THE QUESTION OF TEN-DAY INCUBATION PERIODS

BY MARGARET MORSE NICE

The eggs of a number of birds have been reported as hatching in ten days or even less. These short incubation periods are reported in two connections. One is the baffling method of some authors of counting incubation from the laying of the last egg to the hatching of the first egg—the so-called Kurzbrutdauer, which Swanberg (1950:65) rightly calls "meaningless." The other is the genuine belief in a particularly rapid development of the embryo in the species in question. It is the latter question that I propose to discuss here.

First, we must have a definition of incubation period. Here we may well follow Swanberg (1950:75) who adopts Heinroth's (1922) rule: By incubation period is understood the time which, with regular, uninterrupted incubation of a newly laid egg, elapses until the young has left the egg. In nature this can be checked by counting the time from the laying of the last egg to the hatching of the last egg, when all eggs hatch. This criterion is used by Moreau (1940), Nice (1937a), Skutch (1945), Sutter (1946), and many others.

A firm conviction has existed that little birds must have short incubation periods. Yet before the 19th century I can find no published statement of an incubation period shorter than 11 days. Audubon (1831:251) seems to have been the first to report a ten-day incubation period and this was for the Ruby-throated Hummingbird, Archilochus colubris: "Ten days are required for their hatching. . . . In one week the young are ready to fly, but are fed by the parents for another week." The male feeds his mate and "hurries the Bluebird and the Martin to their boxes . . . all these proofs of the sincerity, fidelity, and courage, with which the male assures his mate of the care he will take of her while sitting on her nest." It is clear that the whole story was spun out of his head; the male does not feed the female or the young; he takes no interest in her nesting; she incubates for 16 days; the young are fledged in 21 to 24 days (Kendeigh, 1952). Audubon's misstatements concerning incubation and fledging periods were incorporated into Nuttall's volume (1832) and appeared without change in the 1840 edition and also in "The Popular Handbook," edited by Chamberlain that came out in various editions from 1891 to 1919. Audubon's figure of ten days was given by Evans (1891) and copied by Bergtold (1917).

Others believed hummingbirds must have even shorter periods. A. E. Brehm (1861:262) suggested that "Hummingbirds perhaps need hardly eight days." Gentry (1876, 1882) stated that the female Ruby-throat incubates

eight days, the young leave at eleven days, both parents build the nest, and both feed the young.

The first European bird to be credited with a ten-day incubation period appears to have been the Wren, Troglodytes troglodytes. In 1841, Yarrell wrote, "The young are hatched after about ten days' incubation, during which time the male feeds the female" (1841:176–177); both statements are incorrect. This abbreviated period appears in the lists of Davy (1863:750) and Owen (1866:257). Evans (1891) quotes Yarrell and Owen, while Arrigoni degli Oddi (1902:48; 1904:130) gives Evans as his authority. The European Wren really incubates for 14 to 16 days (Niethammer, 1937; Witherby, et al., 1938).

It is not only very small birds that have been said to hatch in short order. One of Gigliogli's (1890:187) correspondents assigned eight days to the Cirl Bunting, Emberiza cirlus, both European kinglets, Regulus, and four of the Sylviidae, birds that really incubate 12 to 16 days. The same correspondent also gave 10 days for 20 passerine species and 10 to 12 instead of 18 (Heinroth, 1922) for the European Quail, Coturnix coturnix. (In the same volumes other correspondents gave ridiculously long incubation periods for many of these same birds.) Even seven day incubation periods have been reported in this country: White-eyed Vireo, Vireo griseus (Dugmore, 1900), and Hutton's Vireo, Vireo huttoni (Wheelock, 1904); seven days is about half the actual period in these species.

Ten day incubation periods were given for 7 species by Gentry (1876), for 15 North American species by Burns (1915), and for 28 species (half of them from Burns) of birds of the world by Bergtold (1917). Groebbels (1937) gives a few among the two thousand or so of the incubation periods he quotes. Kendeigh (1952: table 51), in summarizing incubation periods of 107 families, gives none. Nowadays it is chiefly our sparrows and warblers that are supposed to develop so quickly.

It would be wearisome to deal with many of these guesses, most of them on species that have been found to incubate from 11 to 14 days or longer. Most of these records have something uncertain about them, usually some assumption as to the start or finish of incubation. This is true of Skead's (1952) ten-day incubation periods of the Bronzed Cuckoo, Chrysococcyx caprius, and of Gross' (1921) and Crabb's (1923) ten days for the Dickcissel, Spiza americana, while Bowdish (1906) does not state whether all five eggs of his Blue-winged Warbler, Vermivora pinus, hatched. In some cases, although the dates published plainly give eleven days between the laying and hatching of the last egg, the authors say incubation lasted ten days; examples are: Robert's Yellow Warbler, Dendroica petechia (1932:210), Dubois' Horned Lark, Eremophila alpestris (1935:58), and Wright's Blue-winged

Warbler (1909)—"ten or eleven days," interpreted by Bergtold as 10-14 days. Skutch (1945) said the Ruddy Quail-dove, *Oreopeleia montana*, hatched in ten days but later (1949) found it to be over eleven.

With two non-passerine species there are records which appear to be well-authenticated cases of ten day incubation periods. In his intensive study of the development of the Great Spotted Woodpecker, Dendrocopos major, Bussmann (1946:146) recorded six eggs laid April 26 to May 1; four young hatched May 10, and the last two were out by 10 a.m. May 11. Spencer (1943:14) observed 10 and 11 day incubation periods in nests of the Blackbilled Cuckoo, Coccyzus erythropthalmus. A nest with one egg was found July 2, additional eggs were laid July 3 and 6, the last hatching July 16. The other nest also contained one egg when found July 7; other eggs were laid July 8 and 10, the second egg of the set hatching July 19.

Woodpeckers are well-known to have short incubation periods (Heinroth, 1922), hatching in a slightly less developed state than most altricial nestlings. The Black-billed Cuckoo egg that hatched in ten days was laid three days after the previous egg; it may have been retained in the oviduct for an extra 24 hours and thus have been at a more advanced stage when laid than the egg that hatched at 11 days.

It is neither a woodpecker nor a cuckoo, however, that is the most famous example of a reputed ten-day incubation period. Two passerines vie for the distinction of holding the record for "the shortest incubation period of any bird"—the White-eye and the Cowbird.

INCUBATION PERIOD OF Zosterops

White-eyes or Silver-eyes, of the family Zosteropidae, are small birds, four to five inches in length. The family, comprising one genus and 80 species, is widely distributed throughout Africa, southern Asia, Australasia, and many islands of the Pacific. White-eyes have long been cited as having the shortest incubation period of any birds—nine to ten days. We find this statement in books and articles from New Zealand and Australia to England, France, Germany, and North America.

What is the basis of this belief? Its source is a statement by Buller in his "History of the Birds of New Zealand" (1887–8, 1:86) in regard to Zosterops caerulescens (=lateralis)—a bird self-introduced from Australia—"Mr. Potts informs me that, in Canterbury, this species begins nesting early in October. In one instance, within his observation, the birds commenced incubation on October 16, the young were hatched on October 25, and left the nest on November 4." We are not told when the nest was found nor when the eggs were laid.

This supposed nine-day period might well have passed unnoticed, as so many statements, bad and good, have been, had it not been for William Evans, who published an important and influential review of incubation periods in *The Ibis* in 1891. He said: "The shortest period I have seen recorded is that of the tiny New Zealand Zosterops caerulescens, namely 9 to 10 days, as given by Buller on the authority of Mr. Potts, evidently a careful and systematic observer" (this characterization of Potts being quoted from Buller).

This 9-10 day period was included in Gadow's (1891) resumé of Evans' table. Campbell (1901) in "Nests and eggs of Australian birds" noted that "Mr. Potts observes that incubation in the case of the White Eye lasts about ten days." Bergtold (1917) quoted 9-10 days from Evans and 10 days from Campbell.

A ten day incubation for Zosterops received support from reported experiences in some aviaries. Perreau (1911) wrote that "incubation lasted ten days" with his pair of the Indian White-eye, Z. palpebrosa, but gave no details. Page (1911) gave June 27 as the date of finding the nest of his pair of the same species with its full complement of three eggs which hatched ten days later: "I regret that my data are somewhat modified by the fact that the birds had commenced to incubate, but I think it may be safely assumed that they had but just begun their incubatory duties when the nest was discovered." He reported the same event in another journal (1912a), saying his data were "somewhat doubtful." Bergtold quoted from Page's book (1912b) the period of 10-11 days for Zosterops palpebrosa.

The African White-eye, Z. virens, bred in Lovell-Keay's (1915) aviary. The date of laying of the first egg is given, but not the date of hatching: "The incubation period is almost exactly 10 days, certainly not more, as I watched the hen feeding 11 days after the first egg was laid." Neunzig (1921:130) gave the incubation period of the Cape White-eye, Z. capensis, as 10 days, but with no details or authority. Note that the only aviculturist who gave the date of hatching was not sure of the date of laying.

To return to the Antipodes, Oliver (1930) stated that the period of incubation of Z. lateralis in New Zealand "as observed by Mr. Wilkinson of Kapiti Island is ten days," and this was reiterated by Mrs. Wilkinson in 1931. Serventy and Whittell (1948) wrote in regard to the Silver-eye, Z. australasiae, "Incubation takes 9 to 10 days"; in 1951 they say "9 to 12 days." The nine to ten-day period for Zosterops has been quoted far and wide. To give only two examples: Baerg (1941) tells us, "The shortest period on record is nine days, for the Silver-eye of Africa," while Grassé (1950:614) writes "Zosterops furnishes us with the lowest figure with ten days."

Zosterops is a widely distributed genus, abundant in some places. What careful studies have been carried out on its nesting?

Schmitt (1931) bred Z. japonica simplex in his aviary in Hungary. The birds attempted seven nestings in three years, the eggs hatched in five cases. Many details are given of behavior and development. Schmitt says, "After eleven days the naked young hatched."

In New Zealand, Fleming (1943) made a study of the Silver-eye based on color-banding. He watched two nests. "In one case the time from the appearance of the last egg of three to the hatching of the last chick was 11 days (\pm 12 hours): in another clutch of two eggs the same period was 12 days (\pm 12 hours). In the former instance each egg had 10 days' incubation, and the two oldest hatched a day before the third."

Mr. Fleming kindly looked up his original notes and wrote me (June 3, 1952) that in the "Swing" nest the eggs were laid October 12-14, two young hatched October 24 and the third October 25. In the "Eugenia" nest the eggs were laid October 29 and 30 and both hatched November 11. "I think that the period for the 'Swing' pair is 11 days, not 10 as published, and for the 'Eugenia' nest 12 days. Please use these data and correct my misstatement. It would always pay to publish actual data!"

Mr. Robert Stidolph of Masterton, New Zealand, gave me an important record from the notes of Mrs. Wilkinson on a nest watched by her after her 1931 paper had been published. She made daily visits to it from November 20, 1931; the three eggs were laid November 23, 24, and 25; on December 5 no eggs were hatched, but on the 6th there were two young. One egg did not hatch. This gives a minimum period of eleven days.

As to Australia, Dr. Serventy wrote me on June 28, 1952: "The incubation period of Zosterops australasiae in our book appears to be an error. The only definite records which I can personally give are 12 days."

After I had traced the course of the nine to ten-day tradition for Zosterops as outlined above, I received very interesting information from Mr. W. R. B. Oliver of Wellington, New Zealand. He quoted two statements made by Thomas Henry Potts himself. In 1870 Potts published an account of a newly finished nest of Zosterops lateralis found December 4, which he visited daily: "On the 8th it contained three eggs; the next day a fourth egg was laid; on the 19th one callow nestling was exhibiting its ugliness. . . . The day following his ugliness had a companion." The other two eggs did not hatch. Mr. Oliver comments: "This account shows that the minimum incubation period is 11 days. And if the eggs laid presumably on the 5th and 6th were the ones that hatched, the incubation period would be 13 days."

Strangely enough, in 1884, Potts wrote that in this species, "Incubation lasts about ten days." Between 1870 and 1884 he must have found the nest

that started all the trouble; he assumed that incubation had just begun and evidently had forgotten his own daily observations on the first nest.

So here in four nests of the New Zealand Silver-eye recorded from 1870 to 1943 and in five nests of Z. japonica simplex, incubation was found to last at least 11 days, and in Z. australasiae, 12 days. The original nine day period was based on a guess as to when incubation started and the same was true of the ten day period reported by Page in his aviary. Perreau's and Lovell-Keay's statements appear to be of the same character. Mr. Oliver (personal letter) in his new edition of "New Zealand Birds" is "giving eleven days, occasionally twelve, as the time taken to incubate the eggs of the Silver-eye."

INCUBATION PERIOD OF THE COWBIRD

The tradition of the ten day incubation period of *Molothrus ater*, like that of Zosterops, is traceable to two sources, both ambiguous. Alexander Wilson (1810:145) was the first ornithologist to publish on the parasitic habit of the species; he observed it himself and had been told "in a vague way, that the Cowbird laid in other birds' nests. . . . From twelve to fourteen days is the usual time of incubation with our small birds; but although I cannot exactly fix the precise period requisite for the egg of the Cow Bunting, I think I can say almost positively, that it is a day or two less than the shortest of the above-mentioned species!" He quotes from the experiences of his friend, Dr. Nathaniel Potter of Baltimore, who tried to determine the incubation period, but the two nests he was watching came to grief. In his third attempt, "Being obliged to leave home, I could not ascertain precisely when the process of incubation commenced, but from my reckoning, I think the egg of the Cowbird must have been hatched in nine or ten days from the commencement of incubation. . . . I ought to acknowledge here, that in none of these instances could I ascertain exactly the time required to hatch the Cowbird's eggs" (p. 158). All this was repeated in each edition up to the last in 1879, but I can find no quotations of this presumed nine to ten day incubation period.

In the meantime Audubon (1831:497) had given the incubation period as "nearly a fortnight," although he also said, "In every case the Cow Bird's egg is the first hatched." This period was quoted by Evans (1891) and by Bergtold (1917) who attributed it not to its original source but to Evans; otherwise it appears to have been ignored.

The next year Nuttall (1832:192) wrote: "the young of the Cow-bird, I believe, appears about the 12th or 13th day of sitting," and this was reprinted until 1919. I cannot find that this guess made any more impression than Wilson's shorter and Audubon's longer guesses. I have not found the subject mentioned in any other 19th century book until Bendire.

Bendire evidently was the main source of the ten day belief, as he was of so many of our statements as to length of incubation. Whether he was influenced by Wilson we cannot say; he very seldom mentioned sources for any of his assertions. In "The Cow-birds" (1895a) he said that the egg "usually hatches in from ten to eleven days." He quoted M. A. White of Matthews, Virginia: "It was on the 9th of June, 1891, that I placed a fresh egg of the Cowbird in the nest of a Chipping Sparrow containing two of her own that had an advance of one and a half day's incubation. About the 19th Mr. Cowbird emerged from his prison walls, large and vigorous. A day later a little sparrow came forth from his delicate shell." The same story is repeated verbatim in Bendire's "Life Histories of North American Birds" (1895b:438). There are two ambiguities here. We do not know when the Cowbird's egg was laid; the "fresh" egg might have already been incubated for a day or two. And why "about [italics mine] the 19th"? All in all, a shaky foundation on which to base a categorical assertion.

Many books now began to give the incubation period of the Cowbird as ten days, although no one cited evidence or even any authority. Coues had given no incubation period for this species in his first four editions from 1872 to 1892, but in his fifth in 1903 he said 10 or 11 days. Knight (1908) gave 10 days, Eaton (1914) "about ten," Burns (1915) 10, Forbush (1927) 10-12, Roberts (1932) 10, and Chapman, who from 1897 to 1912 had not mentioned the matter, wrote in 1932 "ten days, about the shortest period of any of our passerine birds."

Unfortunately Friedmann accepted the consensus of opinion. He even wrote a paper (1927) on "A case of apparently adaptive acceleration of embryonic growth in birds," giving the incubation periods of the South American cowbirds as $11\frac{1}{2}$ to 13 days, but of *Molothrus ater* as 10 to $10\frac{1}{2}$ days. "No bird in the world is known to have a shorter incubation period; few have one as short." In his book, "The Cowbirds," (1929:187) he says, "The incubation period of the Cowbird is ten days, about the shortest of any of our passerine birds."

All this time collectors were collecting sets with Cowbird eggs, while other observers regularly removed the abhorred object. Friedmann (1929:305) wrote of "the great number of bird-students and bird-lovers who invariably, and not without some reason, throw out Cowbird eggs when they find them." This "enemy [that is, the egg-removers] also affects nestling Cowbirds and in regions where nature study is commonly indulged in, this class of enemies is of no small importance as a check upon the species." No one thought of verifying the accepted incubation period.

The first instance of leaving a Cowbird's egg alone and reporting when it hatched since the days of Dr. Potter and Mr. White seems to have occurred

at the Iowa Lakeside Laboratory on Lake Okobojii in 1917. On June 27, Nelle E. Shaver (1918) who was studying under Dr. T. C. Stephens, found a nest of the Maryland Yellow-throat, *Geothlypis trichas*, containing three eggs of the host and one of a Cowbird. The nest was visited daily and on July 8 the Cowbird was hatched and on July 9 two of the Yellow-throats were hatched. This gives an incubation period of at least eleven days for the Cowbird. No one seemed to notice that it was longer than it should have been. Eleven years later Hoffman (1929) reported a Cowbird egg in the nest of a Song Sparrow, *Melospiza melodia*, hatching in twelve days, the host eggs hatching in thirteen.

Up to this time I had been one of the Cowbird-egg-removers, but when I started my study of Song Sparrows, I realized that I should not interfere. To my astonishment I found the Cowbird never hatched in ten days. I first published my observations in 1933, saying that with the Song Sparrow as host Cowbird eggs hatched in slightly over eleven or twelve days, occasionally more, never less (p. 594). Four years later (1937a:153) I wrote: "It has long been believed that the one respect in which Molothrus ater ater was specialized was that of a short incubation period—'only 10 days.' "With the Song Sparrow as host Cowbird eggs hatched as follows: 5 eggs in 11 days, 9 in 12, 3 in 13, and 2 in 14, an average for the 19 of 12.1 days. Twice again (1937b, 1939) I crusaded against the myth of the Cowbird's ten-day incubation period.

Packard (1936) found on May 25 two Cowbird and four Black-capped Chickadee, Parus atricapillus, eggs in a nest box; on June 6 the Cowbirds hatched, on June 8 two chickadees, making a twelve day incubation period for the Cowbird. In his detailed study of the Ovenbird, Seiurus aurocapillus, Hann (1937:204) found "that the incubation period of Cowbird's eggs ranged from approximately 11.1 days to 11.8 days, with an average of 11.6, which is 0.6 of a day less than the average for the Ovenbird's eggs." Dr. Hann writes me that these averages are based on 15 Cowbird eggs. Finally, Norris (1947:95) in his study of Cowbirds with a variety of hosts writes: "I have recorded the incubation period accurately for only 10 eggs, but none of these hatched in 10 days. Five hatched in 11 days, one in 11.5 days, one in 12 days, two in 12.5 days, and one in 13 days. This gives an average of 11.6 days, exactly Hann's figure."

Thus, between 1918 and 1947 47 records of 11 to 12 day (and occasionally longer) incubation periods were published for this species, yet still the fable goes on. I have also received 15 unpublished records: 12 days in a Cardinal, Richmondena cardinalis, nest (Amelia Laskey), 11 days, 22 hours, 36 minutes in a House Sparrow, Passer domesticus, nest (W. E. Schantz), four 11 and three 12 day periods in Indigo Bunting, Passerina cyanea, Song Sparrow,

and Bobolink, *Dolichonyx oryzivorus*, nests (John L. George), and four of 11 days, one of 11-12, and one of 13 in Yellow-throat nests (P. B. Hofslund). Let us hope that these 62 observations of 11 days or more, and not a single one of 10 days, will make some impression.

Does the Cowbird's incubation period show any adaptation to parasitism? *Molothrus ater* and the Shining Cowbird, *Molothrus bonariensis*, (Friedmann, 1929:89) have similar periods—11 to 12 days. As to other icterids, at least two have equally short periods: Tricolored Red-wing, *Agelaius tricolor*, 11 days (Emlen, 1941:216), and Red-winged Blackbird, *Agelaius phoeniceus*, 11 days in twelve cases, 12 days in two cases, as reported to me by Edwin Willis of Baltimore, Maryland. I think we can answer our question in the negative.

DISCUSSION

Thomas Henry Potts was an important ornithologist, called by Buller a "careful and systematic observer" and by Oliver (1930) "one of the truest naturalists New Zealand has had the good fortune to possess." Major Charles Bendire was a distinguished ornithologist, a founder of the American Ornithologists' Union, and Honorary Curator of the Department of Oology in the United States National Museum. The words of these men carried weight. People thought they were safe in believing such eminent authorities and the reported ten day incubation periods for Zosterops and the Cowbird were copied throughout the world.

Ten day incubation periods should not be lightly assumed; any such report should be accompanied with fullest detail and be scrutinized with extreme care. Very occasionally an egg may be retained for 12 to 24 hours in the oviduct (Sutter, 1946). Hoffman (1929) caught a Cowbird that appeared to be egg-bound and kept her over night; next morning he found two eggs in the cage. One of these eggs would have had an extra day of development before it was laid, and, if immediately incubated, might conceivably have hatched in ten days.

Let Zosterops and the Cowbird be a lesson to us. Leaders in ornithology must be especially careful of their pronouncements, for they have a heavy responsibility. And the rest of us must leaven our respect with a measure of skepticism. Instead of accepting everything in print we must demand the evidence and weigh it, and ourselves observe and experiment. Remember Louis Agassiz's precept: Study Nature, not books.

SUMMARY

Incubation period can best be determined by counting the time from the laying of the last egg to its hatching.

Audubon in 1831 appears to have been the first ornithologist to assign a ten day incubation period to any bird. Since then many such assertions—and even of shorter periods—have been made both in the Old and New worlds, but authenticated incubation periods of less than 11 days prove to be rare.

Zosterops, the White-eye or Silver-eye, has attained world-wide fame for the shortest period of any bird—9 to 10 days. This rumor started in a careless observation in New Zealand in the 1880's. In eleven or more nests that have been carefully watched from 1870 to 1943 the incubation period lasted 11 to 12 days.

For sixty years Cowbird eggs have been stated to hatch in ten days—"about the shortest period of any of our passerine birds." This myth was started through a guess by a friend of Major Bendire and was generally accepted, although no good evidence was ever produced. From 1918 to 1952 there have been 62 cases reported of Cowbird eggs hatching in 11 to 12 days and not one case in ten days.

The unquestioned acceptance of these blunders for 60 to 80 years clearly shows that we need greater care in observation and less reliance on the printed word.

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