEDING SEASON[1]

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Abstract. We studied the molt of adult Cory's Shearwater *Calonectris diomedea borealis* breeding at Vila Islet, Azores. Breeders appear to undergo a complete annual molt that overlaps considerably with the breeding season. Molt is minimal during most of the prelaying and early incubation periods (March–June). The cycle starts at middle incubation (main period July), with ventral body feather replacement at a locus on the upper breast that progresses downwards and laterally to the belly and flanks. Dorsal body molt apparently follows similar topographical and temporal patterns to those of ventral body molt. Primary renewal seems to be simple and descendent and it is estimated to take a mean of 207 days for completion, between 28 August and 22 March. Rectrix renewal apparently starts on the wintering grounds since it is advanced but not completed in March–May; then it is apparently suspended until August, when the renewal of the few remaining old rectrices is concluded in most birds by September. Such an overlap of wing molt and breeding has not been previously described in a pelagic and highly migratory seabird as the Cory's Shearwater. We suggest that the timing of molt in the species is dictated by intrinsic rhythms acquired by evolution rather than imposed by nutritional or energetic constraints.

Key words: Cory's Shearwater; Calonectris diomedea borealis; *breeding adults; molt; Azores.*

INTRODUCTION

There have been relatively few studies of molt in procellariiforms. Most species are wholly pelagic outside the breeding season and, hence, molt is difficult to study in the hand, since there is generally little overlap between the energetically costly activities of breeding and molt in birds (e.g., Payne 1972).

It has been widely reported that long-distance migratory shearwaters (e.g., Manx, *Puffinus puffinus*; Great, *P. gravis*; Sooty, *P. griseus*; Short-tailed, *P. tenuirostris*) delay primary molt until reaching their winter quarters (Marshall and Serventy 1956, Stresemann and Stresemann 1970, Brown 1988, Brooke 1990) despite some renewal of body and contour feathers while breeding (Warham 1990). In contrast, species with restricted post-breeding dispersion (e.g., fulmars, giant petrels, Balearic Shearwater *P. mauretanicus*) may not experience such a delay in primary molt (Warham 1990) and in some cases start it around egg hatching (Hunter 1984).

The Cory's Shearwater *Calonectris diomedea* is the largest breeding procellariiform of the North Atlantic and adjoining seas. It has three well marked subspecies (Warham 1990): *C. d. diomedea* (Mediterranean), *C. d. borealis* (off Iberia and Canary, Madeira, Salvages and Azores archipelagos), *C. d. edwardsii* (Cape Verde archipelago). Subspecies *borealis* attends the breeding colonies during nine months, from late February to late October and its main pelagic wintering area seems to be off eastern South America (Cramp 1977, Mougin et al. 1988, Monteiro et al. 1996). Subspecies *borealis* also shows a high degree of synchronization both within and between colonies, with laying from late May to early June, hatching in late July and fledging from late October to early November (Zino et al. 1987, Granadeiro 1991, Monteiro et al. 1996). Whereas the breeding phenology of *diomedea* matches closely that of *borealis* (Granadeiro 1991), its wintering area seems to be off western South Africa (Mougin et al. 1988). The biology of *edwardsii* is poorly known. Their breeding season appears to be the same length as the other two northern subspecies and their non-breeding range seems to be off western Central-South Africa (Hazevoet 1995).

The timing and sequence of molt in the Cory's Shearwater *Calonectris diomedea* are poorly known (Cramp 1977, Warham 1990). Some information has been provided by Mayaud (1949–

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1950), who described an extended and slow molt cycle for body feathers from a sample of museum skins of *diomedea* and *borealis,* Jouanin and Roux (1966), who reported the start of body molt in breeding adults of *borealis* at hatching, and Brown (1990), who described the molt of primary feathers in birds of unknown reproductive status, and presumed to be *borealis,* during August off Nova Scotia, Canada. There is a complete lack of information on the molt in the wintering areas. Here, we present molt observations obtained during the breeding season while we were collecting feathers of this species to monitor mercury contamination in the marine environment (Monteiro and Furness 1995). This study may well be representative of the molt cycle throughout the species range, considering the overall resemblance of breeding phenology among the three subspecies.

METHODS

The observations were made on individually banded adults breeding on Vila Islet, off Santa Maria, in the Azores, between 22 March–20 October 1994. Designation of feather types followed Brooke and Birkhead (1991).

All birds handled were examined for molt on the breast and scattered observations were made of other ventral and dorsal body feathers, tail and wing feathers. The molt stages of flight feathers were scored (Ginn and Melville 1983): O (= old feather remaining), 1 (= feather missing or in pin), 2 (= new feather emerging from the sheath up to one third grown), 3 (= new feather between one and two thirds grown), 4 (= new feather two thirds to full grown and with remains of waxy sheath or blood in calamus) and 5 (= new feather fully developed with no trace of waxy sheath and no blood in calamus). The fully renewed primaries scored 50 (ignoring the minute 11th primary) and the fully renewed tail scored 60. Since molt in the two wings is normally symmetrical only the right wing was examined. The sequence of replacement of primaries was assessed using the methodology devised by Langston and Rohwer (1995). We used linear regression of calendar date on primary molt score (Pimm 1976) for all birds captured in September–October and March to estimate molt parameters. Breast molt was recorded as 'in progress' when a minimum of five feathers were in pin or emerging from the sheath. In May and September, some birds were fully marked with picric dye on the ventral body surface to assess feather replacement in the following months; the proportion of new feathers on the ventral surface was scored 0 (= no new feathers), 1 (<26% new), 2 (26 to 50% new), 3 (51 to 75% new) and 4 (>75% new). Dorsal and head molt was detected by the presence of darker grayish feathers compared to abraded and brown old feathers, fading probably occurring as a result of disintegration of some of the cornified cell layers of the feather (Miller 1928).

In mid-June 1993, one primary 1 and primary 10 (in alternate wings) together with an outer rectrix were plucked from five breeding adults (three female and two male) to assess the feasibility of studying energetic costs of reproduction by ptilochronology (Grubb 1989).

RESULTS

WING MOLT

Primary molt of breeding adults had started in mid-September (scoring 4.4 ± 0.50 SE, range 0 to 15, $n = 63$) and progressed in October (scoring 12.1 ± 2.02 SE, range 4 to 28, $n = 13$); the median scores differ significantly between these months (Mann-Whitney U test, $Z = 3.73$, $P < 0.001$). In September, 68.3% of the birds observed were molting primaries (43/63) and among those 39.5% (17/43) had dropped primaries 1 and 2 and 44.2% (19/43) had dropped primaries 1 to 3. Up to five primaries were found molting (incompletely grown or missing) at one time. The outermost molting primary was the fifth in September and the sixth in October. The stage of wing molt observed in September did not differ significantly between sexes (29 females: 4.8 ± 0.73 SE; 28 males: 4.1 ± 0.77 SE; Mann-Whitney U test, $U = 361.0$, $p = 0.47$) nor between members of pairs (females: 5.7 ± 1.13 SE; males: 3.6 ± 1.27 SE; $n = 9$, Mann-Whitney U test, $Z = 1.18$, $p = 0.24$). Correlation of primary molt scores between members of pairs approached significance ($r = 0.63$, $p = 0.072$). Primary renewal was ending early in the breeding season, as indicated by mean wing scores in late March (49.4 ± 0.07 SE, range 48 to 50, $n = 32$). By then, renewal of all primaries was concluded in 34.4% (11/32) of the birds observed and in 62.5% (20/32) only primary 10 was incomplete, scoring 4 and showing blood in the calamus.

Primaries 1 to 6 were dropped in simple de-

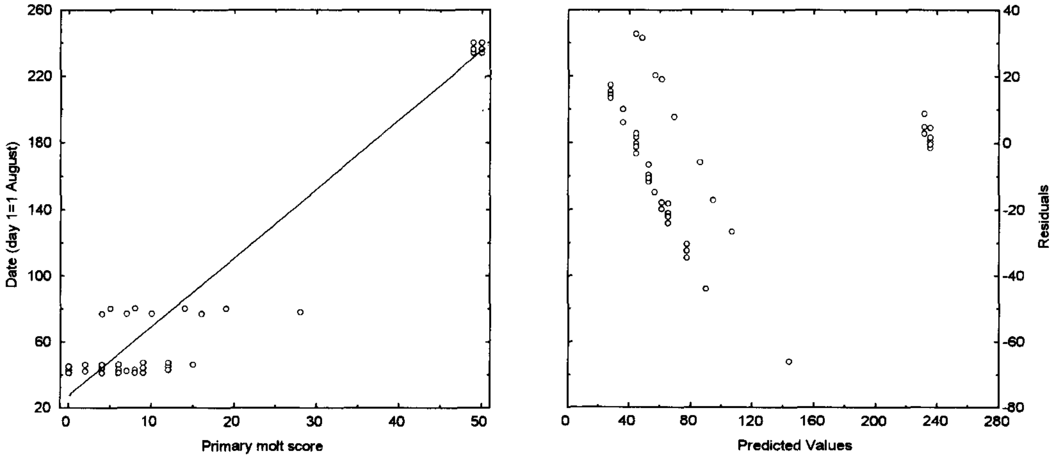

FIGURE 1. Scatterplots of calendar date with primary molt score (left) and residuals with predicted values (right) for adult Cory's Shearwater breeding on Vila Islet, Azores. For regression equation see text.

scending sequence from the innermost outwards, i.e., from proximal to distal. Indeed, in all birds showing actively growing primaries (September and October), the focal feather (Langston and Rohwer 1995) was less advanced in its growth than the next proximal feather, which was always also growing. The sequence of primary replacement ends with primary 10 (above) and the renewal of the P7–9 series presumably follows the simple descending sequence observed for the P1–6 series. Estimates of timing and duration of primary molt were derived from the linear regression equation of calendar date (day 1 = 1 August) on molt score (Fig. 1; DATE = 27.6 ± 2.2S.E. + 4.16 ± 0.08S.E. * SCORE, $r = 0.98$, $F_{1,106} = 2851.2$, $P < 0.0001$). The mean duration estimated in this way was 207 days and the mean estimated starting and completion dates were 28 August and 22 March.

Molt of secondaries was not observed during the study period. In March–May, six out 47 birds observed had one or two old secondaries. The greater secondary coverts were virtually all new in March. In birds molting primaries 1 to 3 during September, half or more of those greater coverts had been shed in exact sequence inwards towards the body and replacements were in pin and emerging; the median and lesser coverts of secondaries and all types of primary coverts were old and very abraded in that month. The renewal of upperwing coverts progressed in October. Then, most birds were molting all types of secondary coverts (three out of 13 had renewed completely the greater coverts) and some were shedding the greater primary coverts.

TAIL MOLT

The renewal of rectrices was advanced but not concluded at the beginning of the breeding season, as indicated by mean tail scores in late March (49.8 ± 3.34 SE, range 25 to 60, $n = 16$) and early May (55.7 ± 0.98 SE, range 45 to 60, $n = 35$). Old rectrices were observed in 50.0% (8/16) of the birds in March (up to 5) and in 37.1% (13/35) of the birds in May (up to 3). Actively growing rectrices were observed in 37.5% (6/16) of the birds in March (up to 2) and in 20.0% (7/35) of the birds in May (up to 6, the second maximum being 2). Subsequently, in June–July both worn and fresh rectrices were present, but no missing or incompletely grown ones, suggesting suspension of tail molt. In August shed rectrices started to be found in the colony and 47.0% of the birds (31/66) presented one to two growing or fresh rectrices; this frequency decreased significantly to 7.9% in September (5/63) ($\chi^2 = 24.41$, $P < 0.001$).

The uppertail coverts were all very abraded between March and July. Their molt started in August, when 81.8% of the birds (54/66) exhibited a mix of old, new and missing feathers. The molt of this tract progressed during September (all feathers renewed but some still growing) and was concluded in 76.9% of the birds (10/13) birds in October.

BODY MOLT

Ventral surface body molt started in early May (a few weeks before laying) at a locus on the upper breast and continued towards October (Table 1). The sex ratio of birds showing breast molt deviated significantly from 1:1 in May but not in June (respectively $\chi^2 = 7.65$, $P < 0.01$ and $\chi^2 = 2.90$, $p = 0.088$, with Yates correction). Females initiated breast molt in early May, i.e., a month earlier than males. It intensified in both sexes from early June to early July, when it was observed in 98% of the incubating birds. During that month ventral body-surface feather replacement progressed downwards and laterally to the belly and flanks. Then shed ventral body feathers began gradually to accumulate around the nests.

The average ventral molt score of birds marked with picric dye (Table 2) increased significantly from June to October (Kruskal-Wallis test, $H = 150.36$, $P < 0.001$). In June and July most birds scored 0 since new feathers were not fully grown yet. In August and September birds scored mainly 1 and 2, respectively, and showed a scattered distribution of new feathers over the ventral surface, with higher density in the breast region than in the belly/flank region. The maximum score observed was 3, in 2 out of 4 birds examined in October. On a return visit in March 1995, ventral molt was scored in some birds originally marked with picric dye in May 1994 (4.0 ± 0.0 SE, $n = 21$; all birds had exclusively new feathers, except for three with a few old feathers) and in September 1994 (1.8 ± 0.4 SE, $n = 5$). This, together with data from Table 2 strongly suggests that the entire ventral plumage is renewed between May/June and March.

Dorsal body molt showed the same temporal pattern as lower ventral body-surface molt. It started at a locus on the crown of the head in early July and progressed in August to the back region and tail coverts. Among the birds observed in August ($n = 66$), most showed a mixture of new (and growing) and old feathers in the back region (89.4%), uppertail coverts (81.8%), crown of the head (77.3%) and scapulars (57.6%). Fresh scapulars were also observed in late March, with some still showing blood in calumus.

INDUCED FLIGHT FEATHER GROWTH

None of the five adults involved in the ptilochronology feasibility assessment had begun to regrow primary 1, primary 10 or the outer rectrix until at least August, when they were checked for the last time in the year.

TABLE 1. Monthly frequency of breeding Cory's Shearwaters with breast molt by sex.

Month	Female		Male	
	n	Fr(%)	*n*	Fr(%)
March	25	0.0	30	0.0
May	50	20.0	49	0.0
June	52	5.8	54	18.5
July	48	97.9	43	97.7
August	26	100.0	25	100.0
September	19	100.0	24	100.0
October	6	100.0	7	100.0

DISCUSSION

Molt and breeding overlap to a great extent in Cory's Shearwater (Fig. 2). Molt begins during incubation (main period July), when ventral body-surface feather replacement starts at a locus on the upper breast and progresses downwards and laterally to the belly and flanks. Dorsal body molt apparently follows similar topographical and temporal patterns to those of ventral body molt. Primary renewal seems to be simple and descendent, with mean estimated starting and completion dates of 28 August and 22 March. Rectrix renewal apparently starts on wintering grounds and it is advanced but not completed in March–May; then it is apparently suspended until August, when the renewal of the few old rectrices left is concluded in most birds towards September. Molt is reduced to a minimum during most of the pre-laying period and early incubation (March–June). The species appears to exhibit a complete annual molt but this was demonstrated only for the replacement of ventral plumage and primaries.

Apparently there are no major differences in the timing of molt between sexes of Cory's Shear-

TABLE 2. Monthly variation of ventral molt scores (mean ± SE) of breeding Cory's Shearwaters marked with picric dye in May 1994.

Month	Score	*n*
June	0.0 ± 0.00	65
July	0.1 ± 0.03	66
August	1.0 ± 0.11	39
September	1.4 ± 0.10	34
October	2.5 ± 0.29	4

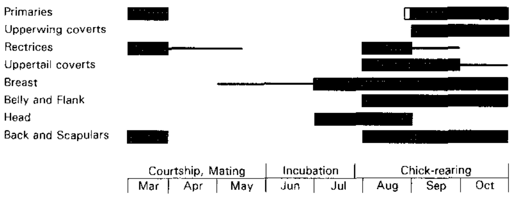

FIGURE 2. Phenology of molt of different tracts of the plumage of Cory's Shearwater in relation to phenology of breeding in breeders on Vila Islet, Azores. Dark blocks indicate observed main molting periods (in more than two thirds of birds examined) and lines indicate marginal molting periods (in less than two thirds of birds examined). For primaries, white block refers to estimated start (August) of renewal.

water, though sex differences have been found in other procellariiforms (Hunter 1984). Despite most birds being fairly synchronized in their stage of molt, some birds exhibited particularly advanced or delayed features that might relate to some extent to their recent breeding history, as reported for Yellow-nosed Albatrosses *Diomedea chlororhynchos* (Furness 1988). Also, it has been shown that non-breeding and failed breeding procellariiforms molt earlier and sometimes faster than do successful breeders in several species (Stresemann and Stresemann 1970, Hunter 1984). This might be the case for Cory's Shearwater. Brown (1990), using a technique that underestimates the actual number of molting birds, reported primary molt in 15 out of 121 birds observed in 15–31 August off Nova Scotia, Canada. He suggested that these birds were likely non-breeders and apparently their stage of primary molt is slightly advanced in comparison to breeders reported in this study. However, the difference is relatively small. More work on birds of known status and sex (and eventually age) is clearly needed to determine typical patterns.

Primary molt in breeding Cory's Shearwater starts about a month after peak hatching and two months before peak fledgling. This is particularly interesting because all migratory species of shearwaters and other wide-ranging procellariiforms apparently do not shed wing and tail feathers while breeding (Warham 1990, Prince et al. 1993). To the best of our knowledge, Cory's is unique among all long-distance migratory shearwaters in not delaying wing molt until winter quarters have been reached. The estimated duration of primary renewal in the study species (207 days) compares with about 90 days in Great and Short-tailed Shearwaters (Stresemann and Stresemann 1970) and 159 days in pre-breeding Sooty Shearwater (Cooper et al. 1991). The remarkable difference in duration of primary molt between Cory's and Great Shearwaters, two similar sized long-distance migrant species whose adults spent relatively short periods on wintering grounds (approximately two to three months), suggests an unusual slow molt in the study species and/or some interruption in the wintering grounds.

Molt strategies are determined by either endogenous factors such as hormones, exogenous constraints, or a combination of these (Hall et al. 1987, Murphy and King 1987, Furness 1988). The ability of Cory's Shearwater to undertake two energetically demanding activities like molt and chick-rearing simultaneously suggests an abundant food supply at their breeding grounds and, hence a lack of nutritional or energetic constraints. This is supported by further evidence we collected on the failure of Cory's Shearwater to regrow flight feathers plucked during incubation. The energetic cost of renewing such feathers did not seem to represent a critical addition to the normal daily energy budget of the birds, since it is precisely during incubation they attain the peak body mass of the entire breeding season (Monteiro et al. 1996). The suspension of tail molt (with just less than three old feathers) during June–July and the incapacity to regrow induced flight feathers in July–August at a time when molt of body feathers is progressing strongly suggest that the timing of molt in this species is dictated by intrinsic rhythms acquired by evolution rather than imposed by exogenous constraints.

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