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Hourly Laying Patterns of the Pearly-eyed Thrasher (*Margarops fuscatus*) in Puerto Rico

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ABSTRACT.—Temporal aspects of egg deposition are important factors governing avian reproductive success. I report hourly egg-laying patterns of the Pearly-eyed Thrasher (*Margarops fuscatus*) in the Luquillo Experimental Forest in northeastern Puerto Rico during 1979–2000. Initiatory eggs were laid by early morning (median = 0642 hrs, AST) and almost half of the eggs were laid by 0723 hrs. Many penultimate and eggs completing a clutch, however, were laid later in the morning and some not until mid afternoon (1429 hrs), thus extending egg deposition to 8 hrs. Delayed laying of the last eggs in a clutch may be an adaptive strategy triggering brood reduction to ensure survival of older and more robust siblings during periods of physiological stress and food shortages. *Received 20 March 2007. Accepted 21 February 2011.*

There is substantial variation in the precise hour of egg laying in birds (Scott 1991, McMaster et al. 2004), but most birds generally lay their eggs in the morning. Many north-temperate passerines lay one egg per day, often within 2–3 hrs shortly before or after local sunrise until the clutch is complete (Skutch 1952, Brackbill 1958, Nolan 1978, Scott 1993, Haftorn 1996, McMaster et al. 2004). Temporal aspects of egg deposition affect all aspects of avian reproduction, e.g., egg size, hatching patterns and synchrony, size, fitness, and viability of nestlings (Williams 1994, Maddox and Weatherhead 2008). Egg size, usually expressed in volumetric or longitudinal measures (Barta and Szekely 1997), is often correlated to hatchling size, fitness, and subsequent nestling development (Slagsvold et al. 1984, Deeming and Birchard 2007). However, Ricklefs (1984) cautioned using egg size or mass as a measure of egg quality as actual composition, e.g., the amount and quality of yolk, is usually independent of linear or volumetric measures. Even variation in embryonic metabolic rates influences time of hatching and hatchling size, and maturation and fitness (Badzinski et al. 2002). Maddox and Weatherhead (2008) suggested that other maternal factors, e.g., asynchronous hatching, override many of the previously espoused endogenous and environmental factors.

Knowledge of timing of laying appears to not have been reported for the Pearly-eyed Thrasher (*Margarops fuscatus*). The objective of this paper is to report the chronology and pattern of egg deposition for a montane population in Puerto Rico and relate it to the asynchronous hatchings observed in this population.

METHODS

The study area was within the 11,330-ha Luquillo Experimental Forest (LEF) in eastern Puerto Rico

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TABLE 1. Number of nest visits (n = 1,089) for the egg of the day. The proportion of nests containing a new egg changed from <50 to >50% by 0829 hrs (**bold**).

Hrs	Nest visits	Egg of the day		Present	
		Yes	No	Proportion	Percent
0530–0629	3	0	3	0/3	0
0630–0729	27	12	15	12/27	44[a]
0730–0829	**85**	**63**	**20**	**63/83**	**76**[a]
0830–0929	132	110	24	110/134	82
0930–1029	181	163	18	163/181	90
1030–1129	228	222	6	222/228	97
1130–1229	160	156	4	156/160	98
1230–1329	85	82	3	82/85	96
1330–1429	56	54	2	54/56	96
1430–1529	34	34	0	34/34	100

[a] Two time periods between which the increase in the proportion of EOD's (egg of the day) was significant (z-test for rates and proportions using Yates correction).

(18° 19′ N, 65° 45′ W). Average annual rainfall and temperatures range, respectively, from 200 cm and 25° C in the foothills to >500 cm and 19° C on peaks reaching 1,075 m asl (García-Martinó et al. 1996). The forest is comprised of four major vegetation associations that are altitudinally stratified and placed into separate life zones (Wadsworth 1951, Ewel and Whitmore 1973).

Egg-laying was monitored from December 1978 to July 2000 (study design and protocols are described in Arendt 2006). I used a standard method to estimate the hour of egg laying (Scott 1993), which entails recording the hour each nest is visited during days females are laying eggs and noting whether the 'egg of the day' (EOD) is present. Scott (1993) also proposed a method for calculating the median time for the 24-hr laying interval; this is the time when the proportion of nests containing a new egg changes from <50 to >50%. Few nest visits in the present study occurred during crepuscular and early diurnal hours (0530–0630); some early-laid eggs may have gone undocumented, especially first eggs. I calculated the median time for egg deposition as there were >100 observations between 0530 and 0829 hrs AST, the period within which the proportion of nests containing a new egg changed from <50 to >50%. I used a z-test for rates and proportions (using Yates correction) to examine the two hourly ranges between which the increase in the proportion of EODs was significant (α = 0.05).

RESULTS

One egg was laid each day until the clutch was complete (n = 1,089 observations during 1979–2000). Most eggs were laid in the morning (0630–1129 hrs; median lay hour = 0723). Forty-four percent were laid by 0729 hrs and 76% were laid by 0829 hrs. However, the latter eggs (2nd, 3rd, 4th eggs in 2-, 3-, and 4-egg clutches) are laid later in the day, and all EODs were not found in the nest until 1529 hrs (Table 1).

The first two eggs of a clutch were generally laid by mid morning (0630–0929 hrs), whereas the last egg (usually the third, and much less frequently a fourth) was often laid later in the day (until 1429 hrs) and was responsible for expansion of the hourly laying period (Fig. 1). Almost 90% of the eggs initiating a clutch were laid by 0729 hrs, and most were present by 0829 hrs (median = 0642 hrs). Second-laid eggs were not always laid in the early morning hours as were initial eggs of a clutch because second-laid eggs in 151 nests completed the clutch and some were laid as late as 1529 hrs. Only about half of second-laid eggs were present by 0729 hrs (median = 0713), whereas most (88%) were not present until 0929 hrs. All second-laid eggs were present well after mid-day (1529 hrs at the latest) (Fig. 1). Most third-laid eggs were laid between 0729 and 0829 hrs (median = 0826) when 39% were present, and 74% were present by 1029 hrs. All third-laid eggs were present by 1529 hrs. None of the 22 fourth-laid eggs was present until between 0830 and 0929 hrs (median = 0957) when 25% were recorded. All fourth-laid eggs were present by 1029 hrs (Fig. 1). There was no significant trend for day of the week initiatory eggs were laid, although there was a continuous increase each day from Sunday to Friday, with prominent increases from Sunday to Monday and Thursday to Friday (Fig. 2).

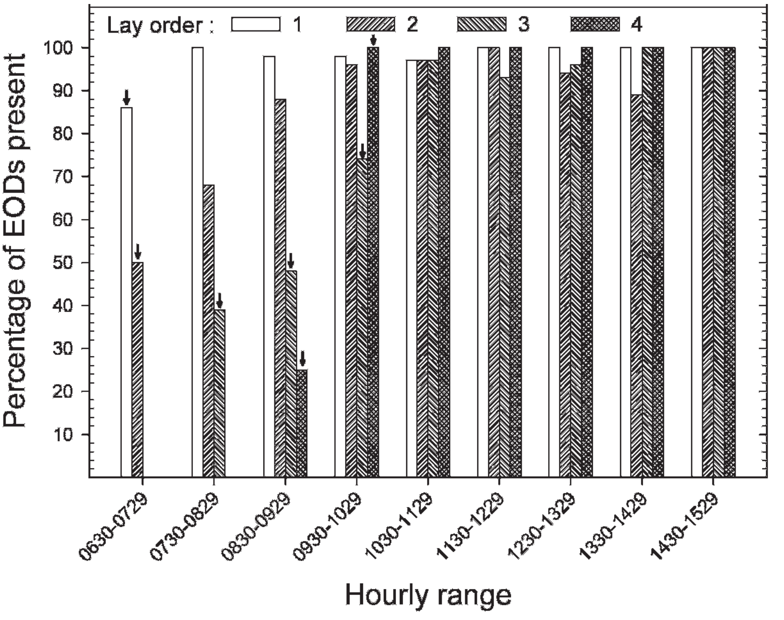

FIG. 1. Hourly egg-laying patterns by lay order for Pearly-eyed Thrashers in the Luquillo Experimental Forest, Puerto Rico (Dec 1979–Jul 2000). Sample sizes for the four categories: first-laid (343), second-laid (401), third-laid (323), and fourth-laid (22). Arrows indicate when the proportion of EODs (egg of the day) present was greater ($\alpha = 0.05$) than within the previous hourly range.

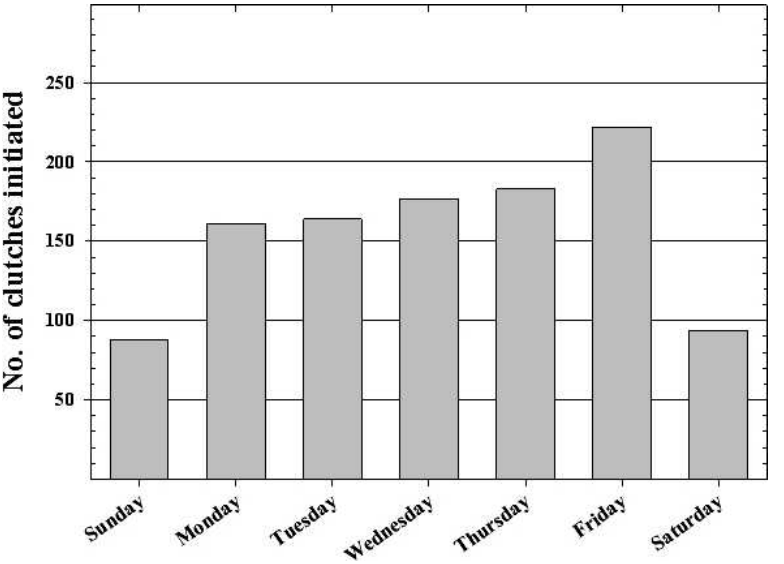

FIG. 2. Number of clutches initiated each day of the week. There was an increase from the first to the penultimate, but a precipitous decline on the last day.

DISCUSSION

The median hour of egg deposition for the Pearly-eyed Thrasher population studied was 0723 hrs, which is similar to the median hour of laying (0700 hrs) calculated for the Gray Catbird (*Dumetella carolinensis*) (Scott 1993). Official sunrise in Puerto Rico varies 73 min (0547 to 0700 hrs; median = 0613 hrs) throughout the year (U. S. Department of Commerce 2011). The Pearly-eyed Thrasher has an extended laying period, laying most of its eggs by 1129 hrs, or ~5 hrs and 7 min after local sunrise, and can delay deposition until at least 1429 hrs. This pattern is similar to its close relative, the European Starling (*Sturnus vulgaris*), which also has close phylogenetic affinities with the Gray Catbird (Meijer 1992:fig. 2; Ericson and Johansson 2003:fig. 1). Other members of the superfamily Muscicapoidea, e.g., thrushes and flycatchers, are also known to lay in the afternoon (Brackbill 1958, Weatherhead et al. 1991). Oppenheimer et al. (1996) reported that much of the variation in laying times reflects phylogeny, which is reflected in the pattern recorded for the Pearly-eyed Thrasher.

The initial egg mass at laying for most birds is an important factor affecting hatchling mass (Deeming and Birchard 2007). The first two eggs in the laying sequence of the Pearly-eyed Thrasher are heavier and are laid earlier in the day than the last one or two eggs completing the clutch (Arendt 2006). Initial eggs of a clutch laid early in the day contribute to a greater age gap between older and younger siblings, giving older siblings developmental and survival advantages over younger nest mates during periods when food and other resources may be critically limited (Esler 1999, Maddox and Weatherhead 2008). First- and second-hatched Pearly-eyed Thrasher fledglings had a higher probability of being recruited into the breeding population and dispersed earlier and farther than younger siblings (Arendt 2006). First- and second-hatched thrasher fledglings, heavily parasitized by philornid (*Philornis* spp.) botfly larvae (Diptera: Muscidae), lived significantly longer and survived better than younger siblings with comparable larval numbers (Arendt 1985, 2000). Unparasitized third- and fourth-hatched siblings would often fledge at similar body masses and appendicular measurements as those of older siblings but, during food shortages, many would lag in development, eventually becoming runts. They would be trampled to death by older siblings, or simply disappear from nests. I observed females on several occasions carrying runt nestlings and discarding them 20–30 m from their nest boxes (Arendt 2006). Delayed laying in the LEF population of the Pearly-eyed Thrasher of the final eggs of a clutch may be an adaptive strategy triggering brood reduction to ensure survival of older, more robust siblings during periods of physiological and environmental stress, e.g., food shortages (Knight 1987, Murray 1994, Maddox and Weatherhead 2008).

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