INCUBATION AND NESTLING PERIODS OF CENTRAL AMERICAN BIRDS

BY ALEXANDER F. SKUTCH

RECORDS of the incubation and nestling periods of birds are of both practical and theoretical importance. The incubation periods of numerous kinds of North Temperate birds have been published both in special lists, as those of Burns (1915) and Bergtold (1917), and in life-histories of particular species. The nestling periods have, on the whole, received less attention. For tropical birds, very few periods have been published—indeed, tropical ornithology, in every respect save pure systematics, is a branch of the science still in its infancy. An outstanding exception is the list of incubation and fledgling periods of African birds published by Moreau and Moreau (1940), which breaks ground in this field. No comparable information for Neotropical birds has, to my knowledge, ever been presented. As to Central American birds in particular, I doubt whether a score of incubation periods have been given in print, and those chiefly in my life-history studies that have from time to time appeared in 'The Auk.'

The incubation and nestling periods given below have been gathered over a space of fifteen years, in Guatemala, Honduras, Costa Rica, and Panamá. They represent the successful harvest of a very much greater number of attempts to determine these intervals, which failed because of the premature loss of nests. In heavy lowland forest, especially, the gathering of this information is a most discouraging business, for the great majority of birds' nests are prematurely destroyed. Of 35 nests that I attempted to follow through in lowland forest in Panamá, in 1935, only five, or 14.3 per cent, came to a successful conclusion—that is, produced at least one fledgling. In other forested regions of the lowlands, my luck has been scarcely better. But in the Guatemalan highlands, between 8,000 and 9,000 feet above sea level, 37 of 67 nests, or 55.2 per cent, were successful.

There has been a lamentable lack of uniformity in the mode of determination of incubation periods, so that if one wishes to make a comparison of different species—to investigate, for example, whether there is an acceleration in the time of hatching with increasing latitude—he is at a loss to know what data it is safe to accept. Some writers have measured the incubation periods from the laying of the last egg to the hatching of the first nestling, which may give a value too short, as the bird may begin to incubate before the set of eggs is complete. The best recent practice has been to calculate the period from the laying of the last egg to its hatching (Nice, 1937). By this method, the uncertainty as to whether the earlier eggs received any incubation before the set was complete will not introduce an unknown quantity into the results. Sometimes the bird will incubate only sporadically during the first day or so after the set is complete, only gradually 'warming up' to the task. This introduces another element of uncertainty into our periods. But since it rarely happens that the observer has both the time and the patience to watch the nest continuously on the day the last egg is laid, it is a source of error that in practice can scarcely be avoided. The best we can do is to define the incubation period, somewhat arbitrarily, as the interval between the laying of the last egg and the hatching of the last nestling.

It might be objected that after the first egg hatches, the parent leaves the nest to find food for the nestling, with the result that the remaining eggs are no longer warmed as constantly as before, and the rate of development of their embryos is retarded. Actually, studies of a number of species, in which one or both sexes incubate, show that there is, as a rule, only a slight decrease in the total time the nest is covered during the first day or two after the nestlings hatch. I have known female birds whose mates began promptly to bring abundant food—as a Streaked Saltator and a Gray-headed Nightingale-Thrush —to increase their time on the nest after the hatching of the first egg. If, as usually happens, all the eggs in the set hatch within a day or two, there is no reason to suppose that the hatching of the last has been retarded by lack of warming.

I use, to fix the end of the incubation period, the hatching of the last nestling, rather than of the last of the eggs to be laid, because, unless we mark the eggs, we can not be sure that the last laid was the last to hatch. In my own experience, when I have marked eggs, they have hatched in the order of laying; but the Moreaus noted exceptions to this rule. While with fairly large eggs in an open nest within convenient reach, marking the shells presents no difficulties, for a great many species, especially between the Tropics, it is a hazardous undertaking. Woodpecker eggs can not be marked unless we saw a hole in the side of the trunk and remove them from the cavity; no matter how carefully this is afterwards closed, we have decreased the birds' chances of a successful nesting. Other nests are in thickets and vine-tangles above our heads; to reach them we must set up a ladder, disturbing the surrounding vegetation and making the nest more easily discoverable by predators. Many eggs are in closed nests with doorways so narrow that it is difficult or impossible to remove them without injuring the structure; and still others, like those of hummingbirds, are so minute and delicate that we hesitate to apply the point of a pencil to their shells.

For these reasons, I have come to depend more and more upon mirrors for looking into closed nests of all sorts, and into open nests above the level of my eyes. When necessary, the dark interior of the nest is illuminated by inserting a small electric bulb. The one uncertainty which the use of mirrors introduces into the determination of the incubation period is whether the last egg to be laid is the last to hatch, since the eggs are not marked. This uncertainty assumes serious proportions when one or more of the eggs in the set fail to hatch, for then one can not be sure that the last to be laid has hatched. By way of compensation, fewer nests are lost. If eggs do not always hatch in the order of laying, then there is a variability in the length of the incubation period which will appear if determinations are made at a number of nests.

As a general rule, I have made only daily visits to my nests. As the Moreaus have pointed out, this allows a certain error in the determination of the periods, but not, I believe, as great as they suppose. Except in a few species—as Anis and Pauraques—eggs are normally laid before the middle of the morning. Hence, if the nest be visited once each day, after 11 A. M.—or better, in the afternoon—there is little room for doubt as to the dates when the eggs were laid. Nestlings as a rule leave the nest during the early hours of the morning, seldom in the afternoon, unless frightened by the observer. Although eggs may hatch at all hours of the day, recently I have begun to suspect that the majority of them hatch during the early forenoon. Since the last sentence was written, I have found confirmatory evidence in a study of the Yellow Warbler by F. G. Schrantz (1943), who states that of 119 eggs, only nine hatched during the afternoon, the remaining 110 at night or in the early morning. Might there not be a diurnal periodicity in hammering at the shell by the birdling within, similar to the periodicity in such activities as feeding, singing, and nest-building, which many birds exhibit? Or does the constant application of warmth during the night, instead of the intermittent heating that the eggs receive during the day when only one parent incubates, influence the time of hatching? Because of the tendency for eggs to be laid and to hatch, and for the young to depart, during the morning, it seems probable that incubation and nestling periods might in fact be approximately whole days more often than would be possible if these events occurred at random hours. This subject deserves further study.

Be this as it may, I have calculated the periods to the nearest whole day; for although I have from the first made a practice of visiting nests late in the day, in my earlier records I did not as a rule set down the hour. For example, if the last egg was laid between my visits on the first and second of the month, and the last nestling hatched between the visits on the thirteenth and fourteenth, the incubation period would be given as twelve days. Where visits were more widely spaced, or made early in the morning, allowance is made in the statement of the results (*e. g.* "12 or 13 days").

It is necessary to distinguish clearly between nestling and fledging periods. The nestling period, as given in the following list, is the interval between the hatching of the young bird and its departure from the nest. Usually the second is an event no less definite in time than the first; with patient watching, we would be able to give the minute of the departure of the nestling. Most of the birds treated here do not return to the nest once they have severed contact with it. A few, among them woodpeckers and wrens, may use their nests as dormitories and return to them in the evening, along with one or both parents; but after their first departure they are away most of the day, and are clearly no longer nestlings. Rarely a young bird, of a kind that does not sleep in a dormitory, will return to its nest after a brief venture beyond it; but this behavior is, in my experience, exceptional, and not often repeated. If alarmed, anis, Hoatzins, and a few other birds scramble out of the nest before they are feathered, and return later if they can reach it; but the great majority of altricial birds do not return even if prematurely frightened out; often they can not be made to stay in the nest, even if replaced by a well-intentioned bird-watcher.

"To fledge" is defined in Webster's Collegiate Dictionary (5th Edition) as "to acquire the feathers necessary for flight." Many ground-nesting altricial birds, as Skylarks and Song Sparrows, may quit the nest before they can fly, hence their fledging period is longer than their nestling period. Woodpeckers, swallows, and numerous other birds, especially those that are reared in high nests and in holes, are well able to fly—as we can prove by driving them prematurely into the open—days before they normally leave the nest and spread their wings. Their fledging period is shorter than their nestling period. The fledging period is more difficult to determine than the nestling period, not only from the circumstance that the bird may wander out of sight before it can fly, but because flight is a relative thing. Is it correct to say that a bird is fledged when it can merely flutter a few yards on a descending course, as many do when they leave the nest? Even precocious birds—as tinamous and quail—have a nestling period, although often of less than a day's duration.

The accurate determination of the true nestling period—the age of spontaneous departure—is no easy matter. If we are careless, we may frighten the little bird prematurely from the nest. I believe it impossible to determine the true nestling period if we remove the young birds, after they begin to be feathered, for weighing, description of plumage, photography, or the like. Where sufficient nests are available, we should reserve some for these purposes, while in others the nestlings remain quite untouched, to learn the age at which they spontaneously depart. If one is consistent in handling the nestlings, in various nests of the same species, he will find that they all depart at more or less the same age; but this will be the age at which the fear-reaction changes from crouching down in the nest to the attempt to escape from it, not the true nestling period. The interval between the age at which nestlings depart when frightened and that at which they depart spontaneously represents a margin of safety in their lives; if undisturbed, they are certainly safer in the nest until more mature; but if their lives are threatened by a predator, it is better for them to scatter and take their chances in the open.

Many recorded nestling periods are almost certainly too short. With some species, as the Gray-capped Flycatcher, I found that the more care I took to avoid frightening the nestlings, the longer they remained in the nest; for contrary to a general impression, parent birds do not, as a rule, urge their youngsters to depart. The use of a mirror, attached to the end of a long stick if need be, will often show whether the nestlings are still at home, without alarming them by coming too near, or shaking the surrounding foliage. Some of my early records of nestling periods are too short, because I did not take all necessary precautions, or had removed the youngsters for photography. I have indicated such cases in the following list. The nests of some tropical birds—as spine-tails, certain flycatchers, etc.—are of such shape that it is practically impossible to see whether the nestlings are still within, without disturbing them to the extent that they may be driven out if they have not already departed. The only alternative course is to learn by watching for the parents to come with food whether the nest is still occupied.

In calculating the nestling periods, I have followed a different procedure than for the incubation period. An egg is not necessarily incubated as soon as laid; but a nestling grows older from the moment it hatches. When nestlings do not all depart on the same day, I assume that they quit the nest in the order of their age. This must normally be true. But even if this assumption be contrary to fact, the calculations based upon it will give a mean value for the length of the nestling period. For example, if in a nest with two eggs these hatch on the first and second of the month, and the nestlings depart on the 20th and 21st, the nestling period for each would be nineteen days. But if in fact they left in the inverse order of their age—which would not be discovered unless they had been marked as hatched, a difficult matter—their periods were twenty and eighteen days, respectively. Nineteen days is the average value; while we must depend upon observations at a number of nests to give the range of variation.

In a number of instances, the approximate nestling period was determined at nests of woodpeckers, toucans, becards, etc., far out of reach, by noting the date when food was first brought, then watching for the departure of the fledglings. Since the very first food brought to the newly hatched nestlings is apt to escape detection, from being in very small particles held inside the parent's bill, this method is likely to give too short, rather than too long, a period.

In ornithology, no less than in physics, the validity of a numerical result depends upon the number of observations on which it rests. Hence I have thought it desirable to give the incubation and nestling periods of every egg and nestling for which I have been able to determine them. In the following list, the notation "12, 12, 12 (3)" means that in a nest with three eggs, three hatched on the twelfth day after the last was laid. Since, when the eggs have not been marked, one can not be certain that the last has hatched unless *all* have hatched, I have thought it worth while to indicate between the parentheses how many produced nestlings. When the number that hatched is greater than the number of periods given, it will be understood that the others hatched a day or two earlier than the last. So "16, 16 (5, four hatched)" indicates that in a set of five eggs, the last two hatched sixteen days after the set was complete, two more a day or more earlier, and one failed to hatch. While this system of notation may appear a trifle complex, I can think of no more concise mode of presenting all the information which the reader will require in order to judge the exactitude of the determination.

The nestling periods have been calculated as already explained. Here the numerals in parentheses indicate the number of young believed to have left the nest alive.

The size of the egg is one of the factors that have been supposed to influence its incubation period. For a number of the species here treated, egg measurements have apparently never been published; others are to be found in sources so scattered that reference to them would be time-consuming and difficult. Hence I have given the dimensions of the eggs wherever known. The numerals in parentheses indicate the number of measurements upon which the average is based. Since, as already explained, much of my work has been done with mirrors to avoid disturbing the nests, I do not have measurements of all the eggs used in the determination of the incubation periods. In the following list, incubation periods are given for about 90 species of Central American birds, and nestling periods for 120 species. Except where otherwise indicated, the periods are given in days.

Nomenclature, both scientific and vernacular, follows Hellmayr's 'Catalogue of the Birds of the Americas' as far as possible, with little exception. In a few cases substitute vernacular names are proposed parenthetically.

Since some readers may wish to know the localities or regions in which particular data were secured, a letter (in parentheses) has been added after each name in accordance with the following schedule:

(A)—El General, head of Térraba Valley, southern Pacific Costa Rica.
(B)—Costa Rican highlands.
(C)—Carribbean Costa Rica.
(D)—Caribbean Honduras, near Tela.
(E)—Los Amates, humid lower Motagua Valley, Guatemala.
(F)—Guatemalan highlands, Department of Chimaltenango.
(G)—Caribbean Guatemala.
(H)—Western Panamá.
(I) —Almirante, western Panamá.
(J) —Canal Zone.

TINAMIDAE. Tinamous.

Crypturus soui modestus, Cabanis's Pileated Tinamou. (A)
Eggs (14) 43.3 × 32.4 mm.
Left nest less than one day after hatching (1 chick).

PHASIANIDAE. Partridges, Quails, Pheasants.

Odontophorus gujanensis castigatus, Chiriquí Partridge. (A)
Eggs (4) 39.1 × 27.6 mm.
Incubation: between 24 and 28 days (4, all hatched).
Nestling: 20 hours or less (4).

COLUMBIDAE. Pigeons and Doves.

Columbigallina talpacoti rufipennis, Red-winged Talpacoti Dove. (A)
Eggs (16) 23.2 × 17.1 mm.

Incubation: 13, 13 (2); 13, 13 (2); 12, 12 (2); 12, 12 (2).
Nestling: 14, 14 (2); 12, 12 (2); 12 (1).

Leptotila verreauxi verreauxi, Verreaux's White-fronted Dove. (A)
Eggs (7) 29.3 × 22.1 mm.
Nestling: 14, 15 (2).

Oreopeleia montana montana, Ruddy Quail Dove. (A)
Eggs (6) 28.1 × 20.4 mm.
Incubation: 10, 10 (2).
Nestling: 10, 10 (2). As I approached the nest, I found the mother sitting beside the ten-day-old nestlings. She took flight and they followed, flying well until out of sight among the underwood.

RALLIDAE. Rails, Gallinules, Coots.

Creciscus ruber, Red Rail. (D)
Eggs (14) 31.0 × 23.5 mm.
Nestling: 14 hours, little over 1 day (3); 1 day (3).

Ionornis martinica, Purple Gallinule. (J)
Eggs (5) 38.7 × 28.2 mm.
Nestling: 1 or 2 days (4).

CATHARTIDAE. New World Vultures.

Coragyps atratus, Black Vulture. (E)
Nestling: At least 70 days (1). The nestling did not always remain on the same spot on the ground, but wandered along trails it had made through the surrounding pasture grass.

ALCEDINIDAE. Kingfishers.

Chloroceryle amazona, Amazon Kingfisher. (D, E)
Eggs (7) 31.5 × 27.1 mm.
Incubation: 22, 22 (3, all hatched).
Nestling: not less than 29 (4).

Megaceryle t. torquata, Ringed Kingfisher. (E)
Eggs (8) 45.4 × 32.6 mm.
Nestling: between 33 & 35 days (1); between 35 & 38 days (1).

MOMOTIDAE. Motmots.

Aspatha gularis, Blue-throated Green Motmot. (F)
Eggs (11) 28.8 × 22.8 mm.
Incubation: 21 or 22 (3, all hatched); 21, 21, 21 (3); 21 (3, all hatched).
Nestling: 30, 30, 31 (3); 30, 29 (3); 31 (2).

Eumomota superciliosa bipartita, Green-breasted Turquoise-browed Motmot. (D, E)
Eggs (15) 26.5 × 22.5 mm.
Nestling: 28 (4, nestlings handled); 26, 26 (3, nestlings handled). At the age of 26 or 28 days they flew well, but would doubtless have remained longer in the burrow had they not been removed for photography.

CAPRIMULGIDAE. Pauraques, Nighthawks, Whippoorwills.

Nyctidromus a. albicollis, Pauraque. (B)
Nestling: The downy young, less than a day old, may be called by the parents to a position some yards distant from the spot on the ground where they hatched. After they are a few days old, it is difficult to follow their movements.

TROCHILIDAE. Hummingbirds.

Amazilia t. tzacatl, Rieffer's Hummingbird. (D, H)
Eggs (6) 14.0 × 8.8 mm.
Incubation: 16 (2, both hatched); 16, 16 (2); 16 (2, 1 hatched); 15 (2, both hatched).
Nestling: 19, 19 (2, disturbed); 18, 19 (2, disturbed); 19, 20 (2, nest collapsed); 21, 22 (2, disturbed).

Callipharus nigriventris, Black-bellied Hummingbird. (B)
Incubation: At least 16 (2, both hatched).

Colibri cyanotus, Lesser Violet-ear. (B)
Incubation: 16, 16 (2).

Hylocharis, l. leucotis, White-eared Hummingbird. (F)
Eggs (6) 12.5 × 8.0 mm.
Nestling: 26 (1); 23, 26 (2).

Oreopyra castaneoventris calolaema, Costa Rican Mountain Gem. (B)
Nestling: 23 (1); 23, 23 (2).

Phaethornis adolphi saturatus, Dusky Hermit. (A)
Incubation: 16 (2, both hatched).

TROGONIDAE. Trogons, Quetzals.

Pharomachrus mocinno costaricensis, Costa Rican Quetzal. (B)
Eggs (1) 38.9 × 30.2 mm.
Incubation: 17 or 18 (2, both hatched).
Nestling: At least 29 (2); about 31; 23, 23 (2, in an unusually low nest, removed for photography).

Trogon bairdii, Baird's Trogon. (A)
Eggs (2) 33.3 × 25.4 mm.
Nestling: 25 (1).

Trogon curucui tenellus, Graceful Trogon. (A)
Eggs (5) 27.7 × 22.7 mm.
Incubation: 18 (2, one hatched).

Trogon m. melanocephalus, Black-headed Trogon. (E)
Eggs (2) 30.4 × 22.8 mm.
Incubation: at least 19 (3, one hatched).
Nestling: 16 or 17, thrice (3).

Trogon mexicanus, Mexican Trogon. (F)
Eggs (6) 28.9 × 23.5 mm.
Incubation: 19, 19 (2); 18 (2, one hatched).
Nestling: 15, 16 (2); 14 or 15 (1).

CUCULIDAE. Cuckoos, Anis.

Crotophaga ani, Smooth-billed Ani. (J)
Eggs (9) 37.6 × 26.4 mm.
Incubation: 15 or less (9, three hatched). Davis (1940) gives the incubation period of Cuban birds as "about 13 days," range 13 to 15 days.
Nestling: 7 (1). See remarks under following species.

Crotophaga s. sulcirostris, Groove-billed Ani. (D)
Eggs (56) 32.1 × 24.2 mm.
Incubation: 14, 14 (3, eggs marked, two hatched, including last of set); 13, 13, 13 (4, of which last three hatched, all on same day). These periods are calculated from laying to hatching of the last egg. Since these anis were slow in beginning to incubate, the eggs were actually warmed for about 12 days before they hatched.

Nestling: 10, 10 (2); 9 (3). Young anis of both species climb from the nest if alarmed at the age of five or six days, before they are feathered; but when possible, they return to be brooded in the nest until a week old, and linger in the nest tree until 9 or 10 days old.

RAMPHASTIDAE. Toucans, Araçaris.

Aulacorhynchus c. caeruleigularis. Blue-throated Toucanet. (B)
Incubation: 16 (3, all hatched).
Nestling: at least 43 (2).

Pteroglossus t. torquatus, Collared Aracari. (J)
Nestling: at least 44 (at least 2).

Ramphastos piscivorus brevicarinatus, Short-keeled Toucan. (J)
Nestling: Van Tyne (1929) estimates the nestling period at 45 days. I should expect that this toucan, which is much larger than the two foregoing species, would remain in the nest somewhat longer.

CAPITONIDAE. Barbets.

Dicrorhynchus frantzii, Costa Rican Prong-billed Barbet. (B)
Incubation: 13, 13, 13, 13, 13 (5).

GALBULIDAE. Jacamars.

Galbula melanogenia, Black-chinned Jacamar. (A, E)
Eggs (4) 22.4 × 19.4 mm.
Incubation: about 20 days (4, all hatched); 20 or 21 (3, all hatched); 22 (2, both hatched; the pair slow in beginning to incubate).
Nestling: 20, 20 (4, handled); 25, 26 (2, not touched); 21, 22 (2, not touched).

PICIDAE. Woodpeckers, Piculets.

Centurus rubricapillus wagleri, Wagler's Woodpecker. (A)
Eggs (1) 23.8 × 17.1 mm.
Nestling: not less than 31 (2).

Centurus aurifrons pauper, Trujillo Woodpecker. (E)
Eggs (4) 22.4 × 19.4 mm.
Incubation: about 13 days (4, three hatched, the first only 11 days after the set was complete).
Nestling: 30 (3).

Dryobates villosus extimus, Boquete Hairy Woodpecker. (Costa Rica)
Nestling: 28 (1).

Piculus rubiginosus uropygialis, Costa Rican Woodpecker. (B)
Nestling: 24 (1, inadvertently frightened from nest, flew well).

Picumnus olivaceus flavotinctus, Veragua Piculet. (A)
Eggs (3) 16.6 × 12.3 mm.
Incubation: 13 or 14 (3, two hatched).
Nestling: 24, 24 or 25 (2).

Tripsurus chrysauchen, Golden-naped Woodpecker. (A)
Nestling: at least 33 (3).

FORMICARIIDAE. Antbirds.

Thamnophilus bridgesi, Bridges's Ant Shrike. (A)
Eggs (2) 23.0 × 16.7 mm.
Incubation: 14 or 15, 14 or 15 (2); 14, 14 (2); 16 (2, one hatched).
Nestling: 10, 10 (2, the first nestling hatched at about 8:50 A. M., June 2, 1937, and departed while I watched from a blind at 6:51 A. M. on June 12, aged 9 days, 22

hours; the second nestling hatched between noon on June 2 and the following dawn, departed at 6:27 A. M. on June 13).

Cercomacra tyrannina crepera, Dusky Tyrannine Antbird. (A)
Egg (1) 19.4 × 14.3 mm.
Nestling: about 11 (2).

Dysithamnus mentalis septentrionalis, Northern Bush Bird (Antvireo). (A)
Eggs (6) 20.0 × 15.0 mm.
Incubation: 15, 15 (2).
Nestling: 9, 9 (2); 9, 9 (2).

Hylophylax n. naevioides, Spotted Antbird. (J)
Eggs (2) 23.0 × 15.5 mm.
Nestling: 11, 11 (2).

Myrmotherula axillaris albigula, Lawrence's Ant Wren. (J)
Eggs (4) 17.2 × 12.5 mm.
Incubation: 16, 16 (2).

Taraba major obscurus, Red-eyed Ant Shrike. (A)
Eggs (4) 29.3 × 22.6 mm.
Incubation: 17 or 18 (2, one hatched).
Nestling: 12 or 13 (1).

Thamnophilus doliatus pacificus, Pacific Ant Shrike. (A)
Eggs (4) 23.3 × 17.2 mm.
Nestling: 12, 13 (2)

Thamnophilus punctatus atrinucha, Slaty Ant Shrike. (J)
Eggs (6) 23.9 × 16.6 mm.
Nestling: 9, 9 (2).

FURNARIIDAE. Ovenbirds and their allies.

Automolus ochrolaemus exsertus, Chiriqui Automolus. (A)
Incubation: 18 to 20, thrice (3, all hatched).
Nestling: 18, 18, 18 (3).

Pseudocolaptes l. lawrencii, Lawrence's Pseudocolaptes. (B)
Nestling: at least 29.

Synallaxis brachyura nigrofumosa, Sooty Spine-tail (Castle-builder). (A)
Eggs (6) 21.5 × 17.0 mm.
Incubation: 18, 18 (2).
Nestling: 14 or 15, 14 or 15 (2, departure probably premature). It is impossible to see the contents of the nests of Spine-tails without making an opening in the side, which causes disturbances in their routine, and may frighten the nestlings forth prematurely.

Synallaxis erythrothorax, Rufous-breasted Spine-tail (Castle-builder). (D, G)
Eggs (19) 21.1 × 16.7 mm.
Incubation: about 17 (4).
Nestling: 14 or 15 (1, frightened from nest).

Xenops minutus ridgwayi, Ridgway's Xenops. (A)
Incubation: between 15 and 17 (2, both hatched).
Nestling: 13, 14 (2).

DENDROCOLAPTIDAE. Wood-hewers.

Lepidocolaptes affinis neglectus, Southern Allied Wood-hewer. (B)
Nestling: 19, 19 (2); 19, 19 (2).

Lepidocolaptes souleyetii compressus, Thin-billed Wood-hewer. (A)
Incubation: 15 (2, one hatched).

Nestling: 19 (1). A pair of Thin-billed Wood-hewers and a *Dendrocincla anabatina saturata* built in the same hollow palm trunk. Two eggs were laid, and incubated by the *Dendrocincla*, which hatched one and faithfully attended the nestling. As it grew older, its streaked head and soft trill clearly indicated that it was not her own offspring.

TYRANNIDAE. Tyrant Flycatchers.

Elaenia c. chiriquensis, Lawrence's Elaenia. (A)
Eggs (13) 18.5 × 14.5 mm.
Incubation: 15 (1); 15 (2, one hatched); 15 (2, one hatched); 14, 14 (2); 14 (2, both hatched); 14 (2, one hatched); 14 (1).
Nestling: 15 or 16 (1); 15 or 16, 16 (2); 14 (1, frightened); 15 (1); 15, 15 (2).

Elaenia flavogaster subpagana, Northern Yellow-bellied Elaenia. (A)
Eggs (15) 21.1 × 16.4 mm.
Incubation: 15 or 16 (2, both hatched); 16 (2, both hatched); 15 (2, both hatched); 17 (2, both hatched; the nest was above a frequently-used path, and the sitting bird was often disturbed); 17 (2, one hatched).
Nestling: 17 or 18 (1); 17 (1).

Legatus l. leucophaius, Striped Flycatcher. (A)
Eggs (8) 21.9 × 16.5 mm.
Incubation: 16, 16 (3, all hatched).
Nestling: 19, 20 (2); 19, 18, 18 (3).

Megarhynchus pitangua mexicanus, Mexican Boat-billed Flycatcher. (A)
Incubation: about 18 (2).
Nestling: at least 23 (1); 24, 24, 24 (3).

Myiarchus tuberculifer connectens, Matagalpa Flycatcher. (E)
Eggs (8) 20.0 × 15.0 mm.
Nestling: 13, 13, 14 (3, left prematurely, but flew well).

Myiobius a. atricaudus, Black-tailed Myiobius. (A)
Eggs (2) 17.3 × 13.1 mm.
Incubation: about 23 days (1).

Myiobius sulphureipygius aureatus, Southern Sulphur-rumped Myiobius. (A)
Eggs (4) 18.3 × 13.1 mm.
Incubation: 22, 22 (2).
Nestling: 22, 22 (2).

Myiochanes cinereus brachytarsus, Short-legged Pewee. (C)
Eggs (2) 17.1 × 13.5 mm.
Incubation: 15 (3, two hatched).

Myiodynastes luteiventris, Sulphur-bellied Flycatcher. (E)
Eggs (3) 25.5 × 19.1 mm.
Incubation: 16 (3, all hatched).

Myiodynastes maculatus nobilis, Noble Flycatcher. (A, J)
Eggs (3) 27.7 × 18.6 mm.
Incubation: 16 or 17 (3, all hatched).
Nestling: at least 21 (3).

Myiophobus fasciatus furfurosus, Bran-colored Flycatcher. (A)
Eggs (12) 17.3 × 13.0 mm.
Incubation: 17, 17 (2); 17 (2, one hatched); 17, 17 (2).
Nestling: 17 (1); 15 (1); 16, 16 (2).

Myiozetetes g. granadensis, Gray-capped Flycatcher. (A)
Eggs (15) 23.9 × 17.3 mm.

Incubation: 16 (3, all hatched); 17, 17, 17 (3); 16 (3, all hatched); 18, 18 (2); 16, 16, 16 (3); 16, 16, 16 (3); 16, 16, 16 (3); 16 (3, all hatched); 31 or 32 (3; I am at a loss to explain this); 16 (3, last hatched); 17, 17 (2); 16, 16, 16 (3); 16, 16 (3, last two hatched).

Nestling: 19, 19, 20 (3); 20, 20 (2); 21, 21 (3); 20, 20, 20 (3); 19, 19 (2); 21, 21 (3); 20, 20 (2).

Myiozetetes similis columbianus, Colombian Vermilion-crowned Flycatcher (Chipsa-cheery Flycatcher). (A, I)

Eggs (11) 23.5 × 16.7 mm.

Incubation: 15, 15 (3, two hatched); 16 (3, one hatched); 15, 15, 15 (3); 16 (2, last hatched).

Nestling: 17, 17, 17, 16 (4, frightened); 22 (1, departure spontaneous); 20 (1, departure spontaneous).

M. s. texensis, Giraud's Flycatcher. (D)

Nestling: 16 (3, frightened).

Onychorhynchus mexicanus fraterculus, Colombian Royal Flycatcher. (A)

Eggs (4) 19.7 × 14.8 mm.

Incubation: 22, 22 (2).

Nestling: 21, 21 (2); 21 or 22 (2).

O. m. mexicanus, Mexican Royal Flycatcher. (D)

Nestling: 21 (1); 21 or 22 (1).

Pipromorpha oleaginea dyscola, Costa Rican Pipromorpha.

Eggs (7) 20.3 × 14.5 mm.

Incubation: 20 (3, all hatched); 19, 19, 19 (3); 21 (3, all hatched).

Nestling: 19, 19, 19 (3, frightened from nest perhaps a trifle prematurely, but flew well).

P. o. assimilis, Mexican Pipromorpha. (D)

Nestling: 18 (1, handled).

Platyrinchus coronatus superciliaris, Western Golden-crowned Flat-bill (Lawrence's Spade-billed Flycatcher). (A)

Eggs (6) 16.1 × 13.3 mm.

Nestling: 15, 16 (2).

Rhynchocyclus b. brevirostris, Short-billed Flat-bill. (A)

Nestling: about 23 (1).

Serpophaga cinerea grisea, Lawrence's Serpophaga (Black-hooded Flycatcher). (Costa Rica)

Eggs (2) 16.9 × 12.7 mm.

Incubation: 17 (2, both hatched); 18 (2, one hatched).

Nestling: 17 (1).

Terenotriccus erythrurus fulvigularis, Fulvous-throated Flycatcher. (J)

Eggs (4) 15.8 × 11.8 mm.

Incubation: at least 22 (2, both hatched).

Nestling: 19 (1).

Todirostrum cinereum finitimum, Northern Tody-tyrant. (I)

Eggs (2) 15.9 × 11.3 mm.

Incubation: 18, 18 (2); 18 (3, all hatched); 17 (3, all hatched).

Todirostrum sylvia schistaceiceps, Slaty-headed Tody-tyrant. (A)

Eggs (4) 17.5 × 12.7 mm.

Incubation: 19, 19 (2).

Nestling: 21, 21 (2); at least 19 (2).

Tolmomyias sulphurescens cinereiceps, Gray-headed Flat-bill. (A)
Eggs 20.8 × 14 mm. (Carriker).
Nestling: at least 20.

Tyranniscus vilissimus parvus, Lesser Paltry Tyrannulet (Lesser Tyranniscus). (A)
Eggs (1) 16.7 × 13.1 mm.
Incubation: 16 (2, both hatched).
Nestling: 18 (1); 19, 18 or 19 (2).

Tyrannus melancholicus chloronotus, Berlepsch's Kingbird. (A)
Eggs (12) 24.7 × 18.2 mm.
Incubation: at least 16 (3, two hatched); 16 (3, all hatched).
Nestling: 18 or 19 (1).

PIPRIDAE. Manakins.

Manacus aurantiacus, Salvin's Manakin. (A)
Eggs (10) 20.6 × 14.9 mm.
Nestling: at least 17 (1).

Pipra coronata velutina, Velvety Manakin. (A)
Eggs (4) 18.6 × 14.2 mm.
Incubation: 19, 19 (2).

COTINGIDAE. Cotingas, Becards.

Pachyramphus c. cinnamomeus, Cinnamon Becard. (C)
Nestling: at least 20 days.

Pachyramphus polychopterus similis, Slate-bellied Becard. (A)
Eggs (2) 20.0 × 14.7 mm.
Incubation: 18 or 19 (4, three hatched).

Platypsaris aglaiae sumichrasti, Sumichrast's Becard. (F)
Eggs (1) 25.4 × 17.5 mm.
Nestling: at least 19.

Tityra inquisitor fraserii, Fraser's Tityra. (C)
Nestling: at least 25 (3, in nest far out of reach).

Tityra semifasciata costaricensis, Costa Rican Tityra. (A)
Eggs (2) 30.0 × 21.0 mm.
Nestling: at least 21 days.

HIRUNDINIDAE. Swallows and Martins.

Pygochelidon c. cyanoleuca, Blue-and-white Swallow. (Costa Rica)
Incubation: 15, 15, 15 (3); 15, 15 (3, all hatched).
Nestling: 26, 27 (3).

Stelgidopteryx ruficollis fulvipennis, Salvin's Rough-winged Swallow. (C, G)
Eggs (27) 19.8 × 13.6 mm.
Incubation: 16, 16, 16 (5, three hatched); 18 (5, all hatched).
Nestling: 20 or 21 (4).

SYLVIIDAE. Gnatcatchers, European Warblers.

Polioptila plumbea superciliaris, Lawrence's Gnatcatcher. (A)
Incubation: 13, 13, 13 (3).

Ramphocaenus r. rufiventris, Northern Long-billed Antwren. (A)
Eggs (2) 19.5 × 13.9 mm.
Incubation: 17 (2, both hatched).
Nestling: 12, 12 (2).

TROGLODYTIDAE. Wrens.

Heleodytes z. zonatus, Mexican Banded Wren. (F)
Eggs (10) 22.0 × 15.8 mm.
Nestling: 18, 18, 19 (3).
Henicorhina leucophrys collina, Chiriqui Wood Wren. (B)
Eggs (2) 22.2 × 15.5 mm.
Incubation: 19 or 20 (2, both hatched).
Nestling: 14, 14 (2); 17, 18 (2).
Thryophilus m. modestus, Cabanis's Wren (Chinchirigüí Wren). (A)
Eggs (6) 22.3 × 15.6 mm.
Incubation: 18 (2, both hatched).
Nestling: 13 (2, frightened).
Thryothorus nigricapillus semibadius, Salvin's Wren (River Wren). (A)
Eggs (3) 21.5 × 15.4 mm.
Nestling: 16 (1, frightened).
Thryothorus rutilus hyperythrus, Tawny-bellied Wren. (A)
Eggs (3) 18.2 × 13.8 mm.
Nestling: 16, 16, 16 (3).
Thryothorus rutilus petersi, Honduras Spotted-breasted Wren. (D)
Eggs (2) 19.1 × 15.3 mm.
Nestling: 12 (2, nestlings handled).
Troglodytes musculus inquietus, Panamá House Wren. (F)
Eggs (9) 17.5 × 13.4 mm.
Incubation: 15, 15 (4, three hatched); 15, 15, 15 (4, three hatched); 16, 16 (4, two hatched); 16 (4, all hatched); 15 (4, all hatched).
Nestling: 18, 18, 18 (3); 18, 18, 18 (3); 18 (1); 17, 16, 16, 15 (4, frightened); 18, 18, 18, 17 (4, all left spontaneously within space of 4 hours, 40 minutes).
Troglodytes m. intermedius, Costa Rica House Wren. (A)
Incubation: 17, 17, 17 (4, all hatched); 15 (3, two hatched).
Nestling: 18, 18, 18, 19 (4); 18, 18, 18, 17 (4); 18, 19 (2).

MIMIDAE. Mockingbirds, Thrashers.

Melanotis caerulescens hypoleucus, White-breasted Blue Mockingbird. (F)
Eggs (8) 31.6 × 21.5 mm.
Nestling: 14, 15 (2, nestlings handled).

TURDIDAE. Thrushes, Bluebirds.

Catharus g. griseiceps, Gray-headed Nightingale-Thrush. (A)
Eggs (23) 23.7 × 17.6 mm.
Incubation: 13, 13 (2); 15, 15 (2); 13, 13 (2); at least 15 (2, one hatched); 15 (2, one hatched).
Nestling: 14 or 15, 14 or 15 (2); 15 (1); 17, 17 (2); 14, 13 (2); 15, 15 (2).
Catharus occidentalis alticola, Guatemalan Nightingale-Thrush. (F)
Eggs (12) 23.9 × 18.2 mm.
Incubation: 15 or 16 (2, both hatched); 15, 15 (2).
Nestling: 14, 15 (2); 15 or 16, 15 or 16 (2).
Myadestes ralloides melanops, Black-faced Solitaire. (B)
Eggs (3) 25.5 × 19.1 mm.
Incubation: 12 or 13, 12 or 13, 12 or 13 (3).
Nestling: 16, 16, 16 (3).

Sialia sialis guatemalae, Guatemala Bluebird. (F)
Eggs (8) 22.1 × 16.8 mm.
Incubation: 14 (4, one hatched).
Turdus grayi subspp., Gray's Thrush. (A, D–H)
Eggs (22) 28.3 × 20.2 mm.
Incubation: 12, 12, 12 (3); 12 (3, all hatched); 12 (3, all hatched).
Nestling: at least 15 (3); 15, (2); 15 (1); 16, 16 (2); 15 (1); 15 (2).

VIREONIDAE. Vireos.

Pachysylvia o. ochraceiceps, Tawny-crowned Pachysylvia. (A)
Nestling: at least 13 (2).
Vireo virescens insulanus, Southern Yellow-green Vireo. (A)
Eggs (8) 20.5 × 14.7 mm.
Incubation: 14, 14 (2); 14 (3, all hatched); 13, 13, 13 (3).
Nestling: 13, 14 (2); 13, 13 (3); 12 (1); 12, 12, 12 (3; they hatched between 6:00 and 8:23 A. M., May 9, 1943, and departed spontaneously between 6:00 and 6:30 A. M., May 21).

PARIDAE. Titmice, Chickadees, Bush-tits.

Psaltriparus minimus melanotis, Black-eared Bush-tit. (F)
Incubation: 15, 15 (4, all hatched); 15 or 16 (4, all hatched).
Nestling: 17, 17, 18, 18 (4); 17 or 18 (4); 19, 19, 19, 19 (4).

COMPSOTHLYPIDAE. Wood Warblers.

Basileuterus fulvicauda veraguensis, Veraguan Buff-rumped Warbler. (A)
Eggs (10) 21.4 × 15.1 mm.
Incubation: 16, 16 (2); 16 (2, one hatched); 16, 16 (2); 19 (2, one hatched; bird frequently frightened from nest in roadside bank); 17 (2, one hatched; nest in same position as last, a year later; the road now less often used); 17 (2, both hatched); 16, 16 (2).
Nestling: 15 (1); 14, 14 (2); 14, 14 (2); 13, 13 (2).
Ergaticus ruber versicolor, Pink-headed Warbler. (F)
Eggs (9) 17.1 × 13.3 mm.
Incubation: 16, 16, 16 (3).
Nestling: 11, 11, 11 (3, handled); 10, 10 (2, frightened).
Myioborus miniatus aurantiacus, Orange-bellied Myioborus (Orange-bellied Redstart). (B)
Eggs (20) 17.5 × 13.4 mm.
Incubation: 14, 14, 14 (3); 13, 13, 13 (3); 15, 15 (3, two hatched); 15, 15 (2); 15, 15, 15 (3); 15, 15 (3, two hatched).
Nestling: 14, 14 (2); 12, 12 (2); 12, 12, 12 (3); 12 (1); 10, 10 (2, probably left prematurely because they had been removed from the nest for examination).
Myioborus miniatus connectens, Intermediate Myioborus (Intermediate Redstart). (F)
Eggs (3) 17.5 × 13.4 mm.
Nestling: 11 (2, nestlings handled).
Myioborus torquatus, Collared Myioborus (Collared Redstart). (B)
Eggs (5) 18.7 × 13.5 mm.
Incubation: 15, 15, 15 (3).
Nestling: 13, 13 (2).

FRINGILLIDAE. Finches, Sparrows, Grosbeaks.

Arremonops conirostris richmondi, Richmond's Sparrow. (A)
Eggs (13) 25.5 × 18.3 mm.
Incubation: at least 14 (2, both hatched); at least 14 (2, both hatched).
Nestling: 12 (2); 11, 11 (2); 11 or 12 (2).

Atlapetes gutturalis parvirostris, Costa Rican Yellow-throated Atlapetes. (B)
Eggs (9) 23.7 × 17.9 mm.
Nestling: 12 (1); 12 (3).

Atlapetes torquatus costaricensis, Costa Rican Atlapetes. (A)
Eggs (12) 25.7 × 18.5 mm.
Incubation: 15, 15 (2); 15 (2, both hatched).
Nestling: 13 (1); 9, 10 (2, frightened).

Oryzoborus funereus, Lesser Rice Grosbeak. (I)
Incubation: 12, 12 (2).
Nestling: between 10 and 12 (1).

Pselliophorus tibialis, Yellow-thighed Sparrow. (B)
Eggs (4) 24.8 × 18.2 mm.
Nestling: 12, 12 (2).

Saltator coerulescens grandis, Lichtenstein's Saltator. (D)
Eggs (3) 25.6 × 18.7 mm.
Nestling: 15 (1).

Saltator maximus intermedius, Panamá Buff-throated Saltator. (A)
Eggs (15) 27.3 × 19.1 mm.
Incubation: 13, 13 (2); 13 (2, one hatched); 16 (2, one hatched; female kept off nest by a rival).
Nestling: 15 (1); 13 (1); 14 (1); 13 (1); 15 (1).

Saltator albicollis furax, Costa Rican Streaked Saltator. (A)
Eggs (9) 26.1 × 18.0 mm.
Nestling: 13 (1).

Sporophila aurita aurita, Hicks's Seed-eater. (A)
Eggs (8) 17.3 × 13.1 mm.
Incubation: 12, 12 (2).
Nestling: 13, 13 (2); 11, 12 (2); 13, 13 (2); 13, 13 (2).

Sporophila aurita corvina, Black Seed-eater. (C)
Eggs (6) 18.0 × 13.2 mm.
Incubation: 12, 12, 12 (3).
Nestling: 12, 12, 12 (3)

Sporophila torqueola morelleti, Morellet's Seed-eater. (D)
Eggs (13) 16.3 × 12.7 mm.
Incubation: 13 (2, both hatched).
Nestling: 10 or 11 (2); 11, 11 (2).

Tiaris olivacea pusilla, Mexican Grassquit. (Costa Rica)
Eggs (5) 17.0 × 12.9 mm.
Incubation: 13, 13 (3, two hatched); 16, 16, 16 (3); 13, 13 (3, all hatched); 13 (3, all hatched); 13, 13 (2, the second egg was laid before 6:00 A. M., June 26, 1943, and hatched between 5:32 and 6:18 A. M., July 9, giving an incubation period of almost exactly 13 days); 13, 13 (2).
Nestling: 10 (1, departure probably premature); 14, 14 or 15 (2); 14, 14, 13 (3); 15, 15 (2); 13 ,13 (2).

Zonotrichia capensis costaricensis, Costa Rican Sparrow. (B)
Nestling: 12 (1).
Zonotrichia capensis septentrionalis, Guatemalan Sparrow. (F)
Eggs (12) 20.8 × 15.6 mm.
Nestling: 10, 10 (2).

COEREBIDAE. Honeycreepers.

Coereba flaveola mexicana, Mexican Bananaquit. (J)
Incubation: 13 (2, both hatched); 13, 13 (2); 12, 12 (2).
Nestling: 17, 17 (2); 17, 17 (2); 16 or 17 (2).
Cyanerpes cyaneus carneipes, Flesh-legged Honey Creeper. (A)
Incubation: 12, 12 (2); 13 (2, one hatched); 12 (2, both hatched).
Nestling: 14, 14 (2).
Diglossa baritula plumbea, Costa Rican Diglossa (Costa Rican Flower-piercer). (B)
Eggs (4) 17.0 × 12.7 mm.
Incubation: 14 (2, both hatched).
Nestling: 13, 16 (2, the first frightened from the nest).

THRAUPIDAE. Tanagers, Euphonias.

Chlorophonia occipitalis callophrys, Costa Rican Chlorophonia. (B)
Nestling: not less than 23 (3); 24 or 25 (3).
Eucometis penicillata stictothorax, Streak-chested Tanager. (A)
Eggs (7) 23.9 × 17.2 mm.
Incubation: 14, 14 (2); 16 (1).
Ramphocelus passerinii costaricensis, Cherrie's Tanager (Song Tanager). (A)
Eggs (18) 24.1 × 17.2 mm.
Incubation: 12 (2, both hatched); 12, 12 (2); 13, 13 (2); 12 (2, one hatched); 13, 13 (2); 13 (2, one hatched); 13 (2, one hatched); 12, 12 (2); 12, 12 (2); 12, 12 (2); 12 (2, both hatched); 12, 12 (2); 12, 12 (2).
Nestling: 12, 13 (2); 11, 11 (2); 12, 12 (2); 12, 12 (2); 12 (1); 13, 13 (2); 12, 12 (2); 12, 12 (2).
Ramphocelus p. passerinii, Passerini's Tanager (Scarlet-rumped Black Tanager). (C, H)
Eggs (8) 24.3 × 17.0 mm.
Incubation: 13 (2, both hatched); 12 (2, both hatched).
Nestling: 11, 12 (2); 11, 11 (2); 11, 11 (2).
Ramphocelus dimidiatus isthmicus, Panamá Crimson-backed Tanager. (J)
Eggs (4) 22.4 × 17.1 mm.
Incubation 12, 12 (2); 12, 12 (2).
Nestling: 10, 11 (2).
Tanagra l. lauta, Bonaparte's Euphonia. (E)
Eggs (5) 16.2 × 12.6 mm.
Incubation: 16, 16, 16, 16, 16 (5).
Nestling: 17, 17, 17 (3, nestlings handled).
Tanagra luteicapilla, Yellow-crowned Euphonia. (A)
Eggs (3) 17.2 × 12.8 mm.
Incubation: 13 or 14 (2, both hatched).
Nestling: 24 (1); 22, 22 (2).
Tangara gyrola bangsi, Bangs's Green Tanager. (A)
Eggs (2) 20.4 × 14.1 mm.

Incubation: 13, 13 (2); 14 (2, both hatched).
Nestling: 16, 16 (2); 15 or 16 (2).

Tangara icterocephala, Silver-throated Tanager. (A)
Eggs (6) 21.5 × 15.6 mm.
Incubation: 14, 14 (2).

Tangara nigro-cincta fanny and *T. n. franciscae*, Fanny's Tanager and Francisca's Tanager. (A, J)
Eggs (10) 20.1 × 14.9 mm.
Incubation: 13, 13 (2); 15 (1); 14, 14 (2, the second egg was laid before 6:30 A. M., May 3, 1943, and hatched about 8:45 A. M., May 17).
Nestling: 12, 12 (2, frightened from nest); 13 or 14, 13 or 14 (2, frightened from nest); 14, 14 (2); 15 (1).

Thraupis episcopus diaconus, Northern Gray Tanager. (A)
Eggs (16) 22.9 × 16.0 mm.
Incubation: 14, 14 (2); 14 (2, one hatched); 13 (1); 14 (2, both hatched); 13, 13 (2); 14 (2, both hatched).
Nestling: at least 16 (2); 20, 20 (2); 17, 17 (2); 14, 15 (2, frightened from nest); 17 (1); 18 or 19 (2); 17 or 18 (1); 17, 18 (2).

ICTERIDAE. Orioles, Oropéndolas, Grackles and their allies.

Cassidix m. mexicanus, Great-tailed Grackle. (E)
Eggs (62) 33.6 × 23.0 mm.
Incubation: 13, 13 (2); 14 (3, all hatched); 13 (3, all hatched); 14 (2, both hatched); 13, 13 (2); 13, 13 (3, eggs marked, last two hatched).
Nestling: at least 21 (3); 22, 23, 23 (3); 21 (3). These nestlings were raised in the crowns of coconut palms; at the age of about 16 days, before they could fly, if disturbed they would leave the nest and scramble over the neighboring fronds.

Gymnostinops montezuma, Montezuma Oropéndola.
Nestling: about 30 days.

Icterus m. mesomelas, Yellow-tailed Oriole. (E)
Eggs (3) 23.9 × 17.9 mm.
Incubation: 14 (3, eggs marked, first and third hatched).
Nestling: 12 or 13 (2).

Zarhynchus wagleri ridgwayi, Pale-naped Oropéndola. (J)
Nestling: about 34–37 days (Chapman, 1928).

CORVIDAE. Jays, Crows, Ravens.

Psilorhinus mexicanus cyanogenys, Central American Brown Jay. (E)
Eggs (7) 34.5 × 24.6 mm.
Incubation: 20 (3, the female sat very inconstantly); 18, 18 (3, eggs marked, the last two hatched).
Nestling: 23, 24 (2).

WHAT FACTORS DETERMINE THE LENGTH OF INCUBATION AND NESTLING PERIODS?

Several theories have been advanced to account for the great diversity in the length of the incubation periods of different species of birds. Bergtold (1917) believed that the higher the taxonomic rank of the bird, the more rapidly its eggs hatched. Worth (1940), characterizing Bergtold's theory as a "vague empiricism," proceeds to demonstrate that the incubation period of an egg is determined primarily by its volume, but may be shortened or lengthened by ecological factors, such as the amount of predation to which the nest is exposed. This ecological correction provides a convenient escape whenever the observed incubation period of an egg does not coincide with that calculated from its volume; for actual studies of nest losses appear to be lacking for most of the species he classifies as of "slow" or "rapid" incubation. Thus hummingbirds, whose minute eggs hatch far more slowly than we should expect from their volume, fall among the species with "slow" incubation. Yet studies of several kinds of hummingbirds (Skutch, in Bent, 1940) revealed that they lose a high percentage of their nests. We still have far too little precise information on this subject to allow ourselves the luxury of becoming dogmatic!

I believe that taxonomic position, no less than size of egg and ecological factors, influences the length of the period of incubation. Taxonomic position would cover the varying temperatures at which eggs are incubated, for different groups of birds vary in their average body temperature, and in general this increases with taxonomic rank (Wetmore, 1921). Another factor, which apparently has never been considered, is the number of hours each day during which the eggs are actually warmed. Many kinds of birds, among them species of woodpeckers, pigeons, trogons, antbirds, etc., keep their eggs almost constantly covered, day and night, while a number of small flycatchers, swallows, etc., incubate their eggs only about fifty per cent of the day, taking many short sessions separated by brief recesses. Unpublished studies of about a hundred species show that the great majority of birds which incubate alone spend from sixty to eighty per cent of the day in the nest.

On the whole, the song-birds (Oscines) have the shortest incubation periods, while birds at the foot of the taxonomic ladder tend to have long periods. This is undoubtedly in part because the 'lower orders' are bigger birds, in part because many of them breed upon islets, on inaccessible cliffs or in holes and burrows, where eggs and young are exposed to fewer dangers than in open nests in the fields, thickets, and forests of continental areas infested with snakes, rodents, and other predators. But we must remember that our linear systems of classification, which attempt to arrange the orders and families of birds according to their degree of evolutionary development or specialization, can not, in fact, present a true picture of avian evolution.

If birds are, indeed, a monophyletic group, then all have an ancestry equally respectable. Some have developed more rapidly in one direction, some in another. We place the song-birds at the top of the ladder because, among other things, their organs of song—a distinctive attribute of birds—are the most perfect. But flight is also an important attribute of birds; and were we to take the development of the organs of flight as our fundamental criterion, we should be obliged to place hummingbirds and swifts in the proud position now occupied by the song-birds.

The pigeons present an excellent example of a family with a low taxonomic position and rapid incubation. The shortest incubation period I have ever determined—as short as any credible incubation period I have seen in print—is that of the Ruddy Quail Dove, whose eggs hatched in ten days. The nest of this dove is a frail platform of sticks and leaves in the undergrowth of the tropical forest, a habitat with such a high degree of predation that I am not likely soon to make a second determination of its incubation period. The eggs, be it noted, are larger than those of many passerine birds with longer incubation periods. The eggs of the Ruddy Ground Dove, a bird of the thickets and clearings where nesting success is somewhat higher, hatch in twelve or thirteen days, which is the incubation period of a number of finches with smaller eggs. The nests of pigeons are so frail and small that the rapid hatching and swift development of the young are at a premium with them. In respect of speed of embryological development, they have evolved far more rapidly than in anatomical structure. Pigeons' eggs, however, are incubated continuously, while few oscinine species sit on the nest more than from sixty to eighty per cent of the day; this may account in part for the unexpectedly rapid development of their embryos.

The influence of taxonomic position upon speed of embryological development may be illustrated by the flycatchers as compared with the tanagers, finches, honeycreepers, and thrushes among which they nest. My nests of the Gray-capped Flycatcher, "Chipsacheery," Lawrence's and Northern Yellow-bellied Elænias, Bran-colored Flycatcher, Berlepsch's Kingbird, and Striped Flycatcher were situated in the same plantations, pastures, dooryard shrubbery and neglected clearings as those of the Northern Gray Tanager, Fanny's and Francisca's Tanagers, Cherrie's Tanager, Flesh-legged Honeycreeper, Mexican Bananaquit, Gray's Thrush, Gray-headed Nightingale-Thrush, and Yellow-green Vireo. Their eggs present the same range in size; their nests are on the average no better concealed and often far more conspicuous; they are just as readily accessible; and the birds themselves, although on the whole more demonstrative when their nests are threatened, are no better equipped to defend them. Yet the incubation periods of these flycatchers are consistently longer than those of the song-birds among which they dwell. Apparently the flycatchers—at least the tropical species—have not been able to speed up the development of their offspring to quite the same extent as many of the song-birds.

For the slow incubation of another group of flycatchers, whose periods are in excess of twenty days, no explanation occurs to me except the ecological. Perhaps the most surprising figures in all the foregoing list are those of the incubation periods of the Colombian Royal Flycatcher, the species of *Myiobius,* and the Fulvous-throated Flycatcher. These small forest flycatchers all build pendent nests, attached to a thin dangling aërial root, the swinging extremity of a vine, or a slender drooping branch. By far the strangest of all these nests is that of the Colombian Royal Flycatcher. The structure bears so little resemblance to any bird's nest of northern lands that I stood a considerable time looking at my first Colombian Royal Flycatcher's nest without suspecting what it was. It was only the bird's interest in the long, dangling mass of vegetable fibers that caused me to investigate further; and even then I did not at once find the eggs. This remarkable nest is, in my experience, invariably suspended from the extremity of some pensile vine or slender branch above a shaded watercourse, sometimes where a man may with difficulty reach it from the bank, but more often quite inaccessible to him. A well-made example is four or five feet long and relatively slender, composed of fibrous roots, thread-like flower stalks of *Myriocarpa,* small epiphytic orchids, fern rhizomes, and other vegetable materials. Somewhere about the middle, the tangled mass is forced apart to form the nest-chamber, which is hardly more than an open niche, so shallow that in a windier spot the eggs would be in great danger of rolling out. The reddish-brown eggs, darker in general tone than any other flycatcher eggs I have seen, are, despite their exposed position, far from conspicuous in their shallow pocket in the brown, fibrous mass.

The next itself, swinging in the free air above the waterway, is a most conspicuous object. Remembering how it had deceived me when first I set eyes upon it, I once supposed that it escaped predators by its failure to suggest a bird's nest of typical form. But I have since seen toucans—those insatiable nest-robbers!—examine these nests with intention, and have little doubt that the egg-eaters along the watercourses where these birds breed know well enough what their nests are. I believe that they escape disastrous visitations, during their long period of occupancy, by being, in fact, inaccessible to snakes, toucans, small mammals, and other predators of the vicinity. The heavy toucan, despite its long bill, is unable to reach the nest-chamber itself while clinging to the supporting vine or twig, and apparently can not secure a foothold among the thin, loose fibers of the nest, which would seem also to afford poor support to a creeping snake. In a more exposed position, this nest would yield a ready prey to the Swallow-tailed Kite (*Elanoides forficatus*), which hovers on wing while extracting its victims; but these long-winged birds seldom forage beneath the crowns of the forest trees. Of course, not every Royal Flycatcher's nest is inaccessible; but one properly placed and constructed seems to be. How else could so conspicuous a structure escape predation during six or seven weeks of occupancy, in an environment so teeming with nest-robbers that even the tiny hammock of the obscurely colored female manakin rarely eludes detection and spoliation? Of five Colombian Royal Flycatchers' nests with eggs or newly hatched nestlings that I have attempted to follow through, four were successful, while the fifth was lost through an ill-starred experiment of my own. Remembering the high mortality of nests in the forested lowlands, this record must be looked upon either as a most unusual coincidence, or as testimony of a higher degree of safety than most nests enjoy.

The pensile nests of the Short-billed Flat-bill, the two species of *Myiobius,* and the Fulvous-throated Flycatcher, are all shorter than those of the Colombian Royal Flycatcher, and far better enclosed. They swing in a clear space beneath the forest more often than above a stream; they are easy to see but hard to reach; and their occupants develop slowly. Since their success appears to depend upon their being out of reach rather than upon escaping detection, those poorly placed—and there are many—would probably be rifled no matter how short the incubation and nestling periods; but if they attain inaccessibility, the length of these periods is of no great consequence. The beautiful, pyriform, moss-covered nests of the Pipromorpha often dangle from a swinging aërial root beside a trunk or cliff; I have found them in general more accessible than those of the preceding species. They seem to rely more largely upon concealing coloration for safety, and often blend with the mossy trunk or bank beside which they hang. The incubation and nestling periods of these birds are slightly shorter than those of the preceding species.

The pensile nests of the Northern Tody-tyrant (Skutch, 1930) swing from a vine or a slender branch in a plantation, a clearing, or above a watercourse. The similar structures of the Slaty-headed Tody-tyrant usually dangle from the end of a vine beneath a thicket. They seem to be, on the average, more accessible than any of the other pensile nests mentioned here save those of the Costa Rican Pipromorpha; and the incubation period of the eggs they shelter is slightly shorter. The remaining flycatchers, with nests of more 'normal' types, have nearly all shorter incubation periods, although a number lay far larger eggs. Even the hole-nesting Noble and Sulphur-bellied Flycatchers hatch their eggs more quickly than the makers of pensile nests. Size for size, the nestling periods of the birds raised in the cup-shaped and oven-shaped nests, and even in holes in trees, are considerably shorter than of those in the pensile structures.

It seems, then, that among flycatchers, the less accessible the nest, the slower the development of the eggs and young it shelters. It is interesting to speculate upon the long incubation periods of these hang-nest flycatchers. Do we have here a survival of the incubation period of the ancestral flycatchers, which has been progressively shortened through natural selection in the species whose nests are more heavily preyed upon? Or, if the pressure to pass quickly through the highly vulnerable stages of egg and nestling has been somewhat diminished by the development of these peculiar nests, have the periods of incubation and nestlinghood secondarily lengthened?

In fairness, it must be recorded that some of these small flycatchers incubate less assiduously than most of their larger relatives, and than the majority of passerine birds. They appear to find it necessary to devote more time to the search for food. A number that I have watched incubated considerably less than sixty per cent of the day—a very poor record. But a Colombian Royal Flycatcher, during six hours of typical weather, sat for 59.9 per cent of the time and hatched her eggs in 22 days; while a Lawrence's Elaenia, during seven hours, sat in her little cup-shaped nest only 52.8 per cent of the time; yet her eggs hatched in fifteen days.

It is undoubtedly true that if we arrange eggs according to their dimensions, from that of the hummingbird to that of the ostrich—which has a volume more than three thousand times as great!—we find a certain rough correlation between their volume and their incubation periods. Considering the tremendous range in size of birds' eggs, the variation in the length of their incubation periods is surprisingly little; the biggest eggs of existing birds take only six or seven times as long to hatch as the smallest. The periods of gestation of mammals, and the times required for the development of plant embryos, show a far greater variability.

In a study of the relation between egg volumes and incubation periods, the first great source of error lies in the computation of the volumes from the conventional egg measurements. We may be skeptical of any single formula that pretends to give the cubic capacity of solids so diverse in geometrical figure as, for example, the highly pyriform egg of the Murre and eggs almost symmetric about their short axis, as those of hummingbirds, certain doves, and the Dendrocolaptidae. Another source of error is the varying degree of development of the young bird when it escapes from the shell. To turn to mammals for a comparison, the period of gestation of the horse, a 'precocial' animal, is two months longer than that of 'altricial' man; but can anyone doubt which develops more rapidly? It seems to me that the relationship between egg-volume and incubation period had best be investigated exhaustively for a single family before we attempt to extend it more widely. In a single family, egg-form, body temperature, and the condition of the young at hatching are more uniform than as between diverse families. We have seen that in the flycatchers, whatever tendency there might exist for the incubation period to vary with the size of the egg is quite overweighed by the other factors we have attempted to analyze. Yet in this family we have given incubation periods for eighteen species. The eggs of the largest for which satisfactory data are available, the Noble Flycatcher, have about 3.5 times the volume of those of the smallest, the Lawrence's Serpophaga. This result is obtained simply by comparing the products of the measurement of the long axis by that of the short axis squared. As Amadon (1943) has shown, most of the proposed formulae for egg-volume may be reduced to $V = kLB^2$, where V is the volume, L the length of the egg, B its greatest width, and k a constant. In a comparison between two eggs, the k cancels out.

The records for the other families show the same lack of correlation between size of egg and length of incubation period. Among the thrushes, the big Gray's Thrush hatches its eggs in one to three days less than the smaller nightingale-thrushes. Among the tanagers, the eggs of species of *Ramphocelus* require less incubation than those of smaller members of the family, as the Fanny's and Silver-throated Tanagers. In the Icteridae, there is little difference in the period of incubation of the big Great-tailed Grackle and the far smaller Yellow-tailed Oriole. Among the finches, however, the largest species, the Costa Rican Atlapetes, has the longest incubation period. In the antbirds, too, the biggest species, the Red-eyed Ant Shrike, has the longest incubation period; but the other species do not follow in the order of their size.

Few families of birds present a greater range in egg-size than the Procellariidae, in which the Fulmar lays eggs of about 8.6 times the volume of those of Leach's Petrel. Worth gives the incubation period of the first as 55 days, of the second as 35 days. But Gross (1935) says of Leach's Petrel: "The longest record that I could obtain of continuous incubation was 42 days, but in all probability incubation endures for at least 50 days."

As usual, when we attempt an investigation of this sort, we find ourselves handicapped by the paucity of authentic, consistent field-data. It is important to remember that contributions such as those of Bergtold, Burns, Worth, the Moreaus, and the present writer, represent the beginning, not the end, of our attempts to understand the incubation periods of birds; and that meanwhile we must preserve an open mind and collect far more records from all parts of the world. When we recall that from tropical Africa and America together, probably less than two hundred incubation periods have been determined, and that many of these determinations rest upon a single nest, we begin to become aware of the immensity of the task that lies before us. That it is not an easy task, no one is more keenly conscious than myself. When we know the incubation periods of two or three thousand species, each one based not upon a single nest but a good number of them, we may theorize with some degree of confidence in our primary data.

When we turn to nestling periods, we find them on the whole less constant for the species than incubation periods; but this seems to be largely because the young birds are often frightened from the nest somewhat prematurely. Yet where external factors, such as the approach of a potential enemy, shaking of the nest, or the like, do not intrude, I believe that the departure of the young bird from the nest is as spontaneous a process as its earlier escape from the shell. While some writers have described various stratagems of parent birds to bring their youngsters into the open, I have witnessed the departure of nestlings of a number of species without seeing any evidence of successful parental pressure to effect this result. Only exceptionally have the old birds seemed to display any eagerness to have their offspring quit the nest—provided, of course, that they did not appear to be in danger. A pair of Fraser's Tityras, after the departure of their first nestling from the old woodpecker hole high in a dead trunk, seemed very eager to have the other two follow. But their efforts to call forth the laggards were quite without effect until the young birds were ripe for departure. The three fledglings flew from their lofty nursery on successive mornings at very nearly the same hour—7:44, 7:08, and 7:48 A. M.—doubtless in the order of their birth.

As Mrs. Nice (1937) found to be true of the Song Sparrow, a small brood does not necessarily leave the nest any sooner than a large one. Yet Moreau (1940) has shown that, with some species at least, a lone nestling may receive considerably more food than a member of a larger family. Since birdlings as they grow older are often so closely packed in the nest that it would seem that the very pressure of their bodies must force some of them into the open, may it not be that the greater amount of room enjoyed by a lone nestling offsets the more rapid development that may possibly result from more abundant feedings? Three broods of the same pair of Panamá House Wrens, which I was careful not to disturb, left the same gourd at the same age—eighteen days—although two consisted of three fledglings, and the third of only one. In my own experience, nestling periods, when determined with due care not to frighten the young birds, show hardly more variability than the incubation periods of the same species. This is clearly shown in the records for Lawrence's Elaenia, Gray-capped Flycatcher, Colombian Royal Flycatcher, Gray-headed Nightingale-Thrush, Gray's Thrush, Orange-bellied Myioborus, Mexican Bananaquit, and Cherrie's Tanager.

It is instructive to compare, as the Moreaus (1940), following Stresemann, have done, the incubation and nestling periods of the same species. On the whole, my results are in accord with theirs. In general, as they point out, the nestling periods of small altricial birds—except hole-nesters and long-winged species like swallows and swifts—are of about the same length as their incubation periods. It is interesting to observe this rule at work among the small flycatchers with pensile nests. Their nestling periods are as unexpectedly long as their incubation periods, and doubtless from the same cause—relative freedom from predation.

Few land birds remain in the nest two or more times as long as they require to hatch. Of those reported upon in this paper, only the Blue-throated Toucanet and the Trujillo Woodpecker have nestling periods so much in excess of their incubation periods. Doubtless the other woodpeckers would fall into this class, were their incubation periods known; and as recorded elsewhere (Skutch, in press), I have reason to believe that the Prong-billed Barbet takes at least four weeks—more than twice as long as its incubation period—to fledge. The Moreaus report the incubation period of an African barbet, *Tricholaema leucomelan,* as fourteen to fifteen days, and its fledging period five weeks. It will be noted that all of these birds nest in deep holes in trees. The young become feathered slowly, then linger in the nest for a long while after they are completely clothed. Why should their incubation period be so accelerated, their nestling period so protracted? Are the eggs subject to serious perils from which the nestlings are relative immune? If so, my studies of these birds have failed to disclose what these dangers are. Among the trogons, the Mexican Trogon, which nests in a shallow niche in a decaying trunk, has a nestling period shorter than the incubation period; while for the Quetzal, which carves a deep hole, the nestling period is less than twice as long as the incubation period.

Birds which nest in burrows in banks, as kingfishers, motmots, jacamars, and some of the swallows and ovenbirds, are, in my experience, of all birds safest from predatory animals. Their nestling periods are long; but their incubation periods are also long. There is not the contrast between the two periods that we meet among woodpeckers, toucans, and barbets.

Nestling periods markedly shorter than the incubation periods are found in the antbirds. For these denizens of the undergrowth of the tropical forest with its thousand perils, swift hatching would seem to be of great value. Yet, notwithstanding that in most species the eggs are kept almost constantly covered by both parents, the embryos develop slowly, as with all Clamatores (Tyranni). Here again, as with the related flycatchers, we find the trait of a taxonomic group persisting in the face of ecological pressure which, theoretically, should cause a change. The young antbirds hatch blind and quite naked, but develop with surprising rapidity. At the age of eight days they are feathered, and on the ninth or tenth day, before they can fly, young Slaty Ant Shrikes, Bridge's Ant Shrikes, and Northern Bush Birds hop from the nest and disperse through the undergrowth. The Long-billed Antwren, another denizen of the forest undergrowth, which in classification has been bandied about between the Formicariidae and the Sylviidae, likewise has a far shorter nestling than incubation period; the youngsters leave their mossy nest before they can fly.

In the present paper, I have not attempted to compare the incubation and nestling periods of tropical American birds with those of their nearest relatives in the temperate portions of the continent. In some instances, the periods appear to be substantially the same; but in others there is evidence of accelerated development of embryos and nestlings at the higher latitudes. This question is now being investigated.

SUMMARY

Difficulties inherent in the determination of the true incubation and nestling periods of birds are discussed. If the nest is inspected only once each day, the visit should be made in the afternoon, since the critical events—laying, hatching, and departure of the young—occur predominantly in the morning. To learn the true nestling period—the age of spontaneous departure—precautions must be taken not to frighten the nestlings; and they should not be removed from the nest for weighing or measurement after they are feathered.

Incubation periods are given for about 90 species of Central American birds, and nestling periods for about 120 species. The great bulk of these data is here published for the first time. Egg-measurements are given for most of the species treated.

The length of the incubation periods appears to be determined by the taxonomic position of the species, the size of the egg, ecological factors such as the dangers to which the nest is exposed, and doubtless other influences as well. The flycatchers which build pendent nests have amazingly long incubation periods, which appear to be correlated with the relative inaccessibility of their eggs. The long incubation periods of flycatchers, as compared with other birds that build nests of the same types in the same habitats and lay eggs of the same size, are cited as an example of the influence of taxonomic position on the rate of embryological development. The birds considered here present only a small range of egg-sizes (about 3.5 to 1 in the Tyrannidae); and whatever influence the volume of the egg may have on the length of the incubation period is completely overshadowed by other factors. Since the amount of actual incubation which eggs receive during the period of diurnal activity varies from 50 to 100 per cent in diverse species, this must not be lost sight of in attempting to analyze the lengths of incubation periods. Above all, it is emphasized that we need far more carefully determined incubation periods from all parts of the world, before we can draw more than tentative conclusions.

If the nestlings are not frightened, their departure from the nest is, with most species studied, as spontaneous as their earlier escape from the shell. The great variability in the recorded nestling periods of a single species is caused in large part by careless practices of the

observer. When the young birds are not disturbed, the nestling period of a species is almost as constant as its incubation period.

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Finca "Los Cusingos"
Quizarrá de Pérez Zeledón
Costa Rica