

JOURNAL OF FIELD ORNITHOLOGY

Published by the
Association of Field Ornithologists

VOL. 75, NO. 2

Spring 2004

PAGES 113–208

J. Field Ornithol. 75(2):113–122, 2004

A comparative analysis of laying times in passerine birds

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Received 7 April 2003; accepted 22 September 2003

ABSTRACT. We documented the time of day of laying and the total time spent on the nest during laying (laying bout) in 21 species of passerine birds and the brood-parasitic Brown-headed Cowbird (*Molothrus ater*) at Delta Marsh, Manitoba, between 1989 and 1995. Brown-headed Cowbirds laid on average 31.2 min before sunrise, whereas mean laying times of the other species ranged from 11.3 min after sunrise through early afternoon. Species that laid later in the day tended to spend more time on their nests during laying. Smaller species tended to lay earlier in the day and had significantly shorter laying bouts than larger species. Future studies accounting for variation in foraging and reproductive behavior and predation risk between taxonomic groups may explain additional variation in laying time and duration.

SINOPSIS. Anácomparativo del tiempo de puesta en paserinos

Documentamos el tiempo de puesta y el periodo total de tiempo que pasa la hembra en el nido en 21 especies de paserinos y en un tordo parasítico (*Molothrus ater*). El trabajo se llevó a cabo de 1989a 1995 en el marjal del delta de Manitoba. En promedio, el tordo hizo su puesta 31.2 minutos antes de salir el sol, mientras que el tiempo promedio de puesta de otros paserinos resultó ser desde 11.3 minutos luego del amanecer hasta temprano en la tarde. Hubo la tendencia de pasar ms tiempo en el nido entre las especies que pusieron tarde en el día. También hubo proclividad, entre las especies más pequeñas, a poner ms temprano en el día y pasar menos tiempo en el nido que las especies de mayor tamaño. Estudios futuros que tomen en cuenta variaciones en la conducta reproductiva y de forrajeo, además del riesgo de ser depredado (entre diferentes grupos taxonómicos), pudieran muy bien explicar otras variaciones en la hora de puesta y el periodo de tiempo que tome la misma.

Key words: egg-laying bout, egg-laying time, Passeriformes

Knowledge of the hour of laying is important for a complete understanding of the breeding biology and mating systems of birds. The laying times of birds may influence the budgeting of time for foraging, territorial defense, singing,

mate-guarding and copulation, and defense against inter- and intraspecific brood parasitism (e.g., Skutch 1952; Schifferli 1979; Feare et al. 1982; Mace 1986; Scott 1991; Weatherhead et al. 1991; Birkhead and Møller 1992; Neudorf and Sealy 1994; Slagsvold et al. 1994; Perrins 1996). Nevertheless, the evolutionary implications of laying times of wild birds have only just begun to receive attention.

Long ago, naturalists were aware that many songbirds laid their eggs in the morning (e.g., Ord 1836; Payne 1898), but as anecdotal reports accumulated, it became evident that species lay

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at characteristic times throughout the day (e.g., Skutch 1952, 1976; Seel 1973; Schifferli 1979; Feare et al. 1982; Galati and Galati 1985; Scott 1991; Rosengren 1993; Frith 1994). Workers now focus on the causes of variation in laying times among species and consistency within species, thus building upon previous speculations about the possible adaptive value of laying times (e.g., Schifferli 1979; Scott 1991, 1993; Weatherhead et al. 1991; Watson et al. 1993; Meek and Robertson 1995; Slagsvold 1996; McMaster et al. 1999). Five explanations have been presented for the adaptiveness of laying eggs at a particular time of the day: (1) avoidance of egg breakage (Schifferli 1979), (2) enhanced foraging efficiency due to reduction in body mass after laying (Meijer 1992; sensu Norberg 1981), (3) maximization of the probability of fertilization occurring during the female's insemination "window" (e.g., Cheng et al. 1983), (4) reduction of risk of egg predation (Watson et al. 1993), and (5) variation among species that reflects phylogeny but has no selective advantage (Oppenheimer et al. 1996).

Schifferli (1979) hypothesized that early-morning laying reduces the likelihood that birds will damage their fragile eggs before beginning their normal daily activities. This hypothesis predicts that smaller passerines lay in the morning before becoming active, whereas larger passerines with thicker-shelled eggs (Ar et al. 1974; Spaw and Rohwer 1987) are free to lay later in the day. In House Sparrows (*Passer domesticus*), Schifferli (1977) showed that the shell was laid down progressively from around midday until the early hours of the following morning. Because the shell is still soft during the daylight hours, oviducal eggs of birds handled then seemed to resist damage, but eggs of birds captured early in the morning often were irreparably damaged. Schifferli (1979) concluded that incorporation of calcium into the shell while inactive at night allowed birds to be more active during daylight hours (see also Fogden and Fogden 1979). However, larger females may place greater stress on eggs and therefore risk to the egg may not vary with size.

Meijer (1992) suggested that the reduction in total body mass (body mass + egg mass) after laying will enhance foraging efficiency. This hypothesis predicts that smaller birds lay early in the morning (Scott 1991) because of their larger egg-to-body mass ratio. Although

this idea has not been tested, it is known that some small passerine birds do not lay early in the morning (Schifferli 1979). Indeed, Weatherhead et al. (1991) found that female American Robins (*Turdus migratorius*) were equally likely to forage before and after laying. Because the American Robin is a relatively large passerine, however, these observations provide a poor test of this hypothesis.

In the hour following the laying of an egg, the next egg in the sequence is fertilized (Birkhead 1988). Predictions have been made regarding the ideal time for copulation and mate-guarding in relation to laying time (e.g., Møller 1987; Weatherhead et al. 1991; Sheldon and Burke 1994), but tests of these have been hampered by the lack of information on the precise times of laying (Schulze-Hagen et al. 1995; Neudorf 1996). Weatherhead et al. (1991) speculated that the time of laying may reflect selection that favors a particular time for fertilization, which in turn may reflect the best time for copulation. Early-morning laying has been considered the optimal time for copulation to take advantage of the female's insemination window (Cheng et al. 1983; but see Birkhead et al. 1996).

In a population of Common Eiders (*Somateria mollissima*), Watson et al. (1993) did not detect a strong selective advantage to laying around midday based on the timing of egg predation. Instead, these authors concluded that selection may act more strongly on laying intervals than on laying times so that eiders lay at different times and avoid predation. Thus, laying times may be constrained by laying intervals, rather than the other way around. Oppenheimer et al.'s (1996) results support this idea. Dusky Flycatchers (*Empidonax oberholseri*) laid throughout the day and laid eggs more than 24 h apart, often skipping a day. White-crowned Sparrows (*Zonotrichia leucophrys*) laid over three hours in successive mornings consistently at 24-h intervals. Oppenheimer et al. (1996) interpreted the differences in laying times and intervals largely as byproducts of the physiological processes involved in egg formation, ancestral to each taxon. The longer the laying interval, the later successive eggs in the clutch are laid, until a day is skipped during laying, after which the next egg is laid earlier. Unexplained are species that consistently lay at 24-h intervals and lay at specific times of the day.

Without mechanical devices of the types used by Haftorn (1966, 1996) to determine laying times of tits (Paridae), most workers have visited nests twice daily, before and after the eggs are laid, thus bracketing the time of laying (e.g., Skutch 1952; Scott 1991; Weatherhead et al. 1991; Meek and Robertson 1995; Oppenheimer et al. 1996). This method approximates the actual laying time, but it does not provide any information on the behavior of females and males leading up to, during, and after laying, or the time it takes to lay eggs (laying bout; Sealy et al. 1995). Although nests can be monitored using video systems (McQuillen and Brewer 2000), laying times of birds can be determined by watching nests from the time the female arrives to lay until she leaves the nest after laying. A few workers have used this labor-intensive method to determine laying times, but single species were usually involved and in most cases sample sizes were small (e.g., Haftorn 1966, 1996; Nolan 1978; Muma 1986; Rosengren 1993).

As part of a larger study on the interactions between parasitic Brown-headed Cowbirds (*Molothrus ater*) and their hosts, we gathered information on the laying times of the cowbird and 21 species of passerine birds by watching nests during the laying period. With the most extensive data set on laying times to date, our objective was to quantify variation in laying times within and among species and to determine whether relationships existed between laying time, laying bout, body mass, and egg size that could stimulate further research into the evolution of laying times.

METHODS

Nest observations. From mid-May to July, 1989 through 1995, we determined laying times of birds nesting in marsh-edge habitat at Delta Marsh, Manitoba (50°11'N, 98°19'W). Details of the study area and bird community are provided by Sealy (1980) and MacKenzie et al. (1982). We found nests by searching the habitat and observing behavior of nesting birds. Using Muma's (1986) protocol, we monitored most nests daily until the first egg was expected to be laid the next day. An observation blind was then set up for observations the following morning, and we usually used binoculars or a 20× telescope to observe the nest. The blind

was placed far enough away from the nest to avoid interfering with the laying female's normal behavior. The morning the female was expected to lay her second or next egg, we approached the nest a few minutes before 03:30 CST and inspected it to confirm that no additional eggs had been laid. The nest was then watched to determine the time the female arrived to lay and the time she departed after laying. We then confirmed the presence of the new egg. Often the female was on the nest when our observations began, whether at 03:30 or later (Neudorf and Sealy 1994). At these nests, we waited until the female left the nest, recorded the time, and then inspected the nest to record its contents. As some females returned to their nests several times for varying lengths of time before finally returning to begin the laying bout, we checked nests after each departure so that the amount of time spent on the nest during laying could be measured. The moment each female finally arrived at the nest to lay was considered the beginning of the laying bout and was taken as the time of day of laying, even though the egg usually was not laid until several to many minutes later (D. G. McMaster et al., unpubl. data). At many nests, the actual moment the female laid was evident when she rose in the nest (Nolan 1978). At some nests where only the time of day of laying was determined, we began our observations after sunrise, but before the females had arrived to lay.

Laying time calculations. Using Scott's (1991) method, we calculated the time of arrival at the nest to lay in relation to sunrise (SR). To determine the exact time of sunrise at Delta Marsh, Manitoba, for the days on which we watched nests, we used the 1991 Observer's Handbook of the Royal Astronomical Society of Canada. As sunrise times exhibit little year-to-year variation, we used the 1991 issue for all seven years of our study. Sunrise ranged from 04:38 to 04:20 CST over the dates we observed nests. We recorded times of laying as the mean number of minutes (\pm SE for sample sizes greater than 5) before sunrise (SR - min) or after sunrise (SR + min). Laying bouts are from Sealy et al. (1995) and this study, female body masses are from Dunning (1993), and egg measurements are from Bent (1942, 1958), Briskie and Sealy (1990), Moskoff (1995), and S. G. Sealy (unpubl. data). We calculated egg volumes using the formula:

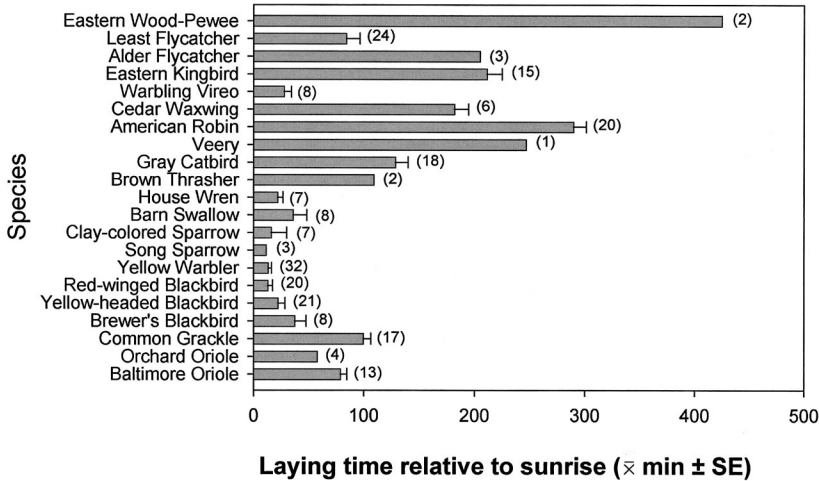


Fig. 1. Mean laying times relative to sunrise (min ± SE, N in parentheses) for 21 species of passerines.

$$V = kLB^2, \tag{1}$$

where $k = 0.515$, $L =$ length, and $B =$ breadth (Hoyt 1979), which is also a good approximation of egg mass (van Noordwijk et al. 1981).

Comparative methods. Comparisons across species may be confounded by common phylogenetic ancestry (Harvey and Pagel 1991; Bennett and Owens 2002). To produce phylogenetically independent data, we calculated standardized linear contrasts (Felsenstein 1985; Harvey and Pagel 1991) using Comparative Analysis of Independent Contrasts (CAIC) by Purvis and Rambaut (1995). We omitted the Brown-headed Cowbird from the analyses because the values for laying time and laying bout were extreme outliers (see Appendix 1 for raw data for all species). To standardize contrasts we assumed that lengths of branches in the phylogeny were of equal length, which represents a punctuated model of evolution. However, results did not differ qualitatively if a gradual model of evolution was assumed. The higher nodes of our phylogeny were based on the molecular phylogeny of Sibley and Ahlquist (1990) and resolution near the tips was derived from other published phylogenetic data (Dunn et al. 2001). All regressions for the purposes of controlling for phylogeny were forced through the origin (Harvey and Pagel 1991). However, the actual slopes of the regression lines forced through the origin may be misleading and were not interpreted (Harvey and Pagel 1991:160).

Statistical analyses. Egg volume was

highly correlated with body mass ($r = 0.98$, $N = 21$, $P < 0.0001$), as noted elsewhere (Hoyt 1979), so we excluded egg volume from the analyses. However, egg volume-to-body mass ratio declined significantly with increasing body mass at the species level ($R^2 = 0.79$, $N = 21$, $P < 0.0001$), indicating that smaller species lay larger eggs for their size than do larger species. So we estimated residual egg mass from the residuals of the regression of egg mass on body mass. We log-transformed the data on laying time, laying bout, egg mass, and body mass for the 21 species prior to analysis in order to render the data normally distributed.

RESULTS

Laying times and bouts. The mean laying times of the 21 species ranged from several minutes before sunrise through early afternoon (Fig. 1). Brown-headed Cowbirds laid 31.2 min before sunrise and spent on average 0.8 min on host nests while laying. Species within the same family generally laid their eggs around the same time of day, but there were exceptions. All species in the Vireonidae, Certhiidae, Hirundinidae, and Fringillidae (except for Common Grackles and Baltimore Orioles) laid within one hour of sunrise, some within 30 min. Both species in the Sturnidae laid about two hours after sunrise. Most species in the Tyrannidae, Bombycillidae and Muscicapidae laid three or more hours after sunrise. One flycatcher, the

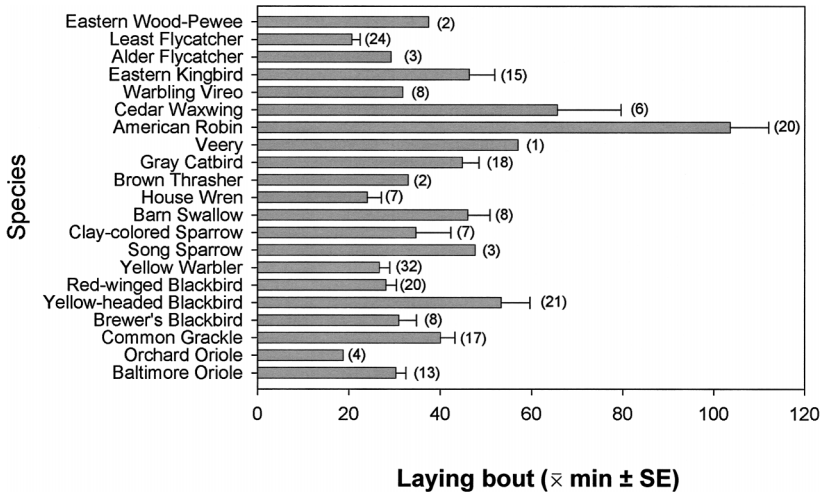


Fig. 2. Mean laying bout (min \pm SE, N in parentheses) for 21 species of passerines.

Eastern Wood-Pewee, laid exceptionally late, in early afternoon. Among the five species of blackbirds, average laying times ranged from 13 min (Red-winged Blackbird) to 99 min (Common Grackle) after sunrise. Mean laying bouts ranged from 18.8 to 103 min among species (Fig. 2), with the mean (\pm SE) overall laying bout for all species being 39.3 (\pm 4.4) min.

Independent contrasts revealed a positive relationship between laying time and laying bout ($P = 0.014$, $N = 17$ contrasts; Fig. 3a). The relationship between laying time and body mass approached significance ($P = 0.07$, $N = 17$ contrasts; Fig. 3b). The negative correlation between laying time and residual egg mass was significant ($P = 0.02$, $N = 17$ contrasts; Fig. 3c). Therefore, species that laid their eggs later in the day tended to spend more time on their nests during laying. Furthermore, larger species tended to lay later in the day than smaller birds. Similarly, species that lay larger eggs relative to their body mass laid earlier in the day.

Laying bout and body mass were significantly positively correlated ($P = 0.018$, $N = 17$ contrasts), but laying bout and residual egg mass were not ($P = 0.12$, $N = 17$ contrasts). Therefore, smaller species tended to lay more rapidly than larger species.

DISCUSSION

Variation in laying times. Our observations confirm the exceptionally early and rapid

laying by Brown-headed Cowbirds (Chance and Hann 1942; Scott 1991). Cowbird behavior may assure that laying occurs before the regular laying period of the hosts (Scott 1991; Neudorf and Sealy 1994). Chance and Hann (1942) speculated that by laying around sunrise, Brown-headed Cowbirds would be less likely to disturb hosts that would be away from their nests foraging before laying their eggs and, hence, less attentive at their nests. On our study area, Brown-headed Cowbirds laid before all potential host species, including the nonparasitic icterids. Therefore early laying by parasitic cowbirds probably is an adaptation for brood parasitism, rather than a primitive icterid trait (Scott 1991). By contrast, some brood parasites lay their eggs after their hosts have laid, possibly to minimize the chances of encountering the nest owners. For example, European Starlings (*Sturnus vulgaris*) parasitized nests around midday, after the nest owners had laid earlier on those mornings (Feare et al. 1984). These authors speculated that this behavior increased the parasites' chances of gaining access to the nests. Although parasitic Cliff Swallows (*Petrochelidon pyrrhonota*) laid from mid-morning through late afternoon, even the earliest of these eggs were deposited after the nest owners had laid, when host nests were left unattended (Brown 1984, Brown and Brown 1989). When parasitizing neighbors' nests, however, the parasites' own nests were unattended and were at risk of parasitism (Brown and Brown 1989).

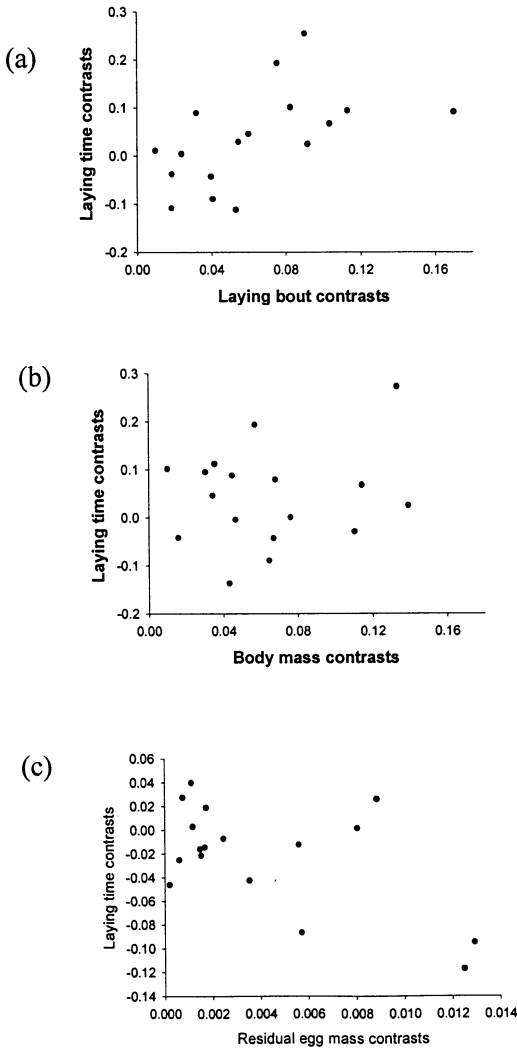


Fig. 3. The relationship between laying time and (a) laying bout, (b) body mass, and (c) egg volume-to-body mass ratio. Points represent independent contrasts.

The other passerine species in our study laid from shortly after sunrise to early afternoon, and were reasonably consistent with published species' laying times where available: Alder Flycatcher (Lowther 1999), Least Flycatcher (Briske 1994), Gray Catbird (Cimprich and Moore 1995), Brown Thrasher (Cavitt and Haas 2000), Cedar Waxwing (Witmer et al. 1997), American Robin (Sallabanks and James 1999), Barn Swallow (Brown and Brown 1999), House Wren (Johnson 1998), Yellow Warbler (Lowther et al. 1999), Clay-colored Sparrow

(Knapton 1994), Red-winged Blackbird (Yasukawa and Searcy 1995), Yellow-headed Blackbird (Twedt and Crawford 1995), Common Grackle (Peer and Bollinger 1997), and Baltimore Oriole (Sealy et al. 1995). Smaller species laid relatively larger eggs than larger species, laid earlier in the day, and took less time to do so than larger species. For example, tyrannids and muscicapids of different body masses laid later in the morning at Delta Marsh, as they do, for example, in the tropics (Skutch 1952). The positive relationship between body mass and laying time confirms the trend noted by Scott (1991) and others. This trend has not been adequately explained, however, although most explanations have invoked enhanced foraging efficiency. Body mass seems to be an important factor in predicting laying time and laying bout.

Previously, we examined laying bout in the context of rapid laying of brood parasites (Sealy et al. 1995), but there is much unexplained variation in laying bouts of nonparasitic species. In general, species that laid later in the day had longer laying bouts, whereas species that laid early may have been under greater time constraints of foraging than those that laid later. Species that lay later presumably have had ample opportunity to forage prior to laying and thus can afford to spend more time on the nest during laying, although it is unclear why a longer laying bout would be advantageous. Perhaps it allows females time to rest after expelling the egg.

Why do laying times vary? Schifferli (1979) hypothesized that songbirds form their eggshells during the night and lay early in the morning to prevent damage to the eggs, at the same time allowing females to make full use of the day for foraging. Perrins (1996) gave other examples. Weatherhead et al. (1991) criticized this idea, pointing out that there is no certainty that normal activity would traumatize an oviducal egg to the same extent as would capturing and handling the female. Indeed, Nolan (1978) did not record damaged eggs laid by Prairie Warblers (*Dendroica discolor*) netted as they arrived at nests to lay; in fact, some females laid eggs in his hand! Female Yellow Warblers are active away from their nests before returning to lay shortly after sunrise (Sealy et al. 2000). The potential for oviducal egg breakage, therefore, seems unlikely to constrain a bird's activity and probably does not influence laying times, even

in small passerines. Do laying times, therefore, vary among groups so that laying conflicts less with foraging?

At issue here is whether foraging around sunrise is important, as many authors have implied. Foraging profitability may be low around sunrise. Kacelnik and Krebs (1982) argued that the profitability of singing at dawn is higher because the profitability of foraging is low due to low light levels. Low temperatures at sunrise may further reduce foraging profitability due to reduced prey mobility at that time. McNamara and Houston (1986) noted that dawn is the time of day at which the greatest number of daylight hours remain and, hence, the cost of eschewing foraging for another activity is lower than at any other time of day. Small, insectivorous birds particularly may lay early in the day to capitalize on the greater availability of their active prey later in the day. Large species such as the American Robin may forage over many hours before laying, possibly because their prey is accessible throughout the day.

Our observations may have implications for mate-guarding, copulation, and timing of fertilization. Weatherhead et al. (1991) suggested that laying time may be a consequence of selection that favors a particular time for fertilization, or, in turn, the best time for fertilization may be the best time for copulation. Thus, solicitations, copulations, and mate-guarding have been expected to be most frequent shortly after laying as fertilization is less successful when there is an egg in the oviduct and is more easily achieved in the insemination window between laying of successive eggs of a clutch (Cheng et al. 1983; Birkhead 1988; cf. Birkhead et al. 1996). Although it would be advantageous to mate during this window, it does not explain why laying times should be as they are.

Examination of recent studies, and re-analysis of data in Cheng et al. (1983), prompted Birkhead et al. (1996) to suggest that all cases of an apparent link between copulation or mate-guarding and laying should be closely scrutinized. They noted that in no studies was the temporal link between copulatory or mate-guarding behavior made explicit because in all studies, except Schulze-Hagen et al.'s (1995), the precise timing of laying was not known. If there is a precise time of day for copulation, in relation to laying, research is needed to identify cues that males use to determine when their

females have just laid. Males cannot rely only on the presence of their females sitting on the nest as an indication of laying because many females sit on their nests many times before actually laying (Sealy et al. 2000). Females that invariably lay around sunrise, however, should be more predictable in their laying times than those that lay at other times of the day (Mace 1986; McMaster et al. 1999).

In this study, body mass and residual egg mass explain variation in laying time and laying bout, but why they do remains unclear. As suggested by Oppenheimer et al. (1996), much of the variation in laying times may reflect phylogeny with no selective advantage. Further comparative studies incorporating factors such as reproductive behavior, foraging behavior, and predation risk may elucidate whether adaptive benefits accrue from variation in laying times and laying bouts in passerine birds.

ACKNOWLEDGMENTS

Order of authorship for DGM and DLHN was determined randomly. We thank the staff of the Delta Marsh Field Station (University of Manitoba) for providing logistical and material support during the field work. The officers of the Delta Waterfowl and Wetlands Research Station and Portage Country Club permitted us to conduct field work on their properties. Ronald Bazin, Warren Bernhardt, Kim Caldwell, Daryl Chudobiak, Marlene Gifford, Sharon Gill, Gloria Goulet, Paula Grief, Percy Hébert, Dorothy Hill, Paul Miller, Adrian Robertson, and Shauna Wiebe sacrificed a lot of sleep to help watch nests. Earlier versions of this manuscript were improved by the comments of Todd Arnold and Patrick Weatherhead. Financial support was provided by Manitoba Conservation (Wildlife Branch) and the Natural Sciences and Engineering Research Council of Canada (grant A9556 to SGS, scholarships to DGM and DLHN).

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Appendix 1. Commencement of laying, laying bout, body mass, and egg volume for 22 species of passerine birds nesting at Delta Marsh, Manitoba. Order and nomenclature follow Sibley and Ahlquist (1990).

| Family | Common name, scientific name | No. of nests | Time laying began (x ± SE min before or after sunrise, SR) | Laying bout ^a (x ± SE min) | Body mass (g) ^b | Egg volume (cm ³) ^c |
|----------------------------------------------|------------------------------------------------------------------|-----------------|------------------------------------------------------------------|------------------------------------------|-------------------------------|-----------------------------------------------|
| Tyrannidae | Eastern Wood-Pewee (<i>Contopus virens</i>) | 2 | SR + 425.5 | 37.5 | 14.1 | 1.7 |
| | Least Flycatcher (<i>Empidonax minimus</i>) | 24 | SR + 84.2 ± 12.3 | 20.7 ± 1.8 | 10.3 | 1.5 |
| | Alder Flycatcher (<i>E. alnorum</i>) | 3 | SR + 205.3 | 29.3 | 13.4 | 1.7 |
| Vireonidae | Eastern Kingbird (<i>Tyrannus tyrannus</i>) | 15 | SR + 211.5 ± 13.7 | 46.4 ± 5.5 | 43.6 | 3.8 |
| | Warbling Vireo (<i>Vireo gilvus</i>) | 8 | SR + 27.8 ± 6.6 | 31.8 | 14.8 | 2.1 |
| | Cedar Waxwing (<i>Bombycilla cedrorum</i>) | 6 | SR + 182.0 ± 12.7 | 65.7 ± 13.9 | 33.1 | 2.9 |
| Muscipidae | American Robin (<i>Turdus migratorius</i>) | 20 | SR + 290.0 ± 11.4 | 103.7 ± 8.4 | 77.3 | 5.8 |
| | Veery (<i>Catharus fuscens</i>) | 1 | SR + 247.0 | 57.0 | 31.2 | 3.3 |
| | Gray Catbird (<i>Dumetella carolinensis</i>) | 18 | SR + 128.7 ± 11.4 | 44.9 ± 3.6 | 36.9 | 3.7 |
| Sturnidae | Brown Thrasher (<i>Toxostoma rufum</i>) | 2 | SR + 109.0 | 33.0 | 68.8 | 5.4 |
| | House Wren (<i>Troglodytes aedon</i>) | 7 | SR + 21.9 ± 4.8 | 24.1 ± 3.0 | 10.9 | 1.4 |
| | Barn Swallow (<i>Hirundo rustica</i>) | 8 | SR + 35.9 ± 12.5 | 46.1 ± 4.8 | 15.8 | 1.9 |
| Hirundinidae | Clay-colored Sparrow (<i>Spizella pallida</i>) | 7 | SR + 15.9 ± 14.2 | 34.7 ± 7.6 | 12.0 | 1.4 |
| | Song Sparrow (<i>Melospiza melodia</i>) | 3 | SR + 11.3 | 47.7 | 20.5 | 2.1 |
| | Yellow Warbler (<i>Dendroica petechia</i>) | 32 | SR + 13.3 ± 2.8 | 26.7 ± 2.3 | 9.2 | 1.3 |
| Fringillidae | Red-winged Blackbird (<i>Agelaius phoeniceus</i>) | 20 | SR + 13.0 ± 4.2 | 28.2 ± 2.2 | 41.5 | 4.1 |
| | Yellow-headed Blackbird (<i>Xanthocephalus xanthocephalus</i>) | 21 | SR + 22.2 ± 6.2 | 53.4 ± 6.2 | 49.3 | 4.3 |
| | Brewer's Blackbird (<i>Euphagus cyanocephalus</i>) | 8 | SR + 37.3 ± 10.2 | 31.0 ± 3.8 | 58.1 | 4.6 |
| Common Grackle (<i>Quiscalus quiscula</i>) | Common Grackle (<i>Quiscalus quiscula</i>) | 17 | SR + 99.4 ± 6.9 | 40.1 ± 3.1 | 100.0 | 6.5 |
| | Brown-headed Cowbird (<i>Molothrus ater</i>) | 13 | SR - 31.2 ± 2.0 | 0.8 ± 0.1 | 38.8 | 3.0 |
| | Orchard Oriole (<i>Icterus spurius</i>) | 4 | SR + 57.8 | 18.8 | 19.6 | 2.2 |
| Baltimore Oriole (<i>I. galbula</i>) | 13 | SR + 78.9 ± 5.7 | 30.3 ± 2.2 | 33.2 | 3.1 | |

^a From Sealy et al. (1995) and this study.

^b From Dunning (1993). Female body masses were used where available.

^c From Bent (1942, 1958), Briskie and Sealy (1990), Moskoff (1995) and S. G. Sealy (unpubl. data).