

# BREEDING AND MOLT IN THE WHITE TERN (*GYGIS ALBA*) ON CHRISTMAS ISLAND, PACIFIC OCEAN

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## INTRODUCTION AND METHODS

Christmas Island lies in the Central Equatorial Pacific at 2° N, 157° W, about 1200 miles south of Hawaii. I made a series of visits to the island during the period March 1963 to February 1964, and one later visit in June 1964. The primary purpose of the visits was to study the sexual cycles of the sea birds on the island. The results of the work on one species, the Sooty Tern (*Sterna fuscata*), have already been published (Ashmole 1965), while the feeding ecology of the various species and the marine environment of the island have been treated elsewhere (Ashmole and Ashmole 1967). The present paper gives results of work on the White or Fairy Tern *Gygis alba*, whose breeding and molt cycles proved, like those of *Sterna fuscata*, to be of special interest.

In this paper the term *sexual cycle* is used to indicate the whole series of events from the laying of the first (or only) egg by the bird or its mate in one breeding period until the laying of the first egg in the next breeding period. Stonehouse (1962a) reasonably considered the sexual cycle to run from the beginning of courtship in one breeding cycle to the same point in the next. I have used the laying of the first egg only because it is a definite occurrence that is easier to record. The *breeding period* (of an individual) is considered as the time period during which an individual is involved more or less continuously in breeding activities, without a pause for a complete post-breeding molt (= postnuptial or prebasic molt—see Amadon 1966).

*Gygis* was studied mainly on Cook Island, an islet about one mile long that lies in the center of the entrance to the main lagoon of Christmas Island. The first visit to Cook Island was from 2 to 9 March 1963, after which there was an interval of seven weeks. Subsequently, no interval was longer than five weeks, and many were much shorter. The original plan called for observations to be continued for at least 13 months, but unfortunately the regular observations had to be terminated on 8 February 1964; however, a final three-week visit to Christmas Island in June 1964 included two weeks on Cook Island. In all, 101 days were spent working on Cook Island. Because the observations were carried out over a relatively short period, and were not continuous, the data are incomplete and difficult to analyze. However, the main features of the breeding and molt regime of this population of *Gygis* were established.

A segment of Cook Island comprising about one tenth of its total area was chosen as a study area.

Within this, an effort was made to locate all active nests; the nests were marked with red paint and numbered with aluminum garden labels, and the activity (if any) at all known sites was recorded at least once on each visit to the island. As many adults as possible were caught and banded during incubation as they left their eggs, while a few more were caught while brooding or about to feed chicks. With few exceptions, adults were banded only if they were known to have an egg or chick. At a later stage in the study a special effort was made to recapture banded birds. This was achieved generally when they were roosting or were involved in a subsequent breeding attempt. The restriction of banding to adults that could be associated with known active nests meant that only a relatively small number (248) could be banded. Many individuals could not be caught with a hand net, and the alternative method, of catching incubating birds at night using a headlamp, was employed only when it was particularly important to recapture a previously banded bird, since it can result in the accidental loss of the egg as the adult leaves the nest in a hurry. On the other hand, every bird banded provided valuable information if it was recaptured, and no time was wasted in catching banded birds of unknown breeding history.

On the routine visits to sites in the study area all chicks found were measured (wing length and exposed culmen length) and weighed when they were first seen, and were also banded. Chicks whose date of hatching was known ( $\pm$  one day) were measured and weighed whenever they were visited. These measurements and weights were plotted against age in order to produce graphs that were used in estimating the hatching dates of chicks whose ages were not known precisely. From these data, approximate laying dates were calculated by assuming an incubation period of 36 days. This estimate is based on the experience of Dorward (1963) on Ascension Island, supported by personal observations. Because of the long incubation period there was little chance of failing to record breeding activity at a site, in spite of the rather long intervals between visits, provided that the egg survived to hatching. However, some eggs must have been laid and lost between visits, and so were not recorded.

During the study 387 examinations were made of the molt of 235 adult *Gygis*; 97 birds were examined more than once, and 29 more than twice. On each occasion the condition of each of the primaries and rectrices was recorded, and at the same time all the primaries and rectrices on the left side were given a nick with a small-diameter paperpunch near the tip of the outer vane. It was thus possible to determine at a subsequent examination exactly which feathers had been replaced in the interval. A rapid check was also made for the presence of growing feathers in various parts of the body, and the state of the brood patches was recorded. In a sample of the birds, the secondaries in one wing were also examined.

Although breeding *Gygis* may be found on Cook Island at all times of year, individuals that have finished breeding seem to leave the island immediately, at about the same time that they start their molt. They are not seen again until they have almost completed their molt, when they return to start courtship for their next breeding period. As a result, the details of the middle part of the molt could not be observed directly, but the general plan became clear from records of the start and finish of molt, and of the retention or loss of punched feathers during the period when the birds were absent.

In recording the state of the individual flight feathers, the numerical method detailed by Ashmole (1962) was utilized (see also table 2). On this system each growing feather is assigned a score, according to its growth stage, of 1 (empty socket or pin feather), 2, 3, or 4. Full-grown new feathers score 5, so that in birds in which a molt wave progresses steadily through a feather series, the position of the wave can be recorded simply by scoring 5 for each feather that has already been replaced, and adding the appropriate lower figures for growing feathers. In the case of *Gygis* and other species in which two or more molt waves are active at the same time in the same feather series, it is necessary for some purposes to record the positions of the separate waves, while for others it is more useful to consider the total effect of the progress in all the waves in a given time period. Each procedure can easily be followed by using the scoring system in an appropriate manner. For instance in the present paper the "primary molt score" used to indicate the molt stage reached by an individual is computed by scoring five points for all primaries replaced since the last breeding period, and adding appropriate scores for all the partly grown feathers present in any of the molt waves. A completed molt scores 100 if both wings are considered, or 50 in a single wing. Individual primaries are referred to by using a letter L or R (left or right) and a number representing the position of the feather in the primary series: thus "L and R 1" identifies the innermost (proximal) primaries in the two wings.

## BREEDING

### THE TEMPORAL DISTRIBUTION OF BREEDING

The most striking feature of the breeding of *Gygis* on Christmas Island is that eggs and chicks can be found at all times of year. Figure 1 shows the temporal distribution of laying, each column representing the eggs laid in one month. The solid black histogram includes data on 228 eggs for which the month of laying was definitely known or could be reliably calculated from measurements of the chick. However, an additional 232 eggs known to have been laid were either lost as eggs or the chicks disappeared before they were measured. The laying dates for these eggs are less precisely known, but have been incorporated as the stippled portion of the histogram in figure 1, by assigning them to the most likely month, on the basis of the record of visits to the site concerned. When the possible time of laying of an egg spanned 10 or more days of each of two adjacent

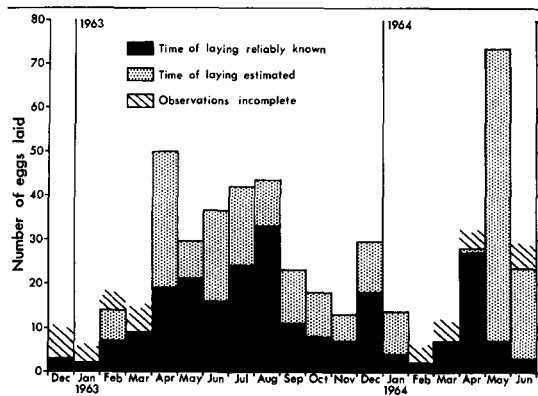


FIGURE 1. Monthly numbers of eggs of *Gygis alba* laid in study area on Cook Island (Christmas Island) in 1963 and 1964. For explanation see text.

months, the egg was assigned half to one month and half to the other. The months in which diagonal lines have been added on top of the columns are those in which the timing of the visits made it certain that many eggs laid were not recorded.

Figure 1 shows that in the first year during which I made regular observations there was much more laying in the period April through August than during the rest of the year, but even the months with least laying (November 1963 and January 1964) had well over one quarter as many layings as occurred in the month with greatest activity (April 1963). However, in May of 1964 there was a peak of laying much higher than any in the previous year. In conjunction with the observations of Gallagher (1960) the data suggest that laying may generally be heaviest during April through August, but it is clear that a substantial amount of breeding takes place at all times of year.

### SUCCESS OF BREEDING AT DIFFERENT TIMES

The available data on the success of breeding in relation to the time of laying of the egg are presented in table 1. However, because of the irregularity of my visits to the island, and the different amounts of time spent searching for juveniles after they had learned to fly, the figures for the different periods are not fully comparable; in all cases they are minima. The results are presented solely to show that throughout the period for which I have data, a fair proportion of the eggs laid produced flying young.

On Christmas Island some chicks from nests in small trees flutter from their nest sites when alarmed even before they are six weeks old, and many do so by the time they are seven weeks old, when they can barely fly. In contrast, on Ascension Island, although

TABLE 1. Breeding success of *Gygis alba* on Christmas Island, 1963.

Laying period	Estimated number of eggs laid <sup>a</sup>	Number known to have hatched	Number of chicks known to have survived to		
			6 weeks <sup>b</sup>	9 weeks	12 weeks
Dec. 1962– Jan. 1963	>5	(5) <sup>c</sup>	(4)	(3)	(3) <sup>d</sup>
Feb.–Mar. 1963	>23	15	11	1	0
Apr.–May 1963	79	35	17	8	3
Jun.–Jul. 1963	78½	37	20	18	12 <sup>d</sup>
Aug.–Sept. 1963	66½	28	22	14	7 <sup>e</sup>
Oct.–Nov. 1963	31	11	(8)	(5) <sup>f</sup>	(1)

<sup>a</sup> Data from figure 1.

<sup>b</sup> Chicks generally become able to fly when between six and seven weeks old. After this they cannot always be found at their nest sites, even if alive.

<sup>c</sup> Data for chicks from eggs laid in December 1962–January 1963 are placed in parentheses because observations started only in March 1963, and those for October–November 1963 because the last regular visit finished on 8 February 1964.

<sup>d</sup> Two of these birds were weak when last seen, apparently from lack of food.

<sup>e</sup> Three of these birds were weak when last seen.

<sup>f</sup> One of these birds was weak when last seen.

the wings of the chicks grow at about the same rate, the chicks mostly begin to fly—from ledges on steep cliffs—only when they are between 60 and 75 days old (Dorward 1963). On Christmas Island (and many other Pacific Islands) the nests of this species are on coral blocks or bushes close to the ground, and it is generally possible for the chicks to return to their nest sites—where they are exclusively fed—even if they cannot fly. The new information from Christmas Island thus supports the suggestion of Dorward and Ashmole (1963) that young of *Anous* spp. and of *Gygis* that are not old enough to be able to fly properly are more ready to leave their nest sites to avoid potential predators in colonies where the nests are close to alternative perching sites than they are in those that are in precipitous places.

Smith (1966) showed experimentally that chicks of *Larus glaucooides*, *L. hyperboreus*, and *L. argentatus*, tested on cliff ledges when 8–9 or 13–14 days old, were much more likely to jump from the ledges when alarmed if they had been raised in nests on the ground than if they had been raised on cliff ledges. It is very possible that the observed differences in behavior of chicks of *Gygis* in different colonies also depend on experience after hatching, rather than on genetic differences.

Between the ages of 7 and 12 weeks the chicks were seen near their nest sites less and less frequently; several were caught when more than 12 weeks old, but it is likely that some leave the island during their fourth month from hatching. Young from eggs laid in the two periods June–July and August–September 1963 were seen in relatively large numbers when more than 12 weeks old (table 1), but this may have indicated a low rather than a

high survival to independence, since six of these old chicks caught between the last week of December 1963 and the first week of February 1964 were found to be strikingly thin and weak. It seems clear from these records that there must have been a food shortage in the last part of December 1963 and in January 1964, but it cannot have been severe since young chicks were not noticeably affected. It may well be that chicks much more than 12 weeks old would normally have started fishing for themselves, but that under slightly abnormal conditions the transition to independent life—and perhaps the time of departure from the island—was delayed. It is of interest that three birds caught when between 16 and 19 weeks old and obviously much too weak to fish for themselves were nevertheless stronger (and in at least one case heavier) a few days later, evidently having been fed in the interval, although they were so old. The food situation clearly improved in the first week of February 1964, since many large regurgitations (of small squid) were obtained from roosting *Gygis* at this time (Ashmole and Ashmole 1967).

#### SEXUAL CYCLES OF INDIVIDUAL BIRDS

On Ascension Island Dorward (1963) found that almost all egg-laying by *Gygis* occurred in the period November through March, although the length of the sexual cycles of individual pairs varied from 8 to 14 months, and most of the cycles were of 11 or 12 months. (However, Dorward assumed that eggs laid in precisely the same site in two successive seasons belonged to the same pair. On Christmas Island, where good potential sites were scarcer, a number of especially attractive sites were used by more than one pair.) On Christmas Island, where laying occurred in all months, an attempt was made to determine the relation between the length of the sexual cycle and the success or lack of success in the included breeding period.

Because the main study could not be continued for more than 11 months, relatively few banded individuals finished a breeding period and the subsequent molt, and returned to breed again, during the period of observation. However, some more birds were recaptured during the visit in June 1964, and 31 birds were caught during two successive breeding periods. A number of other birds were recaptured when in the final stages of the molt following the breeding period in which they were banded, but had not started breeding when I left the island. The sexes are externally indistinguishable in *Gygis*, so I

have no information on possible differences in the relations between breeding and molt in males and females. However, pair-bonds normally persist from one breeding period to the next, so that the length of the sexual cycle is the same in the two members of each pair. The data on the sexual cycles of individuals are not given in full because of their complexity, but are considered to justify the following general statements, which are accompanied by specific examples.

The rearing of a chick occupies about five months, not counting the preliminaries to laying but including just over one month for incubation and about four months during which the chick is dependent. The latter estimate is based on one normal chick that was seen to be fed when just over four months old, plus the three chicks mentioned in the last section that were evidently fed—during a period of food shortage—when more than four months old. However, it is possible that chicks sometimes become independent when only about three months old (cf. Dorward 1963).

Molt occupies almost the entire period between successive breeding periods, and lasts about 5½ to 7 months. For a few weeks at the beginning molt may overlap with the end of the period of dependence of the chick, while molt is generally completed during the courtship period shortly before the laying of the egg. (Molt and its relations with breeding are fully discussed later.)

As might be expected from the above, no sexual cycle in which a chick was raised (which will be referred to as a "successful" cycle) is known to have been completed in less than 10½ months.

An example of a successful cycle is provided by a bird that was banded on 10 August 1963 when incubating an egg subsequently calculated to have been laid about 19 July. The chick was last seen on 17 November, when it was about 12 weeks old. The adult was recaptured on the same day and found not to have started the molt of its flight feathers. On 14 June 1964 it was caught again, incubating an egg laid since 2 June. This bird had completed a successful cycle of breeding and molt in just under 11 months. Similarly, a pair in which both adults were banded hatched an egg on 6 March 1963, the third day of my first visit to the island. The chick was well and could fly on 3 May, when it was 58 days old, and probably survived to independence. On 31 December 1963 one of the adults was found at the same site incubating an egg that must have been laid in the previous two weeks. Unfortunately the egg fell off the site on 20 January, probably dislodged by the other member of the pair as I tried—unsuccessfully—to catch it. A replacement egg was laid in the first week of February, and the second adult was caught incubating. This pair thus had an almost certainly successful sexual cycle that lasted 10½ to 11 months.

Since successful breeding can take place at any time of year, one might expect successful birds to start breeding about a month earlier each year. However, in about half of the breeding attempts the egg is lost or the chick disappears while very young, and the adults generally lay a replacement egg. Thus a bird that is successful at its second attempt in a given breeding period will not be ready to breed again until about a year after its first attempt.

Some of the birds that are unsuccessful in a given breeding period are finished with breeding activities sooner than successful birds. After spending the same time over molt as the successful birds, these individuals return to breed again after about 8 to 10 months.

An example of a short cycle of this kind is provided by a bird that was banded when incubating on 10 August 1963, the egg having been laid during July or early August. By 18 August there was only an empty shell below the nest. The adult was next seen on a new-hatched chick on 2 June 1964, indicating laying about 27 April. The interval between layings was thus about 8½ to 9½ months. Another example is that of a pair that was banded while incubating an egg laid between 6 April and 3 May 1963. By 18 June the egg had gone, and there was no chick. The next egg was laid about 24 December, 8 or 8½ months after the previous one. Both adults were caught during the first 10 days of incubation, and had completed their molt. As in the previous example, it is possible that in the first breeding period an egg was laid and lost before the one I saw, but even in this case the overall sexual cycle would have been much less than a year in length. Another interesting pair hatched a chick about 1 June 1963, but it died shortly before 3 July. No egg had been laid by this pair by the time of my departure from the island on 8 February 1964, but both birds were roosting by the nest site, with their molt virtually completed, and an egg may well have been laid during late February. This would have been about 10 months after the previous laying.

The cycles cited above are among the shorter ones recorded for both successful and unsuccessful breeders. There were a number of cases in which successful breeders appeared to have sexual cycles longer than one year, or in which unsuccessful breeders were found on eggs laid 11 or 12 months after the previous laying. It is probable that in some of these cases the first egg laid in the second breeding period was never seen, and a replacement egg was the one recorded.

An extreme case that will serve to illustrate this possibility is of a bird caught on an egg on 1 May 1963, but whose egg was broken by 3 May, no replacement being seen. On 6 February 1964, two days before I left the island for nearly four months, the bird was found incubating an egg, laid about nine months after the previous one. But on 5 June 1964 the same bird was found incubating again, without

having molted any flight feathers in the interval. If I had left Cook Island two days earlier in February, this bird would have been recorded, with misgivings, as having an unsuccessful sexual cycle lasting 13 months. In fact, the cycle was much less than a year, and the June 1964 egg was probably the third laid in that breeding period.

It is noteworthy that in this bird (and some others) the interval between the laying of the last observed egg in the first breeding period and the last observed egg in the next was a little more than a year, as a result of the loss of an egg or eggs early in the second breeding period, followed by the laying of replacement eggs and consequent long involvement in breeding activities. Another example will serve to illustrate how long this involvement may sometimes be. An adult was banded when incubating an egg that was laid about 13 August 1963, but in which the chick died after pipping. A second egg was present in the site on 3 November, but had gone by 19 November. Although neither parent was caught while incubating this egg, it seems highly likely that one was the banded bird, since it was caught while roosting on 17 November and was found to have fully developed brood patches. On 20 January 1964 it was found on the same site incubating a third egg, laid about 31 December, which hatched about 5 February. Thus this bird—and presumably also its unbanded mate—was involved in breeding activities for nearly six months before it finally hatched an egg successfully. Because I left the island soon after the egg hatched, I do not know what happened to the chick; however, if it was successfully reared, being dependent for about four months, the breeding period of the adult must have occupied nine to 10 months. The molt program of this bird (864 in table 2) was of special interest, and is discussed in the section on the relations between breeding and molt; however, it may be said here that since molt takes about six months, and overlaps only to a small extent with breeding activities, the whole sexual cycle of this individual must have taken much longer than a year, if its chick was successfully reared.

## MOLT

### INTRODUCTION

In his study on Ascension Island Dorward (1963) discovered that a molting *Gygis* normally has, at a given time, growing primaries at either two or three separate points in each wing. The present work was planned to clarify, mainly by the use of punchmarks to identify old feathers, some of the problems raised in Dorward's study. The results confirm that the sequence of molt in the wings of adult *Gygis* is unusual in that two or three waves of molt start simultaneously after breeding and progress outward through the feather series one behind the other, in the same way as in boobies, *Sula* spp. (Dorward 1962).

In many other species of terns a second wave of molt starts from the first primary before the first wave reaches the tenth primary, so that about half of the primaries are replaced twice between successive breeding periods (Stresemann 1963; Ashmole 1963a;

Stresemann and Stresemann 1966). Furthermore, Stresemann has pointed out that in the Least Tern (*Sterna albifrons*) three generations of feathers are present in the wings of breeding birds, because a third molt wave starts at about the time that the first wave reaches the tip of the wing. Stresemann believes that in the White-winged Black Tern (*Chlidonias leucopterus*) all the primaries are replaced twice, and the inner ones a third time, before breeding starts.

Stresemann (1965) and Stresemann and Stresemann (1966) use the term "die periodische Staffelmauser" to describe the type of molt in which one or more new cycles of molt of the primaries begin before the preceding one is completed, but in which molt starts again after breeding only with the first primary. They differentiate "die cyclische Staffelmauser" (1965) or "die kontinuierliche Staffelmauser" (1966) as a molt pattern in which there is again a series of successive molt waves moving simultaneously out through the primaries, but in which the process does not stop before the breeding period, but continues all the time. These terms could be rendered "periodic stepwise molt" and "continual (or cyclic) stepwise molt," respectively, but in the present paper I have generally found it more convenient to employ informal descriptions, using the term "molt wave" to indicate a single sequence of molt travelling along a feather series.

One problem of terminology that arises immediately is that Stresemann and Stresemann include the boobies (*Sula* spp.) in the group having "continual stepwise molt," but Dorward (1962) has shown that in *Sula dactylatra* there is a tendency for molt to be temporarily arrested during the breeding period, continuing afterward from the points where it stopped. A pause in molt during breeding probably also occurs in other birds in this group, for instance in members of the genus *Phaethon* (personal observations). Thus the Stresemanns' "continual stepwise molt" is a slightly heterogeneous category. In some species each molt wave does progress continuously until it reaches the tip of the wing, but in others each molt wave pauses during the breeding period, and resumes its progress afterward from the point where it left off. However, it does seem useful to maintain the distinction that the Stresemanns have emphasized between this category and the other. The important consideration is that in "periodic stepwise molt" all the molt waves stop before breeding, and never continue, since after breeding a new wave starts from

the first primary and is followed later by one or two additional waves, also starting from the first primary. In "continual stepwise molt," on the other hand, each molt wave does eventually reach the tip of the wing, whether or not there is a pause in molt for breeding.

Stresemann and Stresemann (1966), on the basis of the information on *Gygis* published by Dorward (1963), and the examination of museum specimens, came to the conclusion ". . . dass *Gygis*, genau so wie *Sterna albifrons* und *Chlidonias leucoptera*, die Handschwingen periodisch in drei Staffeln erneuert." This implies that after breeding molt would start only with the first primary, and that the triple-wave system would be reestablished only as the first molt wave progressed out through the primary series and second and third waves started successively from the first primary. In fact, however, my field data on the molt of *Gygis*, based on repeated examination of marked birds with punched feathers, show that after breeding each molt wave starts again from the point that it had reached at the time when breeding started and the molt was inhibited. *Gygis* thus has an interrupted "continual stepwise molt" of a kind that has not previously been recorded for any species of tern. In the Christmas Island population I found that one complete replacement normally occurs between successive breeding periods, and it appears that the unusual sequence of the molt is an adaptation permitting rapid replacement of the feathers with minimal impairment of flying ability.

It should be mentioned that one other species of tropical tern, the Black-naped tern (*Sterna sumatrana*), probably has a molt similar to that of *Gygis* (Ashmole unpublished). As in *Gygis*, growing feathers may be found at two or three widely separated points in each wing, but without field data it is difficult to be sure that molt starts after breeding at the several points at which it stopped.

In the following pages all references to specific birds, using band numbers, imply that the available records on the primary molt of these individuals may be found in table 2.

#### MOLT OF THE PRIMARIES

On Christmas Island nine *Gygis* were examined when they were just starting a molt after a breeding period, and the results show that molt starts from several points in each wing, at more or less the same time. Examples are provided by birds 508 and 785 (table 2). However, it is clear that molt does not usually begin at precisely the same date at the different starting points in a single wing, or in

the two wings. For example, in bird 785 primary R 6 was the first to be molted, followed by L 2, 6, and 9; presumably molt waves also started soon with primaries R 2 and 9.

Dorward (1963) found that molt started after breeding (and also finished) at different points in different individuals. This finding is confirmed by the present data. The nine birds referred to above actually provide examples of molt waves starting after breeding with every primary except numbers 1 and 10, whose lack of representation may well be due to chance. In fact, a later examination of one of these birds (859) strongly suggested that molt waves did start with the tenth primaries. Similarly, molt waves may stop before breeding at different points in the primary series in different birds. There is a suggestion from the data that waves may stop most frequently after the growth of primaries 4, 8, and of course 10. This may imply that they most often start with number 1, 5, and 9. However, other patterns of molt are also common.

From each of the starting points a molt wave progresses outward, eventually reaching the next more distal starting point, or the outermost feather (number 10). At this stage all the feathers have been replaced. The available evidence indicates that each molt wave normally stops when it reaches the point where a more distal one started at the beginning of the molt. For example, in bird 801 a molt wave was just starting with L 7 on 18 November 1963, while on 6 June 1964 molt was apparently stopping, and L 6 had just completed its growth. Furthermore, it seems that after breeding each molt wave generally or always starts with the molt of the feather immediately distal to the last one replaced in that wave before breeding. The most certain examples are birds 945 and 508. In the latter case R 8 was the last primary to be replaced in two successive molts, and in each it was still growing after the laying of the egg. The beginning of a third molt was observed, and as predicted a molt wave started with primaries L 9 and then R 9; another wave commenced with L 5 and R 4, indicating that the asymmetry observed in the previous two cycles was being maintained, and would doubtless result in R 8 again being the last feather replaced. The history of this bird thus provides good evidence that the pattern of primary molt is normally the same in successive cycles, and involves one complete replacement of the feathers.

Dorward (1963), in his work on the Ascension Island population, did not find an obvious

TABLE 2. Examples of molt patterns in the primaries of *Gygis alba* on Christmas Island.\*

Bird	Date, breeding status, molt status	Primary number											
		1	2	3	4	5	6	7	8	9	10		
508	4 Mar. 63, egg,	L.	.	.	.	.	.	.	.	.	.	.	.
	molt ending: score 99.	R.	.	.	.	.	.	.	.	4	.	.	.
	20 Jan. 64, egg,	L.	N	N	N	N	N	N	N	4	N	N	N
	molt ending: score 94.	R.	.	.	.	.	.	.	4	1	.	.	.
556	2 Jun. 64, not breeding,	L.	P	P	P	P	4	P	P	P	P	3	P
	molt starting: score 12.	R.	.	.	.	3	.	.	.	.	.	2	.
	30 Apr. 63, egg,	L.	.	.	.	.	.	.	.	.	.	.	.
	no molt.	R.	.	.	.	.	.	.	.	.	.	.	.
785	20 Jan. 64, not breeding,	L.	N	5	N	N	5	1	N	N	2	N	N
	molt near end: score 86.	R.	.	4	.	.	5	1	.	.	3	.	.
	6 Feb. 64, not breeding,	L.	P	P	P	P	P	2	P	P	4	P	P
	molt ending(?): score 92.	R.	.	.	.	.	.	2	.	.	4	.	.
801	15 Jun. 64, egg,	L.	P	P	N	P	P	P	P	P	P	P	N
	no molt.	R.	.	.	.	.	.	.	.	.	.	.	.
	17 Sep. 63, second egg,	L.	.	.	.	.	.	.	.	.	.	.	.
	no molt.	R.	.	.	.	.	.	.	.	.	.	.	.
816	4 Nov. 63, second egg lost,	L.	P	1	P	P	P	1	P	P	1	P	P
	molt starting: score 5.	R.	.	.	.	.	.	2	.	.	.	.	.
	9 Aug. 63, egg,	L.	.	.	.	.	.	.	.	.	.	.	.
	no molt.	R.	.	.	.	.	.	.	.	.	.	.	.
856	18 Nov. 63, not breeding,	L.	P	5	P	P	P	P	1	P	P	P	P
	molt starting: score 3 or 8.	R.	.	.	.	.	.	.	.	.	2	.	.
	6 Jun. 64, not breeding,	L.	N	N	N	N	N	5	N	N	N	N	4
	molt ending: score 99.	R.	.	.	.	.	.	.	.	.	.	.	.
859	10 Aug. 63,	L.	.	.	.	.	.	.	.	4	.	.	.
	molt ending: score 98.	R.	.	.	.	.	.	.	.	4	.	.	.
	2 Jan. 64,	L.	P	P	P	1	P	P	P	P	/P°	P°	P°
	molt starting: score 2.	R.	.	.	.	1	.	.	.	.	/O	O	O
864	18 Sept. 63, chick(?),	L.	.	.	.	.	.	3	.	.	.	.	.
	molt ending?: score 98(?).	R.	.	.	.	.	.	.	.	.	.	.	.
	6 Feb. 64, not breeding,	L.	N	N	3	N	N	1	N	N	N	N	N
	molt near end: score 90.	R.	.	.	4	.	.	3	.	.	4	.	.
864	4 Jun. 64, chick,	L.	P	P	P	P	P	N	P	P	N	P	P
	no molt.	R.	.	.	.	.	.	.	.	.	.	.	.
	18 Sep. 63, egg,	L.	.	.	.	.	.	.	.	.	.	.	.
	no molt.	R.	.	.	.	.	.	.	.	.	.	.	.
864	19 Jan. 64, old chick(?),	L.	P	P	P	P	P	P	P	P	P	/P°	/P°
	molt starting: score 1.	R.	.	.	.	.	.	1	.	.	.	/O	/O
	6 Jun. 64, not breeding,	L.	N	2	N	N	4	N	N	N	2	N	N
	molt ending: score 87.	R.	.	3	.	.	4	.	.	.	2	.	.
864	19 Sep. 63, dead "holed" egg,	L.	.	.	.	.	.	.	.	/O	.	.	.
	no molt.	R.	.	.	.	.	.	.	/O	.	.	.	.
	17 Nov. 63, 2nd egg lost(?),	L.	P	P	P	/P°	P	P	P	4	P	P	P
	molting.	R.	.	.	.	.	.	.	4	.	.	.	.
864	18 Jan. 64, egg (prob. 3rd),	L.	P	P	P	N	/P	P	P	N	/P°	P°	P°
	no molt.	R.	.	.	N	/.	.	.	N	/O	O	O	O
	2 Jan. 64, egg,	L.	.	.	.	.	.	.	.	.	/O	O	O
	no molt.	R.	.	.	.	.	.	.	.	/O	O	O	O
945	1 Jun. 64, not breeding,	L.	3	N	N	2	N	N	N	1	N	N	N
	molt ending: score 84.	R.	N	N	2	N	N	N	2	N	N	4	4

\* Explanation of symbols: L., R., left, right; /, discontinuity between feathers of very different age; N, feather full-grown, but either obviously new or known by the absence of a punch mark to have been molted since previous examination (feathers at stages 1 or 2 could not be punched, and so normally appear as N at the next examination); ., feather of indeterminate age; O, feather conspicuously old, but without a punch mark; P, feather shows punch mark made at previous examination, and thus is known not to have been molted in the interval; P°, feather conspicuously old, and has a punch mark; 1, empty socket or pin feather; 2, growing feather with vane up to one-third grown; 3, growing feather with vane between one-third and two-thirds grown; 4, growing feather with vane more than two-thirds grown but not full length; 5, feather full length, but still with blood in calamus.

relationship between the place where molt finished before breeding and the place where it started afterward, such as might have been expected from the above. However, this can probably be explained by the frequent lack of complete synchrony between the start (and finish) of the different molt waves within a wing. Near the end of a molt one often cannot detect all the molt waves, since some have already reached their stopping points, while in the same bird after breeding the first molt wave to start may not be the one that stopped last (e.g., bird 816).

It is clear that all the primaries are normally replaced between successive breeding periods. Thus of the many individuals whose primaries in the left wing were punched during one breeding period, when they were not molting, and which were examined again shortly before or during their next breeding period, all but one had molted all the punched primaries in the interval. The one exception, whose left primaries were punched when it was incubating in August 1963, still had the punched L 4 when caught on a pipped egg in June 1964; interestingly, R 4 had obviously been replaced in the interval.

As mentioned above, there is a tendency for a molt wave to stop when it reaches the point where a more distal one started, so that each primary should be replaced only once between successive breeding periods. However, there are indications that exceptions do occur.

One bird (801) seems certainly to have replaced primary L 2 twice within a single molt, once between 9 August and 18 November, and again sometime before 6 June 1964. It is possible that this feather was not replaced during the previous molt, like primary L 4 in the bird discussed above, and that it was therefore molted immediately after breeding, and also later in the normal sequence (cf. secondaries of the Black Noddy, *Anous tenuirostris*; Ashmole 1962). Another case for which a similar explanation is possible (although doubtful) is the double replacement of L 9 in bird 856. However, the molt pattern of two other birds, in which certain inner primaries were probably replaced twice, cannot be explained in this way, but nevertheless may represent a fairly frequent occurrence. Bird 945 on 2 January 1964 had age discontinuities (Ashmole 1963a) between primaries L 8 and 9 and between R 7 and 8, the outer feathers being older, indicating that molt waves had stopped asymmetrically with L 8 and R 7; five months later the same asymmetry was apparent, and affected all four molt waves that were then represented. Molt in the left wing clearly started from three points, the most distal wave having replaced L 9 and 10, the next L 5 through 8, and the third presumably L 1 through 4. If so, L 1 was molted twice, since at the last examination a new wave had just been initiated with the molt of this feather. Similarly, records for bird 859 suggest that primaries L and R 2, and per-

haps L and R 1, may have been replaced twice within a single cycle.

Dorward (1963:372, and personal communication) recorded an individual on Ascension Island that had a chick able to fly in February, and that was starting molt in mid-March, with primaries R 7 and R 10 (and also L 4) at stage 1; in mid-September it was near the end of its molt, with primaries R 7 and R 10 at stages 3 and 4, respectively. Dorward originally suggested that these feathers had been growing for six months but were still not complete, but he now considers that they must have completed their growth and then been molted again between the two examinations. This bird thus replaced two primaries in its right wing twice within a single molt lasting a little more than six months. However, there is no indication that any of the primaries in the left wing were replaced twice, so a single complete replacement may be normal in the Ascension Island population, as on Christmas Island.

The records for Christmas Island birds, for instance 785 and 508, make it clear that when molt is initiated after breeding, a molt wave by no means always starts immediately with the shedding of the innermost primary. However, new waves must appear at the proximal end of the series at least once in each molt to maintain the orderly progression of waves out to the tip of the wing. The frequency with which these new waves are initiated, and the speed with which they progress, will determine the spacing of the fronts of the waves along the wing, which is shown in figure 2. In this figure the position of the front of each wave on a scale running from 0 to 50 was computed by allowing a score of 5 for each feather proximal to the wave-front, and appropriate lower figures for partially grown feathers at the wave-front. This is the system described in Ashmole (1962), except that in the present instance only one wing at a time was under consideration, and half-points were used in scoring growing feathers that did not fall easily into one of the categories 1, 2, 3, or 4. In computing the position of an outer wave the presence of other growing feathers at the fronts of inner waves was ignored, so that all feathers proximal to the wave under consideration contributed a score of 5. For example, in bird 785 on 4 November 1963 the waves in the left wing scored 6, 26, and 41, and that in the right wing scored 27.

The overall mean interval between successive waves (omitting the two records shown as circles in figure 2) is 18.5 points (or nearly four feathers), and is represented by the straight line in figure 2. However, it appears that there is a tendency for the interval to be shorter when the outer wave has reached a score of more than 40 than when it is between 30 and 40. The fact that successive waves are closer together distally than in the middle



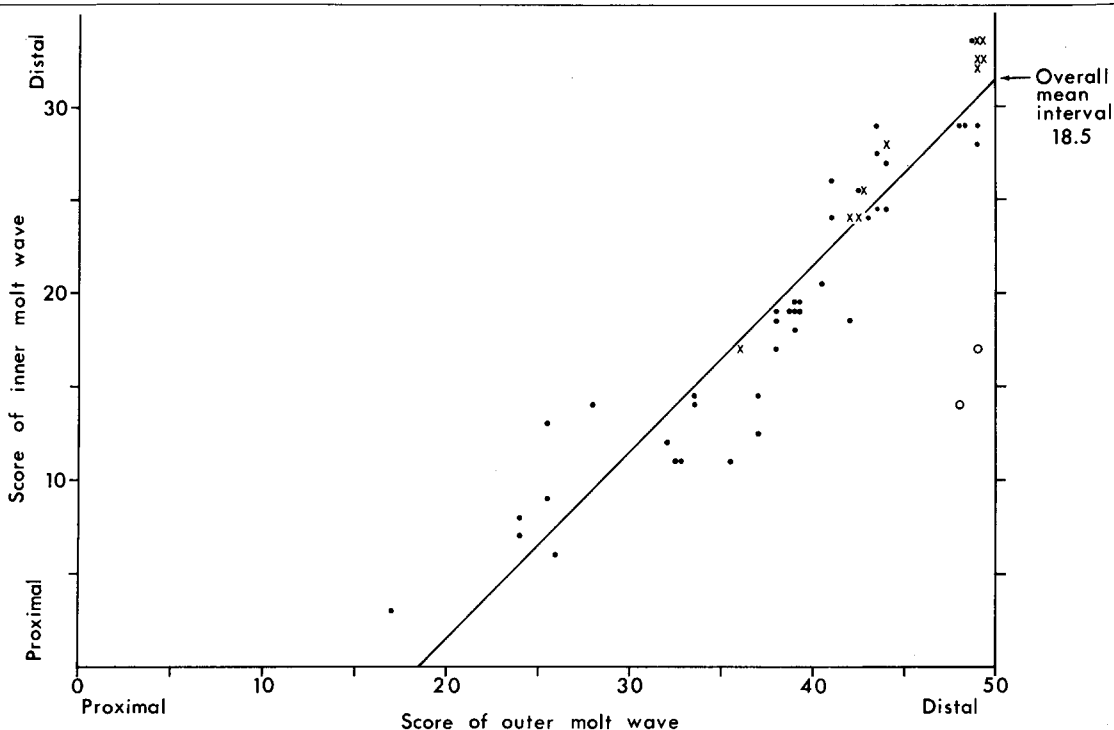


FIGURE 2. Relative positions of molt waves in wings of *Gygis alba* in which two or three waves were found in progress at the same time. For explanation see text. Symbols: ● used in plotting the relative positions of the two most proximal (or the only two) molt waves in a wing; × used in plotting the relative positions of the two most distal molt waves, when three waves were present; ○ used in plotting the relative positions of the only two molt waves in wings of two birds in which an intermediate wave had probably just become inactive.

of the series implies that they catch up with each other as they move outward; this is readily explained by the greater length of the outer feathers, which doubtless take longer to complete their growth. However, there is also a tendency for the successive waves to be very close together when the score of the outer one is lower than 30. The four birds responsible for the six records of closely spaced proximal waves (556, 856, 859, and 945) were all just completing their molt, suggesting that late in the molt new waves may start at the first primary when the preceding wave has barely reached primary four (score about 15). This could result in certain inner primaries being replaced twice within a single molt, as already indicated. The absence of such closely spaced waves in the middle of the primary series must imply that when the next cycle of molt starts after breeding, a wave that had previously reached only the first, second, or third primary may not always become active again until some time after the more distal waves, or may be abandoned altogether and be overrun by a new wave starting with the first primary.

#### RATE OF PRIMARY MOLT

The rate of primary molt is a function of the linear growth rate and length of the feathers, and of the number of feathers that are growing at any one time. Although there are no data on the rates of growth of different primaries in *Gygis*, the inner primaries are so much shorter than the outer ones that it seems certain that the former take less time to complete their growth. (For a discussion of rates of growth of different primaries in other species see Ashmole 1962.) I have only a little information on the total time taken to replace particular primaries. In one bird primary L 3 was molted and the new feather completed its growth in less than 46 days, while in another bird (864) the much longer feathers L 8 and R 7 molted and reached stage 4 in less than 59 days. These and a few other records, together with some information on the rate of progress of single waves of molt over a long period (e.g., bird 859 in table 2), indicate that each of the innermost (shortest) primaries is replaced in little more than a month, and that the longest ones take 1½ to 2 months.

Molting *Gygis* have a high average number of primaries growing at any one time. In most of the Laridae (and other birds) a single wave of molt travels out along the primary series, so that normally one finds growing feathers at only one point in each wing. However, at this point there are often two feathers growing simultaneously, since each primary is normally molted well before its proximal neighbor has completed its growth. (There is much variation in the degree of overlap, both at different stages in the molt and in different species.) In *Gygis* the growth of each primary is almost or quite completed before the adjacent one is molted. Thus on Christmas Island I found only two birds with two adjacent feathers in one wing actively growing at the same time (e.g., 508); in two other birds (e.g., 556) primaries were virtually full length, but perhaps just still growing, after the shedding of their distal neighbors.

However, in this species the rarity with which adjacent feathers are growing simultaneously is more than counterbalanced by the presence of several molt waves, so that molting birds normally have two or three widely spaced growing feathers in each wing. Thus the nine birds examined when their primary molt score was between 77 and 91 had a mean of 2.39 growing primaries per wing. Near the end of the primary replacement the different molt waves naturally do not stop at precisely the same time, so that rather fewer feathers are found growing together. The 31 birds examined when their primary score was between 92 and 99 had a mean of 1.26 growing feathers per wing.

A useful comparison may be made with *Anous tenuirostris*, a species that is closely related to *Gygis* and is similar in size. It has only one molt wave in each wing, but adjacent feathers are frequently found growing at the same time. On Ascension Island *A. tenuirostris* with primary molt scores between 71 and 91 had a mean of 1.72 growing feathers per wing, while beyond a score of 91 they averaged only 1.15 feathers per wing (Ashmole 1962: table 5). I have no data for the middle of the molt of *Gygis*, but the scanty records for the early part of the molt show that it is normal for there to be two or three growing feathers per wing at this time, whereas in *A. tenuirostris* there was generally only one.

This comparison suggests that the time needed for replacement of all the primaries should be shorter in *Gygis* than in *A. tenuirostris* (assuming that the linear growth rate of the feathers is comparable in the two species),

and the data support this expectation. In one *Gygis* seen close to the start and to the end of a primary replacement (bird 859), a score change of 86 was achieved in 139 days, a rate of 0.62 per cent per day. Another bird (856) achieved an even higher rate, with a score change of 90 in 141 days (not counting the completion of growth of the last feather in the previous cycle of replacement), a rate of 0.64 per cent per day. A third individual probably achieved an equally high rate, since it had a score of 94 six months (183 days) after being caught while incubating. Molt probably did not start until some time later. These rates are equal to the highest observed among *A. tenuirostris* on Ascension Island, and imply that a molt may sometimes be completed in less than 6 months. However, one other bird (801) seen when just starting a molt had still not quite completed it 6½ months later, so that it is clear that molt sometimes takes as long as 7 months.

In this context it should be mentioned that in one case where both members of a pair were banded, it was found that although both finished with breeding activities on the same day (when their chick died), one finished its molt several weeks before the other. Clearly, molt must either have started at different times in the two birds or have taken longer to complete in one than in another.

#### SYMMETRY OF THE MOLT OF THE PRIMARIES

Of 50 individuals in which primaries were seen growing and the symmetry of the molt in the two wings could be judged, 13 showed no appreciable asymmetry, in that equivalent growing feathers in the two wings were given the same score of 1, 2, 3, or 4. Twenty-six others showed minor divergences from complete symmetry, ranging from probably merely transient ones (e.g., a feather recently shed in one wing, but not yet in the other) to score differences of 2 or 3 between the wings. The remaining 11 birds had more important asymmetries. (As might be expected, divergences from symmetry in favor of the left and right wings occurred in roughly equal numbers). Of these 11 birds, eight showed differences of about one feather (a score difference of 5), two a little less, and one apparently of two feathers. Among these birds no symmetrical molt waves were seen, and one bird (945) showed asymmetry at four separate points in the wings at the same time. Several of these birds were also examined when breeding, and showed discontinuities at different positions in the two wings, indicating that molt had

stopped asymmetrically (e.g., 945). Bird 508, already mentioned as an individual that showed asymmetry in three successive molts, also demonstrated that molt may start asymmetrically. On 2 June 1964 the difference between the two wings was more than one feather at the proximal wave-front, but much less at the distal one. Since the wave starting with primary R 4 had five long feathers to replace, it is clear that R 8 would again be molted very late, or be retained through a breeding period.

#### MOLT OF THE SECONDARIES

Because examination of the secondaries is very time-consuming, details of the state of molt of the secondaries were obtained at only about 50 examinations. These records are sufficient to show that the sequence of secondary replacement in *Gygis* does not follow the relatively simple pattern exemplified by *Anous tenuirostris* (Ashmole 1962). In the latter species the proximal feathers are molted first, followed closely by the most distal feathers, and a wave of molt then progresses from each end of the series toward the middle. The data suggest that secondary molt in *Gygis* also generally progresses from both ends of the series toward the middle; but one frequently finds a number of separated feathers growing at the same time, indicating that the replacement of the secondaries, like that of the primaries, involves more than one molt wave progressing in a given direction simultaneously. For example, one bird examined when its primary molt score was 84 was growing in the left wing secondaries 3, 6, 13, and 16. Furthermore, among birds whose primary molt was at least four-fifths completed, but still progressing, there were individuals growing each one of the secondaries from number 2 through number 17; even the lack of birds growing the outermost and innermost secondaries could have been due to chance.

Although the data do not permit full analysis of this complex system of secondary molt, it is clear from examinations of wings of breeding birds that all the secondaries are normally replaced between successive breeding periods. The one exception involved a bird that, while it was incubating, had one conspicuously old secondary, which had evidently not been replaced between breeding periods. It is of interest that this feather was the twelfth secondary (counting from the most distal feather inwards), since similar retention of middle secondaries—most often 11 and 12—was sometimes found in *Anous tenuirostris* on Ascension Island (Ashmole

TABLE 3. Relationship of molt of secondaries in *Gygis alba* with breeding and with molt of the primaries.

	Numbers of birds			
	Breeding <sup>a</sup>		Not breeding <sup>b</sup>	
	Molt of secondaries in progress	No molt in secondaries <sup>c</sup>	Molt of secondaries in progress	No molt in secondaries
Molt of primaries in progress, score 1-12	0	0	1	1
Molt of primaries in progress, score 77-99	0	3	18	3
No molt in primaries (score 100/0)	1	17	1	2

<sup>a</sup> Incubation was in progress, or there was a dependent chick.

<sup>b</sup> These birds did not have eggs or chicks, and their brood patches were not fully naked.

<sup>c</sup> In some cases the secondaries were examined on only one side.

1962). In the latter case it was shown that these middle feathers, which would normally have been replaced last, were molted either during breeding or shortly after the start of the next molt.

Table 3 gives the available information on the timing of secondary molt in relation to the molt of the primaries. Birds that had nearly completed molt of their primaries were usually also molting secondaries, and birds that were not molting primaries were generally not molting secondaries either. The data are not sufficient to show whether secondary molt occurs mainly near the end of the primary molt, as it does in other terns.

#### MOLT OF THE RECTRICES

The molt of the rectrices of *Gygis* on Christmas Island occurs largely during the period when the primaries are molting, which is generally when the birds are not breeding (see table 4 and later discussion); however, growing rectrices may occasionally be found at any stage in the sexual cycle.

Most of my observations of molting birds were made during the later stages of the primary replacement (scores between 77 and 99). At this time any of the rectrices could be found growing, but the center ones less frequently and the outer ones more frequently than the rest. My records are as follows (each growing rectrix counted separately): 1's (center feathers) 6 records; 2's 17; 3's 11; 4's 18; 5's 16; 6's 26. This result suggests that a basic sequence of molt in the tail, which might be obvious in young birds undergoing their first molt, has become largely obscured during the lives of the individual birds. A similar sugges-

TABLE 4. Molt of primaries and rectrices of *Gygis alba* at different stages of the sexual cycle. Numerals in parentheses indicate the numbers of birds in each class in which molt of the rectrices was in progress.

	Numbers of birds			
	Incubating	With dependent chick	Unknown breeding status <sup>a</sup>	Not breeding <sup>b</sup>
Molt of primaries in progress, score 1-12	0	1 <sup>c</sup> (0)	3(0)	4(2)
Molt of primaries in progress, score 77-99	11(2)	0	6(3)	26(23)
Molt of primaries in progress, score indeterminate	5(1)	2(0)	2(1)	0
No molt in primaries (score 100/0)	221(9)	54(6)	47(6)	5(3)
Totals	237	57	58	35

<sup>a</sup> This category includes birds known to have recently lost eggs, but which still had naked incubation patches and may have re-laid, as well as other birds whose breeding status was uncertain.

<sup>b</sup> These birds did not have eggs or chicks, and their incubation patches were not fully naked.

<sup>c</sup> Chick was 89 days old.

tion was made, with a little more evidence, in the case of *Anous tenuirostris* on Ascension Island. A basic sequence would also imply a basic symmetry, but this is not detectable in the majority of the adults.

Rectrices are normally all replaced between successive breeding periods, but I have no evidence as to whether any are replaced twice.

#### RELATIONSHIPS OF BREEDING ACTIVITIES AND MOLT

Individual *Gygis* on Christmas Island were generally not molting when they were involved in breeding activities (table 4). Thus, in 237 examinations of incubating birds, 212 showed no molt in the primaries or tail, while in 57 examinations of birds that had dependent chicks 48 showed no molt. In contrast, in 35 checks on birds that were not involved in breeding, 33 showed some molt in the primaries or tail. Similarly, most birds had few or no growing body feathers while they were incubating or had young chicks (see below, and table 5).

The records of birds examined while they had chicks show that a new molt of the flight feathers does not normally start until the chick is three or four months old and nearly or quite independent. Of the nine adults examined when they had chicks more than nine weeks old and well able to fly, six still had complete primaries and rectrices. The

estimated ages of their chicks were 66, 78, 80, 84, 85, and 127 days. In the last of these cases there was evidence that the chick had finally left the nest site and gone to sea within the previous five days, but the adult was found in the nest-tree at night carrying a fish presumably intended for the departed chick. This adult had still not started molt of its flight feathers or tail, although the primaries were badly abraded. Of the three birds that were molting, one was an exceptional individual that was growing certain feathers both while incubating and when it had a chick, while the other two had just started their molt. One of them (859) had a primary molt score of 1 at the time when its chick should have been about 99 days old (it had last been caught 15 days earlier); the other had a score of 5 when its chick was 89 days old.

Although breeding and molt occurred separately in a large majority of the birds studied, a few were molting some primaries or rectrices, or both, while incubating or caring for small chicks (table 4). In this respect the Christmas Island population contrasts with the population of the same species on Ascension Island, where Dorward (1963) found no birds molting primaries or rectrices while they had eggs or small chicks.

Examination of the 25 records of birds that were incubating while growing flight feathers (13 primaries only, 9 rectrices only, 3 both) showed that in about 19 of them the observed situation could reasonably be explained in terms of breeding having started shortly before molt was completed, in contrast to the normal situation in which breeding starts shortly after the end of the molt. It is of interest that two birds (one is 508 in table 2) account for four of the records, each having been found incubating while still growing flight feathers on two separate occasions, in each case about 10 months apart. This finding implies that certain individuals have a persistent tendency to start breeding before molt is completed.

In the other six birds which were growing primaries or rectrices while incubating, it was not clear that molt was just finishing; in some of them feathers had obviously been shed after the laying of the egg, and not all could reasonably be explained as accidental feather losses. Two of these birds are of special interest, since it was almost certain that each had had at least one earlier egg in the same breeding period, and so had already been involved in breeding for rather a long time. One of them molted one primary just before the laying of the replacement egg, and another primary and a rectrix before its chick was two months old. The other replaced two primaries in each wing, as if in the start of a normal molt, during the incubation of its replacement egg and the early life of the resulting chick. However, molt appeared to be stopping at the time when the chick was five weeks old.

Although it was not actually seen molting during its breeding period, it is worth considering here bird 864 (table 2), already discussed as an example of

an individual that was involved in breeding activities for nearly six months before it hatched its egg successfully. When first caught on 19 September 1963, incubating a pipped but dead egg, it had one conspicuously old primary in each wing. On 17 November, when its second egg had probably just been lost, it had nearly completed the growth of new feathers replacing the two old ones. These feathers, clearly representing the most distal wave-fronts in the wings, were probably shed soon after the loss of the first egg. On 18 January 1964 the bird was incubating again, was not molting, but had replaced two more primaries, this time in the proximal molt waves. (My data suggest that, in this species, once a feather has been shed the growth of its successor always continues to completion, even if the bird becomes involved in breeding early in its growth, and further molt is inhibited.)

Five additional birds, examined when they had chicks less than two months old, had growing flight feathers; three had single growing rectrices, one had no less than four growing rectrices, while the other had evidently molted one primary in each wing just before its chick hatched, and subsequently shed a rectrix when the chick was about five weeks old. This last bird was not known to have had and lost another egg previously, but the possibility cannot be excluded.

Thus there is some evidence that in birds laying two or three eggs within one breeding period (because of the loss of the first ones), molt may be initiated at the positions of the wave-fronts at the time, only to stop again as breeding activities continue. This could be the explanation of the curious sequence of records from bird 556 (table 2), since the egg found in June 1964 was almost certainly not the first laid in that breeding period, and although all the primaries had been replaced by February 1964, and molt was apparently stopping, two primaries in the left wing (and probably two in the right wing) had been molted again by June.

Although attention was concentrated mainly on investigation of the molt of the flight feathers, nearly all the birds handled were examined rapidly for growing feathers in the main regions of the body; subsequently, each record was assigned to one of three body molt categories representing negligible, light, and heavy molt. In spite of the subjectivity of this method, the results show striking differences in the proportion of birds in each of the three categories at different stages in the sexual cycle (table 5). Birds examined when they were not breeding were nearly all in heavy body molt. Of the 10 birds examined when they had chicks more than two months old, nine were involved in body molt. Most birds with chicks less than two months old were not molting body feathers, but the nine individuals that did show some body molt included the only two birds that were molting primaries when they had chicks of this age.

TABLE 5. Body molt of *Gygis alba* at different stages of the sexual cycle.

Body molt category <sup>a</sup>	Numbers of birds				
	Incubating		With dependent chick		
	No molt in primaries	Molt of primaries in progress	Less than two months old	More than two months old	Not breeding
1	144	4	34	1	2
2	53	8	9	9	5
3	6	1	0	0	27
Totals <sup>b</sup>	203	13	43	10	34

<sup>a</sup> Category 1 indicates that no growing feathers, or only one or two, were seen in a rapid check of various parts of the body; category 2 indicates that growing feathers were seen only in small numbers, or that they were largely restricted to one part of the body; category 3 indicates the presence of many growing feathers.

<sup>b</sup> I have no information on the body molt of the 26 birds with known breeding status that are not represented in this table but do appear in table 3.

Similarly, although a large majority of incubating birds were not molting body feathers (and hardly any were in heavy body molt), those individuals that were molting primaries while incubating showed a highly significant tendency also to be involved in body molt. This is in accord with the evidence discussed above, that birds involved in a series of unsuccessful breeding attempts sometimes molt a few flight feathers during their extended breeding period, and it suggests a temporary relaxation (presumably during the intervals between successive breeding attempts) of the inhibition of molt activity that normally operated during a breeding period.

In conclusion, it may therefore be said that whereas breeding and molt in this population of *Gygis* are very largely mutually exclusive, they may overlap in three distinct situations. First, some birds start breeding (in the sense of having an egg) before completion of the growth of those flight feathers that were shed last. Second, an unknown proportion of successful breeders start their normal molt some weeks before their chick becomes independent. Finally, some birds that lose one or more eggs in a breeding period may undergo some molt before finishing their last breeding attempts. When they are not breeding, the birds are clearly involved in molt for virtually all the time. They are not seen on the island between the very early stages of the molt and the time when all or nearly all of the old flight feathers have been shed, but the growth of the last feathers to be shed is normally completed during the courtship period, when the pair are spending much time together near the nest site.

## DISCUSSION

## ADAPTATIONS OF THE BREEDING AND MOLT CYCLES

The outstanding feature of the biology of the Christmas Island population of *Gygis* is that breeding occurs at all times of the year. The fact that in both 1958-59 (Gallagher 1960) and 1963-64 there was a substantial peak in laying in the northern summer cannot be interpreted without further data. It is possible, for instance, that *Gygis* in the Christmas Island population retain a degree of the responsiveness to environmental proximate factors, which forms part of the adaptation system for the timing of breeding in colonies where seasonal changes in the environment make it advantageous to breed at a particular time of year. Alternatively, it may be that peaks of breeding on Christmas Island occur at different times in different years, and are produced solely by fluctuations in the numbers of birds that are finished with molt and are ready to breed; these fluctuations could be related to such factors as the success in breeding in the preceding months and the number of young birds settling to breed for the first time.

Although it is unfortunate that the reasons for the observed peaks in laying are not understood, the facts remain that a substantial proportion of the population may be found breeding at any time and that individual members of the population are not tied to an annual breeding schedule. These observations are critical in that they show that this population of *Gygis* is exposed to a type of selection very different from that operating on annual-breeding populations of this or any other species.

The vast majority of all birds have evolved in environments in which there are well-developed annual cycles that make breeding much more likely to succeed at one season than at others. In such environments all but a few birds have evolved sexual cycles that last one year, the exceptions being those large species in which successful breeding occupies more than a year. Thus in most bird populations individuals that attempt to breed at times other than the normal breeding season are subject to strong counter-selection, and those birds are favored that respond promptly and accurately to the external stimuli used in timing the normal breeding season.

However, in sea birds and other species with long incubation and fledging periods, individuals that raise chicks successfully are involved in breeding activities for a much

longer period than those that lose their eggs, or their chicks when they are small. Thus, assuming that the molt takes a roughly constant period, the total time required for a successful breeder to complete breeding and then molt will be considerably longer than the time required by an unsuccessful bird (see, for example, Stonehouse 1962b). Since, as already mentioned, nearly all bird species have evolved cycles in which successful individuals can complete their breeding and molt within a year, and so be ready again at the optimum time in the next season, it follows that unsuccessful individuals will have some "surplus" time.

This surplus time, inevitably wasted in annually breeding populations, can be used in environments that permit the species to breed at any time of year. In a population colonizing a constant environment from a seasonal one, an individual that completes one unsuccessful breeding attempt and the subsequent molt in less than a year will be favored by selection if it starts breeding again at once, since it will on the average produce more young than birds that do not. Thus in constant environments one can expect to find that birds are no longer dependent on environmental proximate stimuli to initiate breeding, but that they are brought back into breeding condition as soon as possible by an intrinsic cyclical tendency, sometimes supplemented by response to social stimulation. Breeding and molt should alternate with each other continuously, and the molt should be as rapid as possible.

However, it must be borne in mind that it is not necessary or likely that any environment has an entirely constant suitability for breeding throughout the year. If one season is on the average only slightly better for breeding than others, it will still be selectively advantageous for a bird that is ready to breed at another time to attempt to do so rather than waiting, if there is a reasonable chance of being successful. For any species in a given environment, the breeding regime that is evolved will be determined by the probabilities of successful breeding at different seasons and the lengths of the unsuccessful and successful sexual cycles. It may also be influenced by the extent to which the species, in other parts of its range, is dependent on social stimulation in timing its breeding activities. For instance, the extremely social nature of *Sterna fuscata* may be one of the reasons why breeding of this species is closely synchronized even on Ascension Island and Christmas Island, although it is not restricted to one particular

season. Since species living together in a given environment exploit it in different ways, it is not surprising to find that in certain environments where seasonal influences are slight, some species have retained annual breeding while in others nonannual regimes have been evolved. The sea birds of Ascension Island provide one good example (see papers in *Ibis*, 103b, 1962-63), while on Christmas Island dramatic contrasts are found even within the terns. *Anous tenuirostris* and *Procelsterna cerulea* maintain annual breeding schedules, *Sterna fuscata* breed at six- or 12-month intervals according to their breeding success (Ashmole 1965), and *Gygis* show great variety in the length of their sexual cycles.

Since *Gygis* breed on Christmas Island at all times of year, and individuals can complete unsuccessful—and sometimes successful—cycles in less than a year, we may assume that the observed sexual cycles have been subject to selection of the kind discussed above, so that molt should be as rapid as possible, and there should be no “wasted” time. In fact, as already shown, birds in this population spend virtually all their time either breeding or molting, and there is sometimes a little overlap between the two. No data are available on the length of time occupied by the molt in annual-breeding populations of *Gygis*, but this might be expected to be as long or longer than on Christmas Island, and might also show less tendency to overlap with the earliest and latest stages of breeding activity. On the other hand, the length of time for which birds are involved in breeding activities need not be shortened by the type of selection operating on Christmas Island. In successful breeders the length of this period is determined mainly by the growth rate of the chick, and there is circumstantial evidence that in sea birds that lay a clutch of one egg this has evolved primarily in relation to the rate at which parents can collect food during the breeding period (Ashmole 1963b). For birds that lose an egg or small chick one or more times during a breeding period, selection for the laying of replacement eggs will be critically dependent on the length of the period suitable for breeding. In most strongly seasonal environments this period will generally be short, and the laying of replacement eggs—inevitably much later than the optimum time, if the first egg was laid close to it—will be relatively uneconomic since it will rarely lead to the successful rearing of a chick. But in environments in which breeding is possible at any time of year, there will be selection in

favor of making repeated attempts to breed, if the first is unsuccessful, before abandoning the chance of successful breeding in that breeding period and starting postbreeding molt.

Thus the record of a *Gygis* on Christmas Island that was incubating an egg in early February and another in early June of the same year, without having undergone an intervening molt, is not unexpected, in spite of the fact that if it raised a chick from the last egg its sexual cycle would have lasted longer than a year. Another record of a bird that had an equally long ( $4\frac{1}{2}$  month) interval between the laying of its first and last egg, but which did molt a few flight feathers during this period, has already been detailed.

In an environment that shows strong seasonal variation in the availability of food, no bird can afford to spend so long in late attempts to breed in one season that it is not ready to breed at the optimum time in the next year. But in *Gygis* on Christmas Island, which has a good chance of breeding successfully in any month, it may be that the only factor limiting the time that may be spent in breeding attempts in one breeding period is the need to replace the plumage before it becomes grossly inefficient. Possibly there is also a limit to the time for which the gonads can remain active, but present evidence suggests that this factor is readily modified by selection (*e.g.*, Miller 1959); indeed, the example, just mentioned, of a bird whose last (probably third) egg in one breeding period was laid four and a half months after the first is impressive evidence of such modification, when it is compared with the situation found in most tern populations.

It may thus be concluded that the environment of Christmas Island is such that *Gygis* can breed at any time, and that the species has evolved a flexible breeding schedule that virtually eliminates “wasted” time, when the bird is not either breeding or undergoing feather replacement at the maximum rate. In comparison with other sea birds the most conspicuous feature of the ecology of this population is the frequent completion of sexual cycles in less than 12 months, thus giving those adults successful in one breeding period a chance to raise two chicks in less than two years. However, the occasional occurrence of very long sexual cycles, in which pairs spend more than one year over a breeding period and the subsequent molt, is also dependent on the seasonless environment and the flexibility of the breeding regime.

The molt sequence shown by *Gygis* appears

to be an exceptionally efficient one for birds that depend critically throughout the year on their agility in flight. In most tern species two or more adjacent primaries may be found growing at the same time. Thus the aerodynamic characteristics of the wing must be very different when the bird has a complete set of remiges and when it is at various stages of the molt. In *Gygis* this effect is minimized, since one primary normally completes its growth before the next is shed, and the slot left by the molt of one feather is partly covered by the adjacent feathers. By having two or three widely spaced growing feathers in the wing at the same time, molt can be completed rapidly, but the effective shape of the wing is very similar at all times.

Although the present description of the molt of *Gygis* relates to the Christmas Island population, it is known that two or more molt waves can be found progressing simultaneously through the primary series in individuals from other populations. It has been shown that primaries are normally replaced only once between successive breeding periods on Christmas Island, but it is possible that in populations in which breeding occurs at strictly annual intervals unsuccessful breeders may continue molt after the first replacement has been completed, until it is time for breeding. If so, the molt sequence found in this species would be especially advantageous, since it would allow extra replacement of old outer primaries, which are most subject to abrasion, as well as of inner ones, which suffer less wear. In contrast, in those Palearctic terns in which primary molt continues after all the feathers have been replaced once, it is only the inner feathers that are replaced again, and all the outer ones are relatively old when breeding starts.

The evolution of a different sequence by *Gygis* could be made especially advantageous by the fact that its feathers are entirely unpigmented. Since feathers with melanin are in general much more resistant to abrasion than those without, it would be especially disadvantageous for *Gygis* to start breeding with old outer primaries. It is worth mentioning in this context that many other species of terns have evolved pale-colored—but not translucent—wings by means of two complementary mechanisms. First, they have a superficial “frosting” or “silvering” on the wing feathers, “due to elongated, curved and frilled barbules on the distal sides of the barbs” (Dwight 1901), which largely obscures the dark pigment below when the feather is new. Second, the inner webs of the primaries,

except the part nearest to the shaft, are white. In the spread wing viewed from below, the white part of each primary largely obscures the dark pigment in its proximal neighbor, but at the same time is itself physically supported by its neighbor, and so does not become abraded quickly. The fact that *Gygis* (and *Sterna sumatrana*) have not evolved these arrangements implies that the translucence (as well as the whiteness), which is a most conspicuous feature of their plumage, is advantageous to them and outweighs the disadvantage of having primaries more subject to abrasion. The possibility that the advantage lies in reduced conspicuousness to their prey is discussed in another paper (Ashmole and Ashmole 1967). It is doubtless significant that *Sterna sumatrana*, which is the only tern apart from *Gygis* to have unpigmented primaries (except in juveniles), is also the only other tern thought to replace its primaries by an interrupted “continual stepwise molt” (Ashmole, unpublished).

#### CONTROL OF MOLT OF THE REMIGES

The pattern of molt of *Gygis* brings into focus the largely unsolved problem of how a protracted sequential molt of the flight feathers, which is of common occurrence among birds, is controlled physiologically. Although experimental work has clarified some aspects of the endocrine control of molt, most of it has been concerned primarily with demonstrating what substances or procedures can stimulate or inhibit “a molt” in fowls, and has thus been only marginally relevant to the problem of the control of a complex molt that may last for more than six months, or almost all the time that a bird is not breeding. The present data on the molt of *Gygis* do not provide a complete solution to this problem, but they do indicate some of the facts that satisfactory theories must explain. Some preliminary alternative hypotheses have been presented here in the hope that they may help in the planning of future experiments. Only the molt of the flight feathers—and mainly of the primaries—is considered in this discussion. Once the mechanisms involved in the control of molt of the primaries are understood, it will probably be easy to interpret the molt of the secondaries. The control of molt of the body feathers is a rather separate problem, and the present study did not provide much critical information about it.

The most general fact requiring explanation is that the pattern of molt of the remiges in most species of birds involves a definite sequence of molt that is adhered to rather



precisely. Whether the molt lasts for six weeks or six months, it is unusual for a feather to be molted out of the normal sequence. For instance in the Christmas Island population of *Gygis* every molt wave for which adequate information is available travelled out through the primary series in exact sequence from proximal to distal feathers. The more proximal of two adjacent feathers never molted after the more distal, and each feather was invariably nearly or completely grown before its distal neighbor was shed.

Two general hypotheses seem possible at first sight. First, one can suppose that the physiological state of the bird becomes suitable for molt at a definite time in relation to breeding activities, that molt starts at certain points in the feather series that are genetically determined, and that the sequence of molt thereafter is determined by the reactions of the different feather follicles to the general physiological state, and by interactions among the follicles. It is not necessary in this case to postulate that the intensity of any systemic molt stimulus changes during the course of the molt. One version of this hypothesis was proposed by Miller (1941) in a paper on the molt centers in the secondaries of the Falconiformes. He suggested that given a general internal stimulation of molt, and a relatively high threshold for response to this stimulation in the follicle, the follicles with the best blood supply might initially be the only ones to react. Then, if the shedding of these feathers improved the blood supply to the adjacent follicles, one would expect to find an orderly molt sequence of the kind that in fact occurs. Another version of the same general hypothesis would be that after molt started at genetically determined points, the growth of these first feathers would stimulate the molt of the adjacent ones. Molt would then continue, each growing feather stimulating its neighbor, until the end of the feather series was reached. To explain the fact that in some species several adjacent feathers may be growing at the same time, while in others a feather is molted only as its neighbor completes its growth, one has only to postulate minor differences between species in the stimulus-response mechanism between one follicle and its neighbor. However, this hypothesis is less satisfactory when applied to feather series in which the molt is irregular, or in which the molt sequence does not correspond with the linear arrangement of the feathers. Both these situations arise in the rectrices of various species. Furthermore, this type of hypothesis cannot easily be applied to

species in which several waves of molt travel simultaneously through the feather series, but in which the waves start after breeding at different points in different individuals. Two examples of such species are *Gygis* and *Sula dactylatra* (Dorward 1962); in both, molt starts after breeding from the points where it stopped at the start of breeding, and not from genetically fixed positions.

The second general hypothesis is that of a gradient and threshold system, in which it is assumed that a general molting stimulus increases gradually in intensity, and that each follicle in a feather series has a slightly different threshold of response, so that an orderly molt is achieved. It is necessary and reasonable to assume that a follicle that has just produced a feather is refractory to further stimulation during the rest of that molt, so that it does not molt again in spite of the (assumed) steadily increasing molt stimulus.

This mechanism is a very likely one for controlling the molt of the many species in which a single molt wave progresses rapidly through a feather series, and in which the length of the molt may be measured in weeks rather than months. However, it seems rather improbable in species in which molt is almost continuous between one breeding season and the next that a general molt stimulus should increase in strength throughout this period. Furthermore, this hypothesis appears definitely not to be sufficient to explain the molt of species like *Gygis*, in which molt starts after breeding with different feathers in different individuals, and probably sometimes with different feathers in a single individual in different years. Difficulties also arise in applying it to species (including many terns—Stresemann 1963; Stresemann and Stresemann 1966) in which a new molt wave starts with the molt of the innermost primaries before the previous molt wave has reached the outermost ones.

Before attempting to explain the observed features of the molt of *Gygis*, I shall consider briefly the molt of some species of Palearctic terns that show interesting differences from *Gygis*. Although my most nearly complete data are for the Black Tern (*Chlidonias niger*), the molt of the Common Tern (*Sterna hirundo*) and many other species (but not the Arctic Tern, *S. paradisaea*) is apparently similar (Stresemann 1963; Stresemann and Stresemann 1966; Ashmole, unpublished). The normal pattern is for primary molt to start near the end of the breeding period (at least sometimes pausing during southward migration) and to proceed continuously until the start of the northward migration in the following

spring. A molt wave starts with the innermost primaries and progresses outward until it reaches the outermost ones. But shortly before the first molt wave reaches the outermost primaries, a new wave starts with a second replacement of the innermost feathers. This wave progresses usually as far as the fourth, fifth, or sixth primary (sometimes replacing one more primary in one wing than another) before it stops at about the time of the northward migration. Breeding birds thus have a sharp discontinuity at some point in the primary series, with new feathers proximal to it and older ones distal to it. After breeding, molt starts again with the innermost primary, not at the discontinuity. The outer primaries are therefore replaced once each year, but the inner ones twice.

It seems useful to present a preliminary hypothesis as to the kind of mechanism controlling this molt sequence in Palearctic terns, and to suggest a way in which the mechanism could have been modified during evolution to give rise to the molt pattern found in *Gygis*. First, it must be emphasized that in most species of Palearctic terns, as in *Gygis*, molt of the primaries is continuous except when the birds are breeding or migrating. This implies that the normal physiological state of the adult bird is one that permits molt of the flight feathers, molt being inhibited only under certain specific circumstances. In most tern species the postbreeding molt starts with the shedding of the innermost primaries, even though these are not the oldest primaries present. It therefore appears that there is a genetically determined tendency for molt of the primaries to start with the innermost feathers. This might be mediated by their having an especially low threshold to stimulation, so that as the hormonal inhibition of molt that is generally associated with breeding gradually dissipated, they would be the first to respond. After the molt of the innermost feathers, molt progresses outward in a single wave, although some outer primaries are older than the inner ones and there is an age discontinuity in the middle of the series. If it is assumed that an active follicle provides a stimulus for the onset of activity in its distal neighbor, the precision of the progress of molt out through the heterogeneous feather series can be explained by its being under local rather than systemic control.

To account for the fact that a second cycle of primary replacement starts in most tern species before the first one is completed, one may postulate that the innermost primaries (and presumably also the others) have a

refractory period, during which they do not initiate another molt wave, even though the general physiological state of the bird permits the first wave to continue its progress out through the primary series. The length of this refractory period, and the rate of progress of the first molt wave, will determine the extent of overlap between the two successive molt waves in the primaries. This postulate also provides an explanation of the sequence of molt in juvenile Palearctic terns; it is known for a number of species that the second complete replacement of the primaries of young birds, starting with the innermost feathers, is initiated before the first cycle of replacement has been completed by the molt of the outermost ones (Stresemann 1963; Stresemann and Stresemann 1966; Ashmole, unpublished). If the initiation of the first molt with the shedding of the innermost primary is controlled by an age-dependent change in the general hormonal balance in the young bird, and subsequent progress of the molt wave is at least partly locally controlled, the start of the next molt wave (and of subsequent ones) can be explained as depending solely on the completion of the refractory period of the follicle of the innermost primary. Each molt wave will then continue its progress out through the primary series, and be regularly succeeded by new waves, until a general inhibition of molt takes place, as in breeding.

Although the ontogeny of the molt pattern of *Gygis* is not yet known, Dorward (1962) has given an account of molt in young *Sula dactylatra*, another (unrelated) species in which adults have two or three simultaneous waves of molt in the primaries. In this species the juvenile primaries are replaced by a wave of molt progressing from the innermost primaries outward, but another wave is initiated with the innermost feathers when the first has reached primary 6 or 7; from that time onward new waves start regularly at the innermost primary, so that for the rest of their lives the birds have several molt waves in each wing, though these are generally inactive when the birds are breeding (Dorward 1962). It seems extremely likely that the ontogeny of the molt pattern in *Gygis* is similar to that in *Sula dactylatra*, and thus essentially the same as in other juvenile terns. In this case there is no need to postulate a different physiological control mechanism.

The critical difference between adult *Gygis* and *S. dactylatra* on the one hand and adult Palearctic terns on the other is that after breeding is finished molt in the former species continues from the several points at which it

stopped, while in the latter group it starts again only from the innermost primaries. A possible explanation of this is that a modification of the normal control mechanism has been evolved, such that in adult *Gygis* (and *S. dactylatra*) a feather follicle that has just produced a new feather has a very high threshold to stimulation, but that this threshold declines steadily with time, until eventually molt will occur even without stimulation by a molting neighbor. Thus when breeding stops, and the general hormonal balance of the bird again permits molt, the several oldest feathers in each wing will be molted first, irrespective of their positions. This will, of course, result in molt starting from all the discontinuities at which it stopped before breeding, and not necessarily with the innermost primary, unless it happens to be one of the oldest primaries left in the wing.

This hypothesis leads to the view that in *Gygis* and *Sula dactylatra*—and perhaps also in some other birds—the molt should be considered not so much as a precisely programmed discrete event starting after breeding, but as a continuous process initiated by the shedding of the juvenile first primaries and progressing in a single sequence throughout the life of the bird, interrupted only by the inhibition imposed by breeding activities. This view is in full accord with the observations that a few individual *Gygis* (e.g., bird 864 in table 2) molted a few primaries—in the normal sequence—after the failure of one breeding attempt, but stopped molt again during another attempt a few weeks later. The implication is merely that the hormonal inhibition of molt was temporarily relaxed between breeding attempts, permitting the shedding of the oldest feathers before the resumption of breeding activities.

If, in *Gygis*, the age of a feather is of critical importance in determining the timing of its molt, the period after a follicle has produced a new feather should be viewed as a “preparatory” rather than as a “refractory” period, stimulation over a considerable period being a prerequisite to further response (at normal levels of stimulation). There are some indications that a “preparatory” process in the feather follicle may also be important in the control of molt in certain species besides *Gygis* (and *Sula dactylatra*). For instance, in *Anous tenuirostris* on Ascension Island (Ashmole 1962) it was shown that whereas all secondaries are normally replaced during the later stages of the primary molt, finishing with the middle ones shortly before breeding starts, some of these middle secondaries are occasion-

ally retained through the breeding period. They are then replaced early in the next molt. If the control system had involved fixed thresholds and a graduated molt stimulus, or if the molt of each feather (except those with which molt commences) was controlled by stimuli from molting neighbors, one would have expected the retained feathers to be replaced late in the next molt, rather than as it started. However, an experimental approach to the problem is clearly desirable.

Although this is not the place for a review of the extensive data on the hormonal control of molts (Assenmacher 1958; Wagner 1962; Stresemann and Stresemann 1966), it seems relevant to mention that it cannot be considered established that cyclical changes in thyroxine levels provide the main control of natural molt. Juhn (1963) argues that there is little evidence that under natural conditions the thyroid shows special activity at the time of initiation of the molt. Furthermore, she points out that growing feathers, which in the fowl show a clear structural response to thyroxine administration at a level far below that stimulating molt, do not show these modifications when grown during the normal molt period. Juhn also investigated the mechanism of progesterone-induced molt in capons and found that feathers regenerating during treatment with progesterone were similar to those grown by untreated birds, but the feathers grown by birds treated with enough thyroxine to induce an equivalent amount of molt showed the usual structural response to this hormone. The implication is that molt-stimulation by progesterone does not act by stimulating thyroid output. Juhn (1963) provisionally concluded that “molt is essentially an autonomous process, the primary seat of the cyclical renewals being the feather papilla proper.”

Stresemann and Stresemann (1966:14) came to a similar conclusion. Commenting on the statement of Rawles (1960:230) that “feather primordia in different positions on the body exhibit orderly and characteristic differences in threshold of reaction to known doses of hormones (thyroxine and estrogen),” they say: “It seems to us that some peculiarities of the sequence can be explained only by another hypothesis. This is that the different reaction of the feather germs to a known dose of hormone depends not on the different height of their thresholds but on the fact that the feather papillae do not develop their sensitivity to this ‘known dose of hormone’ simultaneously, but in a determined sequence of a plan.”

Wagner (1962), on the basis of experimental work on body molt in passerines, suggests that the sex hormones may have an important regulating (*Zeitgeber*) effect in the natural molt cycle through their inhibition of molt. This suggests that in some other species, as in *Gygis*, molt may not depend on a special hormonal stimulus; rather, it should be viewed as a process occurring whenever the bird is in a normal physiological state, provided that it is not inhibited by the presence of hormones related to reproduction or migration, or by certain other circumstances. These latter circumstances are not well understood, but it is possible that the inability of a bird to obtain adequate food acts directly as a proximate stimulus resulting in cessation or slowing down of molt, or delaying its onset. Probable cases of all these phenomena in a population of *Anous tenuirostris* were described by Ashmole (1962). Conversely, a sudden improvement in the availability of certain foods may stimulate molt. Wagner (1962) records that molt in some caged birds may be evoked at unusual times by generous feeding with mealworms or fresh ant eggs. Effects of nutrition on molt presumably operate through changes in metabolic activity; however, the nature of the changes and the role of the thyroid in regulating them are not yet understood. In addition to the proximate effects of food supply on molt, the cycle of food availability in the environment is doubtless a major ultimate cause of the type of molt cycle that is evolved in a bird population.

In birds in which molt can occur without a special internal stimulus, there must be a mechanism to ensure that it follows a definite program and that feathers are not replaced unnecessarily often. As discussed above, the evidence suggests that in *Gygis* and certain other species this mechanism involves time-dependent processes in the feather follicles, such that after a follicle has produced a new feather it will not again become active until it has been exposed for a considerable time to a physiological climate permitting molt. A mechanism of this kind could be sufficient to prevent further molt in the fall after the complete postbreeding molt that occurs in most birds.

In conclusion it is useful to emphasize the need, when attempting to determine the physiological control of molt, to remember that the evolution of different molt regimes in different bird species has necessarily been accompanied by divergent adaptations of the control mechanisms. Full understanding of natural molt will therefore have to await

further field evidence, and also experimental work on a wider range of species than has hitherto been used.

#### SUMMARY

Sexual and molt cycles of the White Tern *Gygis alba* on Christmas Island (Pacific Ocean) were investigated by following the histories of banded birds with individually marked primaries and rectrices, in a study area in which the events at all nest sites were recorded.

Breeding birds are found on the island at all times of year—though not always in the same numbers—and successful breeding apparently occurs at all seasons. The sexual cycles of individuals vary widely in length, lasting at least 10½ months in birds that rear a chick successfully, but often substantially less in unsuccessful breeders. Within these cycles, molt occurs almost entirely when the birds are not breeding, and occupies about 5½ to 7 months; during most of this time the birds are absent from the island.

One complete replacement of the primaries and rectrices normally occurs between successive breeding periods. The primaries are replaced by a series of simultaneous molt waves, each progressing steadily outward and separated by about four feathers from the adjacent waves. Thus, although several feathers grow simultaneously in each wing, there is minimal variation in aerodynamic characteristics.

*Gygis* on Christmas Island are considered to have adapted to an environment in which seasonal changes are slight by evolving the ability to start a new breeding period whenever their molt is completed. They also sometimes continue breeding efforts (*i.e.*, lay replacement eggs) over an unusually long period if the first attempt is unsuccessful.

Data on the unusual sequence of molt in *Gygis*, and on the molt patterns of some Palearctic terns, are used in considering the type of mechanism involved in the control of complex and lengthy natural molts. In *Gygis* and some other species an extended period of exposure of the follicle to a physiological climate permitting molt may be a prerequisite for the molt of each feather, so that when molt starts after a pause, the oldest feathers are shed first. It seems possible that in some bird species there is no special internal stimulus for molt, but that old feathers are replaced whenever molt is not inhibited by hormonal or other factors.

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