

THE NESTING SEASONS OF CENTRAL AMERICAN BIRDS IN RELATION TO CLIMATE AND FOOD SUPPLY

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I. INTRODUCTION.

That in a tropical region where the temperature is always summer-like, where the rainfall is sufficient to keep the landscape perennially green, and in every month some plants flower and some set fruit, the birds should have nesting seasons which in many instances are as short and definite as in northern lands with snowy winters, is, if we consider it closely, a surprising fact. Many people, I believe, are under the impression that, with tropical birds, singing and nesting continue freely throughout the year. When I first went to Central America, towards the end of 1928, I was unfamiliar with the literature of tropical ornithology and expected to find the birds always nesting. But during the clear, delightful days which prevailed on the Caribbean coast of western Panamá during January and February, when mild weather and an abundance of blossoms and unfailing verdure seemed to invite all birds to sing and to build, I found scarcely any nests except the tiny downy cups of hummingbirds and the great, clustered, swinging pouches of the oropéndolas, visible from afar in their lofty tree-tops. During March I noticed a variety of birds nesting and laying, and on 1 April recorded in my notebook, with all the warmth of an original discovery: "I am now convinced that the birds here, at 9 degrees North, have a definite nesting season, and its beginning coincides with the return of spring." Additional field work carried on over a period of nearly two decades, and an examination of published records, have shown that this conclusion is substantially correct, although I had not been the first to reach it.

The periodicity in breeding of Neotropical birds was considered long ago by Euler (1867), but in a locality—Cantagallo in the Province of Rio de Janeiro, Brazil—so near the Tropic of Capricorn that stronger seasonal fluctuations might be expected there than in regions nearer the Equator. Beebe (1917) gathered data on the breeding seasons of the birds at Kartabo, British Guiana. Harrower (1936) compiled the published and manuscript records on the nesting of the passerine birds of Central America, and prepared tables which give the number of species breeding each month in the area as a whole, in the several altitudinal zones, and in the arid and humid regions. Belcher and Smooker (1934–1937) collected a wealth of information on the nesting of the birds of Trinidad and Tobago, which lie in the same latitude as southern Central America, and presented a few general conclusions on the periodicity of breeding and its relation to the climate. In the Old World

tropics, Moreau (1937a) made a comprehensive study of the breeding seasons in an East African evergreen forest as related to climate and other environmental factors, and summarized the pertinent literature. Nice (1937 : 97-107) considered the factors which influence the start of laying in the Song Sparrow *Melospiza melodia* and reviewed the observations of other workers on both temperate zone and tropical birds.

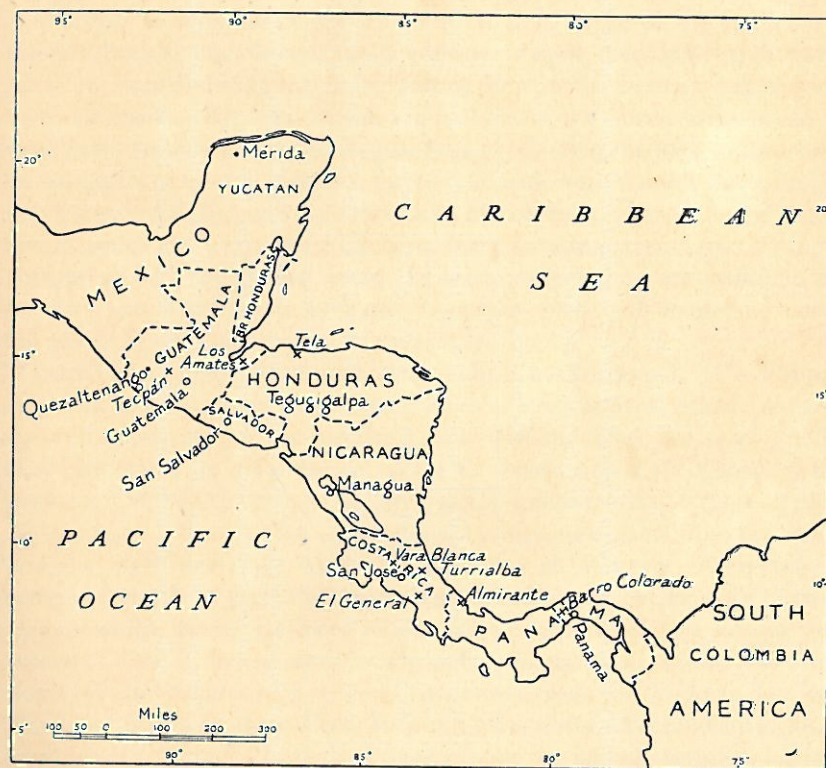
The available information from British Guiana, Venezuela, Trinidad and Central America makes it clear that over a wide area in tropical America, from within six degrees of the Equator northward, the peak of the breeding season is March to June or July, inclusive, with a reduced but still important amount of nesting activity in August and September, whereas only a small proportion of the birds have nests from October to February. Turning now to the southern half of the Tropics, Moreau presents evidence that in the mountain forests of East Africa, from Chirinda at 20° S. to Elgon at 1° N. there is for the majority of the birds a single breeding season lasting roughly from the beginning of October to the end of February, with the earlier part of this period the more important. When we recall that June in the Southern Hemisphere corresponds to December in the Northern, the data from the two hemispheres are in substantial agreement. We may summarize them by stating that in humid or forested localities of the Tropics, at least 5° from the Equator, most of the birds breed while the sun is on their side of the Equator, with the peak of the nesting season between the spring equinox and the summer solstice of the hemisphere where they reside. In tropical regions too dry for the development of closed forest this generalization may fail to hold. In such localities the nesting of the birds appears to depend principally upon the advent of the rains. At localities so diverse as Amani and Chirinda in East Africa, Kartabo, Trinidad and Central America in northern tropical America, and Cantagallo in southern Brazil, the main breeding season of the birds of forested areas begins toward or at the end of a period of reduced rainfall, and at least the latter part of the nesting season is quite wet, although, perhaps, not the wettest part of the year.

The greater part of my own information on the nesting of Central American birds has been gathered in localities remote from well-equipped meteorological stations. Hence it is not possible, as would be desirable, to correlate the fluctuations in the date of nesting, as observed in different regions or in different years at the same locality, with quantitative variations in rainfall, temperature and other measurable factors in the environment. Yet it is still most informative to consider these divergences in the date of nesting in relation to features of the weather obvious to everyone who is interested in Nature or agriculture and lives much out of doors, and which are reflected, if not actually measured for the particular locality where the observations on nesting were made, in the rising and falling curves of precipitation and temperature at distant meteorological stations.

2. THE CLIMATE OF CENTRAL AMERICA.

The observations reported in the present paper were made at points ranging from the Canal Zone 9° north of the Equator to localities in Guatemala 15° north of the Equator (see map). This takes in most of the length of Central America, a great curving isthmus about a thousand miles long, and for the most part extremely broken, mountainous country.

Text-figure 1.



CENTRAL AMERICA.

In a region of such complex topography the climate may vary markedly at stations only a few horizontal miles apart. Although the analysis of all the local climates of Central America would be an endless task, we may here attempt to delineate some of the bolder climatic features of the region as a whole. Unlike some other tropical areas with two annual periods of rain, Central America has each year a single dry season and a single wet season (see Table 1). The dry season begins earliest, lasts longest and is most

TABLE 1.
Average monthly rainfall at Barro Colorado Island, Panamá Canal Zone, and in the Valley of
El General, Costa Rica.

Millimetres.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Barro Colorado (1925-1946)	48.5	31.2	37.1	70.9	282.7	286.3	300.0	319.0	265.9	334.5	490.2	297.4
El General (1937-1943)	19.1	6.4	52.7	135.8	407.3	338.2	294.2	351.8	415.2	494.0	405.4	130.1

Average for 22 years at Barro Colorado, 2763.8 mm. Range : 1944.9 to 3642.9 mm. (From 'Annual Report of the Smithsonian Institution for 1947', pp. 145-146.)

Average for 7 years in El General, 3050.2 mm. Range : 2333.4 to 4243 mm. (Records from Pedregoso in the Valley of El General kindly furnished by Señor don Isaias Retana.)

severe on the Pacific side of the continental divide. In western Guatemala it usually starts about the middle of October and continues until about mid-May, with few showers to interrupt this long period of drought. On the Pacific side of southern Central America the dry season begins somewhat later and may end slightly earlier. On the Caribbean side the drier weather begins earliest in the south, sometimes in December in the Canal Zone, and usually in January in Costa Rica, but often not until February, or even March, on the Caribbean coast of Honduras and Guatemala. It is seldom so pronounced as on the Pacific side; and there is some question as to whether it is proper to recognize a dry season at all along much of the Caribbean littoral; but although there is rarely a severe drought, there is no doubt that for a few months during the earlier part of the year the weather is drier and more agreeable. By April in the south, June in the north, rains have in most years become heavy and frequent again. During the long wet season, on both sides of Central America, there are considerable monthly fluctuations in the amount of rain; and one hears much of a *canicula*, or break, in the rainy season, which in my experience has never lasted more than a few days. Except perhaps in very exceptional years, the rains, once begun, are sufficient in quantity and frequency to keep the vegetation green and flourishing until the advent of the single annual dry season.

Local variations in climate are both altitudinal and horizontal. The former are of the same nature in Central America as in other tropical regions, and are too well known to warrant repetition here. Of the latter, the chief which need concern us are the presence, on the Caribbean side of the Cordillera in northern Central America, of valleys—as the interior parts of those of the Motagua and Negro Rivers—so sheltered by high mountains from the rain-bringing north-east trade winds that they bear an arid type of vegetation composed chiefly of cacti and thorny scrub; and on the Pacific slope of two regions which receive far more rainfall than is general on this side of the isthmus. One of these areas of locally high precipitation lies on the southern slopes of the volcanoes of western Guatemala, near the Mexican border. The other covers southern Costa Rica and parts of the adjacent Panamanian province of Chiriquí. In both of these regions the humid evergreen forests are as tall and heavy as over most of the windward Caribbean slope, and contrast sharply with the lower, more open and deciduous woodlands, the gallery forests with intervening thorn-scrub and cacti, or the savannas, of which one thinks as typical of the Pacific side of Central America. It was in one of these wetter parts of the Pacific slope, that in southern Costa Rica, that most of my records of birds' nests were gathered.

This brief delineation must suffice for the picture of the climate of Central America as a whole. We shall refer to local and annual variations when considering the breeding seasons of the different classes of birds.

3. THE DISTRIBUTION OF NESTS THROUGH THE YEAR.

During the past twenty years I have collected records of nests at a number of localities in Panamá, Costa Rica, Honduras and Guatemala. The great majority of these nests were found in the Valley of El General, which is the name applied to the mountain-rimmed basin at the head of the Río Grande de Térraba, one of the principal rivers of Costa Rica, which enters the Pacific Ocean near the southern boundary of the country. The region known as El General lies between 9° 15' and 9° 28' N. and 83° 33' and 83° 50' W.; most of my nests were found between 2000 and 3000 feet above sea-level, a few slightly higher. My periods of residence in this region were from the end of November 1935 to mid-June 1937; the first half of the year 1939; 22 February to 20 June 1940; and during the five years from 1942 to 1946, inclusive, almost without interruption. Although the amount of time actually spent afield has varied from year to year as other occupations claimed attention, I have at all seasons passed many hours out of doors, and not only searched for nests myself but had people in my employ reporting them to me. My longest period of continuous residence, from 1942 to 1946, was spent on my farm in the district of El General known as El Quizarrá, in the valley of the Río Peña Blanca and at about 2500 feet above sea-level. The farm includes much primary forest as well as pastures, cultivated fields, and resting land covered with second-growth vegetation varying greatly in age and height. Many nests were found in each of these habitats; but I have not dealt with those of the primary forest separately from those in the cleared lands, because so many of the forest birds come into the adjoining clearings to build and rear their young, although the reverse tendency is far more rare*.

Table 2 records the distribution by months of 1357 active nests of 140 species found in the Valley of El General up to the end of 1946. Wherever information is adequate, the nest is entered under the month when egg-laying began; thus a nest of the Song Tanager, found with feathered nestlings which left on 24 May, would be credited to the month of April, because the incubation and nestling periods of this species are each normally twelve days, and egg-laying requires two days more. I have not in general included nests found under construction in which I did not later see eggs or, in inaccessible nests, evidence of incubation; but a few such nests were entered in the table if they belonged to a species for which I had no more complete records as a means of dating the breeding season. In computing the percentage of the total number of nests found in each month, I have applied a correction factor to compensate for the varying number of years in which I was present

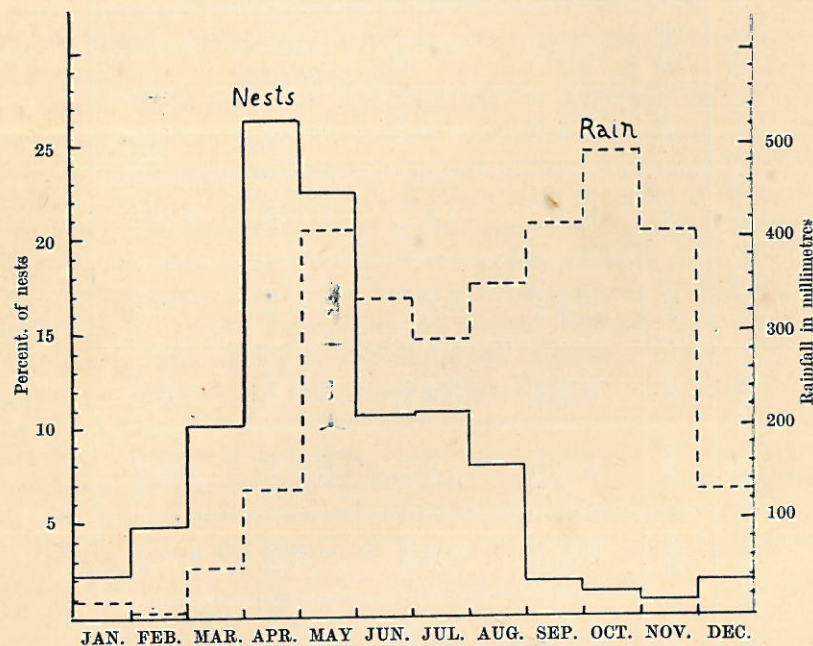
* The monthly distribution of 152 nests of 43 forest-dwelling species (some of which at times build in adjacent clearings) shows a higher proportion of nests in March than is found among the birds of clearings and secondary vegetation. This is in accord with the findings of Belcher and Smooker (1934), who state that in the forests of Trinidad the nesting season appears to be earlier than outside the forest.

TABLE 2. Nesting of birds in three Central American localities throughout the year—all species.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
El General (2-3000 ft. a.s.l.):												
Species (140)	20	34	53	89	81	53	32	32	13	6	6	15
Nests (1357)	28	68	155	401	344	148	91	68	15	11	7	21
Per cent. nests	2.1	4.8	10.1	26.1	22.4	10.6	10.7	7.9	1.8	1.1	0.7	1.8
Census area at El General:												
Species (30)	0	2	8	11	19	15	8	6	1	0	0	1
Nests (152)	0	3	15	44	36	26	19	7	1	0	0	1
Per cent. nests	0	2.0	9.9	29.0	23.7	17.0	12.5	4.6	0.7	0	0	0.7
Vara Blanca (5-6000 ft. a.s.l.):												
Species (51)	1	3	9	25	28	14	2	4	0	1	0	0
Nests (152)	2	7	11	50	50	18	8	5	0	1	0	0
Per cent. nests	1.3	4.6	7.2	32.9	32.9	11.8	5.3	3.3	0	0.7	0	0
Tecpán (7-10000 ft. a.s.l.):												
Species (28)	1	1	4	14	11	8	2	0	0	1	2	4
Nests (88)	2	1	4	28	19	11	2	0	0	3	11	7
Per cent. nests	2.3	1.1	4.5	31.8	21.6	12.5	2.3	0	0	3.4	12.5	8.0

in the region during a given month. In nine years (through 1946) I have been afield practically all the months of March, April and May, whereas in October and November I have looked for nests in El General during only six years; hence a correction factor of 1.5 was applied to the totals for each of these months—these totals, as given in Table 2, being the actual number of nests seen. The graph in text-fig. 2 was constructed from the compensated totals.

Text-figure 2.



Rainfall and nesting in the valley of El General, southern Costa Rica, 2000–3000 feet above sea-level.

The broken line gives the average monthly rainfall at Pedregoso during the seven years from 1937 to 1943, inclusive. The continuous line gives the monthly distribution of 1357 occupied nests found from 1936 to 1946, inclusive, expressed as a percentage of the total number, after compensating for the varying periods spent by the writer in the field in different years. Wherever sufficient information was available, the nest was entered under the month in which eggs were laid in it.

During the two-year period from 1 September 1943 to 31 August 1945 I tried to find all the nests built in my yard and the shady pasture in front, an area of $3\frac{3}{4}$ acres (1.5 hectares) containing many fruit and ornamental trees and much shrubbery. It is bounded on the south by tall second-growth woodland merging at no great distance into primary forest, on the east by

the Rio Peña Blanca and an affluent creek, on the north by this same creek, with thickets and plantations on the farther side, and on the west by open pasture and a small coffee grove. Doubtless some small and well-hidden nests escaped our notice, but certainly the great majority of those built in this area during the two years were found. There was a total of 152 nests of 30 species, and their monthly distribution is given in Table 2 as a small but selected sample. These same nests, of course, are included in the larger total for the region as a whole, in which sampling was necessarily more random. In this small area, as in El General as a whole, egg-laying was at its peak in April and May. But whereas the larger sample gave more nests with eggs in March than in June and July, the converse was true in the area of intensive study. This is chiefly because the big sample contains a greater proportion of pigeons, goatsuckers, woodpeckers and other larger birds that nest early, whereas these groups were poorly represented in my yard and pasture, where passeriform birds predominated.

The second locality for which data are presented in Table 2 is Vara Blanca, on the northern or Caribbean slope of the Cordillera Central of Costa Rica, at $10^{\circ} 9' N.$, $84^{\circ} 10' W.$ Here I resided from 8 July 1937 to 11 August 1938, with absences from 11 November to 7 December and 14 December to 12 January, when nesting was at a minimum. The cottage that I occupied was situated amidst pastures almost surrounded by vast forests, and my field work was done chiefly between 5000 and 6000 feet above sea-level. A brief account of the climate of this excessively humid region is given on page 199. During my year here I found 152 nests of 51 species.

Still farther in the north, I passed the whole of the year 1933 in the mountains above Tecpán (or Tecpam) in the Department of Chimaltenango in west-central Guatemala, at $14^{\circ} 45' N.$, $90^{\circ} 59' W.$ Here I studied the bird-life among woods of oak and other broad-leaf trees, with an admixture of pine, or of cypress in almost pure stand, alternating with bushy pastures and cultivated fields. The nests were found between 7000 and 10000 feet above sea-level, but chiefly from 8000 to 9000 feet. An account of the climatic variations in this mountain range is presented on page 198. Table 2 gives the monthly distribution of the 88 nests that I found, representing 28 species. A comparison of the records from Tecpán and Vara Blanca with those from El General makes it evident that at higher altitudes the peak of reproductive activity is narrower than in the upper part of the Tropical Zone; a larger proportion of the total number of nests was found in the months of April, May and June, while during the remaining months the number of birds nesting was relatively smaller. In his analysis of all published and unpublished records (including my own up to that date) of nests of Central American birds available to him in 1935, Harrower (MS.) found that the concentration of nesting during these three months was greater in the highlands than in the lowlands.

Although these three are the only localities for which I can present year-long records of nesting activities, I am able to give data for the first half of the year from three other points, all on the Caribbean slope. The southernmost of these is Barro Colorado Island in Gatún Lake in the Panama Canal Zone, at 9° 10' N., 79° 50' W., and at an altitude ranging from 85 to 500 feet above sea-level. This small island, set apart as a biological reserve by the government of the United States, is entirely covered by rain-forest, in part primeval and in part secondary, except for a narrow clearing a few acres in extent where the buildings stand. Here, in addition to some shorter visits, I worked from 17 December 1930 to 24 January 1931, and from 6 February to 2 June 1935. Taken together, my records (Table 3) for these two periods show very well the gradual rise in reproductive activity from January to May, although of course they reveal nothing of its decline during the second half of the year. They include 102 nests of 39 species.

In the valley of the Río Pejivalle, a tributary of the Reventazón, near Turrialba, Costa Rica, at 9° 50' N., 83° 43' W., I resided during most of the period from 12 January to 3 March 1934, and continuously from 5 April to 14 June 1941. On this last date I went to Murcia, in the same district but about 1000 feet higher, where I remained until early July 1941. In all I found at these neighbouring points 53 nests of 37 species, and although observations for the month of March are lacking, my records, I believe, present a fair picture of the gradual increase in number of nests during the early part of the year (Table 3).

TABLE 3. *Nesting of birds in three localities on the Caribbean slope of Central America during the first half of the year—all species.*

	Jan.	Feb.	Mar.	April	May	June
Barro Colorado (85-500 ft. a.s.l.):						
Species (39)	6	10	18	22	17	—
Nests (102)	6	13	24	29	30	—
Per cent. nests	5.9	12.7	23.5	28.4	29.4	—
Turrialba (2-3000 ft. a.s.l.):						
Species (37)	4	1	(1)	19	13	9
Nests (53)	4	1	(1)	23	15	9
Per cent. nests	7.4	1.9	1.9	43.4	28.3	17.0
Alsacia (500 ft. a.s.l.):						
Species (40)	—	6	8	28	20	8
Nests (139)	—	10	39	45	34	11
Per cent. nests	—	7.2	28.1	32.4	24.5	7.9

On "Alsacia" Plantation near Los Amates, in the Motagua Valley of Guatemala, at 15° 18' N., 89° 6' W., and at about 500 feet above sea-level, my sojourn extended from 17 February to 23 June 1932, and during these four months I was intensively engaged in the study of the birds. The distribution by month of laying is given in Table 3 for 139 nests representing 40 species. In this series the number of species nesting each month gives a fairer picture of the progress of the breeding season than the number of nests, which includes those of two colonial species of Icteridae. Thus a single colony of Great-tailed Grackles *Cassidix mexicanus* provided 31 of the 39 March nests, but only 4 nests in April, 6 in May and 4 in June. An inaccessible colony of Montezuma Oropéndolas *Gymnostinops montezuma* that I found late in February, but did not revisit, contained nests where incubation was apparently in progress and others still unfinished. In order not to distort the picture, I arbitrarily allowed for this colony five nests with eggs when computing the data for the table. It is probable that the number of nests with eggs was greater than this; but so, too, there must have been, in the area over which I ranged, many small, inconspicuous nests that I failed to discover. If we exclude these conspicuous colonial birds, whose nests are so much easier to find than those of most species, or if we confine our attention to the number of species nesting each month, it is evident that at "Alsacia" the increase in reproductive activity from March to April is considerably sharper than at Barro Colorado, six degrees farther south. Harrower (MS.) likewise noticed the somewhat more gradual increase in nesting activity in southern Central America than in northern Central America during the first quarter of the year.

From "Alsacia" Plantation I went at the end of June to the village of El Rancho in the Motagua Valley, where the rainfall is much less than at Los Amates, and cacti and thorny scrub replace the heavy rain-forest and banana plantations of the lower valley. In this more arid region, the birds in general seemed to be at an earlier stage of the breeding season; but an attack of fever cut short my visit here before I had made enough observations to permit sound conclusions. It is regrettable that an all-year record of nests is not available for any of the more severely arid portions of Central America. It should reveal some interesting relationships.

4. SONG AS AN INDICATION OF BREEDING.

For the Central American birds as a whole song is a good indicator of the amount of nesting activity. It is at a minimum during those months when few species nest, at a maximum, both as to the number of birds that sing and the volume of sound they make, in March and April, when so many birds are building, laying and incubating, and before the feeding of the young has begun to make demands upon the time and strength of the males. During

the beautiful, clear, mild days of the early part of the dry season in December and January relatively few birds are tuneful; their silence during weather so delightful has perhaps been in part responsible for the misconception once prevalent in northern lands that tropical birds are deficient in song. The torrential rains that often fall in May and June, while many birds are still attending nests, greatly reduce the volume of song, and, after this, spells of more agreeable weather later in the year stimulate at best a sporadic renaissance of music.

There are, however, great variations in the relation of song to nesting in the several families and species of birds; in some, singing is almost wholly confined to the months of active reproduction; in others it occurs more or less freely at other seasons. Among the latter are the wrens, many of which sing throughout the year, and in the gloomiest weather; their songs, delivered by both sexes, but more fully by the male, serve, instead of simpler call-notes, to keep the constantly mated pair in contact as they forage, hidden from each other by the dense vegetation. In the thrush family a number of species are almost perennial songsters, silent only for periods while apparently they moult. Such are those glorious musicians the solitaires (*Myadestes obscurus*, *M. unicolor*, *M. ralloides melanops*) and some of the nightingale-thrushes (*Catharus aurantiirostris*, *C. fuscater*), whose simple lays arise through most of the year from the low second-growth thickets or the underwood of the forest where they lurk. On the other hand, in the highlands of Guatemala I heard the song of the Russet-headed Nightingale-thrush *C. occidentalis* only while it nested, and the song of thrushes of the genus *Turdus* (*T. grayi*, *T. infuscatus*, *T. ignobilis plebejus*, *T. assimilis*, *T. rufitorques*) is closely associated with their breeding season and scarcely ever heard during half the year, which in these tropical species seems strange when we recall that in England the Song-thrush *T. ericetorum* is more or less musical through practically the entire year. The Pepper-shrike *Cyclarhis gujanensis* sounds his far-carrying, ringing notes at seasons when I feel sure that he has no nest. Among wood-warblers, the Buff-rumped Warblers *Basileuterus fulvicauda* sing much during the half of the year when they do not reproduce, male and female sometimes answering each other in songs differing surprisingly in type but equally beautiful. In the finch family, the forest-dwelling Blue-black Grosbeak *Cyanocompsa cyanooides* and Orange-billed Sparrow *Arremon aurantiirostris* sing through much of the year, although they nest chiefly during the early part of the wet season.

Other birds which maintain a long silence after the close of one nesting season begin to sing far in advance of the next. Examples of this are the Black-striped Sparrow *Arremonops conirostris*, the Pink-headed Warbler *Ergaticus versicolor* of the Guatemalan highlands, the Neotropic Kingbird *Tyrannus melancholicus*, which even in February sounds his high-pitched twitter in the grey dawn, and many others. The Yellow-green Vireo *Vireo*

virescens flavoviridis, arriving from South America at about the end of January, already sings freely, although it rarely nests before April. Yet the males of numerous other species begin to sing little, if any, before the females start to build. This is true of the Song Tanager *Ramphocelus passerinii costaricensis*, the Oleaginous Pipromorpha *Pipromorpha oleaginea*, which all day long performs tunelessly in the depths of the forest, the Gray-capped Flycatcher *Myiozetetes granadensis* and the related Chipsacheery *M. similis*, each of which sings in its own peculiar fashion at daybreak. The simultaneous beginning of song and nest-building will no doubt surprise those versed in the theory of territory as based upon studies of northern birds. When it occurs among tropical species the birds have been long established with their mates upon their nesting territory (as in *Myiozetetes*), or they hold no territory (as in *Ramphocelus*), or they fail to pair (as in *Pipromorpha*); and construction, especially of the season's first nest, usually takes far longer among the resident birds of the Tropics than among the migratory birds of extra-tropical lands.

5. THE BREEDING SEASONS AND THE FOOD SUPPLY.

For Central America as a whole, and the bird population as a whole, the principal breeding season falls in the second quarter of the year, or from the vernal equinox to the summer solstice of the Northern Hemisphere, with April, May and June the months of greatest reproductive activity and, in the lowlands, a reduced but still important amount in July. There is, however, in nearly all localities a scattering of nests throughout the year, which need not surprise us in a tropical region when it is recalled that the same is true of the British Isles, where the Wood-pigeon *Columba palumbus* has been found breeding in each of the twelve months, and the Redbreast *Erithacus rubecula* sometimes lays in mid-winter.

Of the inland birds of Central America, whose breeding season differs markedly and consistently from that of the generality of the avifauna, several classes may be distinguished:

- A. Nectar-drinkers, including the hummingbirds and some of the honey-creepers (which may also eat minute insects found in the flowers).
- B. Grass-seed-eaters, chiefly small finches of the genera *Sporophila* and *Tiaris*.
- C. Ground-feeders, including a number of passerines and other birds.
- D. Grasshopper-eaters, especially the anis (*Crotophaga*).
- E. Big, far-ranging birds, including hawks, oropendolas, the larger woodpeckers, etc.

A. THE NECTAR-DRINKERS.

Let us first consider the nectar-drinkers, since they provide one of the most remarkable instances that have come to my attention of the dependence

of a bird's season of reproduction on the food supply, in a manner which is clearly unrelated to taxonomic affinities and in defiance of apparently inimical features of the climate.

I spent the year 1933 in an intensive study of the breeding habits of the birds on the Sierra de Tecpán in the highlands of west-central Guatemala. Between 8000 and 10000 feet above sea-level I found nests of four kinds of nectar-drinkers. Three of these were hummingbirds, the fourth a passerine bird, an aberrant member of the honeycreeper family, the Guatemalan Slaty Flower-piercer *Diglossa baritula montana*. The short, uptilted bill of this tiny, dull-coloured bird differs from that of any other bird I know and is a most effective instrument for extracting the nectar from flowers. An abrupt hook at the tip of the upper mandible fits over the base of a tubular corolla and holds it firm, while the short, sharp, awl-like lower mandible pierces the delicate tissue, forming a perforation through which nectar is extracted, doubtless by the peculiar tongue. The flower-piercer can take care of blossoms of most varied sorts and of surprisingly great size, provided they have a tubular portion at the base of the corolla, and operates so rapidly that it visits many during the course of a minute. Like hummingbirds, it supplements its diet of nectar with minute insects caught on the wing, its rictal bristles facilitating their capture.

During the dry months of the northern winter, heavy frosts whitened open fields and pastures on the Sierra de Tecpán every clear and windless night. The last frost was noticed, at 8500 feet, on 2 April 1933. The birds of most kinds were now building their nests or had already laid their eggs. The ground was very dry after five months of little or no rain; there were scarcely any flowers, but deep-rooted trees and shrubs were in full foliage, the oaks of numerous species in particular having recently renewed their leafage in spite of the drought. During April, May and June I found not a single one of these nectar-drinkers nesting and never heard them sing, although later in the year all sang with amazing persistency if with little melody. The rains began in mid-May, and the majority of the birds concluded their nesting operations as soon as their single brood was on the wing. Because of prevailing low temperatures, the vegetation responded to the life-giving rains more slowly than it would have done in lower and warmer regions; flowers only gradually became abundant. About the middle of October the long and unusually severe rainy season came to an end; but with clear nocturnal skies and the sun already on the other side of the Equator, frosts soon became heavy on the open fields. Now the combination of sunny sky and moist soil brought flowers to their greatest profusion. During November and December the traveller finds the *altos* of Guatemala one great flower-garden, and the fact that during the two years I was actively engaged in botanical collecting in the highlands of this country permits me to make statements on the seasonal abundance of flowers based upon something

more than mere impressions gleaned in passing. As the dry season continued frosts became heavier at the same time as the ground became drier; flowering herbs were gradually killed by freezing and drying, and next the shrubs and trees felt the effects of the drought. By January there was a rapid decline in the abundance of blossoms.

Despite freezing nocturnal temperatures at ground-level—felt first on level fields and the lower reaches of open slopes—hummingbirds and the flower-piercer nested during the early part of the dry season. During the chilly nights of this period I used to lie in bed, none too warm under all the heavy Indian blankets I could lay hold of, and think wonderingly of the tiny young hummingbirds in their downy nests out on the frosty open mountain-sides. Strong cold winds were also of frequent occurrence at this season. These smallest of all the birds, along with the flower-piercer, were the only ones I found nesting between October and February. When flowers became scarce in January they rapidly ceased to sing and to nest. My actual records of their reproductive activities, as manifested by the "singing" of the males as well as by the presence of nests, are as follows:

White-eared Hummingbird *Hylocharis leucotis*.—Song first noticed in late August but not delivered freely until October; full in November and December; no longer heard in early February. Nest-building first noticed 17 October. Nests: 1 building in October, 14 all stages in November, 2 in December.

Violet-ear *Colibri thalassinus*.—Sang from mid-October to February. Nests with eggs: 1 in December, 2 in January, 1 in February.

Cazique *Lampornis amethystinus*.—Sang a little in late September and freely from mid-October to end of January. Nests: 2 with eggs in November, 2 with nestlings in December.

Heloise's Hummingbird *Atthis heloisa*.—Sang from mid-October through December. Nest not found.

Broad-tailed Hummingbird *Selasphorus platycercus*.—Flight display witnessed in December, January and February. Nest not found.

Garnet-throated Hummingbird *Lamprolaima rhami*.—A female was building in January.

Guatemalan Slaty Flower-piercer *Diglossa baritula montana*.—Sang from July to end of year. A fledgling seen on 15 December must have hatched from an egg laid in November; two nests with eggs were found in December (see Table 4).

From July 1937 to early August of the following year I studied the birds in the vicinity of Vara Blanca, on the northern slope of the Cordillera Central of Costa Rica. The area I worked most intensively lay between 5000 and 6000 feet above sea-level. These mountains-slopes, exposed to the full sweep of the north-east trade-winds that blow unobstructed from the Caribbean Sea over the forested lowlands of eastern Nicaragua and north-eastern Costa Rica, are excessively wet—a condition reflected in the tremendous masses of epiphytes that burden the trees. During the period of my sojourn there was nothing that could be called a dry season; but in February and March there was perhaps a little more sunshine and fewer long-continued

storms of wind-driven rain than during the remainder of the year. Frost is unknown at this altitude in Costa Rica; and with perpetual moisture there was no lack of bright blossoms in any month. Yet here, too, the nectar-drinkers had breeding seasons distinct from that of the great majority of birds, which here, as elsewhere in Central America, nested chiefly in April, May and June. Actual records of reproductive activity of the nectar-drinkers in this region were as follows :

Chestnut-bellied Mountain Gem *Lampornis castaneiventris*.—1 nest with eggs on 31 January, 4 in February. A nest begun in early April was not finished, but a female was feeding a full-grown youngster on 30 July.

Violet-ear *Colibri thalassinus*.—1 nest with eggs in October, 1 in March.

Black-bellied Hummingbird *Eupherusa nigriventris*.—1 nest with eggs in August, 1 with nestlings in March.

Costa Rican Slaty Flower-piercer *Diglossa baritula plumbea*.—Sang from late June through July, August and September and, after an interval of silence, again in January. I found 1 nest with young in September, 2 with eggs in February and 1 in March. Females were discovered building on 15 March and 15 July but did not complete their nests.

Although the actual records of breeding are not numerous, it is noteworthy that no nest of these four nectar-sipping birds was discovered in April and May, when nests of other kinds of birds were most abundant, and that at the time the hummingbirds and flower-piercer were breeding scarcely any other species did so.

Next we consider the nesting of nectar-drinking birds in the basin of El General on the Pacific side of southern Costa Rica. In this locality, between 2000 and 3000 feet above sea-level, I have kept records of nests during the whole of five years and during the first half of five other years. This is one of the wettest districts on the Pacific slope of Central America, with a rainfall fluctuating from 2200 to 4250 millimetres per year. After the height of the wet season in October or November the rains become lighter through December; but in some years, and in the more exposed parts of the basin in most years, showers fall well into January. February is the driest month. In late or, sometimes, in early March precipitation is resumed in the form of usually light afternoon showers; during April these are more frequent and heavy, while May is at times the month of heaviest rainfall in all the year. The drenching rains, which fall chiefly in the afternoon, are of almost daily occurrence until the end of the year. A tendency toward the double rainy season of some tropical regions is shown by the drop in total precipitation during June, July and August; but rarely less than 250 millimetres falls during each of these months, and sometimes August may be the rainiest month.

In El General seasonal variations in the aspect of the vegetation are not so extreme as in the highlands of western Guatemala, where the dry season is far longer and more severe and frost adds its weight to drought. The

lofty rain-forest is evergreen, although its canopy becomes somewhat more open during the dry season, when scattered trees shed their foliage, usually only to replace it with more abundant new leafage even while the weather is driest, and after only a week or two of nudity. In years of more severe drought the pastures become dry and brown by February, although this does not often happen on the slopes at the northern side of the valley, as at Quizarrá, where most of my observations have been made. Flowers bloom throughout the year, but with great fluctuations in abundance. In November, while rains are still heavy, but diminishing in intensity, many of the plants that bloom at the beginning of the dry season open their earliest blossoms. December and January are the months of greatest floral display, especially in the clearings. With increasing drought there is a progressive diminution of flowering through February and March, particularly in the driest years. Even in relatively wet years exceedingly few native plants are in blossom at the end of March. Although the swollen buds of coffee, species of *Miconia*, *Hasseltia*, and other woody plants open promptly in response to the first showers of March, April and May, the first two months of abundant rainfall are for most plants, especially those of the clearings, a time of vegetative growth rather than of reproductive activity, and flowers are not conspicuous amid the profuse verdure of this period. In the forest they are, during the early part of the wet season, more abundant than in the clearings. Yet in every month of the twelve many plants are in blossom.

In El General, too, nests of nectar-drinking birds are not numerous from March through May, when those of other kinds are most abundant. This is true in spite of the fact that the several species of hummingbirds differ among themselves as to the dates and length of their nesting-seasons. Despite the abundance of these birds, their tiny nests are by no means easily discovered, and those of several species common enough in the locality have escaped me year after year. As with the hummingbirds of the highlands, subsidiary evidence on the periods of reproduction is furnished by the "singing" of some species. The available information may be summarized as follows :

Rieffer's Hummingbird *Amazilia tzacatl*.—This is the commonest resident hummingbird of the clearings and has "sung" persistently in my yard nearly every morning at daybreak for the last six years. The males are silent only for a period of a month or two at the end of the dry season, ceasing to sing in late February or, in wetter years, at the beginning of March—when most other birds are starting to sing!—and resuming their vocal performances in mid-April or, in very dry years, early in May. In 1947, when the short dry season was relieved by occasional showers, they were songless at dawn only from 2 March to 7 April; but in 1948, when the dry season was longer, they ceased performing on 18 February and did not resume until 30 April. Nests with eggs were recorded as follows : 1 in May, 2 in July, 1 in October, 2 in November, 3 in December (had nestlings in early January).

Guimet's Hummingbird *Klais guimeti*.—The males are most persistent "songsters". Beginning in a tentative fashion at the end of October or in November,

they sing increasingly until the end of the year. In January and February they are in full song and perform all day. In March, or in dry years even by mid-February, when there are few flowers, their song wanes and they soon become silent. In April, after the rains begin, or sometimes not until the beginning of May, there is a brief renaissance of singing; but by mid-May they enter a long period of silence. I found a total of 11 nests, 5 of which had eggs in February when one other was being built, 4 held eggs in March, and 1 in April.

Cuvier's Hummingbird *Phaeochroa cuvieri*.—Sings tirelessly all day throughout the wet season from early April or early May through December, and breeds during the same period. 1 nest was found under construction and another with eggs in May, 2 with eggs in June, 1 in July, 1 in August, 1 in September, 2 in October, 1 in December, and 1 in January.

Elicia's Golden-tail *Hylocharis eliciae*.—Males sing a little on bright mornings from mid-September onward. With sunnier weather in December, January and early February they are vocal most of the day; but they become silent during the second fortnight of February or in March, when flowers are scarce. In April there is a renewal of full song, but it does not last beyond early or mid-May. In 1948, premature showers in early March stimulated renewed singing after several weeks of silence, but then a return of the drought caused another period of silence. 1 nest with eggs was found in December.

Snowy-breasted Hummingbird *Amazilia edwardi niveoventer*.—This is not a persistent songster like the foregoing species. 1 nest with eggs was found in November, 3 in December.

Adorable Coquette *Paphosia adorabilis*.—This ornate little hummingbird is rather silent. 1 nest was found in December and 1 in January.

Wood-nymph *Thalurania furcata*.—Another silent species. 1 nest with eggs was found in February.

Barrot's Fairy *Heliothrix barroti*.—1 nest with eggs in January.

Longuemare's Hermit *Phaethornis longuemareus*.—Males gather in assemblies in dense thickets and sing persistently through most of the year, except at the end of the dry season in March and sometimes also in February. 2 nests were found in April, 1 in May, 2 in June, 4 in July, 1 in November.

Buff-browed Hermit *Phaethornis superciliosus*.—I have found no singing assembly locally, although these are quite conspicuous in some districts. 1 nest with eggs was found in January, 1 in May, 2 in June and 1 in July.

Green Hermit *Phaethornis guy*.—Sings throughout the year except during the driest months. Nests were found at altitudes between 3400 and 4000 feet (somewhat higher than those recorded for the foregoing species), 1 in December and 1 in February.

Barbed-throat *Threnetes ruckeri*.—Although I have not found the nest of this bird of the forest undergrowth, its season of song resembles that of the passerine birds more than any other hummingbird of the region. In wet years it begins its elaborate song in March, but in very dry ones not until May, and continues until August.

To summarize: 55 nests of 11 species of hummingbirds found in El General were distributed through the year as follows: 3 in April, 4 in May, 6 in June, 8 in July, 1 in August, 1 in September, 3 in October, 4 in November, 10 in December, 4 in January, 7 in February, 4 in March. In each instance the nest was attributed to the month in which the eggs were laid or calculated to have been laid. With a single exception, all the species known to "sing"

performed freely in December, most in January and February, but all became silent in March, when flowers were fewest, although at this time most of the birds of other groups were becoming songful.

Aside from the hummingbirds, the one constant visitor to flowers which I have discovered in the basin of El General is the Mexican Bananaquit *Coereba flaveola*. This little honeycreeper pushes its rather short, sharp, down-curved black bill into the throats of flowers, only exceptionally puncturing the base of some of the longer corolla tubes, as hummingbirds also will sometimes do. Although its bill is not so highly modified as an instrument for extracting nectar as that of its highland relative, the flower-piercer, and its mode of operation is in consequence different, the bananaquit appears to be no less dependent upon nectar as a food. It supplements its liquid fare with minute insects and spiders gleaned from the foliage and amidst the flowers, rather than caught in the air after the fashion of the flower-piercers. It is a profuse if not melodious songster, and in El General sings through most of the year. In the latter part of the wet season it performs exuberantly and, aside from the hummingbirds, is almost the only feathered creature to indulge freely in song. In dry years it becomes silent in January; but if occasional showers keep the vegetation green and flourishing into February, it may even sing much in this usually dry month. In March it falls silent along with the hummingbirds, to resume singing after the rains have caused an increase in flowers. I have records of 21 occupied breeding nests (others are used for sleeping) from El General, which contained eggs as follows: 1 in May, 3 in June, 1 in July, 4 in August, 1 in September, 2 in October, 1 in November, 2 in December, 3 in January and 3 in February. It is noteworthy that there is no record of nesting in April, when for most passeriform birds breeding activity is at its height.

We saw that in the highlands the flower-piercers parted company with all other passerine birds, to nest at a season when only the hummingbirds were breeding. At these altitudes there was no other member of their own family. But in El General there are, in addition to the bananaquit, five species of honeycreepers. These differ from the bananaquit as greatly in their dietary habits as in their more brilliant plumage of blues, green and black. All five are far more fond of fruits, and four of them come frequently to eat bananas on my feeding-shelf (which the bananaquit mostly ignores), hunt a good many insects, and probe flowers less regularly than *Coereba*; and, as we should expect, they nest, so far as I have been able to discover, along with the great majority of passerine birds in April, May and June, when bananaquits breed sparingly or not at all. Of the Blue Honeycreeper *Cyanerpes cyaneus* I have found eight nests, of the Green Honeycreeper *Chlorophanes spiza* two, of the Scarlet-thighed Dacnis *Dacnis venusta* one, and of the Turquoise Dacnis *D. cayana* one, which was never finished, and all in April, May and June (see Table 4).

TABLE 4. Nesting of nectar-drinking birds (hummingbirds, Diglossa, Coereba) in three Central American localities throughout the year.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
El General:												
Species (12)	5	4	1	2	5	4	5	2	2	3	4	7
Nests (76)	7	10	4	3	5	9	9	5	2	5	5	12
Vara Blanca:												
Species (4)	1	3	1	0	0	0	0	2	0	1	0	0
Nests (13)	2	7	1	0	0	0	0	2	0	1	0	0
Tecpán:												
Species (4)	1	1	0	0	0	0	0	0	0	1	2	4
Nests (24)	2	1	0	0	0	0	0	0	0	3	11	7

TABLE 5. Nesting of grass-seed-eaters (Sporophila, Tiaris) in El General, 1936-1948.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Nests of <i>Sporophila</i>	2	0	0	0	4	16	19	11	0	0	0	1
Nests of <i>Tiaris</i>	1	0	0	1	20	14	12	12	0	3	0	3
Total nests	3	0	0	1	24	30	31	23	0	3	0	4

On the Caribbean coast of Central America the dry season is rarely so pronounced even as it is in El General, which is one of the wetter parts of the Pacific slope. Here, where the vegetation is continuously more flourishing and flowers more uniformly abundant, both Reiffer's Hummingbird and the bananaquit nest continuously through the first half of the year, not ceasing to breed for a period as they do in El General. I have no all-year records of birds' nests for any locality on the Caribbean coast, but available information (Skutch 1931) reveals that Rieffer's Hummingbird nests throughout the year; and I should not be surprised if the bananaquit does likewise, at least in Panamá, as it does in Trinidad (Belcher and Smooker, 1937: 518) and other portions of its vast range.

B. THE GRASS-SEED-EATERS.

In tropical America there are a number of species of tiny, thick-billed finches which subsist to a large degree upon the seeds of grasses, although they eat also small seeds of plants in other families, and, of course, include a certain amount of insect food in their diet. In regions with a long and severe dry season, the grasses, in company with other herbaceous plants, are more adversely affected than the trees and shrubs whose roots reach deeper. Their stems and leaves often turn brown and dry while the woody plants in neighbouring groves and copses bear abundant leafage and even flower or ripen their fruit. Other shrubs, such as coffee and many of the melastomes, merely await the earliest showers to open their already swollen buds. But the grasses must, when they have died back to the ground, form new leafy shoots before they can flower and set seed. No matter how swiftly they respond to the life-giving rains, there is usually a delay of at least several weeks before they come into fruit. Let us see how this delay affects the nesting of those birds which lean heavily upon them for food.

We may consider first the little Yellow-faced Grassquit *Tiaris olivacea*, a bird widely distributed in the Caribbean region. At Pejivalle, 2000 feet above sea-level on the wet eastern side of Costa Rica, the pastures and grassy roadsides where the grassquits dwell usually remain verdant throughout the year. Here I found a nest with newly laid eggs on 12 April 1941, and numerous others during the remainder of this month. Thus the grassquits' breeding season began little later than that of the other small passerines of the clearings. But in El General, on the opposite side of the Cordillera, where during the early months of many years pastures become brown and dry and grasses cease to grow and set seed, the grassquits nest considerably later than their relatives at about the same altitude on the wetter, windward slope, and also later than the small birds of distinct dietary habits with which they mingle. Not only this, but the date when they begin to build depends upon the length and severity of the preceding dry season, being earlier in wetter years. In wet years they lay in May: in 1937 I found my

earliest egg on 1 May, in 1942 on 17 May, in 1943 on 13 May. Compare this with three years when the dry season was severe: in 1936 I recorded the first egg on 11 June, in 1940 on 14 June; while in 1945, a year of unusually severe and prolonged drought which led to many bush fires, no nest was found until mid-July, and this never contained eggs.

The situation is similar with seedeaters of the genus *Sporophila*. In the Caribbean lowlands of Honduras and Guatemala, Morellet's White-collared Seedeater *Sporophila torqueola morelleti* began to lay at the end of April 1930. At Pejiville, Costa Rica, Black Variable Seedeaters *Sporophila aurita corvina* had eggs at the beginning of May 1941. But during the eleven nesting seasons I have passed in the Valley of El General, the type race of the same species, *S. a. aurita*, has always started to breed somewhat later, the date of the beginning of nesting varying greatly from year to year according to the severity of the preceding dry season, in the same manner as with the Yellow-faced Grassquit. In 1942, a wet year, two nests with eggs were discovered on 13 and 14 May, respectively, whereas in the devastatingly dry year 1945 I found my earliest eggs on 21 June, when they were newly laid, and two other sets within the week. The early part of the year 1946 was almost as dry as that of the preceding year, and the first egg was not found until 28 June. But in 1947, when again enough showers fell during the dry early months to keep the pastures green, I found a nest in which laying began on 16 or 17 May. Thus in a single locality the initiation of nesting by this seedeater may vary by about six weeks. After the close of the principal breeding season, in August or September, both the Variable Seedeater and the Yellow-faced Grassquit rest for a period, then may nest sparingly in December and January, a time when scarcely any other passerine bird of the region is engaged in reproduction, save the Mexican Bananaquit and an occasional wren or antbird. This subsidiary nesting season, of far less importance than the earlier one, corresponds in time with the ripening of an aftercrop of seeds by the tuvarrá grass *Paspalum*, which is one of the principal sources of food of the seedeaters of this region. In some years I have found no evidence of the second nesting season of these two little finches (see Table 5).

The few available dates of local nests of the Dark-backed Goldfinch *Spinus psaltria*, another small eater of seeds, suggest a similar distribution through the year; and I suspect that if its nests were not so exceedingly difficult to find, the breeding-seasons of the abundant and widespread Blue-black Grassquit *Volatinia jacarina* would present a similar picture; the periods of song and display of the males suggest that this is true. The Blue-black Grosbeak *Cyanocompsa cyanooides*, a big finch of the forest and adjoining clearings which feeds upon the immature and mature grains of maize and rice as well, apparently, as of the heavier native grasses, also breeds

late; of my six nests found in El General, two held fresh eggs at the beginning of May and four in July and August, when these grains were ripening.

In Trinidad and Tobago, species of *Sporophila* and other sedge-breeding passerines have an extended nesting season which may be said to have its centre in August—that is, considerably later than that of most of the birds (Belcher and Smooker 1934: 574–75). Elsewhere (*op. cit.* 1937: 543) these authors state that the nesting of species of *Sporophila* depends upon the rains. Moreau (1937a: 645) remarks that in the highland forests of East Africa the few seed-eating birds tend to form a class of exceptions as to their seasons of breeding; and in the north the American Goldfinch *Spinus tristis*, which subsists largely upon the seeds of Compositae and other herbs, is among the latest birds to nest, waiting to hatch out its brood until the tall weeds are setting seed.

C. THE GROUND-FEEDERS.

It will be recalled that on the Sierra de Tecpán in Guatemala, between 8000 and 10,000 feet above sea-level, I found the great majority of the birds (except the nectar-drinkers) nesting principally in the brief interval of six or seven weeks between the last frosts of early April and the onset of the rainy season in mid-May. These birds included both fruit- and insect-eaters. At this dry period berries were borne by deep-rooted woody plants, and the insects then active apparently found the water necessary for their development in the foliage or other tissues of the same shrubs and trees, many of which were lushly verdant despite the long-continued drought; but three species of passeriform birds which hunted chiefly on the ground nested distinctly later than their neighbours. Two of these, the White-breasted Blue Mockingbird *Melanotis hypoleucus* and the Chestnut-capped Atlapetes *Atlapetes brunnei-nucha* searched for food by flicking dead leaves and other ground litter aside with their bills to expose the small creatures lurking beneath; the third, the Russet-headed Nightingale-thrush *Catharus occidentalis*, also foraged on the ground, but was not seen to proceed in just this way. Although in April and early May the more profoundly rooted plants could draw water from deeper layers of the soil, the surface and its litter were at this period exceedingly dry, and it is probable—although, unfortunately, no detailed study of this point was made at the time—that the invertebrates which dwell in this litter were few and mostly quiescent. The return of the rains in mid-May must have caused a considerable increase in both the number and activity of the creatures inhabiting this layer, and made food easier for the mockingbird, the atlapetes and the nightingale-thrush to find. Five nests of the White-breasted Blue Mockingbird contained newly laid eggs between mid-May and the first week of July. At Dueñas, Guatemala,

considerably lower than Tecpán, Salvin and Godman (1879, 1 : 30) recorded eggs of this species from the end of May onward. Four nests of the Chestnut-capped Atlapetes on the Sierra de Tecpán held eggs from about 10 May to mid-June. Nine nests of the Russet-headed Nightingale-thrush contained fresh eggs between mid-May and early July. By the date when these three species began to lay, the majority of birds of other kinds were already feeding young; and since nearly all the birds of this elevated region were single-brooded, these others completed their reproductive activities for the year well ahead of the three ground-feeders. Some observations that I made while watching nests from a blind help to elucidate the ability of the ground-foragers to feed their young at a season when the heavy, cold rains appear to make it difficult for many other birds to find enough food for belated families. While hard showers fell, a Slate-throated Redstart *Myioborus miniatus*, who caught insects among the foliage and in the air, lengthened her absences from the eggs she was incubating; whereas, under similar circumstances, a female White-breasted Blue Mockingbird shortened hers.

In regions where the rains begin earlier, the ground-feeders do not delay to nest until well after their neighbours with distinct modes of foraging. Thus in El General the Striped Atlapetes *Atlapetes torquatus*, whose manner of hunting on the ground is much the same as that of its chestnut-capped relative, begins quite generally to nest in April, along with the majority of the passerine birds. Exceptional individuals may in wet years lay as early as the end of February; but in severely dry years like 1945 the nesting of the species is delayed until late May or June. In a wet region like Vara Blanca, the Russet-headed Nightingale-thrush *Catharus occidentalis* began to lay before the middle of April, a full month earlier than I found eggs of this species in western Guatemala. In El General the Orange-billed Nightingale-thrush *C. aurantirostris*, also a ground-feeder, commonly has eggs by the 1st of April in a wet year, somewhat later when the dry season has been severe.

At lower elevations ground-feeders may have very broad breeding seasons, which include both wet and dry seasons. In Central America the Red-winged Talpacoti Dove *Columbigallina talpacoti rufipennis* nests from January until September, if not throughout the year. The Blue Ground Dove *Claravis pretiosa* nests from February through September in El General. In the same locality, the White-fronted Dove *Leptotila verreauxi* has eggs from January until September; the Rufous-naped Cassin's Dove *L. cassinii rufinucha* from March until October. The Pileated Tinamou *Crypturellus soui*, which hunts over the ground amidst low, dense vegetation, incubates from August to April; of the 13 nests recorded from El General, 5 were found in the dry month of February, which apparently is the height of the breeding season.

D. THE GRASSHOPPER-EATERS.

The Groove-billed Ani *Crotophaga sulcirostris* nourishes its nestlings largely with grasshoppers and other insects, which it catches among lush pasture grasses and other low vegetation. Throughout Central America it is a consistently late nester, rarely laying before June and continuing to breed until September. The earliest of my 32 nest records from widely separated parts of Central America is of a nest in El General which held eggs on 26 April 1942. It is of interest that this exceptionally early nest should have been found in a region where the ani is only precariously established, and far more rare than in most parts of Central America at the same altitude and with equal areas of cleared lands. It should be noted here that 1942 was an unusually wet year, when heavy rains fell through most of March. It appears that the ani delays its nesting until several weeks of rain have encouraged the development of the lush herbage among which it finds most of its food.

The breeding of the Smooth-billed Ani *Crotophaga ani* appears to be stimulated by the change of diet which follows the return of wet weather. Davis (1940 : 202) found that in Cuba these abundant birds subsist largely upon vegetable matter during the latter part of the dry season, which here continues from November to mid-May. During the wet season, which covers the remainder of the year, they prefer insects, lizards and other animal food. During 1937, when 8.78 inches of rain fell during May and had turned the fields green by 1 June, the earliest eggs of the ani were found on this date. In the following year, when the rainfall in May was only half as great, and by 1 June the fields were still brown, the first eggs were found on 10 June.

E. MISCELLANEOUS EARLY NESTERS.

In a number of species of birds one occasionally finds a pair nesting well in advance of the majority of their kind. Such early nesting may be induced by abnormal weather or by individual aberrations, and does not seem to be as important to our present inquiry as that of species which consistently breed much earlier than the great mass of birds. These are likely to be big, wary birds whose high nests are difficult to discover. Accordingly, for most of them I have only few and scattered records, but these appear to be worthy of our consideration.

I have exceedingly few records of the nests of hawks and vultures, but all I know about them indicates that they breed early. One nest of the Black Vulture *Coragyps atratus* had nestlings in January and two others held young in March. A pair of Laughing Hawks *Herpetotheres cachinnans* sheltered a downy nestling at the beginning of March. The Large-billed Hawk *Buteo magnirostris* is also an early nester. Vultures gorge on the carcasses of cattle and other animals, which die at all times of year. The Laughing Hawk

subsists largely upon snakes, which are no less numerous in the dry than in the wet season. The Large-billed Hawk eats lizards, some of which are most active in hot, dry weather, and perhaps are easier to find during the rainless months when the herbage is more sparse. Since food is no problem for them, these big birds find it convenient to rear their broods during the rainless months. But my two nests of the Swallow-tailed Kite *Elanoides forficatus*, which seizes insects while soaring and plucks the young of small birds from high and exposed nests, were found in April and May when insects are abundant and many birds have nestlings.

The oropéndolas, both the Montezuma *Gymnostinops montezuma* and Wagler's *Zarhynchus wagleri*, begin in January to weave their great swinging pouches in crowded clusters in high tree-tops. Although they start nesting and rear their first broods in the dry season, the bigger Montezuma Oropéndola, at least, continues well into the wet season, and in Honduras I have found it feeding nestlings in early September. These big birds feed largely upon the fruits of forest trees and fly far and wide in search of them. There are at all seasons some trees in fruit in the Central American forests, and with their wide cruising radius the oropéndolas can find some of them within reach of their nesting colonies.

Some of the bigger woodpeckers breed very early. In El General I have found the White-billed Woodpecker *Phloeoceastes guatemalensis* incubating in November and December, but also a pair which in October were feeding a well-grown youngster that probably hatched during August. In the same region Lineated Woodpeckers *Ceophloeus lineatus* begin to incubate early in January and bring forth their fledglings in February, although the young of belated broods may not take wing until April. My three nest-records for this species from the Caribbean slope in Costa Rica and Guatemala indicate later breeding, in March, April and May. Even the minute Olivaceous Piculet *Picumnus olivaceus* nests very early, in El General beginning in January and continuing until May. Here the Red-crowned Woodpecker *Centurus rubricapillus* begins to incubate in February and may attempt to rear a second brood in May. The Golden-naped Woodpecker breeds later, beginning to incubate in March at earliest, so far as my experience goes, often not until April, and sometimes in May. The first two of these woodpeckers, the White-billed and the Lineated, dig deeply into decaying wood to uncover boring insects which develop slowly and are probably no less abundant in the larval stage in the dry season than in the wet. The Lineated Woodpecker also feeds freely upon the *Azteca* ants which perennially swarm in the hollow stems and branches of the *Cecropia* trees so abundant in second-growth woodland. The tiny piculet nourishes its brood largely with the larvae and pupae of ants which it laboriously extracts from the pith of slender dead twigs; such ants are plentiful at all seasons. *Centurus* and *Tripsurus* have a more varied diet, which includes

a good deal of fruit—they are the only wooddeckers which visit my feeding-table to eat banana and plantain. This appears to be significant in relation to their later nesting.

Kingfishers also nest early. In the Caribbean lowlands of Guatemala I found Ringed Kingfishers *Ceryle torquata* beginning to incubate in late February or early March; Amazon Kingfishers *Chloroceryle amazona* in late February, March or April. When these kingfishers dig their burrows in the low, sandy banks of rivers it is important that they bring out their brood before the heavy rains come in May, for the swollen current may wash away the banks. Also, it is probably easier for the birds to catch minnows when the rivers are low and clear than when they are high and turbid.

Another early nester is the Pauraque *Nyctidromus albicollis*. Of 10 nests found in El General, 1 contained eggs in February, 7 in March and 3 in April. In the Caribbean lowlands of Central America eggs are found from February to June, with the height of the breeding season probably in March or April; and in Trinidad, Belcher and Smooker (1936: 23) found nests from February to July, with the peak of the season between February and April, in the drier weather. Since the Pauraque, like other goatsuckers, lays its eggs directly upon the earth or fallen leaves, it would appear to be advantageous to it to hatch them and brood its tiny young while the ground is dry and relatively warm; torrential rains that spread even a thin sheet of water over the ground would seem to be disastrous to the eggs and downy nestlings. The flying insects upon which it subsists are probably more abundant after the rainy season sets in; but on dark moonless nights its hunting is restricted to the twilight, and earlier in the year it is more certain to enjoy fine weather during this brief, critical period.

F. THE PRINCIPAL NESTING SEASON.

We have discussed first those species whose seasons of reproduction differ from that of the majority of birds in the regions where they dwell. There were several reasons for doing so. The consideration of the nesting seasons of hummingbirds, honeycreepers, seedeaters and other groups which depart from the general mass has greatly influenced my own thought on the subject, and in my own mind, at least, clarified a number of perplexing points. It seems best to lead the reader by the same path which was helpful to me.

These species with aberrant nesting seasons show us clearly that in Central America birds can reproduce at any period of the year so long as conditions are favourable for rearing their offspring. Of these conditions, abundance of food appears to be the most important. We find hummingbirds, which are among the smallest of feathered creatures, hatching their eggs and bringing up their nestlings (that never know a father's care) on the high mountains at a season when heavy nocturnal frosts are of normal occurrence but nectar-producing flowers are abundant. At lower altitudes we find

some species, as Cuvier's Hummingbird, nesting in El General in October, a month which often has over 600 millimetres (24 inches) of rain. We find that dietary habits are of more importance than taxonomic relationship in determining when a bird shall breed; those honeycreepers which consume large amounts of nectar—*Diglossa* and *Coereba*—nest at the same time as the hummingbirds, parting company with other members of their own family whose diet is not so specialized, as well as with the great majority of passerine birds. We find seedeaters breeding later than most other finches and small passerines, and the date of the initiation of their nesting fluctuating greatly from year to year according to the time at which the rains restore life to the grasses upon whose seeds they subsist. In numerous other instances we have pointed out relationships between the nesting season of a species of bird and the abundance of its own particular food.

When I first gave attention to the nesting seasons of Central American birds, and found the great majority of them breeding in the same quarter of the year, I looked for some general regulatory influence, astronomic or climatic, which determined their period of reproduction. Now it appears that if such an influence does exist, be it duration or intensity of sunlight, rainfall, humidity, or something more obscure, it does not affect all species of birds in the same manner. If any single astronomic or climatic cycle tends directly to stimulate the reproductive activities of birds, its action is so weak that any species which finds conditions peculiarly favourable for reproduction at some divergent season of the year may escape its control. Whence I suspect that if any Central American bird continues to march with the crowd and rear its family in April, May and June, it does so because it finds this a kindly period for attending its young, rather than because it is coerced into nesting then by some ineluctable control such as increasing length of day or the beginning of the rains. It may be worth our while to examine those circumstances which might make the second quarter of the year a period especially propitious for nesting.

During the months of the northern winter the avian population of Central America is tremendously increased by the presence of millions of migratory birds which nest in the United States, Canada and neighbouring regions. Since the North American continent is far broader in its extra-tropical than in its tropical portion, those migrants which do not pass on to the vast expanse of South America are funnelled into a winter territory much less extensive than their summer breeding range. Thus the Chestnut-sided Warbler *Dendroica pensylvanica* winters chiefly, if not wholly, in southern Central America, in an area probably not much over one-tenth as great as that over which it breeds. Naturally it swarms through the forests of Costa Rica and Panamá, while snows cover its summer home. It is difficult to estimate what proportion of the entire January bird population of Central America is made up of winter visitants, but it is certainly a high proportion. For

the smaller birds the northward return begins in March and gains impetus in April; by May, when the nestlings of the resident species are clamouring for food on all sides, the great majority of these visitors have departed. The withdrawal of so many mouths in itself causes a tremendous increase in the amount of food which the breeding birds of Central America find available for their offspring in late April, May and June. A slight compensation for the departure of the winter visitants is made by the arrival of species which "winter" in South America and breed in Central America; but this region has less than one species of summer visitant for every score of winter visitants. South of the Equator, migrants from the North Temperate Zone arrive in October when the resident birds nest in increasing numbers, and hence would compete with parents seeking food for their young. But in both South America and Africa the region between the Equator and the Tropic of Capricorn is very broad and quite distant from the points of origin of these immigrants, which apparently are far less concentrated than in Central America (see Moreau 1937 b : 21).

It is clear, then, that there would be more food available for the breeding birds of Central America in May even if there were no actual increase in production; but I believe that the supply of both vegetable and animal food is considerably augmented during the second quarter of the year. The dry early months are the period of flowering of many trees and shrubs whose fruit ripens after the rains begin in April or May. This is in general true of the Lauraceae, a multitudinous family in tropical America, whose fleshy fruits, enclosing a single big seed, are eaten by many birds; the cultivated avocado is an example of this periodicity. Of the innumerable species of small trees and shrubs belonging to the Melastomaceae, many flower during the dry months, or with the first rains, and by May or June ripen small, sweet berries that are greedily devoured by birds. In March, in El General, succulent fruits are rare in the forests and thickets, and birds of the most varied sorts, from thick-billed finches and tanagers to thrushes, pigeons, flycatchers, slender-billed honeycreepers and wintering Tennessee Warblers *Vermivora peregrina*, feed largely on the dry, harsh, green fruits of the *Cecropia* tree. By May more tasty berries are available. One who dwells in an isolated region on the Pacific slope of Central America, where transportation is primitive and his food restricted largely to things that can be produced locally without irrigation, finds a tiresome sameness in his diet during the latter part of the dry season. By May his board is plentifully laden with fruits and vegetables from his own farm. It would not be surprising if the birds' fare is correspondingly enriched during the same period. At Amani, in Tanganyika Territory, East Africa, Moreau (1937 : 650) believes that a maximum in the amount of fruit available to the birds is reached in January, which there, at 5° S., corresponds to July in Central America.

Insects also become more numerous and active in the early part of the wet season. My house is unscreened, yet during the dry season my reading lamp attracts few insects even on dark moonless nights, and rarely enough to be troublesome. But in April and May small flying creatures of the most varied sorts come in swarms to the light, fall into the food and draw ink lines across the paper when I write. It is necessary to close doors and windows in order to concentrate on the nest-records which engage my evenings at this period. Beetles of many sorts become abundant, from small, blackish ones which in the lower parts of the valley are attracted to lights in such numbers that they rain down on the floor early in the night, to big, iridescent green fellows that cover the fruit trees. Butterflies are more numerous, and a friend who is an enthusiastic lepidopterist regards April and May as the best months for collecting them. Horseflies of various sorts increase after the rains begin, and by June or July are a scourge to the poor animals; and in the evenings, after the first soaking rains, the winged brood of the termites fills the air and makes flycatchers of all birds, from graceful members of the family of this name to clumsy anis and toucans; but since the winged termites soon pass, they probably are of little importance as a sustained addition to the birds' food supply. These are some of the ways in which insects, always numerous in the Central American lowlands, come increasingly to the attention of the layman during the second quarter of the year, when the nesting season of the birds is at its climax. It would be valuable to have detailed studies on this subject by professional entomologists.

It seems, then, that the majority of the birds of Central America breed during the second quarter of the year because their food is most abundant during this period, although species with peculiar or highly specialized diets may find another season more favourable and nest at that time. One of the puzzling facts in my personal ornithological experience in Central America is that, in the highlands of western Guatemala, I found the main breeding season starting about the 1st of April, in the midst of a long drought which would continue six weeks more; whereas in El General, when the great mass of the birds begin to nest at about the same date, it is in most years raining freely. Although in the latter region May is not infrequently the rainiest month, with more than 400 millimetres of precipitation and at times nearly twice this amount, the birds continue to nest through it and into June or even much later; but in the Guatemalan highlands most of the birds were single-brooded and ceased to nest as soon after the rains began in mid-May, as they could bring forth the family which then engaged them. The fairly warm showers between 2000 and 3000 feet above sea-level affect both insect life and vegetation in a manner quite distinct from the cold precipitation at 8000 and 10000 feet. In this high region some belated broods caught still unfledged by the rains were found dead in the nest, apparently as a result of exposure and insufficient food. This fate befell

a brood of Rufous-browed Wrens *Troglodytes rufociliatus* in their sheltered cranny in a stump, and even some broods of such late-nesting ground-feeders as the Russet-headed Nightingale-thrush and the Chestnut-capped Atlapetes, if they hatched after the middle of June. At very high altitudes cold rains make it necessary for the parents to devote more time to brooding the nestlings just when insect food seems harder to find. This combination of circumstances apparently sets a limit to the breeding of many species, especially those in which the female receives no help in brooding from her mate.

In Central America the activities of man also make the second quarter of the year more favourable than the first for the nesting of the birds. In the cut-and-burn system of agriculture so extensively practised on the rougher lands throughout the region, the forest and second-growth thickets are cut down during the dry months of the year—the forests, which dry more slowly, earlier than the lighter vegetation. This work is usually finished before the birds begin to build their nests in numbers at the end of March. If they nested earlier, the loss of nests through agricultural operations would be far greater than it actually is. The cut-and-burn or "milpa" system of agriculture was practised by the Indians long before the discovery of America by Columbus. Many species of birds dwell and nest by preference in certain successional stages of the vegetation which overgrows crop-lands between the harvest and the next sowing, a variable number of years later; they must constantly shift their territories as the vegetation of each field becomes too heavy for them, or is cut down for planting corn, rice or beans. It would seem that for these birds of the second-growth thickets, in particular, the proper adjustment of their breeding season to the agricultural practices of man would have survival value.

If the breeding season of birds depended solely upon agreeable weather, I should expect most of those in Central America, at least at lower altitudes, to nest during the beginning of the dry season, when limpid blue skies, mild rainless weather and a verdant and flowery earth make this the most delightful period of all the year, to man at least. It lacks only the singing of the birds to fill the measure of its amenity. But in many parts of the region this delectable season all too soon changes to a period of parched earth and drying vegetation, of burning fields and thickets, of oppressive, sultry, smoke-laden atmosphere, of scarcity of fruits and flowers. Were the birds to respond to the immediate situation and build their nests in December or January, their young would be fledged in February or March, the most disagreeable, niggardly and dangerous period for them in all the year.

6. WHAT REGULATES THE BEGINNING OF NESTING IN TROPICAL BIRDS ?

There is growing recognition of the fact that breeding seasons have been adjusted to secure the optimum conditions for rearing the young (Moreau 1937a: 651, Lack 1946: 101-102). But even when we are able to point

to the conditions which make a given season the most favourable period for the reproduction of a certain species, our inquiry is only half done. To bring the young birds into the world requires a fairly long period of preparation, internal and external—maturation of the reproductive organs, building the nest, laying and hatching the eggs. This preparation must in many instances begin at a period when environmental conditions are far from optimum, and may in fact start when they are least favourable. As I write, this at the end of March, the birds about my house in El General are building their nests, and a few even incubating their eggs, at a time when supplies of food seem to be at their lowest ebb, although with the rainy season at hand they should soon increase.

It is necessary, then, to look for some timing mechanism or physiological stimulus, other than the effective conditions themselves, to bring the birds into the reproductive stage at the proper time. Chapman (1929: 84–85), from his studies of Wagler's Oropéndola, concluded that an internal rhythm caused these birds to build their nests at nearly the same date each year, in spite of pronounced variations in weather. "Each bird carries its calendar within itself." But as Moreau (*loc. cit.*) points out: "Given the delays and accidents that we know to happen so frequently to nesting attempts in the forest, an inherited tendency to breed at a certain age could not of itself restrict the breeding season within the observed narrow limits, nor, indeed, within any limits. Some external stimulus or check, or both, must be operative to maintain the limits. Natural selection must be invoked to penalize the unseasonable breeders and to do so with a thoroughness that one would have thought to be beyond the comparatively small seasonal changes in the forest environment." The classic example of an internally controlled rhythm in reproduction among birds is that of the Sooty Tern *Sterna fuscata*, which on Ascension Island in the South Atlantic breeds at intervals of nine months (Chapin 1946), an interval which can bear no fixed relation to any meteorological phenomenon controlled by the annual revolution of the earth.

Since internal rhythms tend to fall out of step with external rhythms if not somehow controlled by the latter, most organisms have been forced through natural selection to develop some mechanism to correlate their own reproductive and other processes with the periodic changes of the environment. At higher latitudes in both hemispheres optimum conditions for the nesting of most birds are reached toward the end of a long period of gradually lengthening days. So strongly fixed is the association of increasing day-length and the attainment of reproductive capacity by northern birds, and so easy is it to alter the bird's time of breeding by artificially manipulating the daily period of illumination, that we are apt to fall into the error of believing that daylength is the ultimate cause of the bird's nesting at a certain season, not merely the timing factor.

When we come to consider the external regulation of the physiological processes of birds, as of other classes of organisms, within the Tropics, the problem is not so easily solved as with animals and plants at higher latitudes. It is questionable whether the slight annual fluctuations in length of day within ten or fifteen degrees of the Equator are in any event sufficiently great to serve as a control of the reproductive processes of the birds. Even if we admit the efficacy of lengthening days in stimulating the reproductive activities of certain tropical species, that lengthening period of daylight can not be universally the controlling factor is certain from the fact that numerous species—for example, the hummingbirds in the western highlands of Guatemala—begin to nest after the autumnal equinox, as days grow shorter. Among plants, we do indeed know species which flower in response to decreasing daily periods of illumination; but the range in day-length necessary to excite response is usually greater than that found within 15° of the Equator.

If we select some other climatic feature, such as rainfall, and attempt to correlate its seasonal fluctuations with the nesting of the birds, we are faced with contradictions as perplexing as those we have found in our consideration of day-length. Were my experiences with birds limited to Costa Rica I might be inclined to believe that they are stimulated to nest by the return of the rains. When the Yigüiros *Turdus grayi* begin to sing, the Costa Rican people say "*Están llamando el agua*" (they are calling the rain). But in western Guatemala I found the great majority of the birds nesting when the dry season was at its height, and there was still no indication of an approaching change in the weather. So also with temperature; Nice (1937: 97–107) was able to correlate the beginning of egg-laying by the Song Sparrow with rising temperatures; but in Central America some birds breed when temperatures are rising, others when they are falling. In most parts of Central America the annual fluctuation in temperature is at best small as compared with extra-tropical regions; in the Canal Zone, where also most of the birds have a definite nesting season, the mean temperature of the coldest month differs from that of the warmest by one or two degrees centigrade.

Moreau (1937a: 651) concludes his study of the breeding seasons of East African birds with this statement: "The observed uniformity and restrictions of the breeding season among the diverse elements in the East African mountain forest avifauna certainly suggests at first sight the operation of a single ruling factor; but on consideration I think it more likely that the result is due to a variety of congruent causes, both limiting factors and stimuli, external and internal." My consideration of the problem in relation to Central American birds leads me to the same conclusion. These factors are apparently different for diverse species; and it seems likely that the responsiveness of a species to any particular set of conditions may have

much to do with its restriction to one, or a few, of the numerous climatically and biologically distinct regions of Central America.

I believe that the most promising approach to an understanding of the relative importance of the several factors which may influence the beginning of nesting is through phenology. First we may consider possible fluctuations in the date of nesting at the same locality in years which differ in the march of rainfall, temperature or other features. Second, it is enlightening to consider differences in the time of breeding in neighbouring regions which differ strongly in climate—such regions are not difficult to find in a mountainous tropical country.

Some birds begin to nest at very nearly the same time in consecutive years which differ greatly in the distribution of rainfall. Chapman (1929 : 84-85) records that, on Barro Colorado Island, Wagler's Oropéndolas began to build on 8 January in both 1926 and 1927, and on 2 January in 1928, although the preceding rainy season had ended on 6 December in 1925 but not until 12 January in 1927. Hence in 1926 his oropéndolas began building 32 days *after* the termination of the rains, but in 1927 4 days *before* their cessation. A pair of Red-crowned Woodpeckers *Centurus rubricapillus*, which I followed through much of the years 1936 and 1937, reared young which left the nest-hole on 23 March in the former year and 29 March in the latter; yet during 1936 the three preceding months had been practically rainless, whereas in 1937 there were numerous showers during this period. With these two species fluctuation in rainfall appears to exert little influence upon the date of nesting.

With other birds the contrary is true. Of species which nest earlier or later as the rains come earlier or later we have already given examples: the Yellow-faced Grassquit (p. 205), Variable Seedeater (p. 206), Orange-billed Nightingale-thrush (p. 208). To these several others may be added. The Song Tanager *Ramphocelus passerinii costaricensis* is particularly sensitive to the weather, and the first refreshing shower at the end of a pronounced dry season seems often to stimulate the male's earliest essays of song. At my house in El General, the date of the beginning of sustained singing has, during the course of five years, varied by more than three weeks, from 13 February in 1947, a wet year, to 9 March in 1945, a year with a severe and protracted dry season. In a locality about eight miles distant I did not hear this bird's song until the last week of March 1939, after three practically rainless months. The female Song Tanagers start to build their nests at about the same time as the males begin to sing. My earliest date for eggs in the immediate vicinity of my house has fluctuated from 5 March in the wet year, 1943, to 3 April in the dry year, 1945. In this dry year another bird common about my house, the Grey-capped Flycatcher *Myiozetetes granadensis* did not start laying until 11 April, although usually its eggs have been found during the last week of March.

The peculiar weather during the early months of 1948 had a retarding and depressing effect upon the nesting of some of the birds about my house, especially the American flycatchers, as it did upon certain agricultural operations. January was fresh and cool, with light showers almost to the end of the month. February gave scarcely any rain, and toward its end was hot, dry and dusty. Then during the first ten days of March good soaking afternoon showers fell, bringing the coffee into blossom, restoring verdure to the browning pastures, stimulating increased singing among the birds, and causing us to plant our maize. My ten years' experience in the region had taught me not to expect many rainless days together after showers so hard in early March. But now followed three rainless weeks which turned the pastures brown again, retarded the growth of the maize, and caused the birds to become more silent. The drought did not end until 2 April.

Apparently as a result of the rather severe drought following a wet spell that stimulated the development of their larvae and pupae, insects seemed scarcer during the following April and May than in any other year I can recall. Certainly they gave me less bother by coming to my lamp, and some kinds of beetles, ordinarily conspicuous at this season, were not seen at all. This shortage was apparently felt by the flycatchers. The abundant and noisy Grey-capped Flycatcher, which in some years begins its dawn-singing by mid-March, did not start in earnest until 5 April. During each of the preceding five years I had found, in the yard and pastures surrounding my house, from three to five accessible nests, most of them containing three eggs, for early broods laid at the end of March or during the first half of April. But this year there were only two nests, neither of which held an egg before 10 May. (Even in the severely but continuously dry year, 1945, Grey-caps began laying a month earlier.) Each nest received only two eggs, and only three of the four hatched. The Yellow-bellied Elaenia *Elaenia flavogaster*, whose sets of two eggs I usually find in my yard in April, did not lay this year until May, and in each of two nests hatched only a single egg. Nests of other kinds of flycatchers were not so abundant as usual. Although the nesting of finches and tanagers seemed to proceed in normal abundance, if somewhat delayed, on the whole the birds appeared to have an unfavourable season for reproduction.

A traveller may sometimes collect interesting observations on the divergent breeding seasons of the same species of bird in localities not far apart but with distinct climates; yet for a thorough attack on our problem by this method it is desirable to have cooperating resident ornithologists in several stations. We have already mentioned the earlier nesting of the Yellow-faced Grassquit on the Caribbean than on the Pacific slope of Costa Rica. The localities where these records were made are in sight of the same mountain-top. A populous colony of the Great-tailed Grackle *Cassidix mexicanus*, which

in 1932 I studied in the Motagua Valley in the Caribbean lowlands of Guatemala, did not begin building until the end of February; but at Finca Mocá, on the drier Pacific slope of the same country, I found birds of this species feeding nestlings at the beginning of January 1935. Here they must have started to build before mid-December, or more than two months earlier than their relatives on the opposite side of the Cordillera, but at the same latitude.

When I left El General on 17 June 1937 the Gray's Thrushes *Turdus grayi* had about finished their nesting for the year and had ceased to sing a week earlier. But at the end of the same month in the vicinity of Cartago, about 60 miles north of El General, I found Gray's Thrushes in fullest song and nesting on all sides, some building, others incubating, still others feeding feathered nestlings. In El General the first half of the year had been wet and heavy rains had fallen from April onward. At Cartago, on the opposite side of the continental divide, the dry season had ended unusually late and the continued drought had retarded the nesting of the thrushes. The effect was the more notable because as a rule the breeding season of birds ends earlier at higher altitudes, and we should expect it to be over sooner at Cartago, 4500 feet above sea-level, than at Rivas in the Valley of El General, 1500 feet lower.

When the initiation of a bird's nesting fluctuates according to the date when the wet season begins, regulation of the time of breeding appears to be in part internal and in part external. The close of one nesting season is followed by a period of rest, after which there is a gradual return of the organism to the reproductive state. Apparently, after it reaches a certain stage, development is suspended and must await an external stimulus before proceeding to that full maturity which will cause singing by the males and nest-building by the females. This stimulus is somehow associated with the advent of the rains; but whether it is the sight of falling water, the increased cloudiness, the higher humidity, growing abundance of food, or something else, we can only surmise. In the vegetable kingdom we have a parallel example in the blossoming of coffee and other plants; the flower-buds gradually form and swell, then remain dormant until the first showers following a protracted dry spell bring on rapid expansion. Such a combination of internal and external regulation has the inestimable advantage of flexibility; it brings about reproductive readiness at a certain season of the year, yet permits reproduction to proceed a little sooner or later, according to the earliness or lateness of the season. Hence the rains of December do not cause the Song Tanager to sing and build, or the coffee to blossom, because organic development has not proceeded far enough; but the first showers of March or April find the organism ready and waiting to respond. In analogous fashion, the resting buds of temperate zone plants do not open under the influence of a warm week in the late autumn, because

they must be further prepared by winter's cold; but in the spring high temperatures quickly cause leaf and blossom to unfold. With birds like the Song Tanager and Grey-capped Flycatcher, which are somewhat responsive to the vagaries of weather, the timing of the nesting-season does not appear so perplexing as it is in species like Wagler's Oropéndola, which breed at approximately the same date each year in spite of differences in the march of the seasons.

SUMMARY.

This study is based upon records of about 1900 nests, mostly in Costa Rica and Guatemala.

For Central America as a whole, and the birds as a whole, the peak of the nesting season falls between the vernal equinox and the summer solstice, with April the principal month for laying. An important, although minor, number of nests is found in March and in July and August, especially at lower altitudes. Relatively very few birds nest during the half of the year from September to February, inclusive.

At high altitudes the concentration of nesting in April, May and June is more pronounced than in the lowlands. In southern Central America the number of birds nesting increases more gradually during the early months of the year than in northern Central America, where the rise of nesting activity in late March is more abrupt.

On the whole, the number of species singing and the volume of song they produce is a good indication of the amount of nesting. The song of many birds is almost restricted to their season of reproduction, though some birds sing freely at other times of the year.

Certain groups of birds depart radically from the general mass in their time of breeding. Nectar-drinkers, including hummingbirds and the honeycreepers *Diglossa* and *Coereba*, nest chiefly at the beginning of the dry season—from November to February, according to the locality—when flowers are most abundant. Grass-seed-eaters nest later than the majority of the birds, waiting for the seeds of the grasses which spring up with the rains. Where the dry season continues into May, birds that hunt food in the ground litter wait until this has been moistened by the rains, and so nest later than other species. In numerous other instances the special dietary habits of a bird appear to explain its distinct nesting season.

April to June seems to be the principal nesting season because this is when, for the majority of birds, food, both vegetable and insect, is most abundant. But if for any species with peculiar diet food is more plentiful at some other time of year, it may nest then in spite of apparently inimical weather. Thus in the high mountains hummingbirds rear their young when nights are frosty, and small ground-feeders nest beneath chilly, drenching rains.

Minor factors which make the second quarter of the year peculiarly favourable for nesting in Central America are (1) the withdrawal of the countless migrants to North America, (2) the circumstance that the destruction of the birds' habitats by the cutting and burning of brush and woodland, to clear ground for crops, is largely completed before this time.

In the highlands of western Guatemala, where the rains do not come until mid-May, most of the birds breed during the driest period of the year; but in southern Costa Rica, where wet weather returns in March or early April, they nest during the first three months of the rainy season. No single climatic feature, such as length or intensity of daylight, alteration of wet and dry seasons, fluctuations of temperature, etc., appears to regulate the initiation of breeding among the birds as a whole.

A number of species begin to nest earlier or later as the rains come earlier or later; others start at about the same date each year, in spite of annual fluctuations in the rain. For the former it is suggested that the regulation of the date of reproduction is both internal and external. Internally controlled processes carry organic development to a certain stage at which it pauses, awaiting some stimulus associated with the return of the rains, as with the resting flower-buds of certain plants. For birds whose date of nesting is independent of the weather, the timing mechanism is more difficult to visualize.

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