Introduction

Information on the hour of day that birds lay their eggs is important for an understanding of reproductive biology. Laying times may influence the budgeting of time for foraging, territory defense, singing, mate guarding and copulation, and defense of nests against predators and brood parasites. 

Only a few studies, however, have addressed these issues in detail, despite the fact that variation in laying times among species of birds was noted more than a century ago; in fact, accurate laying times of most species have not been determined. My interest in laying times arose during studies, with my students, of interactions between the parasitic Brown-headed Cowbird \((Molothrus ater)\) and its host species, conducted mostly in and adjacent to the dune-ridge forest at Delta Marsh, Manitoba. Results from studies elsewhere suggested that the timing of laying by cowbirds and by their hosts influenced decisions taken by hosts whether to reject parasitism. 

Laying times were determined by direct observations of laying females on nests, from blinds aided by binoculars and spotting scopes when necessary, of 22 species of passerine birds, including the parasitic Brown-headed Cowbird \((Molothrus ater)\) and its host species, conducted mostly in and adjacent to the dune-ridge forest at Delta Marsh, Manitoba. Results from studies elsewhere suggested that the timing of laying by cowbirds and by their hosts influenced decisions taken by hosts whether to reject parasitism. 

Methods and Results

Laying times of the Mourning Dove.—Mourning Doves typically lay clutches of two eggs. Cowbirds laid their eggs consistently during a 25-minute window about 30 minutes before sunrise, whereas the average laying times of the other species ranged from a few minutes after sunrise through mid-morning and early afternoon.
Marsh,\textsuperscript{22} Manitoba (50°11′ N, 98°19′ W), between 30 May and 23 June 1992. Laying times were determined by locating nests containing one egg and checking them on the next day beginning about 08:00 hr (all times CST), which is about 3.5 hours after sunrise, and then inspecting the nest every two hours or so the same day until the next egg was laid. The laying times, all after sunrise (SR + minutes), were calculated as the midpoint between the two nest inspections that bracketed the laying event.\textsuperscript{1,2} To determine the exact time of sunrise at Delta Marsh for the days in 1992 on which I recorded laying, I used the 1991 Observer’s Handbook of the Royal Astronomical Society of Canada because sunrise times for a given latitude exhibit little year-to-variation in the temperate zone. The sunrise times ranged from 04:30 hr (30 May 1992) to 04:23 hr (23 June 1992).

A Mourning Dove was flushed from the nest during all but two nest inspections. In all cases, the second egg was laid the day after the first egg was first observed, although it cannot be construed from this that the eggs were laid on consecutive days. The number of hours that elapsed between laying of the first and second eggs, i.e., the laying interval, was not recorded for any of the nests because the time of laying of the first eggs were not determined. The average laying time of second eggs at eight Mourning Dove nests was SR + 243 ± 11.8 (SE) minutes (08:35 hr; i.e., 4 hours, 18 minutes after sunrise) with a range of SR + 218 minutes (08:00 hr; 3 hours, 36 minutes) to SR + 316 minutes (09:38 hr; 5 hours, 16 minutes). Of the 24 species whose laying times were determined at Delta Marsh,\textsuperscript{5} the Mourning Dove was one of nine species that laid eggs well past sunrise.

Figure 1. Mourning Dove brooding two young, dune-ridge forest, Delta Marsh, Manitoba, June 1981.

Laying times of the Passenger Pigeon.—Passenger Pigeons apparently laid only clutches of one egg,\textsuperscript{23} thus making it more difficult to determine laying times in the field because the day on which the single egg was to be laid would not be known for
sure and, hence, empty nests likely would have to have been checked leading up to the actual laying day. This difficulty is comparable to determining laying times of first eggs of the Mourning Dove and most other species of birds. Fortunately, a sample of laying times of the Passenger Pigeon was determined from captive females that sat on completed nests intermittently for up to two days before laying, thus alerting the observer that an egg was about to be laid. These early observations of laying in captivity provided insight into the time of day of laying in the Passenger Pigeon.

A. W. Schorger’s compilation of information on the former distribution and fragmentary details of the biology of the extinct Passenger Pigeon, published in The Passenger Pigeon, Its Natural History and Extinction, summarized observations of the time of day of egg laying. These data, in remarkable detail, were based on observations of captive birds made between 29 July 1896 and 31 July 1898, and published posthumously by C. O. Whitman in 1919. Ten eggs for which the hour of laying was determined were laid in the late afternoon between approximately 16:00 hr (SR + 11.2 hours) on 29 July 1896 and 18:25 hr (SR + 13.5 hours) on 22 April 1897, presumably CST as Whitman’s aviaries were located near Chicago, Illinois; eight additional eggs were indicated only as laid in the afternoon. Sunrise times for dates of observations in 1897 and 1898 for the Chicago area were obtained from the website of the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/AA/).

Whitman elegantly described (p. 48) a female Passenger Pigeon during the act of laying, at 17.25 hr (SR + 13.4 hours) on 28 April 1897: “[The female] moved forward in the nest and held herself in a more or less erect position. When she dropped the egg she lifted her wings
a little, just as I saw her do in laying a previous egg [in another nest]. Another Ectopistes female stood up for 5 minutes after laying and then sat on the egg. She gave a few low calls shortly before laying.” This is all we will ever know about the laying times of the Passenger Pigeon, which was once one of the most abundant species of bird in North America.24 We must assume that these times reflect the actual time of day that Passenger Pigeons laid their eggs in the wild.

Discussion

In addition to influences that laying times have on the breeding biology of birds, there are practical reasons for accurately determining them, particularly in species such as the Mourning Dove and other species that lay several hours after sunrise. In many studies, nests are inspected each morning, likely preceding laying of first and subsequent eggs, thus resulting in eggs being recorded a day later than the one on which they were actually laid. This problem has apparently hampered attempts to determine accurate laying intervals of the Mourning Dove, and other species of dove and pigeon, because considerable variation in this interval has been recorded, some of it likely erroneous.

Whitman also observed captive Mourning Doves, and recorded eight females laying their first eggs in the afternoon, between 17:00 hr (SR + 12.4 hours) on 2 June 1898 and 18:07 hr (SR + 14 hours) on 24 April 189. These laying times were similar to those he determined for the Passenger Pigeon’s single egg.16 Whitman’s observations are still the only accurate determinations of the hour of laying of the Mourning Dove’s first eggs; other authors, however, have alluded to the laying of this egg in the afternoon.25, 26, 27 Whitman also recorded laying times of four second eggs of the Mourning Dove, all in the morning, ranging from 06:35 hr (SR + 1. 5 hours) on 28 April 1897 to 09:00 hr (SR + 3 hours) on 20 August 1897;16 these times were similar to the laying times of second eggs of Mourning Doves recorded at Delta Marsh. Whitman concluded that Mourning Dove eggs were laid 38-40 hours apart, or on alternative days. Laying the only or first eggs late in the afternoon may be typical of other species of dove and pigeon,27 but determination of these times require nest inspections that bracket egg laying to confirm them.2

It is problematic when authors stated that first eggs were laid in the late afternoon or evening, followed the next morning by the second eggs—an interval less than 24 hours. A minimum of 24 hours or more, without exception, is required for production and laying of successive eggs in birds.28 If the Mourning Dove does lay its first egg in the evening, as the strongest evidence suggests,16 most clutches are likely laid on alternate days. Confusion exists regarding the reporting of this interval, however, because laying times or laying dates of the first eggs, and (or) possibly also the second eggs, were not accurately determined. At the extreme are results from a study of wild and captive Mourning Doves in Iowa, in which it was reported (p. 380) “that eggs were laid when mature regardless of the time of day” (McClure 1943). Times were not provided to support of this variation in laying time, despite detailed notes given on the females’ behaviour before and after the moment of laying. Apparently most eggs were laid 24 hours apart in this study, but several intervals of only 12 hours were also reported.26 The 12-hour intervals were obviously recorded in error, unless this represents a heretofore unappreciated aspect of egg production and laying that requires more careful study (The 12-hour interval was repeated in the most recent account of this species’ biology.)21, Goodwin27 (p. 178) cryptically
questioned such short laying intervals, stating of the Mourning Dove that “the first [egg] is laid in the evening and the second in the early morning of the next day but one after”. What Goodwin meant by “… but one after” is not clear but it suggests that he thought that the second eggs were probably laid two mornings later, thus laid on alternate days.

Other workers reported an interval of about 30 hours between laying of successive Mourning Dove eggs, but this also seems unrealistic, if the first eggs are laid in the evening and the second eggs are laid in the morning. In a detailed study of captive breeding Mourning Doves in Illinois, 17 of 27 clutches (63%) were produced on alternate days and 10 (37%) were laid on consecutive days. Actual laying times were not given in any of these cases and, hence, the intervals cannot be verified. In the closely related White-winged Dove (Z. asiatica), first eggs were laid in the afternoon and second eggs in the morning of the third day, that is, about 36 hours apart, thus, on alternate days. Further studies of laying times of the Mourning Dove and other species of dove and pigeon, and birds in general, are needed to fully understand a species’ breeding biology and to dictate schedules of nest inspection and other activities by researchers to avoid disturbing laying females as much as possible.

As laying times of each species were determined on my study site at Delta Marsh in the late 1980s and early 1990s, students and I adjusted schedules of nest searching to occur after, or in some species that laid later in the day, before each species was expected to lay, so as not to disturb females in the act of laying. Mourning Doves are particularly challenging in this regard, however, as adults sit tightly on their nests after the first egg has been laid, thus leaving little opportunity to inspect nests without disturbing them. Knowing the range of laying times, however, allows field workers to inspect nests well after or before laying and minimize the possibility that nests will be deserted.

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