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PROBLEMS OF INCUBATION PERIODS IN NORTH AMERICAN BIRDS

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Considerable confusion exists in North America on the subject of incubation periods in birds. There is little agreement on definition of the period and many writers seem to have no appreciation of the biological processes involved in incubation. All too many people are content to copy a figure for the incubation period out of a book or article that gives no indication of how this figure was determined, even in cases where it is strikingly inconsistent with the periods established for close relatives of the species in question. Too short periods are usually attributed to hawks and owls, as well as to some shorebirds, rails, terns, hummingbirds, and cowbirds, and too long periods are often attributed to woodpeckers, cuckoos, and some passerines.

Now that a handbook of North American birds is in preparation, it is time to make a thorough investigation of this fundamental subject and to trace the sources from which incubation periods in North America are quoted. Where these can be shown to have been based on guess, clearly they should be discarded. My searching on this subject has been carried out chiefly in the Chicago Natural History Museum and the John Crerar Library. I am much indebted to Louise de Kiriline Lawrence for suggestions on the manuscript.

DEFINITION OF INCUBATION PERIOD

What do we mean by incubation period? In some cases it has been considered the time the parent sits on the eggs. In some it is reckoned from the laying of the first egg of the set until its hatching, in others from the laying of the last egg to the hatching of the first, and in still others no explanation is offered as to what is meant.

In his interesting paper on this subject, Swanberg (1950) points out that it has been known for two centuries that pigeons may sit on the first egg without applying warmth to it (Moore, 1735). He quotes Ryves (1943) as follows: "Incubation . . . is the operation by which the eggs are subjected to the requisite temperature to permit their development." Swanberg then concludes (p. 75) that for the sake of uniformity we ought to adopt and remember Heinroth's (1922) rules: 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 it is generally possible to ascertain the incubation period with satisfactory exactitude by checking the time from the laying of the last egg to the hatching of the last young. To this I will add the qualification, when all eggs hatch.

These criteria are used by Nice (1937), Moreau and Moreau (1940), Skutch (1945), Sutter (1946), Löhrl (1951), and many others. As a rule this method gives the shortest normal incubation period, as the development of the embryo in the last egg continues without the interruptions to which the earlier eggs are subjected, as pointed out by Raspail (1903), Heinroth (1922:174), Kaufman (1938) and Peitzmeier (1953). On the other hand, Sutter quotes Noll (1924) as saying that in grebes and rails the last egg is sometimes neglected and thus takes longer to hatch than the others. It is well known that psychological factors can influence egg laying; in the presence of unfavorable circumstances the bird can retain the egg for some time in the lower part of the oviduct, a fact that has become of special biological significance in parasitic cuckoos (Stresemann, 1927–34:259). A Cowbird (*Molothrus ater*), confined overnight, had laid two eggs by morning (Hoffman, 1929). In such a case in the wild, the first egg might conceivably hatch in 10 days instead of the 11 to 12 days observed in the 62 well authenticated instances I have been able to find for this species (Nice, 1953*a*). Patterson (1910) found that in hens an egg may be delayed 20 hours; Sutter mentions delays of 12 to 24 hours.

The incubation period can be shortened slightly, from 6 to 12 hours, in the incubator, according to Heinroth (1922:175). It can be considerably prolonged through the occasional postponement of the start of incubation (Ryves, 1946), through interruptions due to irregular attendance by the parent, and through inclement weather. Yet to include such aberrant figures merely confuses the picture. What we need to know is "normal" incubation and this may vary a day or more according to season, weather and attentiveness of the sitting bird.

A very interesting table is given by Richdale (1952:65) in which the "normal" incubation time of the Royal Albatross (*Diomedea epomorpha*) is shown to last from 77 to 81 days (5.2 per cent variation), in Black-footed (*D. nigripes*) and Laysan (*D. immutabilis*) albatrosses, from 63 to 67 days (6.4 and 8.1 per cent variation), but in the Yellow-eyed Penguin (*Megadyptes antipodes*) it apparently lasts from 40 to 50 days (25 per cent variation). The albatrosses, perhaps due to the presence of Skuas (*Catharacta lonnbergi*), "sit tightly on their eggs from the moment of laying," while the penquins whose eggs are usually placed under thick vegetation, away from danger from Skuas, "may not sit tightly for some days after the second egg is laid," that is, the start of steady incubation may be considerably delayed.

Several observers have reported on the effects of season and air temperatures on the length of incubation. In 24 nests of the Phoebe (*Sayornis phoebe*) in Iowa, incubation averaged 17 days in the first broods, but 15.5 days in the second (Sherman, 1952:99). European Wrens (*Troglodytes troglodytes*) in Holland averaged 17.5 days on their eggs in April, 16.3 in May, 15.2 in June, and 14.5 in July; early in the season the female has to spend more time finding food for herself than later (Kluijver *et al.*, 1940). Eggs in 10 nests of the House Wren (*Troglodytes aëdon*) hatched in 14 days with an average air temperature of 72°F. (22.2°C.), whereas 13 hatched in 15 days with an average temperature of 60°F. (20°C.) (Kendeigh, 1952:43-44). Four nests of the Chipping Sparrow (*Spizella passerina*) in warm weather averaged 11 days' incubation, whereas five nests in cool weather averaged 12.3 days (Walkinshaw, 1952).

HISTORY OF INCUBATION PERIODS IN THE OLD WORLD

The tendency, still found in many writers, to ascribe too short incubation periods to birds of prey and too long periods to some other species, is traceable to Aristotle. About 350 B.C. he wrote in Book IV, chapter 6, of his Historia Animalium: "The eagle broods for about thirty days. The hatching period is the same for the larger birds, such as the goose and the great bustard; for the middle-sized birds it extends over about twenty days, as in the case of the kite and the hawk" (Thompson, 1910).

Aristotle assumed that all large birds would approximate the domestic goose in length of incubation and middle-sized birds match the hen. In reality the Golden Eagle (*Aquila chrysaëtos*), as well as many other eagles, incubates for 45 days, and the Great Bustard (*Otis tarda*) for about 25. Kites incubate for about 30 days and hawks from 28 to 35 (see Nice, 1953*b* and in press).

Aristotle's guesses were quoted as definite facts by Pliny in the first century A.D., and, with the exception of Frederick II of Hohenstaufen, by all the major writers on birds in the Middle Ages and Renaissance—Albertus Magnus (about 1260), Gesner (1555), Aldrovandi (1599) and Jonston (1657); they were also given by Buffon in the late eighteenth century. Thus the "Aristotelian age in incubation periods" lasted for more than 20 centuries.

In 1742 Zorn published 15 incubation periods of garden birds; some of these must have been based on observation. From 1791 to 1805 two other German ornithologists, J. M. Bechstein and J. A. Naumann, assigned incubation periods, based on the principle of size, for practically all the birds of middle Europe. Too short incubation periods were given to birds of prey, shorebirds, terns, gulls and others, and too long periods to some ducks, pigeons and passerines.

Tiedemann (1810–1814) copied Bechstein; this list was reprinted in the Ibis in 1891 by Evans, and part of it was used by Bergtold (1917) in America; at least one of Tiedemann's short periods (Least Tern, *Sterna albifrons*) was used in this country in 1949 (see table 2). J. F. Naumann in his Naturgeschichte der Vögel Deutschlands (1820–44) presented the same assumed periods as had his father; these volumes had an immense influence in Europe and Great Britain and set the pattern for reports of incubation periods for most of the books written in these countries in the nineteenth century. Their figures are still appearing in some popular works in Germany—Naumann (1905), Brehm (1922–26), Friderich (1923).

The first great investigator of this subject was the Scotch naturalist William Evans. In 1891 and 1892 he published incubation periods of 81 species determined by himself largely through the use of the incubator. He also included in a separate column figures given by others starting with Tiedemann. In his discussion he emphasized some of the worst errors that had prevailed in respect to the Charadriiformes and the Falconiformes, and he pointed out that the latter and owls "incubate for more or less protracted periods" (1891:91). Evans's work stimulated British ornithologists to rely on observation rather than faith. In the pages of the journals The Zoologist and its successor British Birds, there appeared many lists of incubation and fledging periods based on watching birds, while The British Bird Book (Kirkman, *et al.*, 1911–13) and The Practical Handbook of British Birds (Witherby *et al.*, 1920–24) plainly confessed ignorance in regard to many incubation periods. The admirable Handbook of British Birds (Witherby *et al.*, 1938–41) presented incubation periods that are nearly all trustworthy.

The second great investigator in this field was the distinguished German zoologist Oskar Heinroth. In 1908 he published incubation periods of some 80 species whose eggs he had hatched in the incubator. In 1922 appeared his great paper on "Relations between bird-weight, egg-weight, clutch-weight and length of incubation." In this, besides giving weights of 438 females and their eggs, he presented 100 incubation periods determined in the incubator, and he also formulated fundamental principles underlying incubation. Fifteen years later Groebbels (1937) brought out his second volume on Der Vogel in which he summarized nesting data for some 2000 species. For American birds he relied chiefly upon Bendire. In the meantime German ornithologists had been carefully studying their birds, especially hawks and owls; Niethammer's Handbuch der deutschen Vogelkunde (1937–42) presents incubation periods that with few exceptions are reliable.

In recent books on the birds of Sweden (Svärdson and Durango, 1950, and Durango, 1952) and on those of France, Switzerland and Belgium (Géroudet and Robert, 1940; Géroudet, 1942, 1946) the incubation periods are almost all trustworthy. For tropical Africa Moreau and Moreau (1940) published a list, based on their own experience, of incubation periods determined for some 45 species. In New Zealand Richdale has made fine contributions on breeding biology, including observations on a great many incubation periods, of albatrosses, petrels and penguins. Although faulty incubation periods are still current in some popular books in Germany, so far as ornithologists are concerned, statements on this subject in Great Britain and northern Europe are on the whole satisfactory.

THE NEW WORLD

For a long time bird students in North America were too busy describing birds and their more conspicuous habits to spend time on careful life history studies. They possessed the same background as ornithologists in the Old World; indeed, Wilson, Audubon, Nuttall, Bendire and many others grew up across the Atlantic. It is no wonder they shared the firm conviction, handed down through the ages, of too short incubation periods for many birds.

Before Bendire

Alexander Wilson (1809–14) mentioned very few incubation periods: 12 to 14 days for "our small birds," 14 days for the Mockingbird (*Mimus polyglottos*), and a guess by his friend Dr. Potter, that the Cowbird (*Molothrus ater*) hatches in 9 to 10 days. Audubon (1831) gave free reign to his fancy in his tales of bird habits. He seems to have been the first author to assign 10 days as the incubation period of any bird, namely to the Ruby-throated Hummingbird (*Archilochus colubris*) (see Nice, 1953*a*). Evans (1891) quoted thirteen of his periods, five of which were reasonable, but most of the others were too short. All of these were copied by Bergtold and three have plagued us until the present, as shown in tables 1 and 2.

Very few incubation periods appear in the next forty years. Nuttall (1832) adopted Audubon's fabulous account of the Ruby-throated Hummingbird, but suggested that the Cowbird hatches on the 12th day. Turner (1886) followed Old World tradition as to length of incubation of gulls and terns, giving 21 days for the Glaucous Gull (*Larus hyperboreus*), despite Faber's (1825–26) record of 27 to 28 days, and 17 days for the Arctic Tern (*Sterna paradisaea*) and Aleutian Tern (*Sterna aleutica*).

The first American to provide a large number of birds with incubation periods was Gentry (1876, 1882). As he considered that incubation was a most wearisome task for both parent and chick, he compassionately made it short—8 to 10 days for various small birds, 15 to 16 for the Sparrow Hawk (*Falco sparverius*), 16 to 17 for the Sharp-shinned Hawk (*Accipiter striatus*), 18 for the Cooper Hawk (*Accipiter cooperi*), 20 to 21 for the Redtail (*Buteo jamaicensis*), 15 for the Screech Owl (*Otus asio*), 17 to 18 for the Barred Owl (*Strix varia*), 21 for the Great Horned Owl (*Bubo virginianus*), and 24 for the Barn Owl (*Tyto alba*). All in all, his figures seem as ridiculous to us as his flowery descriptions of behavior and his long lists of scientific names of the animal and vegetable food of each species which were much the same for each bird, merely arranged in varying order. But, although these learned-looking lists deceived some people for 50 years (see McAtee, 1912; Zimmer, 1926:239), the incubation periods fortunately were largely ignored except by some of his contemporaries. Even they considered his hawk figures too low, except for the longest, the 21 days for the Redtail. Warren (1888) called Gentry a "close observer and facile writer."

It is evident that at this time in America, as across the sea, people still agreed with Aristotle about the length of incubation in Falconiformes. In 1878 William Wood stated that Red-tailed and Red-shouldered (*Buteo lineatus*) hawks incubate about three weeks, the Broadwing (*Buteo platypterus*) "probably three weeks," and the Golden Eagle 30 days. In 1882, however, he wrote that he had made these statements "on the assertions of my collectors. Some oologists are very positive that hawks incubate 18 to 22 days." In the meantime he had become doubtful and he did a revolutionary thing: ten years before the publication of Evans's paper, he put hawks' eggs under sitting hens.

This appears to be the first instance reported of experimenting to find out the length of incubation of any wild species, except for the unsuccessful attempts of Zorn (1742). When two Red-shouldered Hawk eggs had not hatched after 27 days, Dr. Wood opened them and found two birds "evidently just ready to hatch." His Cooper Hawk eggs were chilled through the accidental shutting out of the hen after 26 days; they proved to be "well-developed." The Marsh Hawks (*Circus cyaneus*) "had cracked the shell on the thirtieth day but were unable to extricate themselves." This early scientist concluded: "I am satisfied that the period of incubation of our Hawks is from twenty-eight to thirty days."

Wood planned to continue his experiments and asked for help. "I have made arrangements this coming season to test the matter with an incubator. If those interested in this subject will send me fresh eggs of our Rapacia, I hope to be able to settle this question." Apparently no oologist could bear to give up an egg, for no further contributions on this subject appeared.

Carpenter in 1882 reported observations of about 27 days' incubation for Red-shouldered and Cooper hawks. In 1883 he found Long-eared and Barred owls hatching 26 days after discovery of the nests.

Warren, however, in his Birds of Pennsylvania (1888) overlooked these important papers and quoted Wood's earlier figures of about three weeks for Red-tailed and Red-shouldered hawks. He rejected Gentry's 18 days for the Cooper Hawk, believing the time required to be "three weeks or over"; he thought the Sparrow Hawk incubated 21 to 24 days.

Bendire

And now came the key figure who set the pattern for reports on incubation periods in North America. Major Charles Bendire had wide experience with birds throughout the western United States. His military career lent itself to his oological pursuits, but not to the time-consuming occupation of waiting for eggs to hatch. He wrote two large volumes on "The Life Histories of North American Birds," covering in the first (1892) the gallinaceous birds, doves, hawks, and owls, in the second (1895), the woodpeckers, hummingbirds, flycatchers, corvids and icterids. For the majority of species he simply stated an incubation period, usually qualifying it with "about." A large proportion of his figures, particularly for hawks and owls, are too short, whereas others, like most of those for woodpeckers, icterids and cuckoos, are too long.

Using size of bird as criterion and assuming that "the majority of Raptores" incubate "probably about four weeks" (1892:317), he alloted this figure to the Golden Eagle, the large buteos and the Osprey (*Pandion haliaëtus*), "somewhat over three weeks" to the Marsh Hawk, 21 to 25 days to the Broad-winged Hawk, about 24 to the Cooper Hawk, and "about three weeks" to the Sharp-shinned and Sparrow hawks. The incubation of the Great Horned Owl "according to the observations of several careful collectors is said to last only three weeks, but I believe that twenty-eight days comes nearer to the actual time required" (1892:382). He assigned 3 to 4 weeks to the Barred Owl, about 3 weeks to the Barn, Long-eared, and Burrowing (*Speotyto cunicularia*) owls and "about two weeks" to the Elf Owl (*Micrathene whitneyi*).

Bendire's figures, like those of practically all of his predecessors in the New and Old worlds, were largely based on guess. He rarely mentioned anyone else's authority, and when he did in two cases, the results were not happy. He quoted from the manuscript of L. M. Turner, whose too short periods for gulls and terns have already been noted: "I cannot speak positively, but I think that seventeen days are required to incubate the eggs" (1892:72) of the Willow Ptarmigan (*Lagopus lagopus*); and in regard to the Spruce Grouse (*Canachites canadensis*) he says, "the young are hatched in about seventeen days" (1892:52). These figures have been quoted many times as positive data (see table 1), even though relatives of these grouse are known to take 24 to 26 days to hatch their eggs.

It is clear that most of Bendire's fellow oologists firmly believed in three-week incubation periods for the larger hawks and owls. Bendire himself had written in 1882 in regard to the Long-eared Owl: "The eggs are hatched in about sixteen days," and this was quoted by Ridgway (1889). Although in 1892 Bendire does not cite Wood's (1882) and Carpenter's (1882, 1883*a*, 1883*b*) papers, he may well have been influenced by them to revise his opinions on length of incubation in raptorial birds. He seems to have been so convinced, however, that the incubation period must be correlated with size of bird that he could not give the Cooper and Marsh hawks and the Long-eared Owl credit for the length of incubation ascertained by experiment and observation.

There is no evidence that he, or anyone else in the United States concerned with this subject, was aware of Evans's papers (1891, 1892). They were not reviewed in The Auk, as The Auk and The Ibis did not exchange until 1908. While Evans started his countrymen on the search for truth, Bendire, like Naumann, gave the impression that things were well known and thus closed the door to inquiry.

Bendire's periods were better than those prevalent at the time both in his native Germany and his adopted country, yet this proved little advantage in the long run. If they had been glaringly bad, they might have been less widely adopted. As it was, despite the qualifying "abouts," his estimates were largely accepted as proven facts and as such have been copied to the present day. Unfortunately, the great majority of Bendire's incubation periods are faulty.

After the publication of Bendire's volumes, incubation periods appeared in a vast array of bird books in the New World. His figures were used by Fisher (1893), Knight (1908), Eaton (1910–1914), Burns (1915), Bergtold (1917), Bent (1921–1940), Forbush (1925–1929), Roberts (1932), and many others. They were also copied in the Old World (Needham, 1931; Groebbels, 1937). But since he did not live to complete the books he planned on the rest of the families, people had to make up many incubation periods of their own. Both Dugmore (1900) and Wheelock (1904) had a predilection for short incubation periods, each crediting some vireos with 7 days. Although Mrs. Wheelock wrote: "in Bird Lore it is never safe to hazard a guess," her incubation periods seem to have been allotted hit or miss, as a sample from the Falconiformes will show: Golden Eagle, 3½ weeks, Swainson Hawk (*Buteo swainsoni*), 21 to 22 days, Marsh Hawk, 18 to 20, Osprey, "little more than two weeks," yet Cooper Hawk, 31 days. Dugmore was quoted by Bergtold, but Wheelock seems to have been almost wholly ignored, the only citation of her work I have found being for 27 days for the Golden Eagle (Forbush, 1925–1929).

In the 21 years following Bendire's first volume, reliable figures were given for three North American birds of prey. [Bergtold's reference to Kobbé's (1900) record on the Sparrow Hawk is an error. This is an article on the Rufous Hummingbird (*Selasphorus rufus*), that incubates "a few weeks"! Kobbé seems never to have written on the Sparrow Hawk.] Hegner (1906) published observations on a nest of the Red-tailed Hawk: on April 5 it was empty, on the 11th it contained 2 eggs; on May 13 in the morning "the first Hawklet broke through the shell"; on May 15 the other egg hatched. This gives at least 34 days for the second egg. Bergtold mentioned this record (as 32 days), but everyone else seems to have overlooked it. The only other observations I have found on incubation period of this species were made in Utah by Hardy (1939); he found it to last 34 to 35 days. Althea Sherman constructed nesting boxes with peep holes in them, and by careful and prolonged watching ascertained the exact time of the laying and hatching of the eggs of a number of species. She found that the incubation period of the Flicker (*Colaptes auratus*) was 11 to 12 days (1910), that of the Screech Owl 26 days (1911), and that of the Sparrow Hawk 29 days (1913). Her pioneer studies, both their technique and their results, did not make the impression they deserved. People continued to quote haphazardly. Forbush said of the Flicker: "period variously given as 11 to 16 days"; of the Screech Owl: "period 21 to 25 days (authors)"; and of the Sparrow Hawk: "period given by some authors as about 21 days, and by others as 29 to 30 days, latter probably nearly correct."

Knight, Burns, and Bergtold

In this century the three men most often quoted on incubation periods in North America are Knight, Burns, and Bergtold. The first two observed to a small extent, but mostly guessed and copied; the third copied.

Ora W. Knight, botanist and ornithologist, specializing in oölogy, published his Birds of Maine in 1908. In the preface he explained that he calculated the start of incubation "from the day when I had reason to believe the female had actually commenced to incubate . . . to the time when the first egg was hatched . . . . It is therefore to be understood that my observations regarding the incubation period are to be taken subject to such variation as may be produced by errors of judgment due to not correctly understanding the true conditions in a given case." This method involves an unknown at the start. Knight's followers, however, seem to have overlooked the preface and trustfully copied the positive statements in the text. While he said nothing about incubation in owls, he credited the Red-shouldered Hawk with 27 days, quoted Bendire for the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) as 14 days, and evidently followed him in the case of other birds, particularly in the too long periods for the Icteridae. He gave many reasonable incubation periods, but also many bad ones: Spotted Sandpiper (*Actitis macularia*), 15 days (see table 1); House Wren and Black-capped Chickadee (*Parus atricapillus*), 11 to 13, instead of 13 to 15; Phoebe, 12 instead of 15 to 17 (Sherman, 1952:99); and Song Sparrow (*Melospiza melodia*), 10 to 14, instead of 12 to 13 (Nice, 1937).

It was Frank L. Burns's list that did much more harm. He was a zealous amateur and originally an egg collector. He was the author of long monographs on the Flicker (1900) and the Broad-winged Hawk (1911), both compilations, and of a pioneer nesting study of a square mile (1901) in which he actually located the nests. In 1915 appeared his "Comparative Periods of Deposition and Incubation of Some North American Birds," in which he gave incubation periods for 225 species and subspecies, in no single instance mentioning his authority. "My conclusions are based upon the statements of authors, the manuscript notes [of 10 correspondants], and my own observations" (p. 276). The list was "compiled from various sources and in many instances from single records, some of which may be inaccurate and are questioned; others may be subject to revision; but none are included without good authority" (p. 281).

The majority of the periods evidently stem from Bendire, although some of these were slightly modified; for instance, where Bendire's figures ranged over 3 to 7 days, Burns chose one or the other. The next largest source appears to have been Knight, although occasionally a good figure from this author was replaced by a bad one of unknown origin. Others were taken from journals and books. Fully half of his records are erroneous, some of them strikingly so, especially in regard to rails, shorebirds, hawks, owls, hummingbirds, icterids, and many other passerines. Heinroth (1922:177) found in this list so many errors, even with the best known birds (Domestic Dove, 14 instead of 17 days; *Fulica,* 14 instead of 22-23; *Lagopus,* 18 instead of 26 days), that he had to "refrain from using it."

The list was welcomed. Stone (1915) in a half page review wrote: "Mr. Burns has done a good work in compiling a list setting forth the time of incubation for some 225 species and races of North American birds. The only weak point in Mr. Burns's paper is that he does not quote his authority for the individual figures, and the list of authors and correspondents from whose statements the list is compiled, must necessarily represent a considerable range of accuracy." He then criticized him for appending a question mark to 29-30 days for the Sparrow Hawk, in view of Miss Sherman's "most careful study of this species. At all events Mr. Burns's list is an excellent foundation on which to build."

It was certainly built upon! The article has a great deal to answer for, as it offered in convenient form in an easily accessible journal the guesses of Bendire and Knight, as well as a scattering of much wilder guesses, all set down as facts, except for the 14 question marks which seemed to have been placed more or less at random. At any rate, this mark after 14 days for the Sora (*Porzana carolina*) did not discourage five authors from copying this figure, although they did prefix "about" or "said to be."

One of the worst features of Burns's list was its lack of references, for no one could check the evidence on which each figure was based. Yet for 36 years this list has been copied, no matter how fantastic the data.

The next list gave the sources. W. H. Bergtold, Denver physician, published in 1917 a book of 108 pages entitled "A Study of Incubation Periods in Birds. What Determines their Length?" Some 800 incubation periods are presented for 625 species of birds of the world. This was by far the largest list until Groebbel's book (1937). The source is given for each period by a figure which refers to the bibliography of 197 abbreviated titles for which dates are largely lacking. Dr. Bergtold said: "Inasmuch as a great deal of the literature used in this study was wholly inaccessible to the writer and had to be copied for him, he fears that some errors incidental to such transcribing may well have crept in, for which he expresses his regret, however unavoidable on his part these errors may have been" (p. 10). He does not, however, indicate which sources he consulted personally. He also stated: "The author is confident that some of the incubation-length records included in this list are grossly incorrect, yet they are incorporated in the data, with a feeling that they will, in the future, be more accurately determined, and in that form recorded, and thus be corrected" (p. 77).

The table of incubation periods includes 225 periods from Burns, 59 from Bendire's first volume (strangely enough the second was missed), 183 from Evans's two papers, 47 from Heinroth (1908), and smaller numbers from various authors in North America, Europe, New Zealand and Australia.

It is unfortunate that the copier did not use better judgment in the figures taken from Evans, for along with some of the reliable ones determined by this ornithologist and others, there are many that are glaringly incorrect. Twenty-two records stem from Tiedemann, and 13 from Audubon with others from Naumann and his followers. At times an ancient guess was preferred to authentic observation, as 21 to 24 days for the Eagle Owl (*Bubo bubo*) instead of 36 found in an aviary, 16 to 17 days for the Stone Curlew (*Burhinus oedicnemus*) instead of a month, 23 days for the White Stork (*Ciconia ciconia*) instead of five other statements of a month, and so on. Eleven records were attributed to Dugmore of which seven are bad, but the worst of all—17 days for the Canada Goose (*Branta canadensis*)—does not occur in any of the editions of Dugmore's book.

Unlike Evans's list, where the results of experiments and observations were clearly divided from the statements of earlier writers, all of Bergtold's periods are listed consecutively with no indication as to the reliability of the source except the key number. And because of the indiscriminate jumbling of Evans's original and historic figures, it is impossible to place reliance upon a figure merely because it is attributed to him.

Stone (1917) devoted two pages to a review of this "valuable contribution to a neglected line of research," his only criticisms being in regard to "evidences of hasty proof reading" and an erroneous citation of the finches of Australia which "are really Weavers." Bergtold's contribution would have been far more valuable had he omitted the many periods he believed "grossly incorrect," or if he had at least indicated which these were. As it was, he merely perpetuated them; they have been quoted by many authors and have been used to bolster inadequate theories (Needham, 1931; Worth, 1940, see Nice, 1940; Huggins and Huggins, 1941, see Nice, 1941). Needham wrote: "What governs the incubation times of birds? . . . by far the best treatment of it in the literature at present is the book of Bergtold." Whereupon he quotes 131 figures, many of them very mistaken. Needham is quoted by Worth and the Hugginses, and undoubtedly will be quoted for many years to come, for biochemists are not as a rule in a position to check upon ornithological facts.

Bergtold's list has been widely used and is still being used for want of something better in this country. Heinroth's great paper remained almost unknown here for many years. In The Auk (1923:366), where many articles were reviewed at length, Heinroth's was listed with the comment: "A lengthy discussion with tables and charts of variation curves." If its true worth had been realized and an adequate review given, Bergtold should not have written in 1929 that "There are available in the literature, so far as the writer has been able to learn, data relating to the [egg] weights of only about sixty bird species." Nor should various superficial theories on length of incubation have later been propounded in this country.

In the last 35 years there have been many studies of individual species in which incubation periods have been carefully determined. The most notable paper by an American dealing with a large number of species is that of Skutch (1945) on "Incubation and Nestling Periods of Central American Birds." In this he summarizes his own careful observations on incubation periods in 90 species and nestling periods in 120. He found that incubation in species of wood warblers, some of the wrens, and some of the tyrant flycatchers was longer than in species of these families at higher latitudes.

An important contribution to the subject of nesting behavior is Kendeigh's book on "Parental Care and Its Evolution" (1952). After describing in detail observations largely made by mechanical records on incubation and care of nestlings in the House Wren and 19 other North American species, he discusses parental care throughout the class Aves with examples that are in the main reliable. Tables 42 to 50 give incubation periods from particular studies for 133 species from the Cuculiformes through Passeriformes. It is a pity that the Bendire tradition was so strong that in the summary on the Falconiformes (p. 193) the incubation period is said to be "commonly about 4 weeks long," a statement belied by the dozen periods of individual species given in the pages immediately preceding, as well as by the figures on page 283. In table 51, in the preparation of which I was privileged to assist, a summary is presented of "attentive behavior by families," in which the range in length of incubation periods is reported according to the best information available. Statements in the text should be checked against this table which contains the latest findings. The book should serve as a guide and stimulus to further research.

A SUMMARY OF SOME OF THE PERSISTENT ERRORS IN NORTH AMERICA

The source and course of some of our popular errors in incubation periods in this country stemming from Tiedemann, Audubon and Bendire to the present are shown in tables 1 and 2.

Table 1

Some Persistent Errors Concerning Incubation Periods of New World Species

Herons to Shorebirds

Species	Audubon 1831	Bendire 1892	Knight 1908	Burns 1915	Bergtold 1917	Different compilations 1920's	1930's	1940's	Correct period
Green Heron, *Butorides virescens*				17	17	17	17	17, 20	20±
California Condor, *Gymnogyps californianus*	29–31				29–31		29–31	29–31	?
Black Vulture, *Coragyps atratus*	32	30±		30	30, 32, 40	30±	28, 39	28	39–41
Sharp-shinned Hawk, *Accipiter striatus*		21±		21	21	21–24	21–24	21–24	34–35
Golden Eagle, *Aquila chrysaëtos*		28±		35	25–35	27, 30	28–35	30	43
Sparrow Hawk, *Falco sparverius*		21±		29–30?	21, 29–30	21, 29–30	29, 30	28, 29	29
Spruce Grouse, *Canachites canadensis*		17?			17		17	17, 24±	24±
Clapper Rail, *Rallus longirostris*	14				14	14		14	21–23±
Sora, *Porzana carolina*				14	14	14	14	14, 16–19	19
American Coot, *Fulica americana*				14	14	21–22, 27	21±	27	23–24
Spotted Sandpiper, *Actitis macularia*			15	15–16	15–16	15–16	15–16	15, 21	21

The references for the 1920's are Bent (1921, 1926, 1927–1929) and Forbush (1925–1929); for the 1930's, Bent (1932, 1937–1938, 1939), Roberts (1932), and Oberholser (1938); for the 1940's, Bent (1940), Hann (1945), E. L. Palmer (1949), R. S. Palmer (1949), and Sprunt and Chamberlain (1949).

In table 1 Burns's 17 days for the Green Heron was quoted up to 1949 (Sprunt and Chamberlain), but that same year R. S. Palmer cited Cooley's (1942) observation of about 20 days. This is consistent with the incubation periods of other herons.

Audubon's statement of 29 to 31 days for the California Condor was based on fantastic stories told to David Douglas, the young Scotch plant collector. This is copied by Needham (1931) from Bergtold via Evans. As yet there is no satisfactory observation on the incubation period of this bird. In his excellent study of this difficult species Koford (1953:85) found it was "at least 42 days." Already in one review this has been changed to "about 42 days" (Tanner, 1953). The South American Condor (*Sarcorhamphus gryphus*) has long been known to take 54 to 56 days in captivity (Evans, 1892; Heinroth, 1922; letter from Mrs. Belle Benchley, former director of the San Diego Zoo). Its eggs average 275 grams in weight, those of the California Condor 298 grams.

The incubation period of the Black Vulture was reported as 40 days by Heinroth (1908) on the authority of Ludwig Wunderlich, director of the Cologne Zoo from about 1888 to 1928. Thomas (1927) found it lasted 39 to 41 days.

I have found no published observations on the incubation of the Sharp-shinned Hawk, but Dr. Alden H. Miller and Dr. Wade Fox, Jr., inform me of a nest in Berkeley, California, in 1944 in which incubation lasted 34 to 35 days. This is consistent with the findings on European accipiters.

The most popular figure for the Golden Eagle in North America was Bendire's of 4 weeks, although Burns's 35 days was sometimes quoted. Apparently this came from Henninger and Jones (1909) who gave some of their "Falcones" incubation periods for which no sources were indicated. Thirty days was quoted as late as 1949 (E. L. Palmer). The only record based on observation that I have found for the American form is that of Walker and Walker (1939) for 43 days.

Althea Sherman (1913) found that the last egg of a set of Sparrow Hawk eggs hatched 29 days after it was laid.

The origin of the 17 days for the Canada Spruce Grouse has already been mentioned. E. L. Palmer repeats this both in 1949 and 1953. R. S. Palmer (1949:162) says: "Incubation probably requires about 24 days." Apparently there are no observations, but this latter figure matches that of related forms.

Audubon's guess of 14 days for the Clapper Rail was copied for 118 years; I have just prevented its reappearance in 1953. In 1949 Kozicky and Schmidt published on this species and gave an average incubation period of 20 days for six nests. But as they considered this period "as starting when the last egg was laid and ending when the first chick hatched," and as hatching spread over 24 to 48 hours, it is obvious that their figure is one or two days too short. I wrote to the authors asking whether they could give me the period from the laying of the last egg to its hatching, but they were unable to do this. They said that observations on five nests in 1950, calculated in the same way as for the first six, ranged from 19 to 23 days, averaging 21.5. From 21 to 23 days would seem approximately correct, until we can get observations made in proper fashion.

Ward D. Tanner has made a special study of the Sora in Iowa; he writes me he found the incubation period in five nests was 19 days and in one 20 days.

Burns's astonishing figure of 14 days for the Coot was quoted by Bergtold, but apparently by no other American. It is, however, continued in Needham's list. Forbush volunteered 27 days and this was used by E. L. Palmer (1949). Gordon W. Gullion, who has made an intensive study of this species (in press), finds that incubation lasts 23 to 24 days.

Knight's guess of 15 days for the Spotted Sandpiper had a great vogue, being quoted as late as 1949 by E. L. Palmer. This in spite of Smith's (1914) finding it was *more* than 17 days, and Nelson's detailed study (1930) that established the incubation period as 21 days, later corroborated by Mousley (1937). Miller and Miller (1948) recorded 20 to 22 days in three nests; I noted 21½ in one nest.

Tiedemann's statement of 14 to 16 days for the Least Tern was quoted by Evans and copied by Bergtold, and since then by Bent, Forbush, Needham, and Sprunt and Chamberlain (1949); this is the longest-lived error in the tables—135 years. I can find no observations on our American subspecies, *Sterna albifrons antillarum,* but Heinroth in 1922 found a period of 21.5 days for *S. a. albifrons.*

In regard to the Black Tern, in 1904 Seton and Chapman reported they had found an egg on June 16 and another on June 18; one had hatched by July 5 "after an incubation period, therefore of seventeen days." Since they knew neither the laying nor hatching date of either egg, this guess of 17 days was unfortunate. It was adopted by Burns and copied until 1949, although Bergtold interpreted the observations as "17 to 19? days." For the European subspecies Haverschmidt (1945) determined that the eggs in three nests hatched in 20 to 22 days. Robert E. Goodwin, who has studied this species in New York state, tells me that marked eggs hatched in 21 to 22 days.

The three owls in table 2 were assigned "about three weeks" by Bendire. Burns interpreted this for the Barn Owl as 21-24 days and thus it has been copied in each decade up to 1949. I can find no American observations, but Witherby *et al.* (1938) give 32 to 34 days and Niethammer (1938), 30 to 34. In 1911 Sherman published her intensive study of the nesting of the Screech Owl in which she found the incubation period of the last egg was 26 days. Burns, however, would not give up Bendire, so stated it to be 21-26 days. The "21" has stuck until 1949, although 30 is also included; this was first proposed by Bent (1938) who said "21-30, probably about 26." The Long-eared Owl was put in the 21 to 24 day class by Tiedemann. Americans followed Bendire's 21 days except that Forbush said 21-30 days with no hint as to the authority for the latter figure, and this was copied by Roberts (1932) and E. L. Palmer (1949). Sumner (1929) found the period to last about 28 days. Evans (1891) and Heinroth (1922) observed that the incubation period of *Asio otus otus* was 27 days.

Audubon assigned a 10-day incubation period to the Ruby-throated Hummingbird and a 7-day fledging period, instead of the 21 to 25 days the young really spend in the nest. The 10-day incubation period appeared in Evans and from there in Bergtold. Hummingbirds have long incubation periods; it is 16 days for this species (Skutch, 1945; Kendeigh, 1952:285).

As to the Belted Kingfisher, Audubon and Bendire guessed 16 days and Finley (1907) 16-17, and this persisted to 1949 (E. L. Palmer). For once Burns was right with 23-24 days; this was what Mousley found in 1938.

The history of the incubation period of the Flicker gives us a perfect example of ascertaining its length, but a sad example of the indifference of others to scientific standards. Miss Sherman (1910) watched the eggs being laid, marked them, and watched them hatch; the last egg in one set took 11 days and 8 hours, in another 11 days and 5 hours. "Roughly speaking, then, the time that our Flickers take for incubation is from eleven to twelve days." In 1900, Burns had published an 82-page treatise on the Flicker but could offer only "one record of the duration of incubation"—14 days, provided by Lynds Jones. In 1915 he gave 11-14 days for this species. Bergtold gave 11-12 days from Sherman's Flicker paper, 11-14 from Burns, and "about 16 days" from Sherman's Sparrow Hawk paper (1913:412). She had said: "The Flickers . . . hatched out their brood on June 6—the first egg having been laid on May 21." Bergtold was thus counting from the laying of the first egg to the hatching of the last, and as the Flickers laid from 7 to 9 eggs in a clutch, this constituted a "grossly erroneous" value. Nevertheless, 16 days was repeated each decade; the only authors of the compilations cited who respected Miss Sherman's work and gave 11 to 12 days as the period were Bent (1939) and R. S. Palmer (1949).

Bendire's 15-17 days for the Eastern Meadowlark have been copied by every one of our compilers up to the present. Dr. George Saunders, who studied this species intensively, writes that he found that incubation lasted 13 to 14 days.

The myth of the 10-day incubation period of the Cowbird has been treated in detail elsewhere (Nice, 1953*a*). R. S. Palmer was the only compiler to notice the many refutations from 1918 (Shaver) on, the most important of which are Nice (1937), Hann (1937), and Norris (1947).

Table 2
Some Persistent Errors Concerning Incubation Periods of New World Species
Terns to Icterids

Species	Tiedemann 1814	Audubon 1831	Bendire 1892–95	Knight 1908	Burns 1915	Bergtold 1917	Different compilations 1920's	1930's	1940's	Correct period
Least Tern, *Sterna albifrons*	14–16					14–16	14–16		14–16	20–22
Black Tern, *Chlidonias niger*					17	17–19?	17	17	17	21–22
Barn Owl, *Tyto alba*			21±		21–24	21–24	21–24	21–25	21–24	32–34
Screech Owl, *Otus asio*			21±		21–26	21, 25	21–25	21–30	26, 21–30	26
Long-eared Owl, *Asio otus*	21–24		21±		21	21	21–30	21–30	21–30	28±
Ruby-throated Hummingbird, *Archilochus colubris*		10	14±	12	14	10, 14, 15	14	14, 16	11, 12 14, 16	16
Belted Kingfisher, *Megaceryle alcyon*		16	16±		23–24	16, 23–24	16–17, 23–24	16–17	16–17, 23–24	23–24
Yellow-shafted Flicker, *Colaptes auratus*			15±		11–14	11–14, 16±	11–16	11–12 11–16	11–13, 14–16	11–12
Eastern Meadowlark *Sturnella magna*			15–16	15–17	15–17	15–17	15–17	15–17	15–17	13–14
Cowbird, *Molothrus ater*		14±	10–11	10	10	10, 10–11, 14±	10–12	10	10, 11–13	11–12

DISCUSSION

Let us examine the factors that have been believed to influence duration of incubation, then consider some related problems that have been neglected, and finally ask ourselves why ornithologists have so trustingly repeated ancient errors for 2300 years. The strong conviction of most ornithologists throughout some 23 centuries has been that length of incubation depends primarily on the size of bird or egg. Various supplementary factors have been suggested. Climate and season were mentioned by Aristotle, Tiedemann and Newton. Gurney (1899) believed that "The period of a bird's incubation seems to have something to do with the length of its life." He thought parrots were an exception, but in reality they support his theory. Some long-lived birds have long incubation periods. This is true of albatrosses, Falconiformes, Strigiformes, and Psittaciformes. Richdale (1952:124) found that the Royal Albatross does not breed until its ninth year. However, geese, swans, gulls, and terns are long-lived, yet their incubation periods are comparatively short. The state of perfection in which the young bird leaves the egg was considered important by Tiedemann, Zorn, and Newton (1893–1896), but not by Burns and Bergtold.

The influence of the temperature of the parent was mentioned by Frederick II (1943). This was also Bergtold's main contention, in favor of which he demolished to his own satisfaction 16 alternative theories, including size of bird and egg, and site of nest—protected or unprotected.

Bergtold cited Heinroth's (1908:22) report that eggs of the Egyptian Goose (*Alpochen aegyptianus*) hatched in 28 days under a hen and in 30 days under a Muscovy Duck (*Cairina moschata*) as experimental evidence of his theory, and this is quoted in turn by Needham and by Huggins and Huggins. Heinroth made no comment on this two-day difference; perhaps the Muscovy had been a poor sitter. In 1922 he gave 28 days as the period for the Egyptian Goose. In this paper (p. 176) he rejected the idea of shorter periods depending on differences in temperature of the sitting bird; if the like-sized eggs of pigeons and Barn Owls (*Tyto alba*) are exchanged, those of the first species take 17 days, those of the second 30, just as under the real parents. Zorn had already (1742–1743) established this in turkeys, hens and pheasants. Did Bergtold, Needham and the Hugginses check the temperatures of Muscovy Ducks and domestic fowl before jumping to their conclusions? Apparently not. In Bergtold's table 6 the temperatures of hens and ducks appear to be about the same, averaging about 107°F. Wetmore (1921) also found the temperature of ducks high, averaging 107°F.; his one example of *Cairina* was 107.7°, his averages for hens 106.4°–106.9°F.

Bergtold does not attempt to match long and short incubation periods with low and high temperatures of the parents. His 9 ostriches with their very short incubations average 100°F.; his 21 adult procellariiforms with their exceedingly slow incubations average 105°. Most of his other birds show somewhat higher temperatures. Gross (1935:391) states that the temperature of adult Leach Petrels (*Oceanodroma leucorhoa*) was 106°F. Wetmore found the temperature of grebes, pelicans, herons and a Turkey Vulture (*Cathartes aura*) ranged between 103.6° and 104.3°F.; that of hawks averaged 106°; gulls and shorebirds 106.7°; ducks 107°; quails 107.6°; passerines 107–108°; woodpeckers 108°; pigeons 108.2°; and cuckoos 108.7°.

Baldwin and Kendeigh (1932:149) point out the incorrectness of Bergtold's assumption that "the optimum incubation temperature for any species is the temperature of the incubating parent." They found the temperature of female birds of eight passerine species in the breeding season averaged 106.3°F. (41.3°C.). By inserting thermocouples in House Wren eggs kept in the center of the nest they recorded an average of 93.1°F. (34°C.) in 26 inattentive periods, and 98.5°F. (37°C.) in 26 attentive periods. Huggins (1941) investigated egg temperatures of 37 species of 11 orders from Ciconiiformes to Passeriformes by inserting thermocouples into the eggs, but allowing the eggs to be moved about by the parents. "The average egg temperature for all orders is 34.0°C., the average for the attentive period 34.3°C., and that for the inattentive period 33.4°C."

Size of bird and/or egg was the yard-stick for Aristotle and his followers, and for Bechstein and Naumann and their followers down to Géroudet, in the Old World, and from Bendire and Burns to Worth and the Hugginses in the New World. Size of egg is related to size of birds; eggs become relatively smaller in larger birds, but each group shows a characteristic size relation of its own (Heinroth, 1922; Huxley, 1927; Amadon, 1945).

Although Bergtold emphasized the inconsistencies in considering egg size the crucial factor in determining length of incubation, ironically enough several people have concluded the opposite, basing their evidence on his list. Needham (1931:478) states, "The length of the incubation period varies more or less with the size of the bird," and he presents a table and chart on double log paper to prove it. Unfortunately, as mentioned earlier, a large proportion of his incubation periods are far from correct. Worth and the Hugginses accepted Needham's conclusions. Worth was unacquainted with Heinroth's papers, and, although Needham and the Hugginses cite them, they show no evidence of having been influenced by them.

Worth (1940) calculated the volume of eggs from their measurements by an elaborate formula rather than using the simple method of Schönwetter (1924, 1932; see Nice, 1937:113) for obtaining weight. Worth chose 104 incubation periods from Bergtold, using single figures or averages, whichever agreed best with his theory. Half of these periods are erroneous. He plotted the egg volumes against these periods and found only 4 or 5 days' deviation on either side of the line representing the "average or expected incubation period." Hence he concludes that with a second formula he can calculate the average incubation period of any egg from its measurements, allowing "an ecological correction not exceeding five days in either direction." Even though one term of his basic material was so faulty, he rightly concluded that birds with short incubation periods are "subject to predation or some other type of environmental onslaught," and that predacious birds develop slowly. But he greatly underestimated the amount of retardation or acceleration, as will be seen in tables 3 and 4.

On the basis of their experiments on egg temperatures, Huggins and Huggins (1941) reject Bergtold's theory. They also consider it "unnecessary to postulate an ecological factor to account for variations in length of incubation compared with egg volume, as Worth does," and conclude: "The evidence presented would seem to indicate that there is a general positive correlation between egg weight or volume and length of incubation." Like Needham and Worth, the Hugginses apply these generalizations to all birds regardless of order or family.

What have the two chief investigators of this subject to say on the factors influencing length of incubation?

Evans (1891:91) concluded that only in "birds possessing a certain amount of affinity" is size of egg correlated with length of incubation.

It is Heinroth who gave the most illuminating analysis of the subject with his extensive table, elaborate charts and discussions (1922:178, 279-285). After pointing out what false conclusions have resulted from Naumann's assumption of the dependence of length of incubation on size of egg, he admitted that *within a group* there *may* be such a relation, but that there are many exceptions. The state of development of the young often has an influence, but again with many exceptions. He believed that very long incubation periods are somewhat primitive and have persisted where the brood is little endangered, as in most birds nesting in holes and on islands, or in birds of prey. Short incubation periods are correlated with danger to the eggs from flooding or predation, and with repeated nesting during a season. Long incubation periods are characteristic of Casuariiformes, Apterygiformes, Sphenisciformes, Procellariiformes, Falconiformes,

Table 3

Some Eggs of Like Size and Their Incubation Periods

Species	State at hatching	Weight of eggs in grams	Incubation period in days	Authority
Cassowary, *Casuarius* sp.	precocial	550	56	Heinroth (1922)
Rhea, *Rhea americana*	precocial	575	35–40	Heinroth (1922)
Royal Albatross, *Diomedia epomophora*	altricial	416	77½–81	Richdale (1952)
Kiwi, *Apteryx mantelli*	precocial	415	75	Harmon (1950), Robson (1948)
South American Condor, *Sarcorhamphus gryphus*	altricial	275	55	Heinroth (1922)
Black Swan, *Cygnus atratus*	precocial	290	35	Heinroth (1922)
White Pelican, *Pelecanus onocratalus*	altricial	165	36	Heinroth (1922)
Canada Goose, *Branta canadensis*	precocial	170	28–29	Witherby (1939)
Little Owl, *Athene noctua*	altricial	16	28–29	Witherby *et al.* (1938–1941)
Stock Dove, *Columba oenas*	altricial	16	16–18	Witherby (*op. cit.*)
Storm Petrel, *Hydrobates pelagicus*	altricial	7	38–40	Lockley (1932)
European Quail, *Coturnix coturnix*	precocial	7	18	Heinroth (1922)
Song Thrush, *Turdus ericetorum*	altricial	7	13½	Lack (1948)

Psittaciformes, Strigiformes, and Trochilidae. Short incubation periods are found in Struthioniformes, Rheiformes, some Anatinae, Turnicidae, Columbidae, Picidae, and most Passeriformes.

Let us examine the incubation periods of 13 species of birds with eggs of like size. In each of the six sets of birds in table 3 representatives of different orders are compared. In five sets the periods are markedly different, ranging from one-third and two-thirds longer in eggs weighing from 16 to 575 grams, and as much as three times as long in two species laying eggs of 7 grams.

As to the state of perfection in which the young are hatched, in only one case does a precocial chick take longer for its development than an altricial chick of like size—the European Quail in contrast to the Song Thrush. In four cases, on the contrary, the precocial chicks have *shorter* incubation periods than the altricials of similar size. The period of the Kiwi deserves notice; this was mistakenly reported as 42 days by Bergtold, Needham and Worth; the source was Evans, his authority being Gould who reported it as such "according to a native" (Brehm, 1875). It is clear that incubation periods of birds of different orders do not correspond to size of egg.

Even more striking are the results when we compare certain eggs of like incubation periods. In table 4 some of the birds are from different orders, but in one set all three are of the same genus. In the three swans the egg of the largest weights 1.7 times as much as that of the smallest, yet all hatch in 35 days. In the sets composed of different orders we find eggs hatching in the same length of time as others 6, 32, and 40 times their size. Here again is striking refutation of the belief that length of incubation depends on size of egg, even in some cases within one family and within one genus.

Table 4

Some Eggs of Like Incubation Periods and Their Weights

Species	State at hatching	Weight of eggs in grams	Comparative size	Incubation period in days	Authority
Emu, *Dromeus novea-hollandiae*	precocial	600	40	56	Heinroth (1922)
Fairy Prion, *Pachyptila turtur*	altricial	24	25	56	Richdale (1944)
Diving Petrel, *Pelecanoides urinatix*	altricial	15	1	56	Richdale (1945)
Ostrich, *Struthio camelus*	precocial	1500	25	42	Heinroth (1922)
Gannet, *Sula bassana*	altricial	102	15	43–45	Witherby (1940)
Puffin, *Fratercula arctica*	altricial	60	1	42	Lockley (1934)
Mute Swan, *Cygnus olor*	precocial	350	1.7	35	Witherby (1939)
Black Swan, *Cygnus atrata*	precocial	290	1.4	35	Heinroth (1922)
Black-necked Swan, *Cygnus melanocoryphus*	precocial	210	1	35	Heinroth (1922)
Stock Dove, *Columba oenas*	altricial	16	32	16–18	Witherby (1940)
Broad-tailed Hummingbird, *Selasphorus platycercus*	altricial	0.5	1	16	Bergtold (1917)
Flicker, *Colaptes auratus*	altricial	7.8	6	11–12	Sherman (1910)
Cowbird, *Molothrus ater*	altricial	3.2	2.5	11–12	Nice (1937)
Lesser White-throat, *Sylvia curruca*	altricial	1.3	1	11–12	Lack (1948)

The greatest contrast in table 4 lies between the eggs of the Diving Petrel and the Ostrich. *The 15-gram egg of the former takes two weeks longer to hatch out an altricial chick than does the hundred-times larger egg of the latter to turn out a precocial bird.*

The very short incubation period of the Ostrich (Mosenthal and Harting, 1877; Watson, 1905), in Africa with its wealth of predators is in marked contrast to the long periods of the Emu and Cassowary in predator-free Australia, as pointed out by Heinroth (1938:43). The development of the egg of the Rhea appears also to have been accelerated in response to enemies.

Two of the birds in these tables with long incubation periods are predators—the Condor and Little Owl. The Condor can have few natural enemies, while the owl is both a predator and a hole-nester. Most of the other birds with prolonged incubation nest in protected places: pelicans and Gannets on islands, the small petrels and the Puffin in holes in the ground on islands, the Kiwi in a hole. Lack (1948:30) has shown that the Nightingale (*Luscinia megarhyncha*) in its open nest incubates 13 days in contrast to 13½ to 14½ days in three hole-nesting Turdidae with eggs of similar or smaller size. In Central America, Skutch (1945:31) gives incubation periods for 18 species of Tyrannidae and concludes that "among flycatchers, the less accessible the nest, the slower the development of the eggs and young it shelters." Hole-nesting ducks take longer to hatch their eggs than do those nesting in the open: 30 days for Wood Duck (*Aix sponsa*), and Golden-eye (*Bucephala clangula*) in contrast to 25 to 26 days for the Tufted Duck (*Nyroca fuligula*) and 22 to 23 days for the Pintail (*Anas acuta*).

In many cases, of course, there is a general relationship between body size and length of incubation, especially in one group. Much larger birds often incubate longer than smaller ones, as in some Anseriformes, Galliformes, Falconiformes, Strigiformes, Psittaciformes, and Passeriformes (Corvidae in contrast to most of the other open-nesters in this order). But even in one genus, species of widely differing size may have the same incubation period, as the swans listed in table 4. The 48-gram egg of the Peregrine Falcon (*Falco peregrinus*) hatches in the same length of time as the 21-gram egg of the Kestrel (*F. tinnunculus*). The same is true for different breeds of the domestic fowl, although the eggs may range in size from 30 to 68 grams (Romanoff and Romanoff, 1949:65). A set of eggs of the 9- to 11-gram Hutton Vireo (*Vireo huttoni*) hatched after 16 days of constant incubation by both parents (Miller, 1953), whereas the eggs of the 16- to 18-gram Red-eyed Vireo (*Vireo olivaceus*) hatch after 12 to 14 days incubation by the female alone (Lawrence, 1953).

Woodpeckers nest in holes, yet many of them have very short incubation periods along with fairly long nestling periods, the young staying in the nest until fully developed. The explanation of the short incubation period would seem to be that they hatch a little earlier in the embryonic development than does a passerine, as is evident in pictures of young nestlings (Bussmann, 1946). The Heinroths (1924, II:221) thus describe a newly-hatched Black Woodpecker (*Dryocopus martius*): "Eyes and ears are entirely closed, and the whole animal gives the impression that it had come too early from the egg; this small degree of development corresponds well with the exceedingly short incubation period." The same situation may pertain in some other families of the Piciformes with short incubation and long nestling periods.

Hummingbirds have long incubation periods—16 to 17 days for their tiny eggs. A state of torpidity at night has been recorded in adult hummingbirds: male and female Anna (*Calypte anna*) and Allen (*Selasphorus sasin*) hummingbirds with temperatures of 18.7°C. in males (Pearson, 1950) and a nonbreeding female Estella Hummingbird (*Oreotrochilus estella*) whose temperature dropped to 14.5°C. (Pearson, 1953). The night temperature of four nesting females of this latter species ranged between 36° and 39.7°C., averaging 37.4°C. (99.2°F.). The average night temperature of females of eight passerine species was 39.7°C. (Baldwin and Kendeigh, 1932:158). Temperature readings for 48 hours at a nest of an Anna Hummingbird by means of a thermocouple placed between the eggs showed "no evidence of torpidity in the parent bird while incubating . . . . The nest was generally maintained about 10°C. warmer than the surrounding air" (Howell and Dawson, 1954). The chart shows that hourly temperatures ranged between 16° and 37°C. These figures could perhaps be best compared with temperatures "at the bottom of the nest" in House Wrens; these average 32.9°C. for inattentive periods and 34.4°C. for attentive periods (Baldwin and Kendeigh, 1932: 153). It seems evident that hummingbird eggs receive somewhat less heat than do most eggs whose incubation temperatures have been studied.

Those who believe that size of egg controls length of incubation assume that development proceeds at much the same rate throughout the class Aves. This is far from true, as has been shown by Heinroth (1922), Lack (1948) and others. Long incubation is usually paired with long nestling periods, as evolution may effect the rate of cell division throughout the period of growth. In contrast to Heinroth's belief that long incubation periods are primitive, Lack (1948:31) makes the interesting suggestion that a slow rate of development might have evolved in some cases as "an adaptation to a scarce and erratic food supply," thus enabling the young to survive periods of starvation. The "swifts and Procellarii" are his chief examples, but he also suggests that this theory might apply to hummingbirds and Falconiformes.

What is the basis of different rates of development, that is, different rates of cell division or different sizes of cells? Kaufman (1929, 1930) found the rate of cell division in chick and pigeon embryos much the same, but pigeon cells were smaller than chick cells and these were smaller than duck cells. All three birds have rapid embryonic development. Byerly *et al.* (1938) studied embryos of bantams and Rhode Island reds and reported comparable growth during the first week, but after that the bantams grew at a "lower" rate than the large breed. Yet they found liver cells were about the same size in both breeds and concluded that there are no "inherent differences in rate of cell division" in the two breeds, hence it is not clear how the greater growth in the larger eggs was effected. If two embryos reach the same stage of development in the same length of time and one is larger than the other, the former must possess either larger cells or more of them.

From the foregoing discussion and the examples presented in tables 3 and 4 it is clear that *the crucial factor in length of incubation is the rate of development of the embryo.* Size of egg sometimes plays a role, but often it does not.

SOME PROBLEMS FOR INVESTIGATION

We now have a considerable body of more or less accurate determinations of incubation periods; yet, considering the number of birds in the world, our knowledge is small indeed. In the Old World the incubation period of such a familiar friend as the White Stork is variously given as 28 to 30 and 33 to 34 days, and such examples can be multiplied easily. In North America the majority of our species could well be studied intensively. We are especially weak on the incubation periods of vultures, eagles, hawks, owls, rails, cuckoos, and woodpeckers.

There are many problems of theoretical interest in this field. Why do river ducks have shorter incubation periods as a rule than diving ducks; falcons than accipiters? Length of incubation in the tropical, temperate and arctic zones should be compared. What is the histological basis of long and short incubations? We need to have some concept of embryology and to realize that after 14 days of incubation a Clapper Rail is a blind, nearly naked creature corresponding fairly well to some newly-hatched passerines.

It is not only the subject of incubation periods for which we have such an appalling array of misinformation in North America, but also for many other topics concerned with nesting. We need to know the clutch size, locality by locality, month by month, year by year, not a meaningless mixture of data from all parts of the country. We need to know which sex incubates; the statements in many of our "standard" books appear to have been set down quite at random. We need to know fledging periods of *undisturbed broods* and the time the young are cared for by their parents. Some material on these subjects of parental care can be found in Nice (1943:69-71) and especially in Kendeigh (1952), as well as a great deal of reliable information in Groebbels (1937) and the British and German handbooks.

CONCLUSIONS

The acceptance of erroneous incubation periods for 2300 years rests upon the stubbornly unscientific bent of the human mind. It takes hard and serious thought to investigate; it demands keen and prolonged observation and experiment, analysis and synthesis, and inductive and deductive reasoning, along with a detached and skeptical attitude and creative imagination. How much simpler for the authority to make a clever guess: since the goose and hen incubate about 30 and 20 days, respectively, here seems to be a law of nature which can safely be applied to the class Aves. And how much easier for everyone else to copy from books and lists these statements based on such a neat law than to undertake the bother of watching the birds in nature or hatching their eggs at home, or even of searching through the journals for the results of other people's first-hand and scientifically reported experiences.

On the subject of incubation periods there have been guessers, copyists and investigators. The chief guessers were Aristotle, Bechstein, Naumann and Bendire; the chief investigators, Evans and Heinroth; the copyists have been legion. Not content with perpetuating the somewhat tentative statements of Aristotle and Bendire as first pronounced, the copyists have magnified the importance of the authorities by consistently omitting the "abouts," with the result that in their versions the original assumptions appear as established facts.

It is impossible to build science on a foundation of heterogeneous mixture of fact and error. Our chief trouble is that we bow to authority instead of cultivating the spirit of inquiry and the habit of evaluating evidence. The non-Aristotelian view of science is well expressed by Johnson (1946:26) who explains how the scientist uses his theory "*as a source of questions,* new questions that have never before been asked by any one. And he uses the new questions to direct himself and others to new observations that have never been made by any one . . . . To be scientific, then, is in a fundamental sense, to ask questions—fresh, meaningful, clear, answerable questions . . . . Our beliefs automatically become questions the moment we realize they are beliefs instead of facts."

This whole problem is a challenging one. We need to watch and study our birds, and to view with suspicion statements unaccompanied with full data as to laying and hatching dates of all eggs in a set. An incubation period is a biological fact, not merely a figure to copy out of a book. As Kirkman *et al.* (1911–1913) said: "To know how little we know is in natural history the beginning of wisdom."

SUMMARY

Confusion still prevails in North American ornithology on the subject of incubation periods. Too short periods are usually attributed to birds of prey, some shorebirds, rails, terns, hummingbirds, and cowbirds, and too long periods to woodpeckers, cuckoos and some passerines.

By incubation period is meant the time required in regular incubation of a newly-laid egg until the young has left the egg.

Aristotle was responsible for the original belief in short incubation periods for birds of prey. He was copied throughout the history of ornithology until late in the 18th century, after which Bechstein and the Naumanns applied to all birds the principle of incubation period matching the size of bird. At the end of the 19th century William Evans investigated this subject with the aid of the incubator and published his findings on 81 species. In 1922 Heinroth published the second great contribution to this field. Recent publications on birds of Great Britain and northern Europe present on the whole reliable information on incubation periods.

In the New World before 1892 only one author, Gentry (1876, 1882) mentioned any large number of incubation periods; these were excessively brief. Charles Bendire (1892–1895) played the key role in the field of reporting incubation periods in North America. He assigned about 28 days to the larger hawks (including Golden Eagle) and

owls, and graded down to about 21 days the incubation periods for smaller raptors and even to about 14 days for the Elf Owl. Some of his periods for cuckoos and passerines were too long. The majority of his guesses were wrong. Yet they have been accepted as facts up to the present. They form the chief basis for incubation periods of North American birds in our most quoted lists, state books, and other compilations.

No reliance can be placed on the lists of incubation periods published by Burns (1915) and Bergtold (1917).

Careful studies have been made on a certain number of species. Skutch (1945) has published incubation and nestling periods of a large number of Central American birds, and Kendeigh (1952) gives much reliable material. Persistent errors in this field concerning 21 New World species are summarized.

Neither longevity nor temperature of the parent is correlated with length of incubation. Within a group, size of egg may or may not have an influence. In general, length of incubation cannot be said to depend on size of bird or egg. Long incubations are found where the brood runs little danger. Heinroth considered slow development a primitive trait, but Lack suggests it may have evolved in some forms in response to an uncertain food supply. The critical factor determining length of incubation is rate of development of the embryo.

The principal figures in this tragedy of errors—Aristotle, Bechstein, the Naumanns and Bendire—assumed that length of incubation must correspond to size of bird or egg, and because of their prestige, this assumption was unquestioningly accepted by the majority of subsequent writers. In the search for truth it is essential to demand the evidence.

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