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EGG LAYING IN DUSKY FLYCATCHERS AND WHITE-CROWNED SPARROWS[1]

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Many birds lay one egg per day, often in the early morning. The time interval between eggs is usually close to 24 hrs, although longer and more irregular periodicities have been noted in a number of species (Skutch 1952, Schifferli 1979, Astheimer 1985). Despite the interspecific variation in laying times and intervals, most of the speculation regarding adaptive significance has centered on the hour of laying (Schifferli 1979, Feare et al. 1982, Weatherhead et al. 1991, Watson et al. 1993).

The purpose of this note is twofold: first, to present data on the laying patterns observed in two passerine species inhabiting roughly the same environment and second, to stimulate new discussion of some of the factors that might influence laying patterns in general.

METHODS

This study was conducted between 1984 and 1995, inclusive, in the Sierra Nevada near Tioga Pass, Mono Co., California. The two species studied, Dusky Flycatcher (*Empidonax oberholseri*) and Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) nested on subalpine meadows (both species) and the vegetated talus slopes immediately above (primarily *E. oberholseri*).

Laying times (noted in Pacific Standard Time) were determined by repeated visits to nests at approximately 1-hr intervals. If a new egg appeared between visits, the laying time was assumed to be midway between the visits. All eggs were numbered on the blunt end with waterproof ink according to laying order. Sitting females were usually left undisturbed and, to minimize error, an attempt was made to check the nest again soon after they had departed on their own accord. Laying times for *E. oberholseri* could sometimes be estimated very closely because as the egg's surface dries within a few minutes after laying, an air sac about 3 mm in diameter forms at the blunt end. The air sac, readily visible through the white shell, grows to about 4.5 mm over the next hour. Thus air sac measurements of recently laid eggs (air sac width smaller than 4.5 mm) allowed us to assign laying times even when nest visits were as much as three hours apart.

For *Z. l. oriantha,* 21 of the laying times were obtained by the multiple nest-visit technique, the other 11 from nest temperatures recorded with thermocouples during laying and attentive periods. When the female came onto the nest in the early morning, nest temperatures typically increased and then decreased sharply upon her departure after laying. Mean (±SD) laying attentive periods were 56.2 ± 10.2 min (range = 36–69 min), and their midpoints were taken to be the time of laying (see Fig. 1 in Zerba and Morton 1983). Modal clutch size for both species was four.

RESULTS

The mean hour of laying was 12:06 for the 117 cases measured in *E. oberholseri* and 05:44 for the 32 cases measured in *Z. l. oriantha* (Table 1). In *Z. l. oriantha* laying times did not vary with laying order (ANOVA: $F_{3,28} = 1.5$, $P = 0.24$), but in *E. oberholseri* the third egg was laid later than any of the others (ANOVA: $F_{3,113} = 5.8$, $P = 0.001$ and Student-Newman-Keuls multiple range test: $P < 0.05$).

Variation in laying time was greater in *E. oberholseri.* The eggs produced by a given female on consecutive days were laid nearly 27 hrs apart, whereas those of *Z. l. oriantha* were almost exactly 24 hrs apart (Table 2). On occasion, *E. oberholseri* skipped laying days and the interval between successively laid eggs became more than 42 hrs (Table 2). In two cases, the penultimate egg was laid before noon and the last egg followed the next afternoon between 13:30 and 15:00. In another two nests, the female laid the penultimate egg after 15:00, skipped the next day, and laid the final egg the following morning before 10:00. In two nests the female laid around 12:00; one laid the final egg the next

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afternoon, and the other skipped a day and laid the final egg before 07:00 the next morning.

Plots of laying times were unimodal for both species. *Z. l. oriantha* laid only in the early morning over a range of about 3 hrs, whereas *E. oberholseri* laid throughout the day over a range of nearly 10 hrs (Fig. 1).

DISCUSSION

Schifferli (1979) suggested that nighttime shell formation and early morning laying enable females to forage actively during the day, reducing the chances of damaging an oviducal egg. While many birds, passerines in particular, have been documented to lay at first light or shortly thereafter (Skutch 1952, Schifferli 1979), the hour of laying in many other species varies considerably (Skutch 1952, 1976, Weatherhead et al. 1991; Meijer 1992; Watson et al. 1993).

If laying times are influenced by energy or mobility constraints motivating birds to expel eggs prior to engaging in normal activity, then we predict that (1) birds with eggs comprising a larger proportion of their body weight should tend to lay earlier and vary less in their laying times than those species whose eggs are smaller, and (2) species relying on foraging techniques that are energy intensive or demanding of agility should tend toward earlier laying times than those in which these factors are less critical.

We therefore predicted that laying times in *E. oberholseri,* an aerial forager, should be earlier and laying times should be more tightly distributed about the beginning of their active day than those in *Z. l. oriantha,* a ground-foraging omnivore. In fact, the data show the opposite pattern. *Empidonax oberholseri* tended to lay much later in the day and demonstrated considerable variation in laying times, even though it relies on aerial agility to catch prey and has slightly larger relative egg size (12%, Pereyra unpubl.) than *Z. l. oriantha* (9% King 1973). This was the case within as well as between females.

Inconsistencies between time of laying and female activity have been noted in two other species as well. In the American Robin (*Turdus migratorius*), an early morning to late afternoon layer, no differences in female activity were observed before or after egg laying (Weatherhead et al. 1991). In European Starlings (*Sturnus vulgaris*), most laying occurred near the end of the peak period of morning social activity (Feare et al. 1982). Laying times in *Z. l. oriantha* were more tightly distributed around an early morning mean, with little of the daily variation seen in *E. oberholseri.* Although they inhabit essentially the same environment and are subject to the same daily photoperiod cues, *Z. l. oriantha* exhibited the early morning laying pattern.

Yolking of ovarian follicles in birds to the point where they are ready for ovulation occurs in a closely controlled hierarchical sequence which, through relatively minor adjustments, can result in a wide range of patterns in egg formation rates and in laying (Astheimer 1985). Using data obtained mostly from quail and domestic fowl, Follett (1984) showed that ovulation occurs about 6 hr after a mature follicle is exposed to a surge of LH. The egg then spends roughly 24 hr in the oviduct before being laid. The ability of the hypothalamo-pituitary system to secrete pre-ovulatory surges in LH is restricted to 8 or 9 hrs per day, the so-called open period. For ovulation to occur on a given day, the presence of a mature follicle must coincide with the open period. In species with 24-hr intervals between successive ovulations, laying happens daily at about the same time. In other birds such as the domestic fowl, Common Eider *Somateria mollisima sedentaria* (Watson et al. 1993) and *E. oberholseri,* it is more common for successive ovulations to occur 2 to 4 hrs later each day and laying occurs at 26 to 28-hr intervals. In such species, the presence of a mature follicle can be expected to drift across the open period until the two no longer coincide and ovulation is skipped for a day and so is laying.

Although virtually all of the work on egg formation in birds has been performed on domesticated species, there are numerous examples of laying time and interval in wild species that fit this model. Rhythmic 24-hr laying periods, such as those exhibited by *Z. l. oriantha,* are common and tend to occur in early morning layers. Among passerines these include some tanagers, fringillids, and icterids (Skutch 1952, Muma 1986, Scott 1991). Longer intervals between successive eggs and varied laying times, such as seen in *E. oberholseri,* are also frequently encountered, but largely among a different set of species including some members of the Tyrannidae, Pipridae, and Cotingidae (Skutch 1952, 1976, Astheimer 1985) and some members of the Ptilonorhynchidae, Climacteridae, and Acanthizidae

TABLE 1. Laying times by egg number of *Empidonax oberholseri* and *Zonotrichia leucophrys oriantha* at Tioga Pass.

	Mean time of day	Range	SD (hr)	*N*
E. oberholseri				
Egg 1	11:37	06:49–14:57	2.4	20
Egg 2	11:13	07:25–14:50	1.9	25
Egg 3	12:59	07:50–16:30	1.9	50
Egg 4	11:35	07:30–14:45	1.8	22
All eggs	12:06	06:49–16:30	2.1	117
Z. l. oriantha				
Egg 1	05:34	04:56–06:39	0.6	8
Egg 2	05:23	04:48–06:01	0.4	8
Egg 3	06:00	04:40–07:30	0.9	11
Egg 4	05:58	05:02–06:47	0.7	5
All eggs	05:44	04:40–07:30	0.7	32

TABLE 2. Number of hours between laying of successive eggs in *Empidonax oberholseri* and *Zonotrichia leucophrys oriantha.*

	Mean	SD	*N*
E. oberholseri (consecutive days)	26.9	1.7	7
E. oberholseri (skipped days)	42.6	2.2	3
Z. l. oriantha	24.1	0.9	16

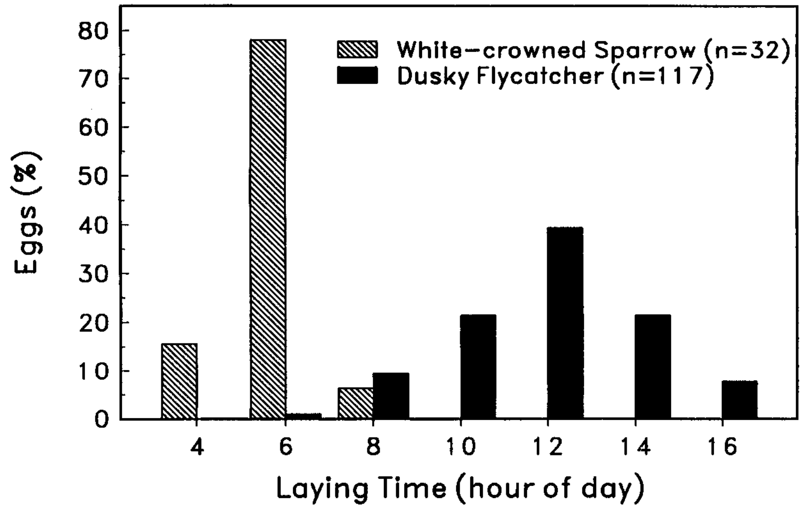

FIGURE 1. Percent of *E. oberholseri* and *Z. l. oriantha* eggs laid at 2-hr time intervals throughout the day. Time interval 4 represents 03:01–05:00, and so on.

(Marchant 1986). Many passerine species with laying intervals longer than 24 hrs begin laying during midmorning or later and at intervals ranging from 1 to 3 days (Skutch 1952, Astheimer 1985).

What dictates the egg laying schedule of birds? This study suggests that the differences in laying times and intervals between *Z. l. oriantha* and *E. oberholseri* are largely byproducts of the physiological processes involved in egg formation. Furthermore, even though the physiological mechanism is an important constraint, food intake or energetic costs most likely affect egg development time in the oviduct (Wiebe and Martin 1995). Yolk, albumen, and shell synthesis have all been proposed as potentially expensive processes that might limit the rate at which egg formation can occur (Williams 1981, Astheimer 1985). For *E. oberholseri,* or any other bird on a laying schedule other than 24 hr, the hour of laying changes day to day, so it is unlikely that there is a "best" hour to lay. These considerations suggest that laying times per se may not be the focus of natural selection in some species. Rather, oviposition intervals may be determined by the physiological mechanism governing egg production.

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