

ACKNOWLEDGMENTS

This investigation was supported in part by PHS Research Grant AI 06072 from the National Institutes of Health, Public Health Service; and in part by a contract with the Communicable Disease Center, Public Health Service. We wish to thank the Gorgas Memorial Laboratory for making available facilities at Almirante; and Gorgas personnel, particularly Dr. Pedro Galindo, Sr. Eustorgio Mendez, and Sr. Rudolfo Hinds, for aid in banding and record-keeping. The Chiriqui Land Company (United Fruit Company) kindly provided housing and other facilities for us at Almirante; we wish especially to mention the late Dr. Gustavo Engler, then director of the company's hospital, for many favors granted. Dr. Merle Kuns of the Middle America Research Unit (NIH) provided nets and labor for intensive netting near Gamboa in autumn 1964. Many local bird students contributed their time and energy to this program. Particularly we wish to acknowledge William Belton, Dr. Nathan B. Gale, Harvey Fischer, Storrs Olson, C. M. Keenan, and A. C. Kupfer for their important contributions. Dr. E. L. Tyson and Frank Chapman did intensive banding for this project in winter 1964.

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Received February, 1965

ANNUAL CYCLE OF THE YELLOW WARBLER IN THE GALAPAGOS¹

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From February 1963 to June 1964 I made regular observations on the Yellow Warbler (*Dendroica petechia*) at Academy Bay on Santa Cruz Island (Indefatigable) in the Galapagos Archipelago, almost exactly on the Equator (0° 45'S). Nests were found throughout both the breeding seasons included in the period of observation, and some birds were trapped in nearly every month, many of them being color-banded. Altogether, 96 individuals were trapped, and 29 recaptures were made. For the two preceding breeding seasons, records have been kindly supplied by R. Lévêque.

The Yellow Warbler is almost certainly a comparatively recent colonizer of the Galapagos. Though described as a distinct sub-

¹Charles Darwin Foundation for the Galapagos, Contribution No. 25.

species (*aureola*), it differs only slightly from the form occurring in coastal Ecuador. The population that was studied lives along the shores of Academy Bay, in the thick fringing growth of mangroves (*Rhizophora*, *Laguncularia* and *Avicennia*) and the tangle of *Cryptocarpus*, *Maytenus* and other bushes and low growth which form a dense strip on the landward side of the mangroves. In this habitat their density is probably greater than anywhere else in the Galapagos. They are however by no means confined to coastal vegetation, as the parent form is on the mainland, but occur, often at very low density, in almost all other vegetated country, including the highlands of the larger islands and some of the most arid and barren of the smaller islands, in both of which they must be exposed to very different seasonal influences from those prevailing in the coastal mangrove strip.

Observations on color-banded birds showed that adults live in pairs throughout the year, and maintain their territories. Song is heard in nearly all months, and besides being used to advertise the territory has a secondary function in maintaining contact between the pair. The singing male is frequently answered by the female when she is at a distance, her harsher call of three or four syllables coinciding with the end of the male's song-phrase.

THE BREEDING SEASON

Table 1 shows the breeding season over four successive years at Academy Bay. In spite of the rather small numbers in the first two years, and the incomplete coverage, it seems clear that the breeding season did not vary much in this period; and the older literature records all fall within the same months, except for one June record from Albemarle Island (Snodgrass and Heller, 1904).

TABLE 1. BREEDING SEASON OF YELLOW WARBLERS AT ACADEMY BAY, GALAPAGOS, OVER 4 YEARS

| Half-month period | Number of nests started (date of first egg.) | | | |
|----------------------|--|---------|---------|---------|
| | 1960/61 | 1961/62 | 1962/63 | 1963/64 |
| Dec. 1 | X | — | X | — |
| 2 | X | — | X | 5 |
| Jan. 1 | X | 1 | 4 | 4 |
| 2 | 1 | 3 | 6 | 3 |
| Feb. 1 | 3 | X | 3 | 2 |
| 2 | 1 | X | 2 | 2 |
| Mar. 1 | 3 | X | 1 | 2 |
| 2 | — | X | 2 | — |
| Apr. 1 | — | X | — | 1 |
| 2 | — | X | — | — |

X: no observations made.

One color-banded pair nested twice in both years, but in neither did they succeed in rearing two broods. However, the season is amply long enough for this, and two broods are probably common. The clutch-size is usually 3, less often 2, eggs. One incubation period exactly recorded (from the laying of the last egg to the hatching of the last chick) was 11 days 16 hours, \pm 9 hours.

The breeding season is rather similar to that of the other Galapagos land-birds (Lack, 1950), and there is no doubt that ultimately it is adapted to coincide with the wet season, which though very variable (and sometimes failing almost completely) usually occurs in the first four months of the year. The proximate factors concerned are, however, less obvious. At least in the arid coastal zone the Galapagos finches, for instance, appear to be like true desert birds and are stimulated to start nesting by heavy rain, which is thus both ultimate and proximate factor (Immelmann, 1963): the Yellow Warbler, on the other hand, began in both years of observation to nest well before any heavy rain had fallen. There was no obvious change of weather which might have been responsible, and the impression was rather of a gradual recrudescence of breeding activity over a prolonged period. It will be shown in the next section that there was considerable variation in the timing of the annual cycle of different pairs.

The population that was studied depends for its food almost entirely on mangroves and other plants which are relatively independent of rainfall, since their roots are either in the sea or reach down to the brackish water which is found a little way beneath the lava near the shore. The insect food afforded by this vegetation is almost certainly less seasonal than that of other vegetation zones in the Galapagos, and it would have been interesting to have made at the same time a comparative study of Yellow Warblers in other habitats.

THE OFF-SEASON

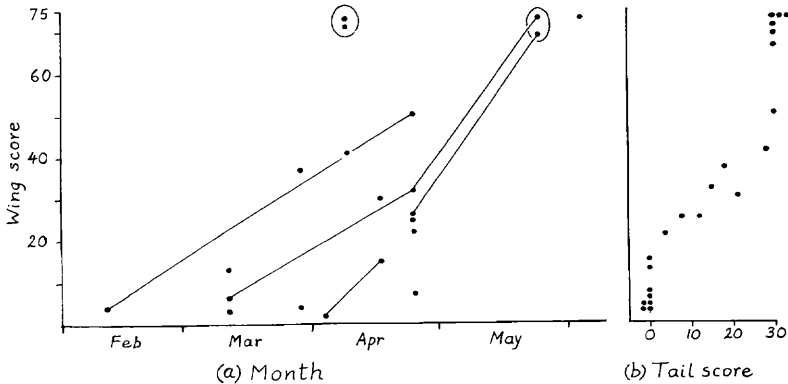
Breeding adults begin to molt as soon as their last nesting is finished. The most striking point brought out by the examination of molting adults was that individual pairs must have had a much more variable breeding season than would otherwise have been suspected. Seventeen birds were trapped while undergoing post-nuptial molt. Of these, the two earliest must have begun to molt in January, soon after the beginning of the composite breeding season, and the rest began more or less evenly throughout February, March and early April.

Fig. 1 presents the data on date of onset and rate of molt, and shows that the complete wing-molt must take a little over 80 days for the individual. The two pairs of which both members were caught in molt at the same time were very closely synchronized, which would be expected if the molt is initiated in some way by the cessation of breeding activities.

In 1963, when systematic observations were made throughout the off-season, song was sustained at moderate intensity throughout

FIGURE 1. Post-nuptial molt in Galapagos Yellow Warblers. (a) State of wing-molt in 16 individuals, including two pairs (circled); molt scores of individuals trapped more than once are joined by a line. (b) Tail-molt in relation to wing-molt.

Molt scores are calculated by allocating the values 1-5 to new feathers according to their stage of growth, and summing these values. For the wing, the three inner secondaries (tertials), which molt in advance of the others, are omitted; the score for a completely molted wing is thus 75 (5 x (9 pr. + 6 sec.)). The score for a completely molted tail is 30, half the tail being used so as to be comparable with one wing. All the tail-feathers usually fall at about the same time, and, as shown in (b), the growth of the new tail is completed within the period occupied by the wing-molt.



the molt and for most of May. There was then a gradual decline, until by the end of August hardly any song was heard. September and the first half of October were also practically without song, and then a little started about the middle of the month. From then onwards it continued and increased, apparently independently of the occasional slight falls of rain and drizzle, until by December song was intense and nesting started.

THE SUCCESSION OF PLUMAGES

Between the juvenal plumage and the adult plumage Galapagos Yellow Warblers undergo two partial molts, which clearly correspond to the post-juvenal and first pre-nuptial molts of the Eastern Yellow Warbler as described in Bent (1953). As in the northern bird, the post-juvenal molt takes place soon after the young bird is independent; but the plumage which is assumed after this molt (equivalent to the "first winter plumage" of the northern bird, though this term is inappropriate to the Galapagos) is very variable, ranging from a "retarded" type in which the juvenal grey and whitish still predominates to an "advanced" type with much yellow. Typically, this plumage is characterized by a whitish throat contrasting with yellower, sometimes faintly streaked underparts, and a grey nape contrasting with a greener crown and mantle. Birds molting into this plumage were trapped as late as May and June, but most of those seen in the field appeared to have finished by April.

In the months May-August, most of the young Yellow Warblers that were caught (30 out of 38) were in this "first winter plumage" and were not molting; and the molt was only slight in those that were molting. In the next three months, September-November, 9 out of the 12 young birds caught were molting from this plumage into a plumage not easily distinguishable from the adults'. This molt, which involves contour feathers and some inner secondaries, was moreover much heavier than was seen in birds caught during the post-juvenal molt. In December three out of seven young birds trapped were still in slight molt, but by January it had finished or nearly finished in all birds examined.

According to Bent, the first pre-nuptial molt of Eastern Yellow Warblers occurs in early spring. Insofar as the equivalent molt occurs in the Galapagos birds in the few months before the breeding season begins, its timing is not essentially different, though it is separated by a shorter interval from the post-juvenal molt. It is also almost certainly more protracted. Thus one young bird was trapped five times before it had acquired its adult plumage. On April 8 and May 20 it was in its "first winter plumage", and was not molting. On June 3 its pre-nuptial molt had begun: bright yellow feathers were growing round the throat. On July 19 the whole throat and breast were bright yellow and there were streaks on the underparts. On September 12 it was molting more heavily: the crown was now brown, as in the adult male, but the nape was still greyish; new major coverts were still growing, and the replacement of the inner secondaries (tertials) was not quite complete*.

SUMMARY

The breeding season of the Yellow Warbler in the Galapagos appears to be relatively invariable: it coincides with the wet season, but is not initiated in response to rainfall as is the case in some other Galapagos land-birds. The proximate factors involved were not determined. The full molt follows immediately after the end of breeding. There is considerable variability in the timing of the annual cycle in different pairs in the same habitat.

Territories are maintained throughout the year, and pairs stay together. Song occurs in almost every month, but it is at a minimum about four months after the end of the molt.

Young birds undergo two partial molts between their juvenal and adult plumages, which correspond to the post-juvenal and first pre-nuptial molts of northern Yellow Warblers, though the interval between them is shorter and the second of them is more protracted in Galapagos Yellow Warblers.

*On the basis of pre-nuptial molt, it is not legitimate to separate the three innermost secondaries (tertials) from the rest. Of 15 birds examined, the three innermost had been replaced in 8, the four innermost in 4, and in 3 a different number had been replaced in the two wings (3 and 4, 3 and 4, 4 and 5). But in the post-nuptial molt it was found in every case that the tertials molted as a unit, in advance of the remaining secondaries.

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ACKNOWLEDGEMENTS

The field work on which this paper is based was carried out while I was Director of the Charles Darwin Research Station in the Galapagos. I am grateful to the Charles Darwin Foundation for the Galapagos and to UNESCO for the opportunity to work at the station, and to R. Lévêque for the use of unpublished data.

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GENERAL NOTES

Preliminary Notes on a Six-Year Study of Rose-breasted Grosbeak Plumages.—For the past six summers (1960 through 1965) I have color-banded the rose-breasted grosbeaks (*Pheucticus ludovicianus*) coming to my feeder in Weston, Massachusetts, and to another about one-half mile away. Following is a summary of the birds banded:

| | <i>Males</i> | <i>Females</i> | <i>Total</i> |
|------|--------------|----------------|--------------|
| 1960 | 2 | 1 | 3 |
| 1961 | 10 | 9 | 19 |
| 1962 | 4 | 0 | 4 |
| 1963 | 7 | 4 | 11 |
| 1964 | 4 | 6 | 10 |
| 1965 | 7 | 6 | 13 |
| | 34 | 26 | 60 |

These were all adult birds. I have made no attempt to band birds of the year, wishing to concentrate my available time on banding every adult visiting my station—so far with 100 percent success.

Of the 27 males banded through 1964, 33 1/3 percent returned in 1965 (1 from 1960, 3 from 1961, 0 from 1962, 2 from 1963, and 3 from 1964); of the 20 females banded through 1964, only 10 percent returned in 1965 (1 from 1963, and 1 from 1964). This is the smallest number of return females so far in this study. In 1964 six returned from previous years (4 from 1961 and 2 from 1963). I have had but one foreign recovery—a female banded in 1959 by C. J. Paine, Weston, Mass., which has appeared from 1963 through 1965.

I have used Parker Reed single-cell traps almost exclusively, hung about seven feet above the ground from high tree limbs. The traps are used as feeders when no banding is being done—the door held open by a snap clothespin. I have used plastic bands (12 colors), putting a single color on each bird in different combina-