Synchronous breeding and moult in the Brown Noddy tern on Soldado Rock, Trinidad.

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Introduction

In most birds the processes of breeding and the main annual moult are mutually exclusive. Breeding usually occurs at times of the year when feeding opportunities are at their highest for the species, so that the parent birds most easily overcome the problems of feeding during incubation and the care of fledglings. In a great many species the breeding cycle is annual, following seasonal changes in climate and vegetation; but in some tropical birds breeding occurs at non-annual intervals, since seasonal fluctuations are less marked.

All birds need to moult at regular intervals, to replace worn or damaged feathers and to promote adequate feather maintenance. While some minor moulting processes may occur at any time, the main moult involves the replacement of all the feather tracts, including the all-important feathers of wings and tail; since the new feathers have to replace those that have already fallen out, the period when flight feathers are being replaced is for many birds a time of stress, when flying is somewhat impaired and normal activities correspondingly reduced. Thus we can expect that the periods of breeding and the main moult will not overlap. In the great majority of species this is so, and the most commonly found regime is that where the moult occurs soon after the end of the breeding season. So during the moult many birds are shy and retiring, and their activity seems to be at its lowest ebb. This period usually lasts perhaps two to three months at most, long enough for the nine or ten primary wing feathers – the normal number in the majority of species – to be replaced without impairing too much the ability to fly. In some waterfowl moult is much more rapid, so that for about three weeks so many primaries are missing or at an early stage of growth that the birds cannot fly at all during this period and are consequently extremely vulnerable.

Seabirds generally resemble land-birds in their moulding process, with the periods of moult and breeding being mutually exclusive. While this seems to be the case in seasonal environments, in some tropical species breeding occurs at non-annual intervals, even as short as six months. In such cases the moult too varies from the annual regime and seems to be "tied" to the breeding periodicity. Ashmole (1965) found that some Sooty Terns, *Sterna fuscata* , bred on Christmas Island at 6-month intervals, following lack of success at the previous occasion. Those birds that were successful, however, would not breed until 12 months later. During the non-breeding period moult was continuous but stopped when breeding commenced, even though incomplete. However, other populations of *S. fuscata* breed and moult annually, and still others at intervals of 9-10 months.

My interest in the moult of the Brown Noddy tern, *Anous stolidus,* began in 1963 when I found that birds breeding on Soldado Rock appeared to be in the middle of a moult cycle. My suspicions were confirmed by an article by Dorward & Ashmole (1963) who found a few moulting Brown Noddies breeding on Ascension Island. My work with the species in collaboration with the Trinidad Regional Virus Laboratory (ffrench 1990) during 1963-1964 suggested that the species completed its moult very slowly over many months. Birds were found to be moulting some primary feathers during all months between April and late October, some even into early January. Moreover, discussions with W.B. Robertson Jr. revealed that this species also moulted during the breeding season on the Dry Tortugas in Florida. Consequently I decided to investigate the phenomenon more closely, to try to determine whether breeding activities influenced the rate of the moult process in any way.

Methods

During 1966 and 1967 I made thirteen visits to Soldado Rock, which is situated 10 km west of Icacos Point, Trinidad (Lat. 10°4'25"N, Long. 62°0'56"W). For a description of the island see my account in the last issue of this journal (ffrench 1990), where I stated that the colony of Brown Noddy terns numbered at least 3000 birds. I intended my visits in 1966 to be fortnightly during the entire breeding season, but unfortunately I had to miss one of the scheduled visits. Table I shows that over the period of the study I captured and examined for moult 596 adult birds, including 197 that were taken during four visits during 1967, made to determine the situation at the beginning and end of the moult, and to establish annual periodicity in this population.

The advantage of the Soldado Rock location was its comparatively small size, which allowed me to concentrate on those groups of birds easiest to catch and observe, so that enough individuals could be identified with coloured bands. Thus I banded 265 individuals, and, of the 596 captured, 233 were birds taken and examined on second or subsequent occasions, some up to five times. Each captive was also examined for moult and its progress recorded, the primary moult being allotted a score according to an established formula (see below). I also spent much time observing specific nesting locations, and was thus able to determine for many individually colour-marked birds the precise stage of their nesting cycle (e.g. eggs, small, medium or large chicks, etc.).

My visits lasted about 24 hours on each occasion. I arrived during the afternoon, spending the remainder of the daylight hours in observation. After dark I caught by hand and

Table I Adult Brown Noddy terns captured on Soldado Rock, Trinidad 1966-1967.

Date of visit	No. of birds examined	No. of birds newly banded*	No. of birds re-captured
2 Apr 66	50	37	-
16 Apr 66	79	44	17
30 Apr 66	13	7	6
14 May 66	46	21	10
11 Jun 66	60	24	24
25 Jun 66	39	7	27
9 Jul 66	41	14	27
24 Jul 66	42	17	19
6 Aug 66	29	12	13
4 Mar 67	36	13	14
18 Mar 67	78	33	35
30 Sep 67	40	21	14
14 Oct 67	43	15	27
Total	596	265	233

* Some captives had previously been banded during 1960-1965, but were retrapped only once in the course of the 1966-1967 study.

examined the birds, using a head-lamp. The greatest success in capturing was always achieved on moonless nights, when birds proved easy to catch on or beside their nests. On some bright moonlit nights I had so little success that I had to resort to trapping by mist-net at dawn, but this method was comparatively little used. On the second day of each visit I concentrated on observing individuals to determine their precise nest-sites and to examine behaviour.

On almost all these visits I was accompanied by at least one person, often my wife Margaret; other people who assisted me were J. Bush, R.M. Clyde, J. Darlington, F. ffrench, E.J. Fisk, J. Frampton, P. Herlin, W. Houston, K. Martin and P. Pawsey. To all of them go my grateful thanks; I am also indebted to W.B. Robertson Jr. for valuable discussions and to the Frank M. Chapman Memorial Fund of the American Museum of Natural History in New York for logistical support.

The method used for scoring primary moult followed that established in several other studies of moult. It was as follows: For each wing containing ten primary feathers an "old" feather scored 0, a feather missing or in small pin scored 1, a feather in large pin or brush scored 2, a half-grown feather scored 3, one between half and three-quarters grown scored 4, and one between three-quarters and fully developed scored 5. Thus each wing had a maximum score of 50 just after the moult was completed, and a score of 0 just before the moult began. Moult was almost invariably at a similar point in both wings at the same time, any variation rarely exceeding one point (but see below). In Brown Noddies the appearance of "old" and "new" feathers is quite clear, the former being paler as well as often damaged or frayed at the tip.

Results

In 1966 the breeding season had already started when I made my first visit on 2 April, and there were many birds with eggs. By 16 April only a few chicks had hatched, but an early rain storm in late April destroyed many clutches, so that on 30 April I found a scene of devastation with many dead chicks and broken egg-shells. On that day no complete eggs were found, but a few young chicks had survived.

However, the colony re-nested, a few new eggs being found on 14 May and many on 11 June. In addition to the few chicks which survived the early storm, many others hatched from the May re-laying, while a few were still unhatched on 9 July. By 24 July all eggs had hatched and there were many chicks. On 6 August there were only a few unfledged chicks left, with many young birds flying; among the adults some had already begun to disperse.

In 1967 I found no eggs at all on 4 March, although there were many adults present; on 18 March about 50 eggs were found, and the number of adults was further increased. By 30 September there was no sign of breeding activity and the population had decreased to the off-season norm of about 1000 birds.

The record of moult scores (both wings) is shown in Figure 1, which confirms that the progress of moult is at least roughly regular for two consecutive years. It also shows that the average rate varied little throughout the entire moulting process, which lasted between 9 and 10 months, from late February to November or December. But of course the problem with average figures is that they may well include considerable numbers of birds that were not at the same stage of the breeding cycle as others in the sample.

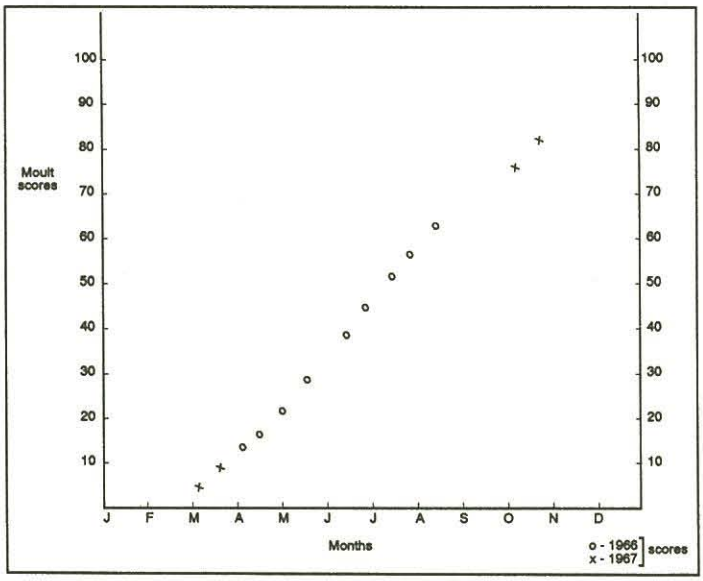

Figure 1. Average moult scores of 596 Brown Noddy terns 1966 - 1967

Table II indicates that for individuals examined twice during their known breeding stages the rate of moult slowed up during the period when young chicks were being fed, but changed barely at all during incubation. It is known that the incubation and fledging periods in Brown Noddy terns are roughly five weeks long in each case (ffrench 1980). Fortunately I was able to obtain more precise data from eight individuals, which I retrapped at regular intervals showing their rate of moult progress at times when I could determine the stage of their individual breeding cycles.

Table III gives individual rates of change for eight birds which were examined between three and five times each, and whose breeding stages were fairly precisely known. Here too parents of young chicks had a noticeably slower rate than those with eggs or older chicks. Clearly, however, we would like to have had larger samples with even more precise data.

As might be expected from the large numbers of birds examined, a few individuals displayed anomalies that could not be explained. One bird, 01870, showed no moult progress at all between 2 April and 16 April (although it was at that time well ahead of the average stage with a score of 30), and by 11 June had continued to progress by only less than half the average rate. Two other birds displayed unbalanced scores for each wing, but in one of these the balance had been restored several weeks later. Two more birds had individual feathers which seemed to have been "arrested" in mid-moult; in both cased later examiniations showed that the "arrested" feathers had "caught up" with their neighbours. Finally, one bird, 86574, had a moult score of 70 in mid-May, showing four months' advance over the general average; unfortunately it was not re-examined.

We may confirm from the data collected in this survey that this population of Brown Noddy terns has an annual moult and an annual breeding cycle. The moult lasts for between nine and ten months, each "new" primary feather taking about four weeks to grow to full length. Clearly, with never more than one primary missing, the bird's flight ability is not significantly impaired. Thus there is no reason for the breeding activities and the moult period not to overlap. However, a slight but definite slowing of the moult rate seems to occur at the time when the younger chicks are being fed and brooded, probably the most stressful period of the breeding cycle.

Further studies with more comprehensive data may elucidate whether the moult rate slows significantly during the whole breeding cycle compared with the periods on either side of breeding. However, the difficulty in practice of obtaining data from sufficient numbers of retrapped individuals at known stages of the cycle should not be under-estimated.

Table II Fortnightly rate of change in moult for breeding Brown Noddy terns

Stage of breeding	Sample size	Fortnightly score change		
		Range	Average	S.D.
No eggs (before laying)	9	3 - 7	5.22	1.227
Egg to egg	24	3 - 7	5.46	1.255
Egg to chick	12	2 - 6	4.75	1.288
Chick to chick	23	1 - 5	3.3	1.195

Table III Moult rates for 8 breeding Brown Noddy terns retrapped several times. The figures show the fortnightly score change during the 10-week breeding cycle; for two birds the figures relate to intervals of 4 or 6 weeks.

Parent	Laying date (presumed)	2-wk-old egg	4-wk-old egg	1-wk-old chick	3-wk-old chick	5-wk-old chick
01704			4	6	2	5
01720		4	5	4		
01865				4	5	
01891			←	15	→	4
86406			7	6	4	
86523		4	5	0	3	
86581			4	6	2	
86585			←	8	→	4	5
Average		4	4.86	4.375	3.57	4.67

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