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Timing of Egg Laying in Yellow Warblers

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Many aspects of the breeding biology of wild birds have been studied thoroughly, but surprisingly little information has been obtained on when birds lay their eggs. For instance, few data exist on the time of day eggs are laid (Scott 1991), and the factors that control laying time are uncertain even for domestic species (Sharp 1980). How long females spend in their nests while laying each egg (i.e. laying bout; Sealy et al. 1995) and the interval between successive eggs in a clutch (i.e. laying interval; Schubert and Cooke 1993) are also poorly known (Scott 1991, Ricklefs 1993). Laying time and interval are important aspects of a species' breeding biology because they have implications for the energetics of the laying female (Astheimer 1985), hatching asynchrony of the resulting clutch (Ricklefs 1993), timing of brood parasitism (Scott 1991, Meijer 1992, Neudorf and Sealy 1994), and timing of pair and extrapair copulations (Birkhead 1988; but see Birkhead et al. 1996).

Repeated inspection of nests has been the technique most frequently employed to obtain an estimate of laying time (see Skutch 1952). Using this technique, the time a female lays her egg is bracketed by visits before and after the egg has been laid, thereby providing an estimate of laying time. Laying times may be determined more accurately by observing nests continuously, either from a blind or with a video camera (Muma 1986, Sealy et al. 1995, Haftorn 1996). Direct observation also allows researchers to record other behaviors at the nest (Sealy et al. 1999) and to determine details of the act of oviposition (Nolan 1978, Sealy et al. 1995, Haftorn 1996).

Laying times of passerines vary among species from several hours before sunrise until afternoon or early evening (e.g. Rosengren 1993, Scott 1993, Frith 1994). Likewise, different species of passerines have characteristic intervals between successive eggs in a clutch, ranging from approximately one day (23 to 27 h) to 48 h (e.g. Astheimer 1985, Morton and Pereyra 1985, Marchant 1986, Meijer 1992). In other species, laying intervals vary within clutches. For example, eggs may be laid successively earlier for the first half of the clutch and successively later thereafter (Feare et al. 1982, Rosengren 1993), or the last egg may be laid much later than the others (Nolan 1978, Meijer 1992). The interval between laying of successive eggs in a clutch, in conjunction with the onset of incubation, contributes to the hatching spread within a clutch (Clark and Wilson 1981, Ricklefs 1993). The amount of time spent laying also varies among species, being dramatically shorter in brood parasites (Sealy et al. 1995).

As part of a larger project on interactions of hosts and the parasitic Brown-headed Cowbird (*Molothrus ater*), we gathered information on the laying behavior of Yellow Warblers (*Dendroica petechia*), a common host of the Brown-headed Cowbird (DellaSala 1985, Sealy 1995). We observed Yellow Warbler nests and recorded laying times, laying-bout duration, and laying intervals for successive eggs in each clutch, and in many cases we recorded the actual time of oviposition. Our objective was to determine the egg-laying patterns of a wild bird species over its entire clutch. We also address several hypotheses proposed to explain both interspecific and intraclutch variation in egg-laying behavior.

Methods.—We observed Yellow Warbler nests in 1993 on the forested dune ridge that separates the Delta Marsh and Lake Manitoba (50°11′N, 98°19′W). Descriptions of study area and nesting habitat are available in MacKenzie (1982) and MacKenzie et al. (1982). Beginning in late May, we located and numbered Yellow Warbler nests under construction. On the evening before a nest watch, we set up a blind close enough to the nest to allow detailed observation of the female without influencing her behavior. We entered the blind the next morning a few minutes before 0330 (CST) and watched nests until one hour had elapsed after the end of the laying bout. Nest watches began before nests were lined to ensure that we would observe the laying of the first warbler egg (i.e. laying day, or LD 1) and each subsequent egg through the last egg of the clutch (LD 4 in 4-egg clutches, LD 5 in 5-egg clutches), unless the nest failed before clutch completion. Additional details pertaining to nest watches are given elsewhere (Neudorf and Sealy 1994; Sealy et al. 1995, 1999).

All behaviors were recorded to the nearest minute. We recorded the time females entered the nest to lay and the time they left the nest after laying. The total

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time females spent in the nest while laying was termed the "laying bout" (Sealy et al. 1995). "Oviposition" refers to the act of laying when the female expelled the egg. The time females began oviposition was usually noticeable because females lifted the front end of their bodies in the nest, increased their respiratory movements, and contracted their abdominal muscles while their eyes were half or fully closed (see Nolan 1978, Tullet 1985, Haftorn 1996). Using these cues, we noted the time females rose in the nest to begin extruding the egg (henceforth initiation of oviposition) and the time females repositioned themselves low in the nest after oviposition. The "oviposition bout" was the total time the female spent expelling the egg.

The time females arrived at their nests was calculated relative to sunrise (SR) using Scott's (1991) method. To determine the exact time of sunrise at Delta Marsh for the days Yellow Warbler nests were observed, we used the 1991 *Observer's Handbook of the Royal Astronomical Society of Canada* (sunrise times for a given date exhibit little year-to-year variation at temperate latitudes).

Most nests were observed each day during the laying period; however, because of predation some nests were watched for only part of the laying period. Observations at five nests that were parasitized by Brown-headed Cowbirds were deleted from the data set because the parasitism event or the parasitic egg could influence Yellow Warbler laying. Although some species characteristically lay very early in the morning while still roosting in their nests (Haftorn 1979, Galati and Galati 1985), most roosting Yellow Warblers left the nest at least once before laying (84 of 88 cases). Therefore, the minority observations were deleted. One female arrived at her nest to lay extremely early relative to other Yellow Warblers (arrival at 0327, 36 min before the next earliest female; oviposition began at 0407); this outlier also was deleted.

All variables were tested for normality using the Shapiro-Wilk test. All variables were normally distributed, with the exception of duration of the laying and oviposition bouts. Data from 4- and 5-egg clutches were examined separately and combined if found to be statistically equal. Laying bouts did not vary significantly between clutch sizes over the entire laying cycle (Fisher's protected least square means $X_r = 1.29$, $P = 0.29$). Because laying bouts on the day the last egg was laid did not differ significantly between clutches (Wilcoxon signed-rank test, $S = 27.5$, $P = 0.43$), we pooled laying bouts for 4-egg clutches on LD 4 with those for 5-egg clutches on LD 5. Laying-bout data for 4- and 5-egg clutches were pooled for LD 1–3; thus, LD 4 represents laying-bout data for 5-egg females only. No other variables differed significantly between 4- and 5-egg clutches by laying day, so data for these variables were pooled along with observations at four nests with 3-egg clutches and where clutch size was not determined because the nest failed ($n = 25$).

Once data were pooled by clutch size, we used linear regression to determine the relationship that sunrise and laying date had on the time females arrived at the nest to lay and on the time of oviposition. Only data for each female's first egg were used in the regression analysis. Differences between laying days for the pooled data were tested using parametric ANOVA and nonparametric Kruskal-Wallis tests. Multiple comparisons were made using the nonparametric Tukey test (Zar 1996).

Results.—Females entered the nest to lay after sunrise throughout the laying cycle and began oviposition a few minutes later (Figs. 1A, 1B). The sun rises progressively earlier each day at Delta Marsh until 14 June, and then rises later each day beginning on 22 June (range 0422 to 0432 over the breeding season). No significant relationship was found between sunrise time and the time females arrived at the nest to lay ($F = 0.06$, df = 1 and 28, $P = 0.80$) or began oviposition ($F = 0.29$, df = 1 and 18, $P = 0.60$). Moreover, neither the time of female arrival relative to sunrise (range SR −19 to SR +38) nor the initiation of oviposition relative to sunrise (range SR −15 to SR +50) varied significantly over the laying season ($F = 2.02$, df = 1 and 28, $P = 0.17$; $F = 0.14$, df = 1 and 18, $P = 0.72$, respectively).

Time of female arrival (Fig. 1A) and time of oviposition initiation (Fig. 1B) did not vary significantly over the laying cycle ($F = 0.49$, df = 4 and 82, $P = 0.74$; $F = 0.20$, df = 4 and 54, $P = 0.94$, respectively). Therefore, the interval between laying of successive eggs was approximately 24 h. Laying bouts, however, varied significantly over the laying cycle ($H = 12.66$, df = 4 and 82, $P = 0.013$; Fig. 2A). Laying bouts on LD 5 were significantly longer than those on LD 1 (Tukey test, $P < 0.05$). The length of the oviposition bout did not vary significantly over the laying cycle ($H = 3.91$, df = 4 and 44, $P = 0.42$; Fig. 2B).

Discussion.—Egg laying in Yellow Warblers followed a rigid schedule that showed little variation over the laying cycle. On average, females entered their nests to lay within 10 min after sunrise, and oviposition occurred over an interval of about 2 min midway through the laying bout. The amount of time females spent in the nest during laying remained constant throughout much of the laying cycle, increasing significantly only on the day the last egg was laid when incubation becomes fully established (McMaster and Sealy unpubl. data).

Why do female Yellow Warblers have such a rigid egg-laying schedule? Laying time in Prairie Warblers (*Dendroica discolor*) also is highly constrained, with females having little or no control over when oviposition occurs (Nolan 1978). The time that Yellow Warblers at Delta Marsh began oviposition relative to sunrise ($\bar{x}$ = SR +18.3 min on LD1) was similar to that for conspecifics in southern Ontario ($\bar{x}$ = SR

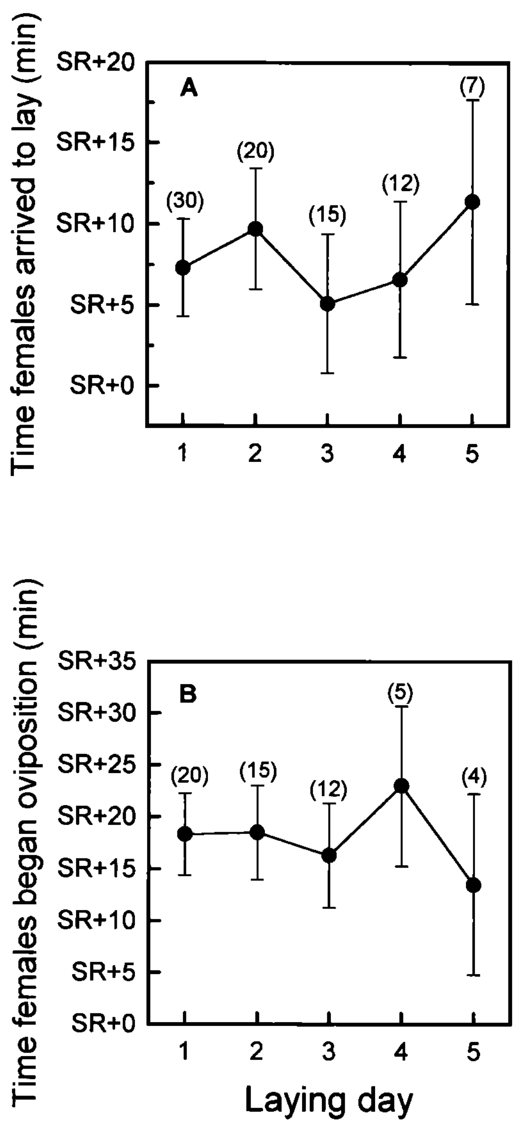

FIG. 1. Mean time (sunrise [SR] ± SE) female Yellow Warblers arrived at their nests to lay (A) and began oviposition (B) for each day of the laying period. Sample sizes in parentheses.

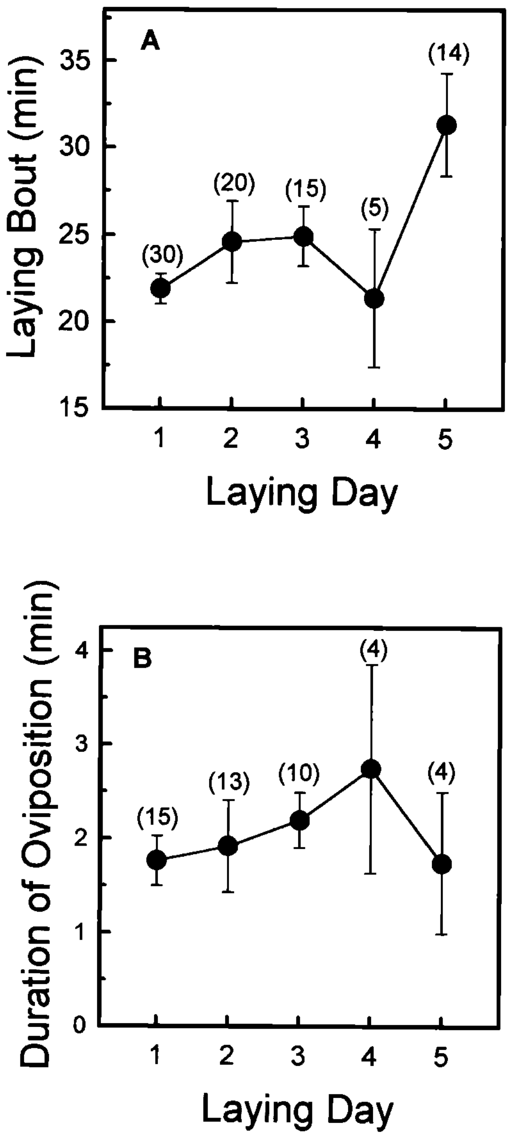

FIG. 2. Mean duration (± SE) of Yellow Warbler laying bouts (A) and oviposition (B) for each day of the laying period. Sample sizes in parentheses.

+18.8 min; Scott 1991), Prairie Warblers in Indiana ($\bar{x}$ = SR +34 min; Nolan 1978), and four species of tits in Europe (SR +1 to 43 min; Haftorn 1996). Data on actual laying times show that Yellow Warblers at Delta Marsh lay earlier in the morning than other parulids at more southerly latitudes (Skutch 1952, Nolan 1978) but later than sylviid warblers and tits at more northerly latitudes (Kuusisto *in* Rosengren 1993, Haftorn 1996). The apparent correlation between sunrise and laying time for these species at various latitudes suggests that sunrise is a cue for the timing of egg laying. Indeed, the time female Red-winged Blackbirds (*Agelaius phoeniceus*) and American Robins (*Turdus migratorius*) begin oviposition is significantly correlated with the time of sunrise (Muma 1986, Weatherhead et al. 1991). The lack of correlation between laying time and sunrise observed for other species (Nolan 1978, Rosengren 1993, this study) may be due to lack of variation in sunrise times. Determination of laying times of a single species at latitudes with significantly different sunrise times might determine the role sunrise and other variables have in influencing the timing of egg laying.

Compared with other species, Yellow Warblers laid during a restricted period of the day (Yellow Warbler oviposition began over a 65-min interval on LD1; European Starlings [*Sturnus vulgaris*] lay from 0600 to 1200; Feare et al. 1982, Meijer 1992) and showed little variation in laying time throughout the clutch (average oviposition time varied by 4 min in Yellow Warblers vs. ca. 80 min in European Starlings; Feare et al. 1982). Therefore, the interval between the laying of successive eggs in the clutch was within minutes of 24 h. Laying intervals within clutches vary from about 23 to 48 h in passerines (e.g. Morton and Pereyra 1985, Marchant 1986, Meijer 1992, Rosengren 1993, Oppenheimer et al. 1996). Laying intervals may be influenced by weather and food availability (Bryant 1975, Nilsson and Svensson 1993), rate or amount of yolk deposited in individual follicles (Astheimer 1985, Meijer 1992), or changes in levels of circulating hormones associated with regression of the female reproductive tract late in egg laying (Ricklefs and Hussell 1984, Meijer 1992). Weather does not appear to influence laying intervals in parulids (Nolan 1978, McMaster et al. unpubl. data), nor are last-laid eggs laid later in the morning, as predicted by Meijer's (1992) reproductive-tract regression hypothesis. Although Yellow Warbler egg mass increases with laying order in the clutch (Hébert and Sealy 1993), in contrast to the findings of Meijer (1992), neither the time female warblers arrived to lay nor began oviposition varied significantly over the laying cycle.

Although the dearth of information on laying times and laying intervals for many species makes generalizations risky, passerines appear to fall into two groups based on laying patterns: (1) species that lay at sunrise show little variation in laying time and have large egg-to-body mass ratios; and (2) species that lay throughout the day show significant variation in laying time and have small egg-to-body mass ratios (Scott 1991, Oppenheimer et al. 1996). Clearly, each of these laying patterns is a result of the time at which the first egg in the clutch is laid and the laying intervals among subsequent eggs. Therefore, hypotheses explaining laying patterns apply to both laying time and laying interval: (1) some selection pressures (fragile eggs [Schifferli 1979]; foraging efficiency [Norberg 1981, Meijer 1992]; behavioral strategy [Weatherhead et al. 1991]; predation [Watson et al. 1993]) act to maintain a certain pattern of laying in the species; or (2) laying time is dictated by the physiology of a species and may simply be an ancestral trait (Oppenheimer et al. 1996). A phylogenetic comparison of a wide range of parameters associated with egg laying for a number of species within a community could elucidate patterns of variation in the daily timing of egg laying among species.

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