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HOW THE MALE BIRD DISCOVERS THE NESTLINGS.

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I. INTRODUCTORY.

How soon after the eggs hatch does the male parent bring food to the nestlings? How does he learn that they have hatched? In many species of birds, especially among non-passerine families, the male spends nearly as much, or even more, time on the eggs than the female, and is often in charge of the nest as they hatch. But among the majority of song-birds the male takes no share in incubation, yet he feeds the nestlings. Since he does not maintain such close contact with the nest as his incubating partner, how does he know when to begin? Does she call his attention to his offspring by some special utterance or gesture? Or must he discover their presence by himself? These questions open up fascinating perspectives in avian psychology. To answer them we must give close attention to all that happens at the nest, not only while the eggs are hatching and immediately afterward, but during the preceding days of incubation; for the male's behaviour during these days has much to do with his promptness in bringing food to the new-born nestlings.

It is not necessary to watch many nests, where the female incubates alone, to learn that her mate does not bring food to the nestlings the moment they hatch. He is not, through some mysterious "super-sense", made aware of this important event as soon as it occurs. An appreciable period must elapse before he makes the discovery, which apparently he does through modes of receiving information quite similar to our own. Often the male parent feeds his nestlings within an hour after they escape the shell; but again several hours may elapse, and more rarely a day or even several days. Perhaps the classic example of delay in beginning to feed the nestlings is given by Mrs. Nice (1932), who tells of a Black-throated Green Warbler *Dendroica virens* so busy repeating his song that to all appearances he was unaware of the existence of his three offspring until his attention was drawn to them by the bustle incident on the departure from the nest of the first two, already eight and nine days old. Then he brought food to the one that remained in the nest, treating it as though it were a newly-hatched nestling rather than one nearly fledged. He was so far out of touch with the happenings in his own family that on the following day he brought food to the nest, which the last of the young had already abandoned.

Apparently few bird-watchers have given attention to this phase of nest-life. When I began to make a preliminary survey of the life-histories of Central American birds I purposely avoided watching their nests immediately after the eggs hatched; for I needed first of all to know whether the male took any share in feeding the nestlings, and a statement in Howard's then newly-published 'Introduction to the Study of Bird Behaviour' (1929) made me doubt whether he would often do so before they were several days old. However this may be with northern birds, I have since learned that male Central American birds as a rule begin far more promptly; and with a little patience one may witness the very first feeding of the nestlings by their father. More recently Mrs. Nice (1943) has briefly treated this question in her compendious work on the behaviour of the Song Sparrow and other passerines. Later we shall have occasion to refer in detail to some of the observations and theories she records there.

2. THE MALE BIRD'S PREPARATION FOR THE DISCOVERY.

Before we are ready to understand how the male bird discovers the nestlings we must consider his contacts with the nest while it still contains eggs. The ways in which he may show interest in the nest during this period are:

A. Incubation.
B. Standing guard.
C. Bringing food.
D. Bringing material.
E. Escorting the female to the nest.
F. Visits of inspection to the nest.

It is desirable to study each of these forms of attention in some detail, and learn their bearing upon our problem.

A. *Incubation.*

Among the majority of the birds placed below the Passeriformes in current schemes of classification, the male takes a large share in keeping the eggs warm. Indeed, there exist a great many facts which lend weight to the hypothesis that among primitive birds the male was chiefly, if not entirely, responsible for incubation; that as family bonds became stronger his mate helped him more and more; and that with increasing development of his voice or nuptial adornments he came to give less and less attention to the nest. It is well known that the male Rhea and the male Kiwi alone attend the eggs and young; and there is a good deal of evidence that this is true also of the tinamous.

It is not so generally known that among woodpeckers the male does the larger share of incubation, warming the eggs through the night, and alternating with the female during the day. In a few genera of woodpeckers, as *Tripsurus* and *Picumnus*, both sexes sleep in the nest-hole together; and it is difficult to determine by direct observation which of the pair actually sits on the eggs through the night. But from analogy with the species that sleep alone it seems probable that the male performs this duty, while his mate sleeps clinging to the wall of the chamber above him. In the cuckoo family, the males of both the Groove-billed Ani *Crotophaga sulcirostris* and the Smooth-billed Ani *C. ani* take charge of the nest during the night; and I am told that this is also true of some of the oriental members of the family. The Ringed Kingfisher *Ceryle torquata*, the biggest representative of the family in the Western Hemisphere, has the interesting custom of alternating in the nest-burrow for twenty-four-hour periods, the male covering the eggs one night and day and the female the next—a situation paralleled, so far as I am aware, only by sea-birds such as the Adélie Penguin *Pygoscelis adeliae*, Leach's Petrel *Oceanodroma leucorhoa* and the Manx Shearwater *Puffinus puffinus*, of which male and female occupy the nest continuously for alternate periods, each of which may be of several days' duration (Levick 1914, Gross 1935, Lockley 1942). With the smaller Amazon Kingfisher *Chloroceryle amazona* and Green Kingfisher *C. americana* the females incubate by night; but the males take long sessions on the nest during the day.

The male incubates for many hours during the day in the families of pigeons, trogons, jacamars, puffbirds, motmots, cuckoos, toucans, barbets and some at least of the goatsuckers. Female trogons, pigeons and jacamars regularly incubate by night; but for the other families mentioned (except the anis among the cuckoos), I have not been able to discover whether this duty falls to the male or the female, for the sexes are alike in appearance. Hummingbirds are exceptional among the non-passerine families of the New World in that the males take no interest at all in nest and nestlings. This is associated with their very specialized habits of courtship, the male

of many species singing from a chosen perch, usually in a gathering of others of his kind and sex, throughout the breeding season.

In that large group of peculiarly neotropical passerines variously called the Clamatores or Tyranni, the share taken by the male bird in the breeding activities varies greatly from family to family and even from genus to genus within the same family. Among the ovenbirds and their allies (Furnariidae) equal participation by both sexes in all the duties of the nest seems to be the rule, to which only a single exception has come to my attention—the only nest of the beautiful *Pseudocolaptes boissonneautii* that I have had an opportunity to study was attended by only one parent. Among antbirds (Formicariidae) we have information upon about a dozen species, and no exception is known to the rule of incubation and care of the nestlings by both parents—indeed, the male frequently sits for somewhat longer periods, and is more zealous than his mate in the defense of the nest. In the family of woodhewers (Dendrocolaptidae), males of the genera *Lepidocolaptes* and *Glyphorhynchus* take a large share in incubation and the other activities of the nest; but among the dendrocinclas I have never been able to discover more than a single attendant.

In the huge and exceedingly varied family of tyrant flycatchers (Tyrannidae), the most diverse situations are found, but incubation seems invariably to be carried on by the female alone. Careful studies of many nests belonging to more than thirty of the tropical species of flycatchers* have failed to bring to light a single instance of nest-relief, even when one member of the pair had been marked for more certain identification. Although it is sometimes stated of some of the migratory flycatchers that breed in North America that the male incubates, the most painstaking studies that have come to my attention fail to confirm this. Incubation by the male is certainly most unusual in the family. In the majority of the species that have been studied the male takes his full share in feeding the nestlings and guarding the nest, and in a few species he even helps to build it. With the distinctive Royal Flycatcher *Onychorhynchus mexicanus* the male remains near the nest and in contact with his mate; but at two nests that I studied carefully he failed even to feed the nestlings. Thus this species is intermediate between the more typical Tyrannidae and that small portion of the family exemplified by the genera *Myiobius*, *Oncostoma*, *Terenotriccus*, *Rhynchocyclus*, *Pipromorpha*, and doubtless others, in which the sexes appear to form no lasting bonds, and the male takes no interest at all in the nest. The pipromorphas possess courtship habits closely approaching those of the manakins (Pipridae), among which the males, so far as known, pay no attention to the nest, but confine themselves, like hummingbirds, to sometimes most elaborate procedures for attracting the opposite sex to their courtship assemblages.

* Throughout this paper "flycatchers" are American flycatchers, Tyrannidae, not Muscicapidae.—ED.

Finally, among the cotingas (Cotingidae) the situation closely parallels that which exists among the Tyrannidae. While the male is not known to incubate in any species, he may help to build the nest, as with the Rose-throated Becard *Platypsaris aglaiae*; or he may limit himself to accompanying his mate while she builds and incubates, later helping her to feed the young, as with the tityras, erators, and becards of the genus *Pachyramphus*; or he may take no notice of either nest or offspring, as with the blue cotingas of the genus *Cotinga*. I make bold to predict that male cotingas which, during the breeding season, are found day after day displaying in a single tree-top, as the Costa Rican Bellbird *Procnias tricarunculata* and the snowy cotingas (*Carpodectes*), take no interest in the eggs or young; but, so far as I know, the nests of these birds of the roof of the forest have never been discovered.

Among the song-birds (Oscines), the most common practice is for the male to take no share in incubation, but to help feed and defend the young, and sometimes also to help build the nest. Yet exceptions to this rule will occur to everyone who has given much attention to the ways of birds: familiar examples of incubating male song-birds (Oscines) are the Barn Swallow *Hirundo rustica erythrogaster*, the Rose-breasted Grosbeak *Pheucticus ludovicianus* and some of the vireos. In Central America I have found incubation by the male in only five species: the Blue-and-White Swallow *Pygochelidon cyanoleuca*, the Black-eared Bush-tit *Psaltriparus melanotis*, the Gnatcatcher *Polioptila plumbea*, the Long-billed Antwren *Ramphocaenus rufiventris* (a peculiar bird which systematists have bandied back and forth between the Formicariidae and the Sylviidae), and the Pepper-shrike *Cyclarhis gujanensis*. This is less than ten per cent of the song-birds I have studied while they incubated.

This rapid survey of the parts taken by the sexes in. incubation and feeding the young serves to indicate the groups of birds to which our problem of how the male discovers the nestlings particularly applies. These are practically all passerines, the Tyrannidae and some of the cotingas among the Clamatores, and the great majority of the Oscines or song-birds. A few of the latter, as a few of the flycatchers and apparently all of the manakins, as well as the humming-birds among the non-passerine families, are excluded because the male does not feed the nestlings. Some of the hawks and other non-passerines apparently do present the problem that interests us; but complete studies of their life-histories are lamentably few, and distinguishing the sexes of the living birds is often exceedingly difficult. When both sexes incubate, either may be in charge of the nest when the first egg hatches, and so be the first to become aware of the presence of a nestling. The other partner will, in the ordinary course of events, first come in contact with its offspring when it arrives to take its usual turn on the nest. So these birds need concern us little in our present investigation; yet I have for them a few observations that shed light upon our problem.

Some years ago I happened to be watching a nest of a pair of Bridges' Antshrikes *Thamnophilus bridgesi* on the morning when the first of the two eggs hatched. In this species, as in all other antbirds that have been carefully studied, the sexes alternate on the eggs through the day, the female sitting by night. But when, at 8.48 a.m., the streaked, grey, female antshrike came through the undergrowth of the forest to relieve her black mate, who for the last hour and a half had been sitting in the black, open nest suspended vireo-fashion between the arms of a crotch, he did not stir from his position. After a minute she flew off to give chase to a trespassing Great Antshrike *Taraba major* and did not soon return. The male Bridges' Antshrike had begun to sit restlessly, frequently rising up to look down into the nest. Finally, at 8.56, he picked up the spotted white cap of an eggshell and caried it away. Two minutes later he was back at the nest and promptly removed the large piece of the empty shell. Returning without delay, he rested upon the rim to peer intently into the nest, then settled down to brood. At 9.24 the female antshrike called softly from a near-by point, her mate responding in very low tones from the nest. Five minutes later he made way for her as she approached the nest, calling softly as she flitted from twig to twig. Alighting upon its rim, she passed several minutes in silent contemplation of its contents. Then she jumped down into the cup to brood. But 13 minutes after his departure the black male returned with food. After a five minutes' delay his streaked mate made way for him to give the nestling its first meal, then brood it. Far less eager than her mate to attend the newly hatched birdling, she lingered out of sight for 83 minutes, returning at length with food. This difference in the relative zeal of the two parents, manifest so soon after the first egg hatched, was displayed until the young quitted the nest. During five alternate mornings of the young antshrikes' brief ten-day nest-life, their father fed them 38 times and brooded a total of 702 minutes ; the less attentive mother bird fed 24 times and brooded 484 minutes.

Here there was no indication that the male antshrike communicated to his mate the fact that an egg had hatched. Apparently she had no intimation of the event until she saw the nestling with her own eyes, for she brought no food until after she had brooded it. Had it been possible for the male to inform his mate by voice of what was taking place, he had an excellent opportunity to do so upon her arrival at 8.48. Even if he insisted upon covering the egg while it hatched, he might at least have risen up to give his mate a peep into the nest and let her see what was happening ; but apparently it never occurred to him to do so. The long period between the female antshrike's departure from the nest at 9.47 and her return with food 83 minutes later makes us pause and reflect. We know that she did not bring the food from habit, for we can be sure that she had not fed a nestling for at least three or four weeks, and possibly never before. If we take the view that the bringing of food is an unconscious reaction set in motion by the sight of the nestling, we shall be obliged to account for the long delay in the reaction, since with ordinary luck in hunting insects the bird might have brought one within two or three minutes. Memory, in the currently accepted sense of the word, supplies a far simpler explanation of her behaviour.

While the male antshrike proved himself quite as competent as the female in caring for the newly hatched nestling, this is not true of all species, even those of which the male incubates. In the mountains of Guatemala I watched a nest of the resplendent Mexican Trogon *Trogon mexicanus*. The male had been in the habit of taking a long session on the eggs every afternoon. On the second morning after they hatched he came with a small insect but, instead of delivering it to a nestling, sat holding it stupidly in his bill for nearly an hour while he brooded, and upon his mate's arrival to replace him he flew away, still carrying the insect. A quarter of an hour later he returned with a large grey moth and settled down to brood, holding it inertly in his bill. Ten minutes later, as he was about to leave in response to the summons of his mate, a squirrel noisily rustling the dry leaves in front of the nest delayed his departure, and while hesitating to go it seemed suddenly to occur to him that he had omitted a duty, for he backed up in the nest and placed the morsel in the upturned mouth of a baby trogon. But thrice again during the course of the morning he brought food only to carry it away again after a period of brooding. The female had also brought food five times, and delivered it all in an efficient manner. If her instincts had been no more perfect than his, the nestlings would probably have died of starvation. But the male Mexican Trogon was capable of improvement, and two days later was feeding the nestlings in the normal manner. Lest it be inferred that male trogons are generally incompetent, I may mention a male White-tailed Trogon *Trogon strigilatus* and a male Quetzal *Pharomachrus mocinno*, each of which attended the nestlings unaided for a number of days after the mysterious disappearance of his mate, and brought them safely from the nest. We shall see later that at times male birds which do not incubate seem at a loss to know what to do with the first morsels of food they bring to the neighbourhood of the nest.

B. *Standing guard.*

When the male bird does not incubate, his activities may or may not be co-ordinated with his mate's periods of sitting and taking recess. Many male birds sing and forage in the neighbourhood of the nest without appearing to give much attention to what the female is doing, although doubtless they know very well where she is to be found at any moment. Or the male may go off for long periods and be out of sight and hearing. But many other male birds co-ordinate their movements with those of the incubating female, and this co-ordination takes two contrasting forms :

(i) Standing guard over the nest during the female's recesses.
(ii) Accompanying the female on her recesses.

The habit of standing guard is best developed in big birds, strong enough to defend the nest from prowling enemies. It is only among such birds that standing guard appears to be a constant specific trait rather than a peculiarity of individual males. The males of the two largest jays of Central America, the White-tipped Brown Jay *Psilorhinus mexicanus* and the crested blue Magpie-jay *Calocitta formosa*, regularly bring food to the female while she sits. Often the females of both species receive nourishment from one or more unmated helpers as well, so that they are able to incubate continuously for long periods, taking only brief and infrequent recesses. These are as a rule initiated by the male's arrival with food. After taking it with loud cries (of satisfaction), the female flies off, leaving him resting upon the rim of the nest, or close beside it, until her return fifteen or twenty minutes later. Here he stands merely upon sentinel duty, for he does not normally incubate.

The Boat-billed Flycatcher *Megarhynchus pitangua* is one of the biggest and most powerful members of its multitudinous family. The female builds the nest in a high and sometimes exposed position, fashioning the open cup of long pieces of vine and the wiry roots of epiphytes, while her mate follows her back and forth, often tirelessly carrying a bit of material that he never troubles himself to place on the nest. After the two or three eggs are laid, the female sits upon them until her mate arrives, usually with a loud, cheery cry, to relieve her. Then he stands beside or above the nest while she goes for food, but he never incubates. If a party of nest-robbing toucans appear in the offing he is among the first of the nesting birds to raise the alarm, and with admirable foresight darts off to confront the peril while it is still a long way from the precious nest. Once the young have hatched he promptly brings food, and remains after each feeding to guard them, as he guarded the eggs, without ever warming them, until his mate returns to feed them, and then brood once more.

The male Neotropic Kingbird *Tyrannus melancholicus* keeps s watchful eye over the frail, conspicuously placed nest during his mate's absences from incubating; but since he does not stand so near the nest as the Boat-bill, merely overlooking the whole vicinity from a salient watch-post, with these flycatchers the habit of guarding lacks the military precision of the regularly alternating Boat-bills. I once watched the nest of a pair of tiny Banded Flycatchers *Myiophobus fasciatus*, birds no larger than the Least Flycatcher *Empidonax minimus* of North America, which the male guarded during his mate's absences from the eggs, although what enemy he might have driven away I could not surmise. His deportment was not entirely consistent; yet he lingered close by the low nest in a thicket far more during his mate's recesses than while she was present warming the two eggs. During a good part of the morning there was a definite alternation between the two—the female sitting, then the male coming when she left for food. While in the presence of the nest he passed the time chiefly flitting about among the

bushes close by, snatching up small insects and now and again repeating his delightfully serious little trilled whistle; but sometimes he remained quietly perching upon the branch from which the nest hung, about two feet distant from it, until his mate's return.

Not long ago a pair of Yellow-bellied Elaenias *Elaenia flavogaster* nested in a tree in front of my house in Costa Rica. The male Elaenia stood guard over the low nest during his mate's frequent short recesses, but in a similarly imperfect manner. His arrival to watch the nest often coincided with the female's departure; but he did not often have patience to remain on duty until her return to the eggs. At another nest of this species, built in Guatemala a dozen years earlier, the male neglected to stand guard.

Among small and weak birds guarding the nest is likely to be an individual trait rather than a habit general within the species. One male Orange-billed Nightingale-thrush *Catharus aurantiirostris* came, whenever his mate left the nest, to sing where he could keep an eye upon the mossy cup from a distance of two or three yards; but while she incubated he never tarried long in sight of the nest. Often his approach was the signal for her departure from the eggs, and her return was promptly followed by his withdrawal into the depths of the neighbouring thicket. The alternation in the attendance of these two Nightingale-thrushes was just as regular as with antbirds, woodpeckers and birds of other families of which both sexes incubate, with the difference that the male merely guarded and never covered the eggs. Yet at other nests of this thrush, as also at nests of the Russet-capped Nightingale-thrush *Catharus occidentalis*, I have looked in vain for the male on guard.

In Maryland a male Catbird *Dumetella carolinensis* would come to sing in a hawthorn tree overlooking his mate's nest in the hedge close by whenever she left her three blue eggs, whereas during her attendance he invariably kept himself at a greater distance. Although the Orange-billed Nightingale-thrush did nothing more effective than protest at my intrusion with catbird-like scolds, the Catbird, after the eggs had hatched, would buffet the back of my head whenever I looked into the nest, his mate at the same time fiercely punishing my outstretched hand with her bill and feet.

Among finches, I have known a male Streaked Saltator *Saltator albicollis* to remain close by the nest during the female's recesses, always drifting away on her return. A second male of this species, breeding in the same region, was less methodical in guarding the nest. Mrs. Mickey (1943) likewise found great individual variation in this respect among McCown's Longspurs *Rhynchophanes mccowni*, some males regularly guarding during the female's absence from the nest, and even while she sat; others apparently never doing so.

With hole-nesting birds guard is rarely kept; yet I have known a male Inquisitive Tityra *Tityra inquisitor* who displayed a definite tendency to

guard the nest in an old woodpecker-hole high in a dead tree at the edge of the tropical forest. During 131 minutes while his mate took recess, he rested upon a stub at the top of the nest-tree, or in a living tree close by the nest, for at least 125 minutes. But during 294 minutes while his mate was in the nest he remained in sight only 66 minutes and was absent 228 minutes. This separation of the pair is the more significant when one considers the tityras' strongly developed habit of flying two by two.

C. *Bringing food.*

Some male birds which do not incubate bring a great deal of food to the nest during this period, others only at long intervals bring a morsel to the sitting mate, and the majority nothing at all. With the Magpie-jay, the American Goldfinch *Spinus tristis*, the hornbills of the Old World tropics, and a few other birds, the food brought to the sitting female by her mate—and sometimes by her " helpers " as well—may be sufficient in quantity to make it unnecessary for her to hunt for herself. Thereby she is enabled to incubate almost or quite continuously. While few female birds that incubate alone and must find the bulk of their own nourishment devote more than from 60 to 80 per cent of the daylight period to warming their eggs, these jays and goldfinches incubate from 85 to 95 per cent of the day ; and the female hornbill remains for weeks in the nest-hole, so sealed with clay as to leave an aperture only just large enough for the male to pass in her food. In such cases the bringing of food by the male is obviously important in diminishing, or quite abolishing, the female's periods of absence, during which the eggs are left exposed. We may distinguish such food-bringing as " sustaining ".

But with the majority of species of which the male brings food to his incubating partner the quantity is insufficient to lengthen to an important degree her periods of sitting. We might look upon such food-bringing as merely a pleasant courtesy, of no practical importance; but it also serves the important function of keeping the male bird in close touch with the nest and of forming in him the habit of bringing food in advance of the hatching of the eggs. When the male brings food so rarely, or in such small amounts, that he fails to increase his mate's time on the eggs to more than 80 per cent of the hours of daylight, we may term his habit " occasional food-bringing ".

In a number of instances that have come to my attention it was clear that the male, when he flew to the nest with food, did not intend to feed his mate, but was anticipating the hatching of the nestlings still tightly enclosed within the eggshells. If the female happened to be at hand, and desired the morsel, she received it ; but it was plainly not brought for her. All such cases of carrying food to the nest we may briefly distinguish as " anticipatory food-bringing ". Much occasional food-bringing may in fact be anticipatory; but since we cannot read the bird's mind, and must depend entirely upon objective criteria, we shall hesitate to call it so unless the evidence for such

designation is particularly clear. Let us consider first cases which left no doubt in the watcher's mind that the male bird brought food for his unhatched offspring, rather than for his mate.

It was at a nest of the Pink-headed Warbler *Ergaticus versicolor* in the Guatemalan highlands that I first saw a male bird anticipate the hatching of the nestlings. While I sat in the hide watching the little oven-shaped edifice of pine-needles in which the red female incubated the two white eggs speckled with pale brown, her equally red mate brought a caterpillar and passed it to her through the doorway. A few minutes later she began her recess; and during her absence he came with a small green insect, alighted in the doorway, and murmured in low tones. I was surprised that he should have brought this offering to the nest while the female was away, because a bird usually knows quite well where its mate is to be found. After repeating his soft murmurs in the entrance, he flew to some bushes in front of the nest, where he hopped about, still holding the insect. Soon the female returned and perched near him in the bush. Instead of offering her what he held, as I had anticipated he would do, he preceded her to the nest, where he stood in the doorway, blocking her return, and voicing soft, low notes as before. As soon as he left the way clear, the female returned to her eggs. Then, after hovering a few times in front of the nest, and once alighting on the roof, the male stood on the sill and passed the morsel to her.

Again in the afternoon the male warbler came to the nest while his mate was taking her recess. This time he brought a whole mouthful of insects and acted most queerly. Resting in the doorway, he bent his head into the nest and called in a thin twitter. He could certainly hear the " chip-chip " of his mate, who was hunting insects down the steep hillside; how could he hope to find her on the eggs? He went off a little way, then returned to the nest and twittered again; he repeated this performance five times in all. Meanwhile he answered the calls of his mate, sounding plainly down the slope, yet would not go to her, but persisted in trying to deliver food to the unoccupied nest. When at length the female returned to the eggs, she received the food as before. By this time I was convinced that the male had not brought these insects with the intention of giving them to his mate, but rather in anticipation of the coming of the nestlings, which would not hatch for six days more. Since there was still no nestling to take the food, the female incidentally received it. I saw the male come to the nest with insects four times during the absence of his mate, and only once while she was within. This could hardly have been mere chance, for the female warbler spent more than twice as much time in the nest as away from it.

Among the wood warblers the male regularly feeds the nestlings, but except in a few species it is not usual for him to bring food to his mate while she incubates. At about the same time that I studied the Pink-headed

Warblers I gave attention to two nests of Hartlaub's Warbler *Vermivora superciliosa*, another highland bird that builds its nest on banks and steep slopes. I watched each of these nests for an entire morning while incubation was in progress. The male did not approach the first nest at all, and only once did the male of the second visit his incubating mate. On this occasion he came with an insect in his bill; but upon his approach the female turned her face to the bank and crouched down in the nest. After delaying a minute on the rim the male flew away, still bearing his intended gift. I believe that he also had come in anticipation of the nestlings rather than to feed his mate. The male Buff-rumped Warbler *Basileuterus fulvicauda* gives food to the female during her recesses from her eggs, and also while she incubates, if she will let him. While most of the morsels that he brings seem to be intended for his mate, at times, especially when the eggs are near the point of hatching, he will go to the nest in her absence and murmur soft, sweet notes as he makes movements which suggest that he is trying to feed the nestlings through the unbroken shells.

In Panamá a male Crimson-backed Tanager *Ramphocelus dimidiatus*, whose nest contained only two blue eggs that would not hatch for four days more, brought caterpillars to it while his mate took her recesses, exactly as the Pink-headed Warbler had done. Perching on the rim, he uttered low, continuous, cheeping notes, as though coaxing newly hatched nestlings to take food. He brought insects thrice during ten hours. On only one of his three visits to the nest did he find his mate covering the eggs, and surrendered the morsel to her with apparent reluctance. She seemed in nowise eager to accept the gift, passed it back to him once, or possibly twice, but in the end was persuaded to eat it. It was evident that the male tanager had not in the first place intended this for his mate, and that she was perplexed by the unwonted attention.

During many hours of watching their nests in southern Costa Rica I have thrice seen male Song Tanagers *Ramphocelus passerinii costaricensis* bring food before the eggs hatched—twice at one nest and once at another. Their behaviour was always the same. Each time, as the female returned to her eggs at the end of a recess, the male accompanied her, bearing a morsel in his bill. Preceding her to the nest, he stood on the rim, bent down his head into the cup, and mandibulated the particle of food, continuing this for about a minute, all exactly as though he coaxed very young nestlings to take nourishment. Then he flew off with the morsel, not proffering it to his mate. I have never seen a male Song Tanager feed the female. At one nest she would not even take food from his bill to pass it to the nestlings. If she happened to be brooding when he arrived to feed them she flew off to clear the way for him. But at a second nest the female took the food from her mate and delivered it to the nestlings.

Other male tanagers feed their mates. The Golden-masked Tanager *Tangara nigro-cincta*, the Yellow-browed Tanager *T. chrysophrys*, the

Silver-throated Tanager *T. icterocephala* and the Blue Tanager *Thraupis episcopus* give her food not only while she sits on the eggs, but also while the pair are at a distance from the nest. The male Turquoise-naped Chlorophonia *Chlorophonia occipitalis* regurgitates food for his mate as she is about to enter the nest; but I have not seen him do so while she sits. I have not witnessed any of these elegant little tanagers offer food to the eggs in the manner of the two species of *Ramphocelus*.

Most of these male tanagers feed their mates infrequently at the nest. For the wide-ranging Blue Tanager four times in three hours is the most rapid feeding I have recorded. At another nest of this species the male was accustomed to bring food as he accompanied his mate to her nest after a recess; but since she was not hungry at these times he would either swallow the morsel in her presence or carry it off. One Silver-throated Tanager fed his mate on the nest twice in the course of a morning; another, once in seven hours. A male Yellow-browed Tanager fed twice in three and a half hours. But in addition to these feedings on or near the nest, it is not unlikely that each of these male tanagers gave his mate other morsels while they foraged together at a distance; for in all of these species the male commonly accompanies the female on her recesses. He almost never stays to guard the eggs in her absence.

The tanager family, so large and so amazingly varied in plumage, has led us away from the strict historical sequence in which we began to consider that strange phenomenon of offering food to unhatched eggs. The Pink-headed Warbler was the first, the Crimson-backed Tanager the second, and the Band-tailed Tityra *Tityra semifasciata* the third species in which I witnessed this peculiar behaviour. The male tityra, a nearly white bird with black trimmings on wings and tail and bright red bare cheeks, on rare occasions brings a morsel of food to the old woodpecker hole or natural cavity in a dead tree where his mate is incubating. When he sees that the brownish eggs lie intact upon the litter of dead leaves, he either devours the food on the spot, or else carries it off, doubtless to be swallowed later. He does not offer it to his mate, even if she happen to be perching close by him. Even after the eggs hatch, the male tityra does not, like so many male birds of other kinds, give the food to the female while she broods, to be passed by her to the nestlings. If he finds her in the nest when he arrives with food, he will wait long and patiently upon some near-by stub until in her own good time she flies from the hole, then go to deliver the morsel in person.

Some years ago, while I was visiting a coffee plantation in eastern Costa Rica, a female Black Variable Seedeater *Sporophila aurita corvina* built a filigree nest in a lemon tree before my bedroom window and laid three eggs. Although I spent much time watching this nest, I saw the male bring food to it only twice before the eggs hatched. On one of these occasions the female was sitting, and the male regurgitated his collected grass-seed into her mouth. But on his second visit he found the eggs uncovered and,

perching on the rim, he bent down his head into the frail cup and went through all the motions of feeding nestlings—which were still half-formed embryos enclosed in the mottled shells.

Last May a Variable Seedeater *Sporophila a. aurita* built her delicate cup in the calabash tree in front of the dining-room window and successfully reared her brood of two. In August she refurbished the nest for a second brood. Late one afternoon, before the first egg had been laid, I saw her black-and-white mate come to the nest with grass-seeds conspicuous on his short, thick bill, and apparently more in his throat. Perching on the rim, he lowered his head into the empty cup and gave a pantomime of feeding, just as the Black Variable Seedeater had done. I did not again see him behave so during the course of incubation, but after the eggs hatched he promptly began to feed the nestlings.

One of the characteristics of anticipatory food-bringing is its unpredictability. In species of which the male bird sustains his mate while she incubates, one may expect to see him come with food every day and at every nest. But, like the habit of guarding the nest among small, weak birds, attempting to feed unhatched nestlings appears at times to be an individual peculiarity, not general in the species. During the period of incubation I have watched two other nests of the Variable Seedeater, each for nine hours, without seeing the male bird bring food or even closely approach the nest. Still, with an act of such rare and irregular occurrence as this appears to be among seedeaters, one must be an indefatigable bird-watcher indeed to be able to state with confidence that it does not happen at any particular nest.

Among other Central American finches that bring food to the nest before the eggs hatch are the big, thick-billed saltators. The male Buff-throated Saltator *Saltator maximus* feeds his mate while she builds the nest and at long intervals while she incubates. A male Streaked Saltator *S. albicollis* gave food to his incubating mate twice during the course of nine hours. I have not seen male saltators of either species attempt to feed the eggs.

Of all the male birds that I have seen feed their mates while they incubated none gave them food more frequently than two Ash-coloured Wood Pewees *Myiochanes cinereus*, although the amount of nourishment each delivered to the female was probably far less than that brought by goldfinches and jays in an equal interval. This is the more surprising because these Wood Pewees belong to a family in which the male very rarely feeds his mate—I have never myself witnessed another instance of this in the Tyrannidae, and I know of only five other species in this great group for which it has been reported by others. These are the Crested Flycatcher *Myiarchus crinitus*, Vermilion Flycatcher *Pyrocephalus rubinus*, Wood Pewee *Myiochanes virens*, Least Flycatcher *Empidonax minimus*, and Eastern Phoebe *Sayornis phoebe*—Gillespie (1924), Lack (1940), Bent (1942), MacQueen (1950), De Kiriline (1948 and 1951). (Apparently such feeding is exceptional in some of these five species.) One of my pewees fed his mate at least 12 times in four hours, the other 10 times is an equal period. Usually the female was fed as she sat in the nest, but at times also while she perched in other parts of the little nest-tree. Sometimes the male pewee would bring his mate back to her duty by going to the nest with a big insect. Then she might dart up and reach the little cup almost as soon as he; the food was passed over the eggs as the twain perched on opposite sides of the rim; the male thereupon flitted away, while his mate settled down to incubute—or sometimes perversely darted off again to continue her recess. Despite these feedings, one of the female pewees incubated for only 66·1 per cent of the time, the other 74·8 per cent. Although this is a high degree of constancy for a small flycatcher, it does not appear to be high enough to characterize the male's food-bringing as " sustaining ".

From time to time, while his mate was away, the male pewee would stand on the rim of the nest and look attentively into it as though to see whether the eggs were about to hatch, often continuing his scrutiny for a minute or two. Again he would bring a small insect and lower it into the cup, as though trying to make the unhatched eggs receive it—" anticipating the nestlings ". Once, upon her return to the nest from a recess, the female pewee brought a small insect and behaved in precisely the same manner, singing the while a pretty, low-voiced song, like the warbled part of her mate's dawn-song.

Of the other two female birds that I have known to anticipate the hatching of the nestlings in this manner, one was another flycatcher, the Chipsacheery *Myiozetetes similis*, and she did so by a very narrow margin of time. The first of her two eggs did not hatch, because the embryo was reversed in the shell—its head in the narrow end—and failed to effect its escape. Although it did succeed in perforating the shell, it was unable to rotate in the narrow space and enlarge the breach laterally until it could push off the end of the shell. Small ants entering through the gap it had made in its prison wall killed the birdling. At 8.35 on the day after I had removed the egg containing this dead embryo I entered the hide before the nest. In the shell of the second egg the birdling was on the point of escaping. Returning to the nest six minutes later, the female Chipsacheery brought a whole billful of small insects. For about a minute she stood in the doorway, as though offering them to a nestling, which certainly had not hatched when last she looked into the nest, and apparently had still not escaped the shell, for she settled down to incubate, holding the insects in her bill. Again and again she rose up to look beneath her. Soon she darted out to snatch up another insect and add it to the store in her bill, already bristling with projecting legs and gauzy wings. Then she returned to the nest, stood a few moments in the doorway, and went through the motions of feeding once again, but

was obliged to resume incubation with a full bill. While she sat the insects vanished—I believe into her own stomach. But at 8.59 she flew from the nest, caught another insect, and repeated the motions of feeding in the doorway. This time she seemed to succeed in giving food to the nestling, then flew away. Going now to look into the nest, I found the birdling lying between the halves of the parted shell, as though it had just escaped, to find its first meal already awaiting the first opening of its mouth.

My final example of a female bird which brought food to her nest before the eggs hatched was an Orange-billed Sparrow *Arremon aurantiirostris*, whose nest I watched for $8\frac{1}{2}$ hours on the third day before hatching. Twice during my watch the sparrow returned to her eggs with a particle of food in her thick orange bill. After entering the covered nest she rose from the eggs and lowered her head beneath her, at the same time rapidly uttering many low notes. Then she ate the morsel and settled down to incubate.

Among Central American birds very few instances of males feeding their mates during the period of incubation have come to my notice except those cited above. Among the orioles (Icteridae), a male Melodious Blackbird *Dives dives* brought food to his incubating mate twice in a morning. A male Rufous-browed Wren *Troglodytes rufociliatus* from time to time took a morsel to his mate as she sat on the eggs in a hollow trunk in the Guatemalan highlands. In both of these families it is quite exceptional for the male to feed his mate. When Lack (1940) prepared his survey of courtship feeding he could cite no instances for either orioles or wrens, but since that date a number of cases have come to light for the wrens. The male has been seen to feed his mate in Bewick's Wren *Thryomanes bewickii*, Carolina Wren *Thryothorus ludovicianus*, Winter Wren *Troglodytes troglodytes hiemalis*, and Rock Wren *Salpinctes obsoletus*—Miller (1941), Laskey (1948), Bent (1948). Among birds of which both sexes incubate, jacamars, toucans, kingfishers, motmots and antbirds may give more or less food to their mates during the period of courtship and nest-building ; but once they have settled down to incubate, and the pair are seldom together except for brief meetings when one member replaces the other on the eggs, such feeding rarely or never occurs, and its consideration is beyond our present scope.

Likewise it would lead us too far afield to consider all the examples of feeding at the nest during incubation that have been recorded in the literature. But anticipatory food-bringing has been so rarely witnessed, or so seldom recognized, that a few additional instances may be of value here. Mrs. Nice (1943) summarizes briefly the experience of other birdwatchers ; her first example is of the Song Sparrow *Melospiza melodia* :

" A curious thing happened in 1935 : as I went to visit 204 M's nest at 5.20 p.m., there was 204 M with a grub in his beak; his mate was on the nest,

but no eggs had hatched. Later when I passed by he was there again, examining the eggs. The next morning two had hatched.

" A male California Thrasher (*Toxostoma redivivum*) was seen carrying insects to the nest at the beginning of incubation (Sargent 1940). A male Ovenbird (*Seiurus aurocapillus*), as shown by the itograph record, came to the nest each morning on the 9th, 10th and 11th days of incubation ; on the 12th he was seen bringing food (Hann 1937). A female Chough regurgitated food into the nest and gave the food call $1\frac{3}{4}$ hours before the first egg was pipped and $8\frac{3}{4}$ hours before it hatched (Schifferli and Lang 1940)."

All of the examples we have cited in our discussion of anticipatory food-bringing are not equally clear. So far as we can ever be certain of what is going on in another creature's mind, I am confident that when the Pink-headed Warbler, the Crimson-backed Tanager, the Song Tanagers, the tityra, and at times the Ash-coloured Wood Pewee, brought food to the nest they wished to feed the unhatched nestlings. But the other tanagers, the saltators, the Melodious Blackbird, the Rufous-browed Wren, and others gave no outward indication of any motive in bringing food to the nest other than to feed their mates. But two or three small insects, more or less, during the course of a day can be of no great consequence to a well-fed adult bird ; and in its practical consequences, if not in its motivation, all such occasional feeding is the equivalent of anticipatory food-bringing.

Male birds which neither incubate nor sing profusely appear sometimes to find time hanging heavily during the days when their mates attend the eggs, and seem eager for some activity. Wrens may build extra nests, some of which are used as dormitories. During this period of waiting for the eggs to hatch, male birds may amuse themselves by feeding nestlings of distinct species (Williams 1942, Skutch 1935) ; and yet others attempt prematurely to feed their own. It would be interesting to know whether male birds which have not previously nested behave so, or only those who have already had the experience of feeding nestlings. The Crimson-backed Tanager and the Variable Seedeater who brought food to the nest in anticipation of the nestlings had reared earlier broods in the same season ; but I am not sure about the others. As we have seen, the female bird far more rarely offers food to the unhatched eggs. Her behaviour appears to be more closely controlled by the physiological phase of the reproductive cycle. Other factors, akin to imagination, anticipation, imitation, and learning in ourselves, if not actually the same, come more strongly to the front in the male. With him at least behaviour during the reproductive period is not so automatically regulated by physiological " cycles " as is sometimes held to be true.

D. *Bringing material.*

Many birds that build very bulky or elaborate nests, or those requiring an unusually large number of billfuls of material, continue to add to them until

the eggs hatch. Thus the castle-builders (*Synallaxis*) are continually bringing new materials and tidying up their great castles of sticks. Both sexes share this work; but since the male castle-builder also incubates, this is but one more link with the nest. So also hummingbirds continue to bring downy stuff and cobweb to their little chalices until the nestlings hatch; but this, as everything else connected with the hummingbird's nest, is exclusively the province of the female. The Rose-throated Becards *Platypsaris aglaiae* construct great globe-shaped nests with a small round entrance in the underside, attaching them to some slender swinging branchlet high up in a tree. The female is the architect and chief builder of the bulky edifice, but her mate brings much material to it. During the course of incubation, which is performed by the female alone, both continue to increase the already enormous mass of material by bringing additional leaves, lichens, vines and the like, the female taking many pieces inside, but the male, so far as I have seen, placing all that he brings on the roof, never entering, as he has never entered during the later stages of construction before the eggs were laid. In this fashion he maintains close association with the nest until the time arrives when he brings food instead of building materials.

Even after the eggs have been laid, the Black-eared Bush-tits *Psaltriparus melanotis* of the Guatemalan highlands continue to add downy stuff to the lining of their beautiful lichen-encrusted pouches. Male and female share this labour, as all the other duties of the nest. But in addition to the pair that built it, other, unmated, males may now bring soft down for the inner walls of the nest. Since in this species the black-faced males outnumber the grey-cheeked females by possibly four or six to one, there is always an excess of the former during the breeding season. The male bush-tits that have been taking material to the nest change to food-bringing after the eggs hatch; and at this time still others become voluntary attendants, so that as many as four males and one female may feed the four tiny nestlings. All now take advantage of the warmth afforded by the thick-walled pouch on cold mountain nights.

The feeding of nestlings by these and other unmated or juvenile birds whose assistance is not essential for the successful reproduction of their kind, as well as the impatience of many mated males to begin to nourish their offspring, suggests that when food is abundant birds find this an agreeable occupation. Among practically all monogamous birds—those which regularly pair—the male takes a share in feeding the nestlings. Nest-building by the male is not so widespread, and incubation rarer still. Stated differently, if the male bird takes any active part in the fabrication or care of the nest or its contents, he will feed the young; yet often he will attend the nestlings without having helped to build the nest nor to incubate the eggs. I am familiar with only two birds which pair, yet the male does not regularly feed but only guards the nestlings: the Royal Flycatcher *Onychorhynchus mexicanus* and the Red-winged Blackbird *Agelaius phoeniceus*,

E. *Escorting the female to the nest.*

When the male bird neither incubates nor guards the nest in his mate's absence he very frequently keeps her company during her recesses from the eggs, then flies with her as she returns to resume incubation. Sometimes he also comes to call her from her duty that she may go off and hunt food with him. This behaviour is far more widespread among birds than the habit of standing guard at the nest during the female's absence; instances of it will be familiar to anyone who has watched birds at their nests. It is especially well developed among the American flycatchers and the tanagers, but is found also among cotingas, wrens, mockingbirds, vireos, warblers, finches, American orioles, and other families. Once the female has settled on her eggs the male usually goes off to hunt food or to sing; but he may at times tarry in the vicinity of the nest.

The point at which the male stops short when he accompanies his mate on her return is at a distance from the nest which varies with the species and the individual. A certain White-breasted Blue Mockingbird *Melanotis hypoleucus*, whose nest I watched, almost always escorted his mate as she came back to her blue eggs in the low thicket, but regularly stopped short when still six feet or more from the nest, never going up to it. But a male Yellow-green Vireo *Vireo virescens flavoviridis*, when he saw his mate returning to her nest, would hurry up and stand close beside it while she settled down to warm the eggs in front of him. The female vireo came to associate this act with her return; and once, when her mate flew to the nest while she was near by, but apparently not ready to resume incubation, she darted up to stand beside the nest, too, for a moment; then both flew away. A male Streaked Flycatcher *Myiodynastes maculatus*, whose mate nested in a box I had put up for her in a mango tree, would usually escort her to the tree, sometimes to the doorway of the box, and more rarely would enter with her, when a low, twittered conversation took place within. With most birds the male is most attentive in the early morning, and as the day grows older follows his mate less frequently to the nest.

A Black Phoebe *Sayornis nigricans* behaved in an odd manner that caused me to ponder much. She had plastered her mud-walled nest on a vertical projection from the underside of a huge overhanging boulder beside a mountain torrent in the Costa Rican foothills. As she returned to her two white eggs after a recess, her mate would often hover beneath the rock, facing the nest and a few inches distant from it; or at other times he would stand on the rim while she settled down before him. Since the rocky shore afforded no site for a hide, I watched this nest without my customary concealment. If I sat only ten or twelve yards from the nest, the female phoebe would not return to her eggs unless the male was close by. But if I increased my distance to fifty feet she would settle on her nest in his absence. It appeared that his near presence gave her courage in the face of supposed danger.

Among a few kinds of very small birds of which male and female together build a closed nest with a round doorway in the side, the female's return to her eggs is made the occasion of a spectacular ceremony. I first witnessed this while watching a pair of Bonaparte's Euphonias *Tanagra lauta* at their nest, a little hollow sphere made of bits of vegetation, bound together with cobweb, placed in a cranny in the top of a decaying fence-post. Male and female, returning together, perched in a low bush in front of the narrow round doorway. When the female started toward the nest the male flew close behind her, and appeared to be racing to reach the entrance first. But the female euphonia won by her own length and entered, while her mate swerved aside just in time to avoid striking the post and winged out of sight. The female sat for a while, then took another recess, and when she returned with her mate the thrilling race for the doorway was repeated, with loud whirring of small wings, and the same result as before. When I saw that the greenish female invariably won the race, I began to suspect that the blue-black male did not really try to reach the doorway first, but merely escorted her.

Continued studies of this euphonia, and also of the Yellow-crowned Euphonia *Tanagra luteicapilla* and Tawny-bellied Euphonia *T. imitans*, failed to reveal that the male ever sits upon the eggs, although his habit of racing to the doorway as though he wished to reach it first is common to all three species. The male Costa Rican Turquoise-naped Chlorophonia *Chlorophonia occipitalis* ushers his mate into the mossy nest in precisely the same manner. So, too, do the male Black-crowned Tody Flycatcher *Todirostrum cinereum* and Slate-headed Tody Flycatcher *T. sylvia* escort their mates to the round doorway in the side of their swinging nest. But apart from these three genera, two in the tanager and one in the flycatcher family, I have never seen male birds conduct their mates to the nest in just the same way.

F. *Visits of inspection to the nest.*

Male birds which do not incubate make visits of inspection to the nest, usually at irregular intervals. Perching upon the rim, or in the doorway if it be a closed nest, they bend forward and scrutinize the contents, sometimes remaining in this attitude for a minute or more. When the male stands guard upon the rim, as with White-tipped Brown Jays and sometimes Boat-billed Flycatchers, he enjoys ample opportunity to see what lies within ; but if he keeps watch over the nest from a greater distance he may from time to time advance to its side for a closer inspection. This was true of an Orange-billed Nightingale-thrush and a Streaked Saltator, both of whom regularly kept vigil over the nest from a point several feet away. Even if a bird escort his mate to the nest after the fashion of the euphonias and the tody flycatchers he may have little opportunity to view its contents unless he make more deliberate visits of inspection. As a rule these careful examinations of the contents of the nest are not frequent, and few male birds make them more than

three or four times in the course of a day. More details of this are given in the histories of individual nests in the following section.

Buxton (1950) concluded that with the Redstart *Phoenicurus phoenicurus* the male learns when the nestlings hatch by visits of inspection to the nest-hole.

2. THE MALE BIRD'S DISCOVERY OF THE NESTLINGS.

A. *Methods of study.*

Now that we have considered the male bird's contacts with the nest during the days when his mate is incubating, we are in a better position to understand how he makes the actual discovery that the nestlings have hatched. Most of my records of the events at the nest at and immediately after the hatching of the eggs were made during watches undertaken for this particular purpose ; but on a few occasions the eggs hatched unexpectedly while I was studying the mode of incubation—these were the experiences that simulated my interest in the subject. As a rule only nests particularly well situated for observation were chosen for these studies ; for it is necessary to see clearly what is taking place, and without undue strain upon the eyes. Nearly always the nests were watched from a hide, or from the window of a house, for I wished to be sure that my presence in no way altered the birds' activities. In order to plan the watches to the best advantage it is preferable to study nests in which the eggs were laid on known dates, and of species whose incubation period has been previously determined. Wherever feasible an entire morning was devoted to watching the nest a day or more before the eggs were due to hatch, in order to learn exactly how this particular pair of birds behaved during the period of incubation, and what changes the hatching of the eggs made in their routine. All too often I made these preliminary watches only to lose the eggs before they hatched.

As the expected date of hatching approached, the eggs were examined at intervals to look for the first traces of chipping, for often there is a variation of a day or more in the length of the incubation period in a single species, sometimes caused by differences in the birds' promptness in settling down to serious incubation. This precaution may obviate long watches which fail of their purpose because the eggs do not hatch on the expected date. As a rule the eggs of small song-birds (Oscines) hatch on the morning following the day on which a roughening of the surface of the shell is first detected with the finger-tip. The eggs of some of the flycatchers—particularly the genus *Myiozetetes*—frequently do not hatch until the second day after the first signs of chipping are discernible. With non-passerines the birdling may first chip the shell two, or even three, days before it manages to effect its escape, hammering assiduously during the interval ; but since with most of these species the male, if he feed the nestlings, also incubates the eggs, they do not interest us in our present study. But even with small song-birds abnormal circumstances may lengthen to two or three days the interval between the

first chipping of the shell and the escape of the nestling. A Buff-throated Saltator, whose mother was frequently driven from the nest by a rival of her own species, did not hatch until the third day after I noticed the first chipping of the shell. The incubation period for this egg was 16 days instead of the 13 days normal for the species.

With surprisingly few exceptions, the eggs in the nests selected for these studies hatched—if the hosts of predatory creatures allowed them to hatch—during the night or the forenoon, usually before the middle of the morning. In only a single instance did the first egg in one of the chosen nests hatch during the afternoon, and then the study was abandoned because of an approaching thunderstorm. This hatching in the morning is a most fortunate circumstance, because in the region where most of these studies were made hard afternoon rains are to be expected during the months when the great majority of the birds have their nests (see Skutch 1952).

It is not practicable to determine the exact minute when an egg hatches. To do so one would need to watch it continuously, which would keep the parent from the nest, chill the egg, and so retard its hatching. Too-frequent visits to the nest are to be avoided, for they upset the routine of the parents. While watching from concealment, rather than emerge from hiding and break the continuity of the record, I have often relied upon indirect evidence to tell me when the eggs hatched. Most song-birds remove the shell, either eating it or carrying it away, almost as soon as the nestling is free of it. Flycatchers are sometimes tardy in this matter, leaving the empty shell in the nest for hours ; but the female is usually quite prompt in feeding the newly emerged nestling. Only exceptionally is a nest so favourably situated that one can actually see the eggs as he watches from a hide ; but the eating or carrying away of the shell, or the feeding of the nestlings, can be plainly seen. Accordingly, for the purposes of the present study, I have in most instances taken the time of the removal of the shell, or of the first feeding by the female—whichever came first—as the time of hatching of the egg ; the interval between this visible indication of hatching and the first feeding by the male bird is his delay in beginning to attend the nestlings. If the eggs hatched during the night, this is still the interval that interests us ; for obviously a diurnal bird cannot be expected to see or feed his nestlings during the hours of darkness.

In some of the species studied the sexes are strikingly distinct in plumage, in others they are essentially alike. But even when upon casual examination the sexes would be pronounced similar, long and attentive watching would often reveal differences in the appearance of the male and female which were sufficient to distinguish the two at close range. This failing, the male's song might be depended upon for recognition. In the last resort, sitting in the nest was taken as the distinguishing characteristic of the female when preliminary and subsequent studies had failed to show that the male ever

replaced her. Flycatchers were sometimes marked by letting them rub against a wad of paint-saturated cotton fastened over the nest on the end of a fine stick ; but Oscines are more careful of their personal appearance, and the method usually fails with them. Moreover, it sometimes upsets the routine of the nest.

Before proceeding to study the history of individual nests it will be well to list the ways in which the male bird might conceivably become aware that the nestlings have hatched, that we may keep them in mind as we go. Aside from some " supersense " or telepathic communication for which we lack evidence, these are :—

1. By direct sight of the nestlings.

2. By seeing the female bring food to the nest, or carry away or eat the empty shell, or a dropping.

3. By a vocal communication from the female, or some sign or gesture of intelligence.

4. By hearing the voices of the nestlings, especially as they grow older.

5. By the female's increased desire for food, if he has been in the habit of feeding her.

We must also devote some thought to our criterion for the male's awareness of the nestlings. If he stands upon the rim of the nest and looks attentively in we may be sure that he has seen them. But he may fly over the nest, or rest upon a higher branch, with or without noticing that there are now nestlings instead of eggs ; we must depend upon his subsequent behaviour to inform us whether he has done so. If we are reasonably certain that he has not brought food to the nest during the period of incubation, we may take the first bringing of food as an indication that he has responded to changed conditions at the nest, or to the altered behaviour of his mate, even if he has not previously seen the nestlings. But if he has brought food in any manner while the eggs were unhatched, his first appearance with food after they hatch tells us nothing definite. Yet if he brought food very rarely during the period of incubation, and does so promptly after the eggs hatch, there is good reason to suspect that he was led to do so by some indication of their having hatched.

But if the male parent does not bring food, I believe that we may safely assume, in most of the species considered here, that he has not discovered the nestlings. Since so many male birds, as we have seen, prove in various ways that they are eager to begin feeding, there is no reason to suppose that they would delay this pleasurable activity once the door has been opened to it. In every instance when I have been certain that the male saw the nestlings he has returned promptly with food for them. If he has been taking food to the female while she incubated, he has abruptly increased the frequency of his visits with food after having seen the young birds. Even when, as sometimes happens, several days elapse between the hatching of the eggs and the first

feeding by the male parent, I believe that we may with confidence conclude that he has remained in ignorance of the presence of the nestlings.

B. *Histories of individual nests.*

Yellow-bellied Elaenia *Elaenia flavogaster*.

This little, high-crested, grey flycatcher of open and bushy country builds a shallow, cup-shaped nest, usually placing it in a crotch and decorating it profusely with lichens on the outside. Both sexes share the work of building. The eggs, never more than two in a set, are laid as a rule on alternate days and incubated by the female alone, hatching 15, 16 or rarely 17 days after the last was laid. The particular nest selected for this study was conveniently situated in a calabash tree in front of my house, where it could be watched from the porch. During the course of incubation the male Elaenia guarded frequently, but not consistently, from a perch beside and above the nest, whence he could see into it. The first egg was addled and failed to hatch ; the second did not hatch until 17 days after it was laid, because the female was slow in beginning to incubate and left it uncovered for the first two nights.

The second egg hatched during the night of 1–2 May 1944. When the female flew from the nest at daybreak (5.19 a.m.) on 2 May the nestling's down was nearly dry. At 5.28 the male alighted on a branch above the nest, but remained only a moment, flying off as the female returned to brood. She sat for half an hour, leaving at 5.58. A minute later the male returned to the branch above the nest, whence he guarded ; but the nestling evidently caught his eye, for he went at once to the rim and stood there about 20 seconds, looking intently inside. As he flew off he carried away a white feather from the lining that stuck up above the rim. At 6.05 the female brought the first food, an insect so big that she was obliged to offer it to the nestling for one minute before it vanished—I am not sure that it was not down her own throat. Then she brooded. At 6.08 the male brought a tiny insect and alighted on the rim of the nest. The female neither took the morsel nor rose up to allow him to feed the nestling, so he flew up to a higher branch. At 6.20 the female fed and carried off the cap of the empty shell, and less than a minute later the male fed the nestling for the first time.

The male Elaenia probably did not notice the nestling on his first brief visit to the nest-tree, but he certainly did so on his second visit at 5.59, 40 minutes after his earliest possible opportunity to discover it. He brought food nine minutes later, and it was not his fault that he could not deliver it to the nestling. The female first fed at 6.05, 46 minutes after she became active in the morning. She removed the cap of the shell an hour after she became active. The large part of the empty shell had not been removed by 8.28 when, going to the nest, I found that the unhatched egg had slipped into it, fitting snugly. I separated the two, and seven minutes later the female carried off the shell. The male Elaenia took his full share in feeding and guarding the nestling until it departed the nest at the age of 17 days, but the mother alone brooded it.

Banded Flycatcher *Myiophobus fasciatus*.

This tiny brownish flycatcher lives in low thickets and bushy pastures. The nest, built by the female alone, is an open cup attached between the arms of a slender forked twig in vireo fashion, usually between 4 and 12 feet above the ground, and regularly contains two eggs. The female alone incubates, and they hatch in 17 days. I have already described how the male of one pair kept an irregular guard over the nest during his mate's recesses from incubation. But although he passed much time flitting about, insect-catching and singing, within a yard or two of the nest, and at times rested upon the supporting branch only two feet from it, he did not once during five hours on the fifteenth day of incubation actually go to look into it. His colours were slightly paler than those of his mate, and possibly he was a young, inexperienced bird, nesting for the first time.

When I reached the nest as it was growing light, at 5.45 on the morning of 22 May 1937, I found that the first egg had just hatched, and the shell had not been removed. At 5.47 the mother returned and went through the motions of feeding the nestling ; but the light was still so dim that I could not make sure that she brought food. At 6.12, however, she jumped from the nest, caught a small insect that flew past, and gave it to the nestling. She removed part of the shell at 6.27 and the other part at 6.41. The second egg had hatched by 6.58, and the nestling that came from it already held up its open mouth for food. I watched the nest until 9.51, a period of four hours, during which the female flycatcher fed the nestlings 28 times and brooded them a total of 131 minutes.

The male guarded the nest as he had done two days earlier, flitting all around it, sometimes perching only two feet away, and driving or attempting to drive away small trespassers such as wrens, castle-builders and nightingale-thrushes. But he did not once feed the nestlings ; and I believe that the reason for his neglect was his failure to take notice of them. In spite of his close association with the nest, he never seemed to give attention to its contents, and never went to the rim to look intently in as the male Elaenia did. Meanwhile, during four hours, the female did nothing which I could construe as a deliberate attempt to draw his attention to the nestlings, although she often passed by him bearing food in her bill; but as she delivered this he usually departed, for her return to the nest concluded his period of sentry duty.

I resumed my watch of this nest at 10.25 the following morning. The male was now feeding frequently, having discovered the nestlings between four and 29 hours after the first hatched. Unfortunately I was not present when he made the momentous discovery. During the next hour he fed the nestlings 12 times to the female's nine. Although, considering how close he

remained to the nest, he was amazingly unobservant and slow in taking notice of the nestlings, he did his full duty once he became aware of them. This Banded Flycatcher shows us that the male may guard the nest yet be very tardy in discovering the nestlings unless guarding is supplemented by more deliberate visits of inspection.

Chipsacheery Flycatcher *Myiozetetes similis*.

This big yellow-breasted flycatcher is a familiar bird of clearings and open places over an immense territory. The nest, built by the female alone while her mate rests close by, is a bulky roofed structure with a round doorway in the more exposed side. It is hardly possible for the male to see what the chamber contains without going to the doorway. The two to four eggs are laid at irregular intervals of one to two days, are incubated by the female alone, and hatch in 15 or 16 days.

Nest 1.—This nest was situated in a low tree in the pasture in front of my house and contained four eggs. On 9 and 10 May 1944, three days before the first egg hatched, I watched for 11 hours from a hide. The male Chipsacheery spent much time in the nest-tree, showing a tendency to be there during his mate's absences. Twice while she was away he went to the nest and clung in the doorway, loking in, while he sang the nest-song—a rapid sequence of low, soft notes.

On 13 May, I entered the hide at 5.10 a.m. while the light was still dim. For the next two hours the female Chipsacheery sat almost motionless, while her impatient mate called, with growing urgency, from neighbouring trees. At 7.00 she at last flew out for a belated breakfast, and going to the nest I found that the first egg had hatched, but the birdling was still partly within the shell. At 7.20 the female returned, stood in the doorway looking down at the nestling, and lowered her head two or three times as though feeding, although I could detect nothing in her bill. Then she settled down to brood, but constantly rose up and snuggled down again, in strong contrast to her earlier motionless sitting. At 7.29 she rose up, picked part of the empty shell from beneath her, and flew out with it. Her mate was at the moment close by, but seemed not to notice this. At 7.32 she returned, bringing a tiny insect in the tip of her bill. The nestling did not swallow the morsel, so she resumed brooding, still holding it. From time to time she rose up to offer it again to the little one, and finally, at 7.45, it vanished—the first indubitable meal. At 8·02 she fed again and removed the other part of the empty shell. At 8.14 she carried out another piece of shell, thereby telling me that another egg had hatched.

The male Chipsacheery, although he passed most of his time in the small nest-tree, and often rested very close to the nest, was unaccountably slow in discovering what had happened within. At 8.24, while the female was in the act of feeding, the male, perhaps because he saw her standing in the doorway,

tail outward, in an attitude she did not often maintain while she merely incubated, became interested and alighted on the twig closest in front of the door, where he sang the nest-song. This perch, although only about six inches from the nest, was unfortunately somewhat below it—had it been a little higher we might have a different story to tell. On this occasion the nestling again failed to swallow the morsel, which was rather too big for it. After the female had settled down to brood, still holding the insect conspicuously in her bill, the male hovered for a moment in front of her. He could not see the nestlings, for she was covering them ; and either he failed to notice the insect she held or the sight of it did not convey any meaning to him. He retired to a slightly more distant perch and resumed his endless preening.

Throughout the morning preening, scratching and stretching his wings were the chief occupations of the male Chipsacheery. Apparently he was annoyed by vermin ; for never have I seen a bird preen more assiduously, nor scratch himself more vigorously. Often through the morning he was preening within a few feet of the nest while his mate fed : but his perch was usually behind or to one side of it, where he could hardly see what she was doing ; for the roofed edifice was on an outer branch, its doorway facing out from the tree. But again at 11.03 he came to rest on the twig close in front of and below the doorway, while his mate delivered food, and again he appeared to take an interest in what she did. Still, his lower position made it impossible for him to see the nestlings, and once more he failed to grasp the significance of their mother's attitude while she delivered food. When I left the hide at 11.40, more than four hours after the female had taken the first food to the nestlings, the male had yet brought nothing, and to all appearances did not known that they had hatched. Yet during all this period he had been in constant vocal communication with his mate.

Returning to the hide at 1.05 p.m., I waited nearly half an hour without seeing the male Chipsacheery bring food to the nest. Then, at 1.29, he followed his mate as she returned with food, and alighted on the perch nearest in front of the doorway, singing the nest-song while she fed the nestlings. When she had completed the feeding and settled down to brood, facing outward as always, he rose to hover in front of her. All this was a repetition of his behaviour at 8.24, five hours earlier. But now the female did something I had not previously seen—she opened her mouth as though begging for food, at the same time rising slightly. This last visit to the nest caused an abrupt change in the male's behaviour. Going first to a neighbouring branch, he darted out and caught a tiny insect. Holding this in his bill, he uttered low, soft notes that followed each other more rapidly and led up to the nest-song. Then he went to the nest and passed the morsel through the doorway to his brooding mate, who rose up and placed it in the mouth of one of the nestlings beneath her. This was at 1.34, six hours after the female

brought the first food to the nest, about 6½ hours after the first egg hatched. As though to make up for lost time, he brought six more meals during the next half-hour.

When the male Chipsacheery went to look into the nest at 1.29 p.m. his mate not only opened her mouth to show that she was hungry, but also rose slightly. It is possible that he caught a glimpse of the nestlings beneath her. It is also possible that he heard the slight, rapid peeping they already uttered. But since we have already seen that he was an unobservant Chipsacheery, I think it likely that the most obvious sign is what caught his attention, and that he brought food because his mate had shown him by " begging " that she was hungry. If this be true, he might not have seen the babies until his second subsequent visit to the nest, when the female was absent, and he fed them himself.

The history of this pair shows us that the female bird can be in the closest association with her mate, constantly exchanging calls with him, yet fail for several hours to convey to him the information that the eggs have hatched. The female's act in opening her mouth while her mate looked in the doorway at 1.29 p.m. was the more noteworthy because, in years of association with this and other species of *Myiozetetes*, I have never seen a male feed his mate, and I have never seen this or any other female behave in this fashion on any other occasion. This gesture, so expressive of hunger, certainly seemed to be decisive in starting the male to bring food to the nest ; but we must not attach too much weight to it, because it is not impossible that the male saw or heard the nestlings at the same time. Probably a combination of factors finally " released " the male's food-bringing.

Nest 2.—This Chipsacheery's nest was situated ten feet up in a sour-orange tree not far from the last and contained only two eggs. The female was a very voluble bird, singing her pretty nest-song nearly every time she passed through her doorway at the end of one of her frequent recesses, and often singing or calling out loudly in the midst of a session in the nest. Sometimes, too, she spread her crown-patch while sitting, the generally concealed crest opening up like a scarlet blossom and lighting up the whole interior of the nest. In all of these habits, as well as her far more frequent comings and goings, she contrasted strongly with her more patient and taciturn neighbour in the lower pasture. Her mate, too, behaved very differently from her neighbour's mate. During my nine hours of watching, on the next-to-last and final days of incubation, he did not once visit the nest nor come nearer than the next tree; yet he often exchanged calls with the female.

This is the nest at which the female, as already recounted, brought food before she could have seen the nestling. The embryo in the first egg, developing in an inverted position, pierced the shell without effecting its release, and died or was killed by invading ants. The second nestling successfully hatched at about 8.58 on 31 May 1944 and was fed at

once with the tiny insects its mother had all ready for it. She removed half of the empty shell at 9.45, the other half at 10.19. When the nestling was slow in taking food the mother frequently coaxed it with the feeding-song, a rapid sequence of low notes bearing considerable resemblance to the nest-song, but softer in tone. I never heard this utterance while she incubated, and the nest-song she then so often repeated was now rarely used. This change in the character of the notes issuing from the nest might have told the male that something had happened there; but he came no nearer than a neighbouring guava tree, whence he frequently answered the female.

As late as the morning of 6 June, six days after the nestling hatched, the male had not begun to feed it. But by the morning of 10 June he was feeding regularly, as a Chipsacheery father should. During three hours he brought food 17 times, the female 22 times, making a total of 39 meals, or 13 per hour for the single nestling. Of all the birds I have studied in this connection this father was the slowest in finding his nestling. My surmise is that he finally became aware of its existence through its increasingly loud calls. At this nest I could easily distinguish the female by the permanent curvature her tail had acquired while she sat in the closed chamber; at the first nest of this species the female could, with close scrutiny, be recognized by her slightly darker face.

It is significant that of the two male Chipsacheeries studied, the one who made occasional visits to the nest while it contained eggs began to feed the nestlings about 6½ hours after the first hatched; the other, who was never seen near the nest toward the end of the incubation period, had not begun to feed on the morning of the sixth day after the nestling hatched. It is often possible, by watching the behaviour of the male parent during the period of incubation, to predict with accuracy whether he will be prompt or tardy in beginning to feed the nestlings.

Grey-capped Flycatcher *Myiozetetes granadensis*.

The jolly, noisy Grey-capped Flycatcher closely resembles its relative the Chipsacheery in plumage, but is readily distinguished by its white forehead and, above all, by its loud, usually harsh notes. The nests and eggs of the two species are less readily separated. A bird of each kind will often build close together in the same small tree; and unless the watcher manages to surprise one or the other in her nest—no easy matter with these shy, alert flycatchers—it is generally impossible to decide which nest belongs to which bird. But I have never known two Grey-caps or two Chipsacheeries to build in the same tree. Like her cousin the Chipsacheery, the female Grey-cap builds her domed nest alone, while her mate watches and calls close by. She lays two, three, or seldom four, white, spotted eggs and incubates unaided by the male, hatching her nestlings 16, or rarely 17 or 18, days after the last egg was laid.

Nest 1.—This nest was built in early May 1943 on a low branch of an orange tree in front of the house. The last of the three eggs was laid on 12 May. On the morning of 19 May I watched this nest for six hours from the hide. As she sat on her eggs, the female often hummed her low, somewhat churring nest-song, and frequently shouted at the top of her voice, to be answered by her mate, who passed much of the morning resting in a neighbouring tree. Once during the morning, while the female delayed upon a near-by branch before returning to her nest, the male hovered momentarily in front of the doorway, looking in. On another occasion he flew past the doorway as she entered. But during six hours on 27 May, the last day of incubation, when the eggs were already pipped, the male did not once go directly to the nest, although he continued to rest much in neighbouring trees. Apparently his interest in the nest had waned somewhat during the long, monotonous period of incubation, but he was still in continual vocal contact with his mate, who was as loquacious as ever.

Two eggs hatched during the night of 27–28 May, the third before 7.40 the following morning. Long before sunrise the mother Grey-cap began to feed the nestlings. At first she brought very tiny insects, held within her bill, where I could not see them, so that it was difficult to be sure exactly when the nestlings received their first meal; but I believe it was at 5.19. Soon she was bringing food at brief intervals, and brooding for short periods (less than one to 16 minutes), so that her flights to and from the nest were much more frequent than on the mornings before the eggs hatched. Her happy nest-song, so often repeated during the early hours of the days while she incubated, was now silenced. I did not hear it until 8.29, when she had been feeding the nestlings more than three hours. If she felt added happiness upon the hatching of her nestlings it took other forms of expression; probably her increased activity demanded the energy she had formerly expended in song. As on other mornings, she called loudly and sharply to her mate both while sitting in the nest and after leaving it. I do not believe that these calls were intended to acquaint him with recent events there. To my ear they sounded exactly like her outcries of previous mornings, and the male did not alter his behaviour upon hearing them, nor make any move to indicate that he had been informed of his newly achieved fatherhood.

At 7.52 the female Grey-cap first brought an insect so large that I could detect a portion of it projecting from her bill. Soon after this I heard a new utterance from her. While standing in the doorway, with her back toward me, apparently coaxing a nestling to take food, she delivered what sounded to my ear like a low-voiced version of the male's dawn-song. It seemed an eager, hurried, possibly slightly vexed expostulation to the nestlings who were sluggish in taking their meal. It is significant that it was first voiced after she had begun to bring larger morsels, which the tiny birdlings might experience difficulty in swallowing. I repeatedly heard

this feeding-song during the remainder of the nestlings' first morning. It is in the same class with the low, melodious murmurings that other birds use to coax newly-hatched nestlings to take food—a sort of cradle-song. It was one of the things that led the male to the discovery of the nestlings. But that it was not primarily intended for this purpose I think is obvious from the fact that it was first uttered at least three hours after the eggs hatched, and continued to be repeated, at meal-time, long after the male Grey-cap himself began to bring food to the nestlings—I heard it as late as their sixth day.

During the first three hours of the morning, as during six hours on the preceding day, the male did not once come within two or three yards of the nest. His reawakening of interest in the nest began when I first noticed somewhat larger insects in the female's bill, and first heard the feeding-song. From his perch above the road he could see his mate as she rested upon a bough of a lower guava tree reaching out towards the nest; and doubtless his keen eyes could discern the insect projecting from her bill, as mine with the aid of the field-glasses. He could also hear the feeding-song. Which of his senses, sight or hearing, played the larger part in leading him to the discovery of the nestlings I find it difficult to decide.

At all events, his first display of interest in the nest, on the morning the nestlings hatched, was made at 8.04, one minute after I first heard the feeding-song, and 12 minutes after I first saw food in the female's bill. All that he did on this occasion was to fly rapidly past the doorway of the nest—he could hardly have seen what was within as he darted by. His next show of interest came at 8.16, when his mate, arriving with a fairly big insect that I could plainly distinguish with the naked eye, perched in the guava tree in front of the nest where he could see her—and doubtless also what she held—from his look-out above the road. He flew down to hover above her as she fed the nestlings; but of course the closed nest did not permit him to see what was going on within. Then, after she had flown off, he hovered twice beside the nest and once above it, but not directly in front, where alone he might have seen the nestlings. This was his greatest manifestation of interest in the nest that I had witnessed during 15 hours of watching.

During the next hour the male Grey-cap remained much of the time on a perch directly in front of the nest, where formerly he had never lingered, instead of on his erstwhile favourite bough above the roadway. He was clearly much interested in what was happening at the nest, but not very intelligent in his efforts to solve the mystery. Again and again, while his mate was in the act of delivering food, or immediately after, he hovered in front of the nest or above it, then returned to the perch a few yards in front. Plainly he had lost his former habit of going directly to the doorway to look in; at first he even seemed somewhat doubtful as to its exact location. But at last, at 9.26, after hovering before the doorway, he alighted upon the door-sill, perhaps in imitation of his mate, who had so many times rested there,

feeding the nestlings, in his presence. Clinging here, back outward, he delayed long enough for a close examination of the babies within. His response to the sight of them was immediate and unhesitating. Going to a nearby tree, he darted out to snatch up the first suitable small insect that winged by, mashed it in his bill as is proper for newly hatched nestlings, and within two minutes was back to feed one of them, singing a snatch of the nest-song in a low voice as he did so.

We have dwelt in so much detail upon the male Grey-cap's slowly achieved discovery of his offspring because his behaviour contrasts so sharply with that of nearly all the other birds we shall consider. Nearly all have, whether early or late, become aware of their nestlings at a single stroke. The Grey-cap, more than any other bird I have watched, seemed to be laboriously striving to solve a mystery. The habits he had formed during the period of incubation helped lead him to the discovery of the nestlings, but were not adequate to do this promptly. He was plainly led to awareness of the nestlings by his interest in the strange new things his mate began to do and say after they hatched. He must be a wiser man than I who would attempt to decide whether the sight of food in his mate's bill, or the sound of the feeding-song, called up visions of nestlings in the male flycatcher's mind, or merely roused his curiosity as to what change had taken place at the nest where, for 16 days, hour had followed hour with monotonous uniformity. There is no evidence that the female tried to acquaint her mate with the fact that the eggs had hatched, by means of a vocal communication used for this end alone; and it is questionable whether the feeding-song, now first heard, was more important than the food visible in her bill, or her attitude in clinging in the doorway as she fed, in leading her mate to the great discovery.

Nest 2.—This nest was built the following year in a lemon tree a few yards distant from the orange tree that held the foregoing nest, and probably belonged to the same pair of birds. The female Grey-cap, if the same, was just as noisy as she had been a year earlier, singing and shouting in her nest through much of the day. The male's favourite perch was now the orange tree where last year's nest had been. Here he had the entire crown of the lemon tree between himself and the present nest, and could not see it. Probably this circumstance accounts for his more tardy discovery of the nestlings.

During six hours on the final day of incubation, when the eggs were already pipped, the male did not once come close to the nest, although he called to his mate and was answered by her. The first egg was infertile and did not hatch. The second—in the order of laying—hatched during the night of 25–26 May; I first saw the nestling when the female flew from the nest at 5.18 the following morning. She possibly fed the nestling at 5.44, and certainly at 5.48. I first heard the feeding-song, delivered in a

very low voice, at 5.59—earlier than at the previous nest. I do not know exactly when the third egg hatched; but the down of the nestling that came from it was already becoming fluffy when, at 8.31, I next left the hide to look into the nest. On neither of the two years was the female flycatcher seen to eat or intentionally remove any part of a shell. Some of the pieces became entangled in her plumage and were inadvertently carried out as she flew from the nest; one worked up under a wing, annoyed her, and was thrown through the doorway by a flick of the wing. Yet the shells of both eggs had disappeared from the nest by noon of the day after they hatched; and since only the parts of a single shell were found on the grass below the nest, those of the other shell may have been tardily carried away. Other Grey-caps have been fairly prompt in removing the empty shells.

As I had expected, the male Grey-cap was slow in beginning to feed his offspring. At 8.49 the female brought a morsel bigger than any I had previously seen and gave the feeding-song somewhat loudly. The male heard this at his favourite perch in the orange tree and flew at once to the lemon tree, where I had seldom seen him. But he did not actually look into the nest, soon went off, and subsequent repetitions of the feeding-song, even when he was within hearing, did not stir his interest afresh. Six hours after the female flew from the nest at dawn, revealing that an egg had hatched, the male Grey-cap had not fed nor even seen the nestlings. But at 1.30 p.m. on the following day he brought a billful of insects to them. Still, he was feeding very slowly, bringing only two meals in as many hours, while the female fed the nestlings seven times. I am not sure what led him to the discovery of the nestlings; but since the feeding-song seemed most to arouse his interest, probably it was this. In the preceding season the feeding-song appeared to be one of the things which led to his seeing, and then feeding, the nestlings.

Sulphury Flatbill *Tolmomyias sulphurescens*.

My observations on this little olive-green bird of second-growth woodlands and the forest's edge are by no means so complete as I should like them; but they seem worth recording here because they introduce us to the problem of how the male finds the nestlings in a structure so well enclosed that he cannot possibly see them unless he enters, yet he does not enter during the period of incubation. The female alone builds the nest, a fabric composed wholly of black fibrous materials, shaped very much like an old-fashioned chemist's retort, hung from a slender vine or twig with the spout-like entrance tube pointing straight downward. The two or three eggs rest in the part that corresponds to the bulb of the retort. The female alone incubates them. During six hours of watching at one nest I failed to see the male enter, although he lingered much in its vicinity. Unfortunately for the completeness of my study this nest was inaccessible. I could not

learn by direct inspection when the eggs hatched; but by 17 May 1940 the female was taking in small insects and brooding. On this morning I twice saw the male approach the nest, holding a small insect in his bill, once while his mate was brooding within, once during her absence. Each time he lingered close beside the nest for a few minutes, holding the insect, then carried it off. Such behaviour confirmed my earlier conclusion that he had not been in the habit of entering for inspection. As with the male Mexican Trogon, his instinct to feed the nestlings was only partially developed, and it was necessary to complete it by learning. My inference was that he had seen the female with food in her bill and was imitating her; but it is possible to think of other explanations of his conduct.

Four days later, this male Sulphury Flatbill was not only bringing food but also delivering it to the nestlings in their well-enclosed swinging cradle. By now their weak cries reached me as I sat on the bank of the river six or seven yards away. Possibly these cries were the added stimulus needed to make their father enter the nest with food he had already been in the habit of bringing to its neighbourhood. Possibly, also, continued observation of his mate completed his education. These seem the two most probable explanations. I believe that in this instance we can safely exclude direct sight as the mode of discovering the nestlings.

Rose-throated Becard *Platypsaris aglaiae*.

With this cotinga the situation is much the same as with the Sulphury Flatbill. The nest is a bulky, roughly globular affair, about a foot in diameter, with very thick walls composed of dead vines, leaves, lichens, moss, wool—in fact, almost anything the birds can find to increase its bulk. It is generally hung high up at the end of some drooping branch so slender that a squirrel could hardly reach it. The entrance is a narrow orifice at one side of the bottom. The blackish, rose-throated male is distinguished at a glance from his brown mate. Both sexes build the nest; but at one structure to which I devoted a good deal of attention the male placed all of his material on the outside; the female alone entered to attend to the lining. During 20 hours of watching while the female incubated I never once saw the male go into the nest, although he continued to bring pieces of lichen and other material and place them on the roof.

Of course it was impossible to learn exactly when the eggs hatched. But on the afternoon of 13 June 1933 the female becard was regularly bringing leaves or fibrous material when she returned to resume incubation; while on the morning of 15 June she brought tiny morsels of food instead of building material, thereby plainly telling me that an important change had taken place within the inaccessible nest. At this time the dark grey male was also taking food into the nest (once a caterpillar too big for the nestlings to swallow), so that he learned about his offspring fairly promptly—

within a day and a half of their birth at most. Since he seemed never to enter the nest while it contained eggs, either the sight of his mate carrying insects in her bill or the nestlings' cries seeping through the thick walls of their swinging cradle must have made him aware of their arrival. Possibly one or the other of these things, or both together, first aroused his curiosity and led him to make a preliminary visit of inspection to the interior of the nest (which must have been so dark that he could see little), after which he brought food. But it is not likely that, as so often happens with birds whose nests are open, his first intimation of the presence of the nestlings was obtained by seeing them, without any preliminary excitation.

White-winged Becard *Pachyramphus polychropterus*.

With the White-winged Becard the problem of how the male discovers the nestlings is equally challenging and equally difficult to resolve. The globular nest is only slightly less bulky than that of the Rose-throated Becard, but it is placed in a fork, generally high in a tree-top, instead of swinging at the end of a twig, and the entrance is in the side rather than in the bottom. The male neither builds nor incubates, nor have I seen him make visits of inspection to the interior of the nest, yet he feeds the nestlings. How does he learn that they have hatched? Observations at one nest showed that he may delay many hours in beginning to bring food; but unfortunately the nest was destroyed by a toucan or other predatory creature before I could complete my study of it.

At another nest the eggs hatched between the afternoon of 29 June and 15.00 on 30 June. The male becard was feeding the nestlings early on the morning of 2 July, at first going to the doorway with considerable hesitancy, but soon delivering the food as efficiently as his mate. Thus he was bringing food about two days after the nestlings hatched. Yet during the course of incubation I had watched this nest for ten hours without seeing the male go to it a single time.

Highland Wood Wren *Henicorhina leucophrys*.

These little wrens dwell in the undergrowth of the mossy, dripping, mountain rain-forests in the subtropical zone. Their thin-walled, nearly spherical nest is entered through a wide, downwardly directed doorway; it is situated in the undergrowth of the forest, or in a bush overhanging the bank beside a mountain trail. Both sexes build; but the two white eggs are incubated by the female alone, as with all other wrens for which we have information. They hatch after 19 or 20 days of incubation.

On 2 and 3 June 1938 I devoted nine hours to watching a nest that held two eggs within four days of hatching. The male did not once come near the nest, but he sang in the forest down the mountain-side; and while she sat on the eggs his mate sang in response to him. The first egg hatched during

the afternoon of 6 June. On the following morning I watched the nest from 6.20 to 9.40 without finding evidence that the male wren had yet begun to bring food. As with nearly all members of the family, the sexes of the Wood Wren are alike in appearance; but I hoped to see him come while his mate brooded. Once, however, a wren which I took to be the male came with food, hopped through the bushes near the nest, then carried off the morsel.

The second egg hatched during the afternoon of 7 June or the following night. On 8 June I watched the nest from 10 to 11 a.m., and thrice saw the male wren bring food and pass it to his mate as she brooded the nestlings. Since he had not been in the habit of making visits of inspection to the nest, what led him to discover the nestlings? I believe it was seeing his mate carry food to the nest.

Catbird *Dumetella carolinensis.*

Once, in Maryland, I removed a newly hatched Cowbird *Molothrus ater* from the nest of a Kentucky Warbler *Oporornis formosus* and placed it in the nest of a Catbird with three eggs still two days from hatching, without removing any of the Catbird's eggs. This was the nest which the male Catbird regularly guarded during his mate's recesses from a hawthorn tree growing about a yard away (page 9). The female promptly returned and alighted on the rim, where she lingered for about two minutes, looking silently down into the nest with its strange occupant, and often lowering her head into the hollow. This was unwonted behaviour (usually she settled promptly on the eggs), but otherwise she gave no sign of surprise by either voice or gesture; and after her prolonged scrunity she settled down to brood the eggs and the nestling so different in appearance from those which would hatch from them. After brooding for four minutes she departed, returned after a minute, sat a minute, then went off once more. Nine minutes later she returned with empty bill, but at once flew off again, and soon returned with some small object almost concealed within her bill. She delivered this to the Cowbird nestling, then sat down to brood, but continually rose up to look beneath her breast. This vacillating behaviour, so different from the business-like procedure of the Gray's Thrushes, Bridges' Antshrikes and other birds at the time their proper nestlings appeared, may have been the result of the confusion and uncertainty arising from the sudden presence of a nestling, without her preparation for the event, by feeling and seeing the hatching of an egg.

At the moment when the female Catbird brought the first morsel to the young Cowbird, her mate, having come as usual to the hawthorn when she went off to hunt food, was resting where he could see the nest from a point well above it and not over two yards distant. Ten minutes later she again fed the Cowbird in the presence of her mate. She brought food twice more; and then at last the male came and gave a grub to the nestling, three-quarters

of an hour after I had placed it in the nest. He had not within this period come within a yard or more of the nest. Whether or not he would have noticed the cowbird nestling itself from this distance it is impossible to decide; but he could hardly have escaped seeing his mate feed it. In this instance, also, the male parent discovered the presence of the nestling with his own eyes. It is of interest that the first food he brought was a white grub about half an inch long, while the female always came with tiny morsels appropriate for a newly hatched nestling.

This experiment suggests an approach to the problem different from that I have followed in all other instances. Instead of waiting for the eggs to hatch in their own good time, the observer might economize his own time by placing a strange nestling in the nest at whatever hour was most convenient to him. The record just given suggests that the course of events might be somewhat different from that attending the hatching of the birds' own eggs; still, this procedure might teach us much about the male bird's manner of discovering the nestlings, and how long he takes to do it. Nearly all of my own studies have been made in regions where birds with the habits of cowbirds and cuckoos breed sparingly or not at all; and one hesitates to rob feathered parents of their own proper nestlings.

(TO BE CONCLUDED IN JULY.)