Museum of Natural History, and several specimens intermediate with or closer to *virginianus* from eastern Colorado. Thus I reexamined the type of *occidentalis*.

Stone (1897) was absolutely right. Unfortunately, he used a pale "western" (from Philadelphia) specimen as the type of *occidentalis*, not knowing the northern form was moderately to highly invasive. Oberholser's concepts of *occidentalis* were (I believe) based on migrants of the subarctic nesting form—or intergrades between it and the various adjacent more southerly populations as evidenced by his recognizing, at least in Colorado, a "dark phase" (p. 191). Thus, as Stone stated correctly, his *Bubo virginianus occidentalis* becomes a synonym of *Bubo virginianus subarcticus* Ridgway (see Browning and Banks 1991).

With *occidentalis* recognized as a synonym of *subarcticus*, the characters of *pallescens* vs. *subarcticus* must now be determined to delimit their ranges in the midcontinent area from Texas northward through the continuous grasslands east of the Rockies to the western and northern prairie provinces of Canada.

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Egg-laying Times of American Robins

PATRICK J. WEATHERHEAD,[1] ROBERT D. MONTGOMERIE,[2] AND SUSAN B. MCRAE[1]
[1]*Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada; and*
[2]*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada*

The time of day when birds lay their eggs has generally not been well studied. Almost all reports of egg-laying times are anecdotal, with few based on more than a handful of observations (Skutch 1952, 1976; Schifferli 1979). We present observations of egg-laying times of American Robins (*Turdus migratorius*) and test the hypothesis that birds lay their eggs at times when they are normally inactive, because carrying a developing egg constrains female activity (Schifferli 1979).

Schifferli (1979) compiled the most comprehensive summary to date of egg-laying times of passerine birds and found that most species lay their eggs at dawn. However, a few species lay their eggs well after sunrise (Schifferli 1979). For example, Feare et al. (1982) found that European Starlings (*Sturnus vulgaris*) lay eggs on average about midmorning. Our first objective in this study was to document laying times of American Robins.

Little theoretical attention has been paid to the question of when birds should lay their eggs. The prevalence of egg laying around dawn may imply that the developing egg in the oviduct before laying constrains female activity (Schifferli 1979). Because females are inactive at night regardless of whether or not they have an egg in their oviduct, then laying in

the morning does not interfere with normal diurnal activity. In support of this hypothesis, Schifferli (1979) showed that the capture and handling of female House Sparrows (*Passer domesticus*) in late afternoon on the day preceding egg laying did not damage oviducal eggs, whereas similar treatment in late evening caused damage. He concluded that oviducal eggs become more vulnerable to damage as they approach completion and that normal diurnal activity before egg laying would damage eggs. The weakness of this experiment is that it is not obvious that normal activity should traumatize an oviducal egg to the same extent that capturing and handling the female would. Our second objective in this study was to test the hypothesis that the activity of female American Robins is constrained when they are carrying an egg in their oviduct.

We report observations collected while studying robin reproductive biology at the Queen's University Biological Station in eastern Ontario in 1987 and 1988 (Weatherhead and McRae 1990). We found many nests before egg laying and determined the time period in which 37 eggs were laid in 19 nests. During the laying period we checked easily accessible nests repeatedly throughout the day. If a female was on the nest she was left undisturbed, and if the nest was unattended
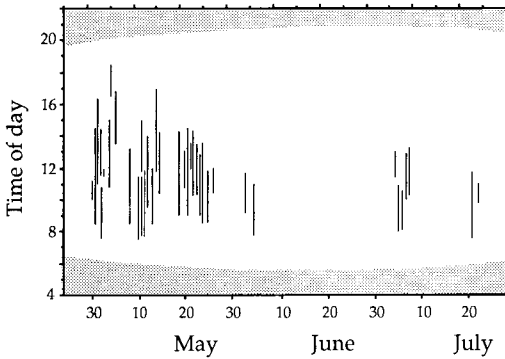
Fig. 1. Seasonal variation in egg-laying times. Each vertical line represents the interval when each of 37 eggs (from 19 nests) was known to have been laid. Shading represents time before sunrise and after sunset.

we checked its contents. We determined the period in which an egg was laid in one of two ways. First, if an egg appeared between two visits, it was laid in that interval. Second, if after first checking a nest we then observed the female on the nest and later found an additional egg, we assumed the egg was laid between the time we first saw the female on the nest and the time we found the new egg. We assumed that females leave the nest soon after laying an egg and only included eggs laid before the onset of incubation (i.e. all but the last egg of a clutch). We restricted our analysis to the 37 observations where the estimated interval of egg laying was <6 h.

As part of our other investigations, we regularly surveyed the study area and mapped the locations of all the robins observed. All birds were individually color-banded. Nearly all observations were of birds as they foraged in open areas because individuals were much easier to identify in those situations. In collecting these data we inadvertently created the opportunity to compare the activity of females immediately before and after they had laid an egg. Because the data were not collected for this purpose, no extra effort was made to spot laying females, so our observations are free from any bias that could have caused those females to be overrepresented before or after laying.

All egg laying occurred between 0730 and 1830 EDT. If we use the midpoint of each laying interval as our estimate of when eggs were laid, the average (±SE) egg-laying time (1132 ± 18 min) was actually closer to midday than to sunrise. Despite this, egg-laying times were significantly correlated with the time of sunrise ($r = 0.40$, $P = 0.01$, $n = 37$). Thus robins may still use sunrise as a cue to time egg laying, as do species that lay soon after dawn (e.g. Red-winged Blackbirds, *Agelaius phoeniceus*) (Muma 1986).

To compare the activity of females immediately be-

fore and immediately after egg laying, we used all our sighting records both for laying females and for all other robins for the period 3 h before and 3 h after each laying event (i.e. 3 h before a female was first seen on the nest and 3 h after we first determined she was no longer on the nest). Over all the prelaying periods we recorded 51 sightings of known individuals, and over all the postlaying periods we recorded 57 sightings. Of these sightings, 8 observations were of females that we knew subsequently began egg laying within the next three hours and 5 were of females that had just completed egg laying in the past three hours. Thus, females were equally likely to be seen just before and just after egg laying ($\chi^2 = 1.11$, $P > 0.05$). This result does not support the hypothesis that having an egg in the oviduct constrains female activity.

Our results provide another example of a passerine that lays its eggs well past dawn. Our evidence that female robins were able to remain active immediately before egg laying suggests that the general passerine pattern of laying eggs at dawn may not be a consequence of the necessity to remain inactive before egg laying. We do not have an explanation for the pattern observed in robins, but we can suggest avenues for exploration that previously have not been considered. For example, egg laying is associated temporally with egg fertilization; in the hour following the laying of one egg, the next egg in sequence is fertilized (Birkhead 1988). Conceivably, the time of egg laying may be just a consequence of selection having favored a particular time for fertilization. In turn, the best time for fertilization might have something to do with the best time for copulation. As a new approach to understanding the patterns of egg laying among passerines, it may prove useful to assess the other reproductive activities associated with egg laying rather than to limit the focus to egg laying proper.

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Comments on the Sample Sizes Used to Test the Effect of Experimental Brood Enlargement on Adult Survival

JEFF GRAVES

Department of Biology and Preclinical Medicine, University of St. Andrews, St. Andrews, Fife KY16 9TS, United Kingdom

Demonstrating that an experimental manipulation does not have an effect on adult survival can frequently be difficult. In particular, a small sample size may be inadequate to have a reasonable chance of finding a real difference between experimental and control groups (type II error). In recent reviews of the literature on experimental studies of the cost of reproduction, Linden and Møller (1989), Dijkstra et al. (1990), and Nur (1990) cited studies of increased reproductive effort on adult mortality in 11 species that was caused by experimental enlargement of brood size. They reported that in only four of these species (Askenmo 1979; Nur 1984, 1988a; Reid 1987; Dijkstra et al. 1990) was there a significant increase in adult mortality for at least one sex subsequent to experimental brood enlargement. Because more experimental brood enlargement manipulations reduced adult fecundity in the next breeding attempt rather than increased adult mortality, it is tempting to conclude that the trade-offs that reduce adult fecundity are more likely than those that reduce adult survival (Linden and Møller 1989). Unfortunately, many of the studies that found no significant effect on adult mortality have sample sizes below that required to have even a reasonable probability of detecting a significant difference between the experimentals and the controls (i.e. inadequate statistical power).

Although several authors commented that small sample size results in a low probability of rejecting the null hypothesis (Nur 1988b, 1990; DeSteven 1980; Linden and Møller 1989), none of the studies that reported failure to find any significant increase in adult mortality after experimental brood mortality also calculated the statistical power of their results. There exist discussions of the problem of determining the sample size required to detect a significant difference between two populations (Fleiss 1981, Cohen 1988). Fleiss (1981) provided a simple formula that gives an approximation of the sample sizes required, and he also provided an appendix that lists the sample sizes necessary to achieve different levels of power with different significance levels and different pairs of proportions for the experimental and control groups. Cohen (1988) has the most extensive treatment, with tables for sample sizes and for calculating the power of any particular test.

Significance levels are now rigidly set by convention at 0.05 or less, but there is as yet no general agreement on the critical level of power. Toft and Shea (1983) recommend that β, the probability of type II error, be set at 0.05, so that the power is $1 - \beta$ (i.e. 0.95 or greater). This would require very large sample sizes; far in excess of what is usually possible in field studies, unless the difference between the two groups was very marked indeed. Fleiss (1981) and Cohen (1988) suggest as a reasonable compromise the criterion that type II error should be set at four times the level set for type I error. Thus, when the significance level is 0.05 the criterion for type II error would be set at $1 - 0.20$ (i.e. 0.80). The acceptance of such a criterion for the statistical power of a test would presuppose that type I errors are in general four times as serious as type II errors (Cohen 1988).

In the case of changes in adult mortality when brood size has been experimentally enlarged or reduced, there is usually some information beforehand on the expected mortality of the controls. Setting the significance level at the usual 0.05 and the type II at 0.80, a curve for the sample sizes required can be generated for any level of mortality for the experimental subjects. There is a very rapid increase in sample size required as the mortality of the experimentals approaches that of the controls (Fig. 1). If the control mortality is 40% and the experimental is 45%, then to have an 80% chance of detecting it at the 0.05 level of significance, 1,573 birds in both the groups will be required.

These results greatly affect the interpretation of most of the studies on brood enlargement and its effect on adult mortality. Of the eight studies that found no effect on adult mortality, six used sample sizes for experimental or control groups of 30 or fewer nests (DeSteven 1980, Harris 1970, Hegner and Wingfield 1987, Korpimäki 1988, Orell and Koivula 1988, Røskaft 1985). With sample sizes as small as this, the experimental birds would have to suffer a massive