# Determinate vs. Indeterminate Laying in the House Sparrow

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Kendra et al. (1988) have reopened the question of whether the House Sparrow (*Passer domesticus*) is a determinate or indeterminate layer. *Determinate* layers are species in which the number of ovarian follicles responding to the stimulation of gonadotropic hormones is equal to the number of eggs laid, and this number is determined when egg laying begins (cf. Klomp 1970). Neither the removal nor addition of eggs during the laying period will affect the number of eggs laid. *Indeterminate* layers are species in which the number of follicles that respond to hormonal stimulation is greater than the number of eggs laid normally. The follicles respond asynchronously to hormonal stimulation so that the development of some of the later-responding follicles may be inhibited during the laying cycle by the presence of eggs in the nest (cf. Klomp 1970). If eggs are removed as laid, laying in these species continues beyond the normal clutch size to an indefinite number.

Kendra et al. (1988) performed removal experiments on six nests. In three, one egg was removed daily beginning with the second day of laying and in three others, one egg was removed daily beginning with the third day of laying. Because two of the females in the first group laid additional eggs while none of the three females in the latter group continued laying beyond the normal clutch size, Kendra et al. concluded that "the female House Sparrow is an indeterminate layer up to a clutch size of 3 eggs" (1988: 86). This assertion supports Witschi's (1935) report that "If . . . one removes daily the egg that the sparrow deposits, she goes on laying up to fifty eggs in succession, often twelve to nineteen on consecutive days" (Witschi 1935: 183). Witschi provided no more details about his experiments. In an experiment that involved daily removal of single eggs beginning with the second day of egg laying in two nests, Brackbill (1960) concluded that the House Sparrow is a determinate layer. I performed egg-removal experiments on 20 nests of the House Sparrow: 2 nests were in Poland in 1977 and 18 were in northern lower Michigan during the 1986–1988 breeding seasons.

In Poland both eggs were removed on the second day of laying, and subsequent eggs were removed as laid. In two Michigan nests, single eggs were removed daily beginning on the second day of laying. In the other 16 Michigan nests, the first egg laid was removed on the day of laying, the second was left in the nest, and the third and subsequent eggs were removed on the day laid. I measured the length and breadth of each egg with dial calipers on the day of laying, and recorded fresh weights with a 5-g Pesola spring balance.

In none of the 20 experimental nests did the removal of eggs induce continuous laying by the female. Females deserted seven nests (including one in Poland) during the egg-laying period (three after the first egg was laid, one after the second, and three after the third). Seven (including one in the second Poland nest) deserted after completion of the laying of a number of eggs equivalent to the normal clutch size (four after four eggs, and three after five). Most clutches of the House Sparrow in both Poland and Michigan contain 4–6 eggs (Pinowski and Wieloch 1972, Anderson MS). Six nests produced nestlings or additional eggs (Table 1). In four, the female incubated the one remaining egg, which hatched 9–10 days after the last egg was laid. "Clutch size" in these four nests ranged from 5(2) to 7(1). Incubation period (*sensu stricto*) in the House Sparrow is ca. 11.5 days (Seel 1968; Anderson 1978, MS); presumably the female initiated incubation after the laying of the second or third egg. In the two remaining experimental nests (both with initial clutch sizes of six), the female resumed laying

TABLE 1. Results from nests in which female did not desert the nesting effort. Day 1 is the date of clutch initiation. (E = egg laid on that day, * = egg removed on that day, N = nestling present in nest.)

| Nest number | Initiation date | Day | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| 8BOG1 | 14 June 1988 | E* | E | | E* | E* | E* | E* | E* | | | | |
| 8BAP2 | 29 June 1988 | E* | E | E* | E* | E* | E* | | | | | | |
| 8BAY1 | 6 July 1988 | E* | E | | E* | E* | E* | | | | | | |
| 8ROJ2 | 19 July 1988 | E* | E | E* | E* | E* | | | | | | | |
| 7BAS1 | 22 June 1987 | E* | E | E* | E* | E* | E* | | | | | | |
| 8BOT2 | 20 June 1988 | E* | E | E* | E* | E* | E* | | | | | | E* |

after an interval of 5 days in one, and 6 days in the other. Four additional eggs (which were also removed as laid) were laid in one nest (8BOT2), after which the female deserted. In the other (7BAS1), the female laid five more eggs (which were left in the nest) and incubated them successfully. Although interruptions occurred in three of the laying sequences (Table 1), egg measurements and coloration indicated that only one female laid all eggs in each of the six nests.

These results do not differ from those of either Brackbill (1960) or Kendra et al. (1988). In both studies laying continued only after an interval of several days. Egg formation in the House Sparrow requires ca. 4 days (Schifferli 1980), which would indicate that the stimulus for the production of additional eggs in the experimental nests did not occur until late in the laying cycle, or until after the cycle was completed. Consequently, the female laid a series of "clutches." The size of each clutch was determined at the outset of laying. Therefore, House Sparrows should be considered a determinate layer (see Davis 1955), unless Witschi's (1935) claim of continuous laying by House Sparrow females is verified experimentally. My observation that four females incubated a single egg to hatching without laying additional eggs also raises questions about the validity of the claim (Kendra et al. 1988) that there are differences in the responses of female House Sparrows before and after the laying of the third egg. Larger sample sizes using both removal protocols described by Kendra et al. would be required to answer those questions.

Murphy (1978) concluded that House Sparrow females, studied near Lawrence, Kansas, and Calgary, Alberta, were genetically predisposed to produce clutches of 4–6 eggs (with a rarely achieved upper limit of 7 eggs). He also concluded that the actual number of eggs laid was determined proximately by the food supply just prior to the onset of egg laying. Each female laid as many eggs as she could produce under the prevailing conditions. My results corroborate this conclusion and demonstrate that female House Sparrows are apparently unable to respond to the experimental removal of eggs with continuous egg production (even if egg removal begins on the first day of laying). This implies that clutch size has been determined before the onset of egg laying. Increased food availability during the laying period would have little or no effect on clutch size in the House Sparrow (see also Anderson 1977, Hochachka and Boag 1987).

TABLE 1. Extended.

| Day | | | | | | | |
|---|---|---|---|---|---|---|---|
| 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| | | | | N | N | N | N |
| | | N | N | N | N | N | N |
| | | N | N | N | N | N | N |
| | | N | N | N | N | N | N |
| E | E | E | | E | E | | |
| E* | E* | E* | | | | | |

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## Polygyny in the Northern Saw-whet Owl

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Although owls are generally thought to be monogamous (Korpimäki 1988), polygyny has been reported in eight species in Europe (see Watson 1957, Scherzinger 1968, Koenig 1973, Schönfeld and Girbig 1975, Korpimäki 1983, Solheim 1983, Norgall 1985, Lehtoranta 1986, Sonerud et al. 1987). The incidence of polygyny appears rare, however, for all species but the Boreal Owl (*Aegolius funereus*; Carlsson et al. 1987; Korpimäki 1988, 1989).

We report two cases of polygyny for the Northern Saw-whet Owl (*Aegolius acadicus*), including the first apparent case of trigyny known for any owl species. We followed Korpimäki (1988) in inferring polygyny when the same male feeds two or more females (or their young) at different nests at which no other male is detected. We assumed in such cases that the male mated with the females. Given the territorial behavior of cavity-nesting owls (pers. obs.), this assumption is reasonable.

*Case 1: Snake River, southwestern Idaho.*—The Snake River Birds of Prey Area (BOPA) is a shrubsteppe desert dominated by big sagebrush (*Artemisia tridentata*) and is not typical Northern Saw-whet Owl breeding habitat (Marks and Doremus 1988). Trees are scarce, and most are too small to provide owl nesting cavities.

Beginning in 1982, nest boxes were placed in trees as part of an ongoing study of Western Screech-Owls (*Otus kennicottii*). The first Northern Saw-whet Owl nest known for the BOPA occurred in one of these boxes in 1986. Twenty-six pairs of boxes (paired boxes placed 1–40 m apart) were available in 1987. On 14 March, female Northern Saw-whet Owls were incubating in seven of these boxes. Three nests were very close together: two were in paired boxes 15-m apart and the third was 130 m away. Males were captured at all nesting sites between 22 and 29 March. Four nests were attended by different males in what appeared to be monogamous relationships. At the three close nests, however, we repeatedly captured and observed the same owl, which we marked in the center of the forehead with a dot of blue paint. This male was captured at both of the paired boxes on 22 March and carried food to all three nests on 12 April. He provisioned young at two of the nests until at least the end of April. No other male was seen or heard near these boxes. We believe this to be a case of trigyny, the first reported for any species of owl.

Nest boxes of the four monogamous pairs ranged from 265 m to >4 km apart. The first eggs hatched on 31 March, 2 April, and 6 April at three monogamous nests, and on 25 March and 9 April at two trigynous nests. A monogamous clutch of seven eggs was vandalized and failed to hatch. The other three monogamous nests produced 2, 4, and 5 fledglings from clutches of 5, 6, and 7 eggs, respectively. The 7-egg clutch from one of the trigynous nests failed to hatch (the eggs were addled). The other two nests produced 5 fledglings each from clutches of 5 and 6 eggs. Thus, the trigynous male produced 10 fledglings vs. a mean of 3.7 fledglings for the monogamous males (vandalized nest excluded). The trigynous male weighed 80 g on 22 March, and 76 g on 25 April. Of two monogamous males, one weighed 76 g (24 March) and the other 78 g (29 March); on 25 April, they weighed 73 and 77 g, respectively. These differences in mass loss between trigynous and monogamous males were slight.

Breeding Northern Saw-whet Owls in the BOPA fed almost exclusively on mice (Marks and Doremus 1988). Mice were unusually abundant near owl nests during 1987 (we saw and heard many), and nocturnal spotlight transects conducted each spring from 1984 to 1988 showed that 1987 was a peak year for mice (Table 1).

*Case 2: Vaseux Lake, south-central British Columbia.*—The Vaseux Lake area, characterized by open ponderosa pine (*Pinus ponderosa*)/Douglas fir (*Pseudotsuga*

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