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Intermittent incubation during egg laying in House Sparrows.—The clutch sizes of many passerine birds show considerable phenotypic plasticity (Perrins and Moss 1975, Hogstedt 1980, Pettifor et al. 1988), but the proximate mechanisms responsible for determining clutch size are poorly understood. Recent studies have suggested that the onset of incubation behavior, which commences gradually during egg laying in some species, may play a role in the proximate determination of clutch size (Haftorn 1981, Mead and Morton 1985, Meijer 1990, Haywood 1993). Anderson (1995) proposed that the mechanism of clutch size determination in the House Sparrow (*Passer domesticus*) involves (1) female condition at some point prior to the beginning of egg laying, establishing both a prospective clutch size and a corresponding schedule for the onset of incubation, (2) tactile feedback from the presence of at least one egg in the nest causing continuation of incubation behavior and resultant increases in prolactin secretion, and (3) rising prolactin levels suppressing follicular development causing egg production to cease at the predetermined number. This proposal would require that incubation begin early in the laying sequence, such as has been observed in several other passerines (Haftorn 1981, Zerba and Morton 1983, Meijer 1990, Hebert and Sealy 1992).

Little is known about the onset of incubation in the House Sparrow. Asynchronous hatching occurs in House Sparrow broods (Veiga and Vinuela 1993, Anderson 1994), which suggests that incubation begins prior to the completion of egg laying. It is also known that female House Sparrows roost in the nest on the eggs during egg laying (Summers-Smith 1963) and spend more time on the nest during the day as egg laying progresses (Summers-Smith 1963, North 1980), but it is not known if heat is being applied to the eggs during these periods. A gradual onset of incubation behavior involving intermittent bouts of incubation early in the laying sequence would be required for the mechanism proposed above, while an abrupt onset late in the egg laying cycle would be inconsistent with it. The purpose of this preliminary study was to determine if such intermittent bouts of incubation occur during egg laying in the House Sparrow.

TABLE 1

DATE OF INITIATION, CLUTCH SIZE AND APPARENT TIME OF EGG LAYING FOR SIX CLUTCHES IN WHICH NEST CUP TEMPERATURES WERE MONITORED DURING THE LAYING PERIOD

Nest-box number	Date of initiation	Clutch size	N	Time of egg laying	
				Range	Mean (SD)
256.1	7/6	6	3	6:55–7:00	6:58 (:03)
256.2	7/23	5	5	6:51–7:11	7:03 (:08)
266	7/23	2	1	7:50	—
209	7/24	4	4	6:50–7:05	6:59 (:06)
251	7/29	5	4	6:30–7:05	6:54 (:16)
284	7/30	4	4	6:30–7:05	6:51 (:15)

Study area and methods.—The study was conducted at a dairy farm near the Univ. of Michigan Biological Station (UMBS), Cheboygan County, Michigan (45°34'N, 84°40'W), from 7 July to 7 August 1995. Six nest boxes located on the inside south wall of an open shed housing dairy cattle were used for the experiment. Nest boxes were visited daily, usually between 07:30 and 09:00 EDT, to check nest contents.

Thermocouple thermometers (20 gauge, type T) were placed in the floor of the nest cup in four nest boxes (three in which egg laying was occurring) during the late afternoon of 7 July. The thermocouples were connected to an OWL/HOOT on-site weather logger (eme systems, 2229 Fifth St., Berkeley, CA 94710). Temperatures were recorded at five-minute intervals, which required downloading of the temperature records every three days, and the weather logger was taken to UMBS at two- or three-day intervals for downloading. This process resulted in a disruption of data collection for approximately one hour, usually around 09:30 EDT. Data for a three-day period (12–15 July) were lost in the downloading process, and data from one 24-h period (9–10 July) were not recorded due to a wiring error.

Two of the laying females abandoned their nests, apparently due to the extensive disturbance during the two hours required to set up the equipment, while the third (256.1) continued to lay. Following the loss of data in downloading mentioned above, the nest contents of four nest boxes were removed on 18 and 19 July to stimulate renesting (see Anderson 1979). Thermocouples were moved occasionally to other nest boxes as nest building or clutch initiation in those boxes occurred. Females were captured and banded during incubation following the completion of their clutches.

One thermocouple was constantly maintained in an inactive nest box to provide continuous data on ambient nest cup temperature (T_a). Different nest boxes served as the control at different times due to changes in occupancy during the study. Nest cup temperatures in occupied nest boxes (T_n) were compared to T_a. Incubation was inferred from sharp rises in T_n in occupied nests or by continuous maintenance of T_n well above T_a. It might be argued that elevated T_n was simply due to radiative heat from the presence of an adult in the nest. The lack of a difference between T_n and T_a during many of the nights during egg laying in several of the nests (see below) when the female was presumably roosting on the eggs (cf Summers-Smith 1963) suggests that the sharp rises in T_n instead represent application of heat from the brood patch of the female. Male House Sparrows do not develop brood patches (Summers-Smith 1963, Anderson, pers. obs.) and, therefore, do not truly incubate.

A sharp rise in the difference betwen T_n and T_a between 06:00 and 07:30 EDT (shortly after sunrise) on each day during the egg-laying period was presumed to coincide with egg

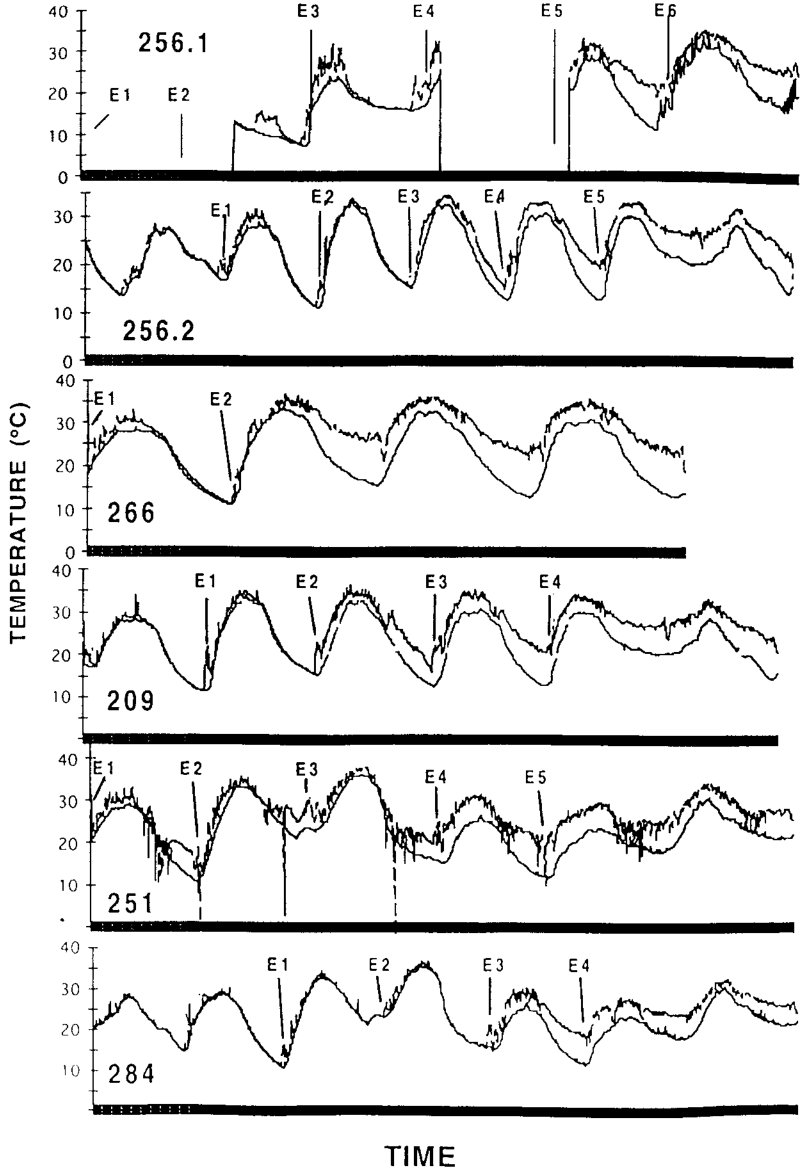

FIG. 1. Traces of nest cup temperatures during egg laying in six House Sparrow nests in northern lower Michigan, July–August 1995. Lower trace in each sequence is ambient temperature in the nest cup of an unoccupied nest box, with the sinusoidal shape representing daily fluctuations in ambient temperature, with the low point in each trough occurring approximately at dawn (about 07:00 EDT). Approximate times of egg laying in the occupied nest-boxes are designated by E1, E2, etc., for first, second, and subsequent eggs in the clutch.

laying, which normally occurs near dawn in the House Sparrow (Summers-Smith 1963, Anderson, pers. obs.). The time of the peak difference between T_n and T_a during this period was interpreted as the actual time of egg laying.

Results and discussion.—Temperature records were obtained for the entire laying sequence for five clutches (256.2, 266, 209, 251, and 284) and for a part of the laying sequence for one clutch (256.1) (Table 1). Anomalous temperature readings occurred at intermittent intervals in nest box 251, probably due to a damaged lead, but the basic pattern of incubation onset was still discernible. The same female laid both clutches in nest box 256 (256.1 and 256.2), while the female laying the abnormally small two-egg clutch (see Anderson 1994) had been captured in the same nest box on 17 July on the 15th day of incubation of a clutch of infertile eggs. The laying histories of the three other females were not known.

Table 1 also contains data on the apparent time of egg laying in the six nests. Egg laying occurred about 45 minutes after sunrise ($N = 21$, mean = 44.9 min, $SD = 18.9$).

Fig. 1 shows the temperature traces for the six clutches. Each trace shows T_n compared to T_a for the same interval. Haftorn (1981) distinguished between incubation *sensu stricto*, any application of heat to the eggs, and the beginning of continuous incubation, the time when the female begins continuous attentiveness to the eggs. Incubation *sensu stricto* began in all six clutches prior to the laying of the last egg. In the five nests for which complete temperature records for the entire laying period are available, all five showed periods of daytime incubation beginning with the day of the laying of the first egg. The intensity and duration of these periods varied among nests (Fig. 1), and, in general, appeared to increase with subsequent days. Some periods of nocturnal incubation were also evident (after the laying of the second egg in 256.1, and after the laying of each of the first three eggs in 251) (Fig. 1).

The establishment of continuous attentiveness also varied among nests. In three nests (256.2, 209 and 251) continuous attentiveness began during the night preceding the laying of the penultimate egg (Fig. 1). In 284 continuous attentiveness began during the day of the laying of the penultimate egg, while in 266 (with the 2-egg clutch), attentiveness began in mid-afternoon on the day of the laying of the last egg. In 256.1, the loss of data precluded identification of the beginning of continuous attentiveness, but it did begin before the laying of the last egg.

In conclusion, the results of this preliminary study clearly indicate that bouts of incubation begin during egg laying in the House Sparrow, usually with the laying of the first egg. These findings are consistent with the hypothesis that tactile feedback from the eggs (through the brood patch) may play a role in the mechanism controlling clutch size in the species (Anderson 1995). They also suggest that egg removal in experiments to test for determinate or indeterminate laying in a species should occur soon after egg laying to obviate the possible effects of tactile feedback from the egg on the termination of laying.

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Individual, brood, and sex variation in begging calls of Western Bluebirds.—Vocal differences in birds are often sufficient for recognition not only of species but of variables such as sex, age, genetic relatedness, and condition. Here we analyze begging calls of Western Bluebird (*Sialia mexicana*) nestlings and test for family, sex, and individual differences. The original impetus for this study was the finding by Gowaty and Droge (1990) that female Eastern Bluebird (*Sialia sialis*) nestlings were fed more often than were male nestlings and that female-biased broods were provisioned more frequently by the adult male attending the nest. If this result is due to an adjustment of parental behavior in response to the sex of the nestlings, then there must be a proximate mechanism by which parents can determine the sex of their offspring. Inasmuch as bluebirds are cavity nesters and nestlings are similar in size, the most likely mechanism for sex recognition is differences in nestling vocalizations or begging calls.

Subsequently, work in our study population has determined that sex-biased provisioning does not occur (Leonard et al. 1994) and, furthermore, that parents do not discriminate against unrelated offspring translocated into their nests (Leonard et al. 1995). These results prompt a somewhat different question than that originally envisioned. Given that Western Bluebird parents do not appear to discriminate among offspring, either on the basis of sex or genetic relatedness, are differences in nestling vocalizations uncorrelated with these factors? If vocalizations are not distinguishable between the sexes or between nests, then one