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PRIMARY MOLT AND TRANSEQUATORIAL MIGRATION OF THE SOOTY SHEARWATER[1]

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Abstract. Examination of beached corpses of 244 Sooty Shearwaters (*Puffinus griseus*) from the southwestern Cape, South Africa, showed that simple descendent primary molt occurs from December to June, with most records being in the months of February and March. Based on percentage feather mass grown, primary molt takes a mean of 159 days for completion, with mean estimated starting and completion dates of 2 January and 10 June. Because the completion of breeding extends from late March to early May, the birds studied cannot have bred successfully in the previous austral summer and were probably prebreeders. Unlike the situation in the North Pacific Ocean, Sooty Shearwaters in the North Atlantic Ocean do not undergo primary molt. The hypothesis that Sooty Shearwaters of breeding age migrate preferentially into the North Pacific, whereas young birds first molt in the South Atlantic Ocean before migrating into the North Atlantic, needs to be tested by extensive banding of birds at the breeding localities.

Key words: *Sooty Shearwater;* Puffinus griseus; *beached specimens; primary molt; trans-equatorial migration; South Africa.*

INTRODUCTION

Seabirds of the Order Procellariiformes are, with few exceptions, wholly pelagic outside their breeding seasons when they cannot easily be studied in the hand. For this reason, there have been relatively few detailed studies of molt in procellariiforms, since for birds there is generally little temporal overlap between the energetically costly activities of breeding and molting (e.g., Payne 1972). Most procellariiforms undertake a post-nuptial molt of their primary feathers (Stresemann and Stresemann 1966), although exceptions to the lack of an overlap have been recorded in the fulmarine petrels of the genera *Daption, Pagodroma, Fulmarus* and *Macronectes* and in the British Storm Petrel (*Hydrobates pelagicus*) (e.g., Harris 1966; Beck 1969, 1970; Hunter 1984).

It has long been known that procellariiforms which undertake long-distance migrations after breeding delay molting their flight feathers until they have reached their wintering grounds (e.g., Loomis 1921, Marshall and Serventy 1956a, Beck and Brown 1972, Brooke 1990). Such a delay has been attributed to the need for a complete set of flight feathers, with no increase in wing-loading and an assumed reduction in flight efficiency, while rapidly migrating long distances between breeding and wintering areas (e.g., Stresemann and Stresemann 1970, Brown 1988). In contrast, closely related species which do not undergo such long migrations may not experience such a delay in commencement of molt (e.g., Marshall and Serventy 1956a, Beck 1970, Beck and Brown 1972, Cramp and Simmons 1977, Brooke 1990).

The difficulty of obtaining procellariiforms to study their molt in the hand has led some workers to base their conclusions on observations made from vessels of birds at sea seen to be actively molting their flight feathers (Watson 1971; Brown 1988, 1990). While useful, such studies do not allow the onset, completion and duration of molt to be accurately calculated, because only the presence of obvious gaps in the wing (as illustrated by Watson 1971 and Ogi et al. 1981) can be used to denote active molt. Birds commencing and completing primary molt will not be so easily discerned and those with inter-

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rupted molt (perhaps as many as half) will also be overlooked (Brown 1988). The usual alternative is to collect specimens at sea, either deliberately (e.g., Stresemann and Stresemann 1970) or by examining birds caught incidentally during fishing operations (e.g., Ogi et al. 1981). For various reasons, it is not always desirable or practical to collect birds at sea. However, pelagic seabirds are prone to being 'wrecked' under adverse conditions, when their corpses may be washed ashore in numbers (e.g., Ryan et al. 1989). Beached specimens offer an opportunity to study the molt of procellariiform species which otherwise are not readily available outside their breeding seasons.

The Sooty Shearwater (*Puffinus griseus*) is a procellariiform seabird which undergoes long and rapid transequatorial migrations between its Australasian and South American breeding grounds in the southern hemisphere and wintering areas in the North Pacific and North Atlantic Oceans (e.g., Bourne 1956, Phillips 1963, Briggs and Chu 1986, Brown 1988). Some birds may winter south of the equator, including in southern African waters (e.g., Stanford 1953, Phillips 1963, Richdale 1963, Ryan and Rose 1989). Here, we discuss the primary molt of Sooty Shearwaters found dead on South African beaches in relation to transequatorial migration.

METHODS

Regular monthly patrols of selected beaches for dead seabirds have been carried out in the southwestern Cape, South Africa since 1977 (Avery 1989 and references therein). Sooty Shearwaters in fresh condition, and considered to have been dead for no more than one week, had the molt of their primary feathers scored on one wing, following the standard 0–5 scale of Ginn and Melville (1983). Birds were not sexed or aged. Primary molt scores were also obtained from nine birds shot at sea off the southwestern Cape for dietary studies during March 1983 and February 1984 (Jackson 1988, Fitzpatrick Institute, unpubl. data).

Fully grown primary feathers were removed from eight birds, dried to constant mass at 50°C in a forced-draught oven, and weighed to the nearest 0.1 mg. The dried masses for each primary were averaged and expressed as a percentage of the total mass of all ten primaries. The primary molt scores were then converted to percentage feather mass grown (PFMG) as described by Underhill and Zucchini (1988). PFMG takes into account the differences in the relative size of the primaries and is used in preference to summing the individual primary feather molt scores. PFMG was assumed to increase linearly with time and was used as a molt index in the Underhill-Zucchini molt model. This model estimates the following parameters (and their standard errors): duration of primary molt τ, mean starting date μ and the variability of starting dates σ. The mean starting date and the variability of starting date are modeled as a normal distribution with mean μ and standard deviation σ. Under the assumptions of the model the distribution of completion dates is also a normal distribution, with mean $\mu + \tau$ and the same standard deviation σ. The model makes it possible to estimate intervals in which, say, 95% of the population commenced or completed primary molt.

The algorithm given by Underhill and Zucchini (1988) uses three types of data to estimate these parameters, data types 2 and 3 are relevant here. With data type 2, it is assumed that the observed molts consist of a random sample of all birds on each sampling date, including birds that have not yet commenced molt, those in molt, and those that have completed molt. All three kinds of data are used to estimate the parameters of molt. With data type 3, only birds in molt are used in parameter estimation, and the only assumption is that the birds observed in molt form a random sample of that fraction of the population which is actively molting on each sampling data: birds with no feathers in molt may be either over-represented or under-represented in the observed sample relative to the population without altering the parameters estimated (Underhill et al. 1990; Underhill et al., in press). If the results for data types 2 and 3 coincide, the implication is that the number of birds observed with complete primaries (either old or new) is representative of the proportions of such birds in the population. For a fuller discussion of this point see Underhill et al. (1990) and Underhill et al. (in press).

RESULTS

A total of 653 Sooty Shearwaters was found on a cumulative total of 8,271 km of patrolled shoreline of the southwestern Cape, South Africa from 1977 to 1990. Most birds (83.5%) were found beached near Yzerfontein (33°21′S, 18°08′E) and within False Bay (34°05′S, 18°10′E),

TABLE 1. Seasonal variation in the numbers and proportions of Sooty Shearwaters found ashore and molting their primaries in the southwestern Cape, South Africa, 1977–1990.

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
No. found on patrols	12	30	5	15	23	29	56	179	163	87	31	23	653
Total no. examined for molt	2	8	1	1	5	5	24	85	71	25	7	10	244
No. in molt	0	3	0	0	0	1	15	82	70	25	7	6	209
% molting	0.0	37.5	0.0	0.0	0.0	20.0	62.5	96.5	98.6	100.0	100.0	60.0	85.7

particularly in the months of January to April (74.3%, Table 1).

Primary molt scores were recorded from 244 specimens during the years 1977 to 1990, of which 209 (85.7%) were actively molting their primaries. Primary molt was simple and descendent and only one case of interrupted molt (both worn and fresh primary feathers present, but no missing or incompletely grown ones) was observed (20 February 1986; molt score 20). Twenty specimens examined had not commenced and 15 had completed primary molt. Nearly all those in primary molt were found during the months of December to June, with three finishing their molts in August (molt scores 46, 49 and 49). 72.7% of molting birds were found in February and March (Table 1). The seasonal distribution of all beached specimens and those in primary molt are broadly similar (Table 1). The proportions of examined birds in active primary molt varied monthly from 0–100% (Table 1). Perhaps because the numbers of specimens found varied greatly between years (3–115), no differences in the seasonal occurrence of molting were noticeable between years.

Up to five primaries were found molting (feathers incompletely grown or missing) at one time (Table 2). The mean number of primaries in molt simultaneously decreased significantly with increasing molt score ($\chi^2_6 = 52.8, P < 0.001$, Table 2).

The dried mass of the tenth and outer primary was 5.3 times that of the innermost feather, representing nearly 19% of the total dried mass of primaries (Table 3). Based on the Underhill-Zucchini model using data type 2, the mean individual duration of primary molt was estimated to be 159 days, with a 95% confidence interval of 143 to 175 days (Table 4). Mean estimated starting and completion dates were 2 January and 4 June. An estimated 95% commenced primary molt between 13 November and 21 February and completed molt between 21 April and 30 July (Table 4). Nearly identical results, with larger standard errors due to smaller sample size,

TABLE 2. Numbers and percentages of Sooty Shearwaters simultaneously molting a given number of primaries at three stages of primary molt and mean numbers of primaries molting simultaneously at each stage in the southwestern Cape, South Africa, 1977–1990.

	Molt score					
	No.	% 1–15	No.	% 16–35	No.	% 36–49
Number of primaries in molt simultaneously						
0	0	0.0	1	0.7	0	0.0
1	2	8.3	13	9.4	10	22.7
2	2	8.3	92	6.1	25	56.9
3	12	50.0	31	22.0	7	15.9
4	7	29.2	1	0.7	2	4.5
5	1	4.2	3	2.1	0	0.0
Mean number of primaries molting simultaneously		3.1		2.2		2.0
Sample size	24		141		44	

TABLE 3. Mean masses of the primaries of the Sooty Shearwater.

Primary no.	Sample size	Average mass (SE) (mg)	Relative mass (%)
1	8	91.0 (4.4)	3.55
2	8	105.6 (7.5)	4.11
3	8	130.7 (9.8)	5.09
4	6	167.8 (10.9)	6.54
5	4	213.5 (4.5)	8.32
6	2	264.3	10.30
7	4	312.4 (9.1)	12.17
8	8	367.2 (7.4)	14.31
9	8	428.9 (23.4)	16.71
10	7	485.5 (21.2)	18.91

were obtained using data type 3 (Table 4). The fact that the parameters of molt estimated using both data types 2 and 3 were essentially identical indicates that mortality is independent of the state of molt. It also indicates that there is no tendency for Sooty Shearwaters to arrive in the southwestern Cape to commence primary molt, or to leave as soon as molt is completed. Therefore, movements of birds in and out of the southwestern Cape are apparently independent of the state of primary molt. The three birds molting in August (Table 1) were diagnosed by the model to be outliers relative to the remainder of the observations (Underhill and Zucchini 1988), and therefore have not been included in the calculations.

DISCUSSION

Sooty Shearwaters are present all year round in southern African waters, but are most abundant during the austral winter (Richdale 1963, Jackson 1988, Ryan and Rose 1989). Because no banded birds have been recovered off southern Africa (T. B. Oatley, South African Bird Ringing Unit, pers. comm.) and because there is no known taxonomic or morphological variation in the various breeding populations of the species (Murphy 1930, Cramp and Simmons 1977, Jouanin and Mougin 1979) it cannot be stated where the Sooty Shearwaters occurring in South African waters breed. Fledging of chicks and departure of successfully breeding adults takes place from late March to early May and prebreeding birds depart from early February onwards at breeding localities in Australasia and the Falkland Islands (Richdale 1944, 1963; Woods 1975; Warham et al. 1982) Because most Sooty Shearwaters in South African waters undertake primary molt from mid-November to mid-July, the visiting population must presumably contain a large proportion of prebreeders and possibly some failed breeders. This cannot be proven without recoveries of birds of known age, because Sooty Shearwaters cannot be aged on external morphological grounds (Cramp and Simmons 1977), but the presence of birds in South African waters in all months of the year supports this assumption. Age at first breeding is not accurately known for the Sooty Shearwater (Richdale 1963, Warham et al. 1982) but is most commonly five to eight years in the closely related Short-tailed Shearwater (*P. tenuirostris*) (Serventy 1957, Wooller et al. 1988), which is also a transequatorial migrant (Serventy 1953, Marshall and Serventy 1956b).

Loomis (1918) reported molting Sooty Shearwaters from late February off California and it must also be assumed that these birds were either prebreeders or had failed breeding early in the season. That young, nonbreeding and failed breeding procellariiform seabirds molt earlier (and sometimes faster) than do successful breeders has been shown variously for several species

TABLE 4. The parameters of molt for Sooty Shearwaters, estimated using the Underhill-Zucchini Model. Standard errors (in days) of estimates given in parentheses.

Mean starting date	Standard deviation of starting dates (days)	Dates between which 95% of birds start primary molt	Duration (days)	Mean completion date	Dates between which 95% of birds finish molt
Data type 2					
2 January (3.4)	25.7 (1.7)	13 November–21 February	159.4 (8.0)	10 June (5.4)	21 April–30 July
Data type 3					
2 January (5.6)	26.4 (2.2)	11 November–17 February	159.0 (13.2)	10 June (8.3)	20 April–31 July

of fulmarine petrels and for the Greater Shearwater (*P. gravis*) (Wynne-Edwards 1939; Carrick and Dunnet 1956; Beck 1969, 1970; Stresemann and Stresemann 1970; Hunter 1984). Peak numbers of Sooty Shearwaters off California do not occur until April–May (Briggs and Chu 1986), at the end of the breeding season. Thus, most Sooty Shearwaters off California, and probably throughout the North Pacific, are likely to be of breeding age.

In the North Pacific Ocean Sooty Shearwaters have been recorded in active primary molt from 22 June–7 August (Ogi et al. 1981; but deduced from a reduction in wing measurements, therefore resulting in an artificially delayed starting date). Brown (1988) observed the presence of active primary molt in the first week of May off California (up to 72% of birds observed) and from the end of April as soon as birds had arrived off British Columbia, where by the end of May 90% showed signs of active primary molt. Chu (1984) recorded primary and secondary molt of 166 Sooty Shearwaters collected at sea in Monterey Bay, California from May to September. By the latter month over half those examined had completed molt. Loomis (1918) recorded the presence of primary molt off California as late as October.

In complete contrast to the situation in the North Pacific, 603 Sooty Shearwaters observed at sea in the North Atlantic by Brown (1988, 1990) during May to November (with one exception of a 30 May individual with a single primary feather missing from one wing) had all completed primary molt and were in fresh plumage. Mayaud (1949–1950) did not observe primary molt in 13 specimens collected off France between August and January which were in fresh plumage, but did record primary molt in an early November specimen. Based on the state of their gonads, Mayaud (1949–1950) considered his North Atlantic specimens to be mostly juveniles. On the above evidence and that of the present study, it appears that Sooty Shearwaters migrating into the South and North Atlantic Oceans are either prebreeders (as already postulated by Brown 1988) and/or failed breeders, whereas birds migrating into and molting within North Pacific waters are mainly adults of breeding age. Sooty Shearwaters that arrive off the eastern seaboard of Canada in early to mid-May (Phillips 1963, Brown et al. 1981, Brown 1988) have presumably completed their molt in the South Atlantic. A few individuals, assumed to be nonbreeders, arrive off Newfoundland in late March (Rees 1964).

A newly fledged "juvenile" banded in the Falklands on 3 May 1962 and recovered at St. Philip, Barbados in the North Atlantic on 1 June the same year (Woods 1975) represents the only transequatorial movement of a banded prebreeding Sooty Shearwater. Transequatorial recoveries of adults banded in their burrows at Australasian breeding localities ($n = 10$) are all from the North Pacific Ocean (Richdale 1957, Hitchcock 1961, Warham 1964, Hitchcock 1966, Warham et al. 1982, R. O. Cossee, New Zealand National Banding Scheme, pers. comm.; K. M. Lowe, Australian Bird and Bat Banding Schemes, pers. comm.). A chick banded in New Zealand and recovered 10 years later in Oregon, U.S.A. (Cossee 1989) also represents an adult movement across the equator.

The fact that many more Sooty Shearwaters migrate into the North Pacific than into the North Atlantic (Phillips 1963, Brown 1988) is not at variance with a migratory separation in two oceans of prebreeders and birds of breeding age, because in an assumed long-lived species the latter category is certain to be the larger one. The closely related Short-tailed Shearwater has been recorded as breeding over more than a 30-year period (Wooller et al. 1988).

There are no previous published estimates of the duration of primary molt in the Sooty Shearwater. Based on 112 examined specimens of the Greater Shearwater, Stresemann and Stresemann (1970) estimated that primary molt took about 90 days in adults of this species, which is also a transequatorial migrant breeding in the southern hemisphere (Cramp and Simmons 1977). Stresemann and Stresemann (1970) also estimated that primary molt of adult Short-tailed Shearwaters, while in the North Pacific (Marshall and Serventy 1956a, Palmer 1962), takes 82–100 days. Brown (1988) considered that Greater Shearwaters completed primary molt in only 40 days off Newfoundland, but this is likely to be an underestimate due to the observation technique used. Based on banding returns (Morant 1977) it is clear that, apparently unlike Sooty Shearwaters, both juvenile and adult Greater Shearwaters migrate to the North Atlantic, where they arrive in late May and early June and adults depart by the end of August (Stresemann and Stresemann 1970, Brown 1988). The relatively

short period spent by adults of this species on the wintering grounds (approximately two months) means that they have to complete primary molt quickly. Stresemann and Stresemann (1970) reported up to five primaries molting simultaneously in the Greater Shearwater. Meinertzhagen (1956) observed Greater Shearwaters in "full wing moult, many unable to fly" in June and August off Greenland, and Voous (1970) observed a near-flightless bird with "all primaries being short" in August in the Bay of Biscay. Greater Shearwaters, presumably young birds or failed breeders, can also molt in the southern hemisphere as early as January (Watson 1971). Stresemann and Stresemann (1970) found that juvenile Greater Shearwaters commenced primary molt earlier than did adults in the North Atlantic.

It is assumed that Sooty Shearwaters molting in southern African waters during December to June are birds of prebreeding age or are failed breeders which may then migrate across the equator into the North Atlantic. Their apparently leisurely molt contrasts with that known for adult Greater and Short-tailed Shearwaters. It remains to be investigated whether successfully breeding Sooty Shearwaters molt their primary feathers more quickly, in a manner akin to that of Greater and Short-tailed Shearwaters and successfully breeding fulmarine petrels. To this end, beached corpses of Sooty Shearwaters in the North Pacific should be examined quantitatively for primary molt. The three Sooty Shearwaters molting in South African waters in August may have belonged to a different subpopulation to that of the remainder of the molting individuals and could have been birds which had bred successfully the previous austral summer.

To elucidate further whether prebreeding Sooty Shearwaters preferentially head north in the Atlantic Ocean whereas adults migrate to the North Pacific requires concerted efforts to band large numbers of both fledglings and breeding adults at different breeding colonies in the southern hemisphere.

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