

## REMOVAL INDETERMINACY AND THE PROXIMATE DETERMINATION OF CLUTCH SIZE IN THE HOUSE SPARROW<sup>1</sup>

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**Abstract.** To test whether or not the House Sparrow (*Passer domesticus*) is a determinate or indeterminate layer, 16 experimental nest sites were used following a removal protocol suggested by Haywood (pers. comm.). In six of the 16 experimental nests the females laid in an indeterminate manner, laying 8-18 eggs at daily intervals, or with breaks of one or two days. Analysis of the egg contents showed that fresh mass and dry masses of yolk, albumen and shell tended to increase with position in the laying sequence, with fresh mass, dry albumen mass and total dry mass of eggs 2-6 being significantly less than those of the supernumerary eggs, eggs 7+. Female condition was unaffected by the laying of supernormal-sized clutches. The implications of these results for the proximate determination of clutch size in the House Sparrow were discussed, including a proposed mechanism for clutch size determination in the species.

**Key words:** Indeterminate laying; clutch size; House Sparrow; *Passer domesticus*; female condition.

### INTRODUCTION

Since David Lack (1947) first proposed that the clutch size of altricial species of birds is selected to maximize the reproductive output of the individual female (or pair) and is ultimately determined by the ability of the parent(s) to provide food to the young, most studies have provided confirmation of the general hypothesis (see reviews in Klomp 1970, Murphy and Haukioja 1986, Martin 1987). Clutch size in some populations has, however, been observed to vary considerably with habitat type, season, density, female age, and year. Studies of the heritability of clutch size have generally found a low heritability of the trait in most species (Boag and van Noordwijk 1987), suggesting that most of the observed variation in clutch size is phenotypic. Perrins and Moss (1975) proposed that female Great Tits (*Parus major*) are able to adjust their clutch sizes to fit local conditions. Such phenotypic plasticity may permit individual optimization of reproductive output where there are predictable levels of local, seasonal or annual variability in environmental quality (see Drent and Daan 1980, Hogstedt 1980, Pettifor et al. 1988), and raises the question of what mechanisms are involved in the proximate determination of clutch size.

The proximate factors involved in the determination of clutch size in birds are not well understood. In species such as the Lesser Snow Goose (*Chen caerulescens*) that arrive on the breeding area and produce a clutch before sufficient food is available for egg production, the role of endogenous energy reserves in determining clutch size is well documented (Ankney and MacInnes 1978). Jones and Ward (1976) proposed that the amount of protein reserves in the flight muscles serves as a proximate determinant of clutch size in the altricial Red-Billed Quelea (*Quelea quelea*). In the House Sparrow (*Passer domesticus*) a correlation was observed between the fat content of the female on the first day of ovulation and the prospective clutch size, suggesting a proximate role for fat reserves in determining clutch size (Pinowska 1979). Loss of protein reserves during egg formation and laying has also been observed in female House Sparrows (Schifferli 1976, Jones 1990). A possible role for inorganic nutrient reserves, particularly magnesium, in laying House Sparrows has also been suggested (Pinowska and Krasnicki 1985).

Cole (1917) classified birds as either determinate or indeterminate based on the response of laying females to the removal or addition of eggs during the laying of a clutch. Species were classified as determinate if experimental removal or addition of eggs did not affect the number of eggs laid, or as indeterminate if females contin-

<sup>1</sup> Received 13 April 1994. Accepted 10 October 1994.

TABLE 1. Results of egg removal experiments on the House Sparrow. In the table E stands for an egg that remained in the nest on the day laid, E\* stands for an egg that was removed from the nest on the day laid, E<sub>r</sub> stands for an egg that was replaced on the day laid, F stands for a female that was captured incubating an egg or eggs at the site, and M stands for a male captured at the nestsite. Subscripts refer to the number of eggs remaining in the nest after the nest check on each day. Replacement eggs occasionally disappeared (i.e., R3092). Nests were normally checked between 07:00 and 11:00 EDT.

Nest Number	Date Initiated	Day													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
B3751	6/28	E* <sub>0</sub>													
B3371	6/16	E* <sub>0</sub>	E* <sub>0</sub>	M <sub>0</sub>	0	0	E* <sub>0</sub>	E* <sub>0</sub>							
B3CC1	6/15	E <sub>1</sub>	E** <sub>0</sub>	0	0	0	E* <sub>0</sub>	0	E* <sub>0</sub>						
A3201	4/29	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E <sup>c</sup> * <sub>0</sub>										
D30J1	6/25	E* <sub>0</sub>	E* <sub>0</sub>	0	E* <sub>0</sub>	E* <sub>0</sub>	E <sub>r1</sub>	E* <sub>1</sub>							
D3CF1	6/23	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	0	0	0	0	0	0	0	0	0	E* <sub>0</sub>	E* <sub>0</sub>
D3CD1	6/23 <sup>b</sup>						E* <sub>0</sub>	0	0	0	E* <sub>0</sub>	E* <sub>0</sub>	0	0	E* <sub>0</sub>
B3202	6/21	E <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>r1</sub>	1	1	1	1	1	E <sub>2</sub>	0	E* <sub>r2</sub>
R3092	6/23	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	0	E* <sub>0</sub>	E <sub>r1</sub>	1	1	1	1	1	1	1	E <sub>r2</sub>
D3251	6/17	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E <sub>r1</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	0	0	F		
D3092	7/2	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E <sub>r1</sub>	1	1	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	1	1
B30P2	6/22	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	0	E* <sub>0</sub>	E <sub>r1</sub>	1	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E <sub>r2</sub>	
D3351	6/20	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	0	E <sub>r1</sub>	1	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	1	1	F
R3511	6/21	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E <sub>r1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	1	1	1	1	E <sub>r2</sub>	E* <sub>2</sub>
D3751	6/16	E* <sub>0</sub>	E* <sub>0</sub>	0	0	E* <sub>0</sub>	0	E* <sub>0</sub>	0	0	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E* <sub>0</sub>	E <sub>r1</sub>

<sup>a</sup> Dead male House Sparrow removed from nest-box.  
<sup>b</sup> Laying sequence and egg coloration suggested that the same female was laying at the adjacent sites of D3CF1 and D3CD1.  
<sup>c</sup> Reduced pigmentation typical of last-laid eggs in the House Sparrow (cf. Lowther 1988).

ued laying beyond the normal clutch size if eggs were removed, or curtailed laying early if eggs were added. Kennedy (1991) and Haywood (1993) have recently reviewed indeterminate and determinate laying in birds. Kennedy (1991) categorized the House Sparrow as a removal determinate, but addition indeterminate layer, while Haywood (1993), basing his conclusions on the results of early reports with incomplete explanations of the experimental protocol (i.e., Wenzel 1908 cited in Haywood 1993; Witschi 1935), categorized the species as tactile indeterminate. Haywood (1993) also based this conclusion in part on the proposed linkage between tactile stimulation of the brood patch by the presence of one or more eggs in the nest, and the proximate determination of clutch size by the onset of incubation behavior and consequent termination of laying. Haywood (pers. comm.) predicted that if each egg was removed as it was laid beginning with the first egg, thereby preventing tactile feedback through the brood patch, female House Sparrows would lay indeterminately.

The objectives of this study were first to test Haywood's prediction that removal of each egg as it is laid would induce indeterminate laying in the House Sparrow, and second, to explore the implications of the findings from this exper-

iment for the proximate mechanism controlling clutch size in the species.

METHODS

The primary study site consisted of three dairy farms in the vicinity of the University of Michigan Biological Station (UMBS), Cheboygan County, Michigan, at which House Sparrow breeding colonies have been studied since 1986 (Anderson 1989, 1994). Many of the experimental nests were located in nest-boxes, although some were located in crevices in buildings. One experimental nest, also in a nest-box, was in a residential neighborhood in Lebanon, St. Clair County, Illinois.

Nest sites in Michigan were visited daily between 07:00 and 11:00 EDT from 15 June to 11 August 1993. Egg-laying in the House Sparrow normally occurs shortly after dawn; between 05:45 and 07:00 GMT in Great Britain (Summers-Smith 1963), and usually before 07:00 EDT at the study site (Anderson, pers. observ.). Eggs were numbered with felt-tip pen on the day laid, fresh mass to the nearest 0.05 g obtained with a 10-g Pesola balance, and length and maximum breadth measured to the nearest 0.1 mm with dial calipers.

TABLE 1. Extended.

																Day			
15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32		
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	0	0	0	0	0	0	0	E* <sub>0</sub> <sup>0</sup>	E* <sub>0</sub> <sup>0</sup>	E* <sub>0</sub> <sup>0</sup>									
E* <sub>3</sub> <sup>2</sup>	E* <sub>3</sub> <sup>2</sup>	E* <sub>3</sub> <sup>2</sup>	E* <sub>3</sub> <sup>2</sup>	E* <sub>3</sub> <sup>2</sup>	E* <sub>3</sub> <sup>2</sup>	E* <sub>3</sub> <sup>2</sup>	F												
E <sub>2</sub>	E <sub>3</sub>	3	E* <sub>3</sub>	3	3	3	F												
E <sub>3</sub>	E <sub>4</sub>	E <sub>4</sub>	E <sub>4</sub>	E <sub>4</sub>	E <sub>4</sub>	E <sub>4</sub>	F												
E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	E* <sub>1</sub>	0	E* <sub>0</sub>	E <sub>1</sub>	E* <sub>1</sub>	E <sub>2</sub>	E <sub>3</sub>	E* <sub>3</sub>	E* <sub>3</sub>	3	3	M <sub>3</sub>	F

At 16 experimental nest sites (11 nest-box sites including the one in Illinois), eggs were removed from the nest on the day they appeared, beginning with the first egg of a clutch. After being marked, weighed and measured, they were refrigerated for subsequent comparison and analysis. To minimize the risk of desertion each fifth egg of a laying sequence was replaced by an egg removed from another House Sparrow nest. Following termination of laying at an experimental site, all eggs laid at the site were examined together for possible differences in pigmentation pattern that might indicate that more than one female contributed to the clutch (intraspecific brood parasitism) (i.e., Kendra et al. 1988), and the entire clutch was photographed. No evidence of intraspecific brood parasitism was obtained, and none has been observed in the Michigan population during eight years of study (Anderson, pers. observ.).

Females were captured at both unmanipulated and experimental nest-box nests during either the incubation or nestling period. Females were weighed to the nearest 0.1 g on a 50-g Pesola balance, and tarsus length was measured to the nearest 0.1 mm with dial calipers. A condition index for each female was calculated by dividing the mass (g) by the tarsus length (cm). This index reduced some of the variation in mass due to

differences in structural size (Anderson, unpubl. data; see also Rising and Somers 1989).

The contents of eggs from six experimental nests in which females continued to lay beyond the normal clutch size (see below) were analyzed. Eggs were boiled for ten min, and then separated into yolk, albumen (white) and shell. These components were then oven-dried to constant weight (48 hr at 60°C), and the dry mass of each obtained to the nearest 0.1 mg on an electronic balance.

RESULTS

The laying histories of the 16 experimental nests are presented in Table 1. As in an earlier experimental study (Anderson 1989), the outcomes differed among nests, and the results in Table 1 are grouped according to these outcomes. In three cases (B3751, B3CC1 and B3371) nests were deserted after the laying of one to four eggs, with interruptions of one to three days in the laying sequences of two of the nests. In two nests (A3201 and D3OJ1) "clutches" of four and six eggs, respectively, were completed, after which the female deserted the site (with no eggs remaining in the nest in A3201, and with one egg in D3OJ1). In A3201 the conclusion that the four eggs represented a complete "clutch" was inferred from the fact that the fourth egg had the reduced pigmentation typical of last-laid eggs in the House

TABLE 2. Means (standard deviations) of fresh egg mass and dry masses of egg components for six House Sparrow nests in which indeterminate laying occurred.

	Nest number					
	D3251	D3092	B3OP2	D3351	R3511	D3751
Number of eggs	9	9 (8) <sup>a</sup>	10 (9) <sup>b</sup>	9	8	18
Fresh mass (g)	2.75 (0.12)	3.05 (0.23)	2.66 (0.08)	3.28 (0.14)	2.80 (0.09)	3.19 (0.17)
Dry yolk (mg)	213 (17)	260 (34)	213 (12)	264 (12)	248 (13)	239 (15)
Dry albumen (mg)	214 (10)	244 (21)	209 (7)	265 (13)	200 (13)	272 (17)
Dry shell (mg)	165 (8)	195 (14)	161 (6)	179 (7)	188 (4)	214 (10)

<sup>a</sup> Sample size of 8 for dry albumen and dry shell due to breakage during processing.  
<sup>b</sup> Sample size of 9 for all dry masses due to breakage.

Sparrow (Lowther 1988). The laying sequence and pigmentation patterns on the eggs suggested that the same female was laying alternately in two adjacent sites (D3CD1 and D3CF1). If this conclusion is correct (as presented in Table 1), this female laid 11 eggs over a span of 22 days with four interruptions of 1–5 days. At two sites (B3202 and R3092) the females laid six and five eggs, respectively, followed by the laying of an

additional four and five eggs after intervals of four and six days, respectively. These results were similar to patters reported in other studies of the House Sparrow (Brackbill 1960, Kendra et al. 1988, Anderson 1989).

In six nests females showed true removal indeterminacy (cf., Kennedy 1991) by laying from eight to 18 eggs on successive days, or with breaks of only one or two days. In one instance (D3751)

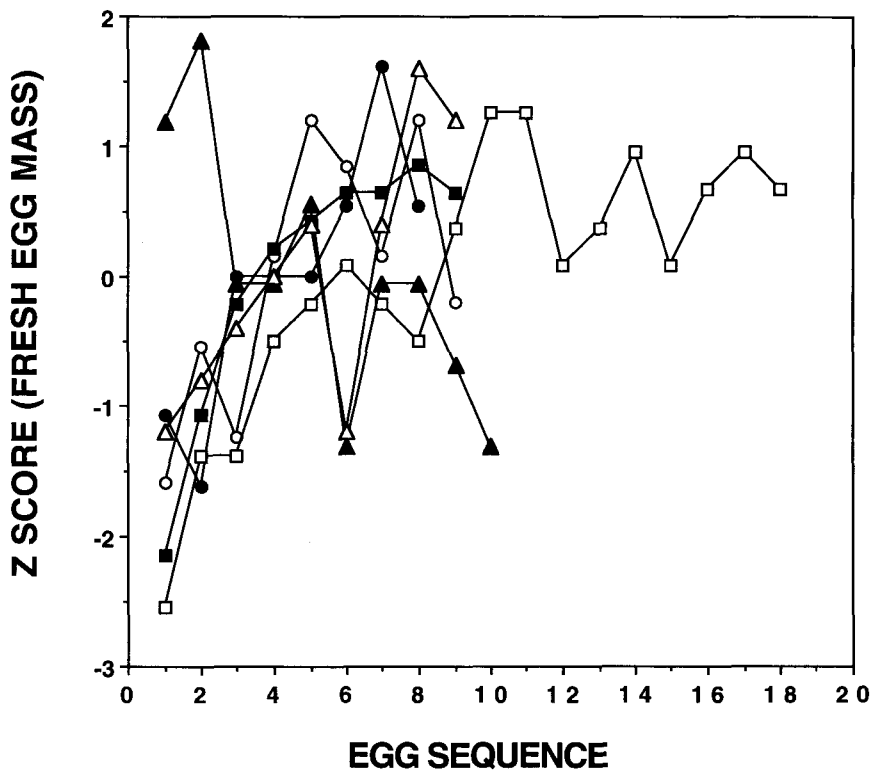


FIGURE 1. Standard scores (z-scores) of fresh egg mass plotted by position in laying sequence for eggs from six House Sparrow nests in which indeterminate laying occurred. Symbols for the six nests are: D3351 (○), R3511 (●), D3751 (□), D3092 (■), B3OP2 (▲) and D3251 (△).

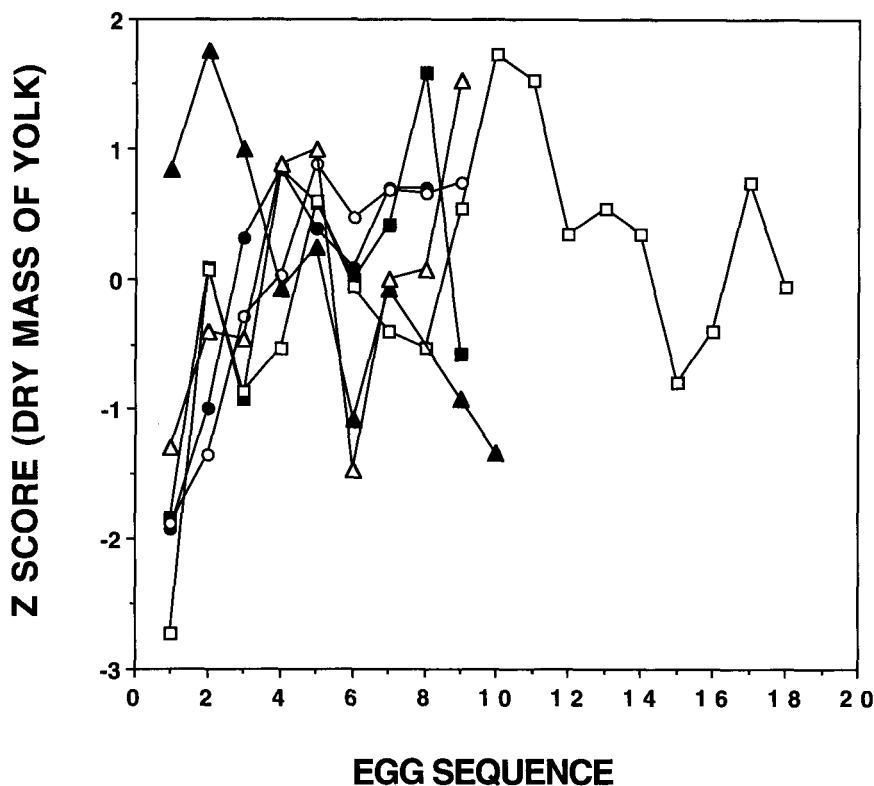


FIGURE 2. Z-scores of dry yolk mass plotted by position in the laying sequence for eggs from six indeterminate nests. Symbols as in Figure 1.

the laying of 18 eggs in 19 days followed a period in which four eggs had been laid and experimentally removed at 1–3 day intervals over eight days. Visual inspection of pigmentation patterns and mensural data (see below) both support the conclusion that the eggs at each site were laid by a single female. Clutch size of the House Sparrow at the study site during 1986–1991 varied from two to eight eggs, with only two of 340 completed clutches having eight eggs (Anderson 1994). The clutch size of 20 unmanipulated clutches during the period of this experiment varied from four to six (mean = 5.35, SD = 0.59), which was similar to the clutch size during this part of the breeding season in 1986–1991 (Anderson 1994).

Table 2 summarizes data on the composition of the eggs in the six nests in which indeterminate laying occurred. Accidental egg breakage resulted in incomplete data on two eggs, the second of nine eggs in D3351 and the eighth of ten eggs in B30P2. Standard scores (z-scores) of fresh mass, dry yolk mass, dry albumen mass and dry shell

mass were calculated for each egg within a clutch, and these z-scores were then plotted by position in the laying sequence for each egg in the six indeterminate nests (Figs. 1–4). In five of the six nests, fresh egg mass of the first egg was more than one standard deviation below the mean, and mass tended to increase with the laying sequence (Fig. 1). In the sixth nest (B30P2), fresh egg mass of the first egg was more than one standard deviation above the mean and tended to decrease with laying sequence. The pattern for dry yolk mass was very similar to that for fresh mass, with only B30P2 having a dry yolk mass of the first egg exceeding the average for the clutch (Fig. 2).

Dry albumen mass of first eggs, however, was less than the mean in all six indeterminate nests (Fig. 3), with the eighth egg in five of the six nests, and the ninth egg in B30P2 (in which the eighth egg was broken accidentally), all having dry albumen masses greater than the mean. No pattern was observed in the relationship between dry shell mass and laying sequence (Fig. 4).

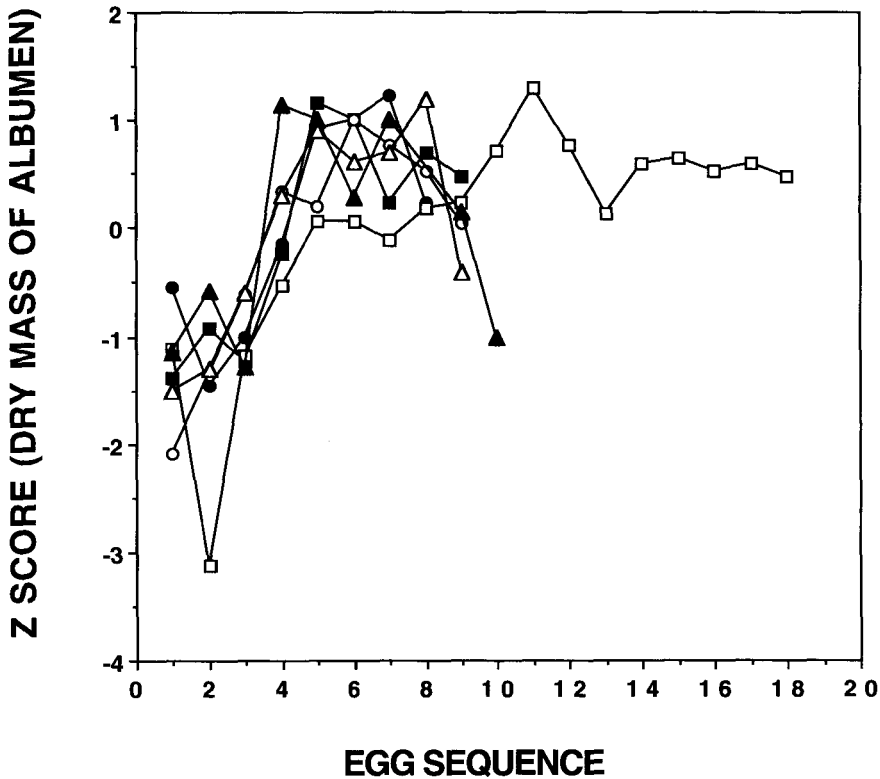


FIGURE 3. Z-scores of dry albumen mass plotted by position in the laying sequence for eggs from six indeterminate nests. Symbols as in Figure 1.

Nested analyses of variance were performed comparing the fresh, dry yolk, dry albumen, dry shell, and total dry masses of the first six eggs in a clutch with those of the seventh and subsequent eggs. In each case the among nest variation in mass was significant:  $F_{3,6} = 6.51$ ,  $P = 0.021$ ;  $F_{5,6} = 6.32$ ,  $P = 0.022$ ;  $F_{5,6} = 13.75$ ,  $P < 0.005$ ;  $F_{5,6} = 30.89$ ,  $P < 0.001$ ; and  $F_{5,6} = 11.34$ ,  $P = 0.005$ ; respectively. In the comparisons between the first six eggs and seventh and subsequent eggs, fresh mass ( $F_{6,51} = 5.31$ ,  $P < 0.001$ ), dry yolk mass ( $F_{6,50} = 2.53$ ,  $P < 0.05$ ), dry albumen mass ( $F_{6,49} = 3.44$ ,  $P < 0.01$ ) and total dry mass ( $F_{6,49} = 3.05$ ,  $P = 0.013$ ) all showed significant differences. In all cases mean masses of the first six eggs were lower than those of the seventh and subsequent eggs. Dry shell mass did not differ significantly between the early and late eggs ( $F_{6,50} = 1.82$ ,  $P > 0.10$ ).

Because the first egg in most of the nests had the lowest mass (see above), and might therefore account for the significant differences noted be-

tween eggs 1–6 and eggs 7+, the nested ANOVA was repeated comparing the masses of eggs 2–6 with those of the seventh and subsequent eggs. Among nest differences in masses were again highly significant: fresh mass ( $F_{5,6} = 11.99$ ,  $P < 0.01$ ), dry yolk mass ( $F_{5,6} = 14.28$ ,  $P < 0.01$ ), dry albumen mass ( $F_{5,6} = 17.66$ ,  $P < 0.01$ ), dry shell mass ( $F_{5,6} = 43.07$ ,  $P < 0.001$ ), and total dry mass ( $F_{5,6} = 23.01$ ,  $P = 0.001$ ). Significant within nest differences were observed only in fresh mass ( $F_{6,45} = 4.66$ ,  $P = 0.001$ ), dry albumen mass ( $F_{6,43} = 3.13$ ,  $P = 0.012$ ) and total dry mass ( $F_{6,43} = 2.67$ ,  $P < 0.05$ ). In each case the mean masses of eggs 2–6 were less than those of the seventh and subsequent eggs. Dry yolk mass and dry shell mass did not differ significantly ( $F_{6,44} = 1.73$ ,  $P > 0.10$  and  $F_{6,44} = 1.61$ ,  $P > 0.15$ , respectively).

Five of the six females laying in an indeterminate manner were captured during incubation following the termination of laying. In two of the cases, R3511 and D3092, females were captured after laying additional eggs after 3–4 day inter-

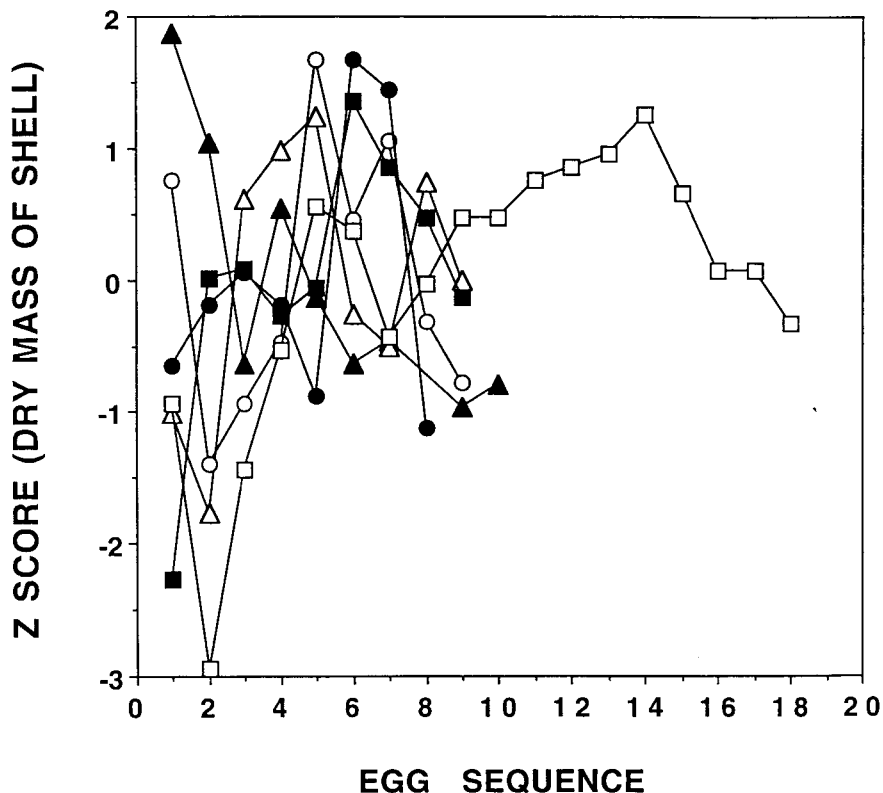


FIGURE 4. Z-scores of dry shell mass plotted by position in the laying sequence for eggs from six indeterminate nests. Symbols as in Figure 1.

ruptions following the laying of the supernormal-sized clutches (see Table 1). Figure 5 compares the condition of these five females to that of 140 females captured on second broods at the same study site during the years 1986–1991 (Anderson, unpubl. data).

#### DISCUSSION

The results of these experiments confirm Haywood's (pers. comm.) prediction, and demonstrate conclusively that the House Sparrow is a removal indeterminate layer. The results also support the conclusion of Krementz and Ankney (1986) that egg production in the House Sparrow is primarily dependent on exogenous energy and nutrient resources, and that the female's endogenous reserves do not directly limit clutch size in the species. The correspondence of the results with Haywood's prediction further suggests that the onset of incubation plays a role in the termination of egg-laying, and therefore in the proximate determination of clutch size.

Several recent experiments have suggested that the House Sparrow is a determinate layer (cf., Anderson 1989). Brackbill (1960) removed the second and subsequent eggs as they were laid from one nest, and the female laid an initial "clutch" of five eggs, and then a second "clutch" of four eggs following a four-day hiatus. He also added four eggs to a nest on the day the first egg was laid, and the female continued to lay, completing a four-egg "clutch." Schifferli (1976) removed the first three eggs as they were laid in ten nests, and observed no apparent increase in clutch size. He also added four eggs to seven nests on the day the first egg was laid, and observed no apparent decrease in clutch size. Kendra et al. (1988) used two removal protocols, removing the second and subsequent eggs as laid in three nests, and removing the third and subsequent eggs in three other nests. In two of the former nests the females continued to lay following intervals of 4–5 days. Anderson (1989) removed the first egg on the day laid and the third and

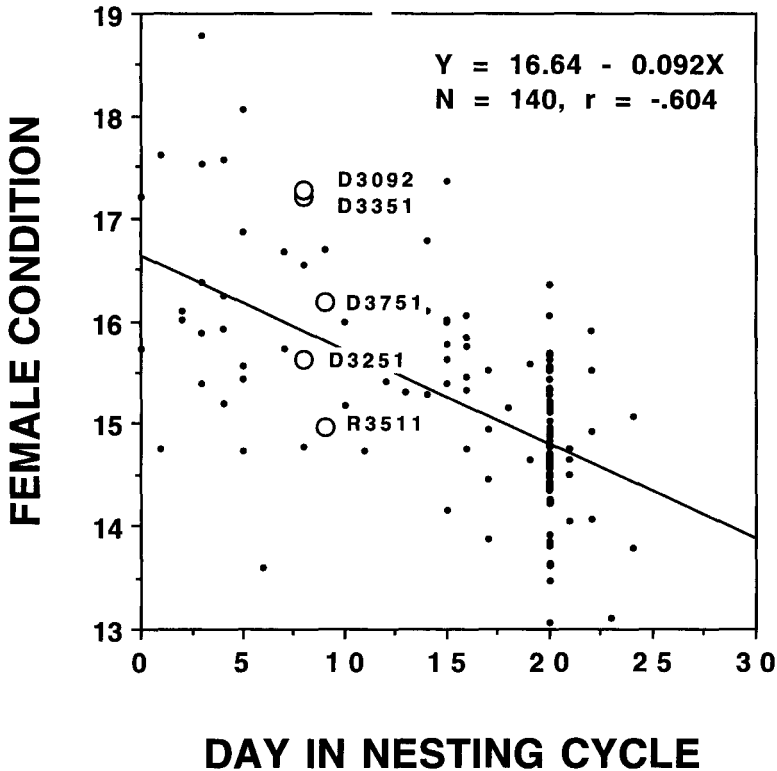


FIGURE 5. Condition of five females captured during incubation at sites at which indeterminate laying occurred compared to a regression of female condition against day in the nesting cycle for 140 females captured on second broods during 1986–1991 at the same study site (Anderson, unpubl. data). Days in the nesting cycle were standardized to the modal clutch size and incubation period (see Anderson 1994), and days 1–5 represent the laying period, days 6–14 the incubation period, and days 15–30 the nestling period.

subsequent eggs as laid, and observed continued laying in two nests following breaks of five and six days. Four other females incubated the one remaining egg to hatching following the same removal protocol. Anderson (1989) concluded that the House Sparrow is a determinate layer, and that the continued laying in several of the experiments following a 4–6 day hiatus represented the laying of replacement clutches rather than indeterminate laying (see Davis 1955).

The laying of 8–18 eggs in the six experimental nests described above represents conclusive evidence that the House Sparrow is a removal indeterminate layer, in contradiction to my earlier conclusion (Anderson 1989), but consistent with Haywood's (pers. comm.) prediction. This indeterminate laying, and particularly the patterns of change in fresh egg mass and dry masses of the three egg fractions (Figs. 1–4), also demonstrate that endogenous reserves of the laying fe-

male do not directly limit clutch size in the House Sparrow. Mean masses of eggs 2–6 in the laying sequence were lower than those of the supernumerary eggs (7+) for all egg components, and nested ANOVAs showed that these differences were significant for fresh egg mass, dry albumen mass and total dry mass. Kremetz and Ankney (1986) determined the daily protein and fat requirements for egg production in laying House Sparrows, and concluded that the costs of egg production do not limit clutch size in the species. The results of this experiment confirm their conclusion.

Although egg production was not directly limited by the energetic or nutrient costs of egg production itself, the number of eggs might normally be limited by the necessity for females to retain sufficient reserves to successfully complete subsequent, energetically-demanding reproductive activities such as incubation and the brooding



and feeding of nestlings (Martin 1987). Although the results in the present study are not definitive due to the small sample size, the fact that the conditions of the five females captured during incubation, following the production of super-normal-sized clutches, were comparable to the conditions of females laying unmanipulated second clutches at the site (Fig. 5), strongly suggests that the females laying 8–18 eggs still maintained normal body reserves.

The difference in these results and those summarized above is undoubtedly due to each of the first four eggs being removed as laid in this study. The presence of even a single egg in the nest is apparently sufficient to induce onset of incubation, presumably through tactile stimulation to the brood patch (see Haywood 1993), resulting in termination of laying. The results of this and other experiments also show, however, that the presence of an egg is not a necessary condition to terminate laying. In A3201, for instance (see Table 1), the female completed a four-egg "clutch" despite the fact that no eggs remained in the nest. In R3092, the female ceased laying after the fifth egg, and resumed laying after a hiatus of six days even though no egg had remained in the nest prior to the laying of the fifth egg. The presence of one egg in the nest is therefore apparently a sufficient, but not a necessary, cause for the cessation of laying.

Mead and Morton (1985) proposed that a direct link exists between onset of incubation and termination of laying in the White-crowned Sparrow (*Zonotrichia leucophrys*). Haywood (1993) discussed two possible hormonal mechanisms that might be involved in terminating egg production: (a) an increase in prolactin levels that inhibits rapid follicular development in the ovary, and (b) suppression of gonadotropin releasing factor secretion from the hypothalamus, which is necessary for release of follicle stimulating hormone from the pituitary gland. Although the two may work in concert, the effect of tactile stimulation of eggs on the brood patch resulting in increased prolactin levels seems to represent a more parsimonious explanation (Mead and Morton 1985, Haywood 1993).

Meijer (1990) studied onset of incubation in captive European Starlings (*Sturnus vulgaris*) by continuously monitoring nestcup temperatures during egg-laying. He found a fixed pattern of daily periods of incubation beginning with the laying of the first egg, with progressively longer

periods of incubation on successive days. He also found that the entire incubation schedule shifted appropriately for different clutch sizes both within and among females (i.e., the entire schedule shifted forward one day in four-egg clutches compared to five-egg clutches). Meijer (1993) recently reported removal indeterminacy in captive European Starlings. Females for which the second and subsequent eggs were removed as laid, or for which the first two eggs were removed following the laying of the second egg, laid in a determinate manner; but many females for which each of the first three eggs were removed as laid, laid 1–3 additional eggs. Six of nine females laid 1–3 additional eggs when egg removal occurred at 15:00 hr on the day the egg was laid, while three of ten females laid one or two additional eggs when removal occurred at 08:00 hr the morning following the laying of the egg (see Fig. 1, Meijer 1993). This difference was significant despite the fact that no incubation normally occurs in the interval between 15:00 hr and 08:00 hr following the laying of the first egg (Meijer 1990). This suggests that some tactile feedback from the eggs may occur when the female covers them at night even though she does not incubate them.

Although the onset of incubation in the House Sparrow has not been as intensively studied as that in the European Starling, it is known that female House Sparrows spend more total time and longer periods of time on the nest on successive days of egg laying (Summers-Smith 1963, North 1980). Assuming that the onset of incubation in the House Sparrow is similar to that in the European Starling, a possible mechanism for the proximate determination of clutch size in the species may involve the following steps: (1) female condition at some point prior to the beginning of egg laying determines both a prospective clutch size within a genetically determined range (Murphy 1978) and a corresponding schedule for the onset of incubation (Meijer 1990); (2) during egg laying, tactile feedback from the presence of at least one egg in the nest causes continuation of the onset of incubation behavior, with resultant increases in prolactin secretion; and (3) rising prolactin levels suppress continued follicular development stopping egg production at the predetermined number. Failure to obtain the tactile feedback due to the experimental removal or natural disappearance of each egg as it is laid may interrupt the schedule of onset of

incubation, with a resultant lack of increase in prolactin levels, leading to indeterminate laying. A somewhat similar model has been proposed for the proximate determination of clutch size in the single-brooded European Kestrel (*Falco tinnunculus*), which shows a seasonal decline in clutch size (Meijer et al. 1990).

If the individual female House Sparrow optimizes its reproductive output under varying environmental conditions, then the information upon which she makes the "decision" of how many eggs to lay must be available during the period of egg formation and laying. Egg formation from the beginning of rapid yolk deposition and follicular enlargement to egg laying requires five days in the House Sparrow (Schifferli 1980). Eggs are laid at daily intervals which means that the female has as many as five eggs developing simultaneously. Natural abortion of developing follicles is rare in House Sparrows, with atretic follicles being observed in less than 2% of large samples of females collected during egg laying in Great Britain and Ontario, Canada (Schifferli 1976, Krementz and Ankney 1988). This means that rapid yolk deposition normally begins in a number of follicles equal to the number of eggs to be laid.

Pinowska (1979) found a positive correlation between lipid reserves of the female on the day of first ovulation (the day before the laying of the first egg) and the number of eggs which the female was preparing to lay, and proposed that clutch size in Polish House Sparrows is determined by fat reserves in the female at the time of first ovulation. The fact that fat reserves in the female do not set an ultimate limit on the number of eggs that can be laid (as evidenced by the indeterminate laying observed in this study) does not preclude the possibility that lipid metabolism in the female is responsible for the proximate determination of clutch size. Lipid reserves in the female increase rapidly just prior to (Schifferli 1976) or during (Krementz and Ankney 1988) yolk deposition in the first developing follicles of a clutch. A plausible hypothesis therefore links lipid reserves in the laying female to the proximate determination of clutch size in the House Sparrow.

Placing of the timing of this proximate determination of clutch size at the day of first ovulation would help to explain the difference between the results of this study and those of Schifferli (1976), who failed to obtain indeter-

minate laying following the removal of the first three eggs as they were laid in Oxford, England. This discrepancy may be explained by the fact that the modal clutch size of the House Sparrow in Oxford is four (Seel 1968, Dawson 1972), while the modal clutch size in Michigan is five, with six being almost as common as five for second clutches (Anderson 1994). Assuming that most of the females in Schifferli's study were preparing to lay four-egg clutches, removal of the first egg after it is laid would occur at a time when initiation of rapid yolk deposition has already ceased. In the present study, however, where most of the females were presumably preparing to lay five- or six-egg clutches, removal of the first and subsequent eggs occurred at a time when initiation of yolk deposition in another follicle was still occurring on a daily basis, creating the opportunity for the lack of tactile stimulation from an egg in the nest to play a role in triggering cessation of laying, thus resulting in some cases in indeterminate laying.

#### ACKNOWLEDGMENTS

I thank J. Teeri, T. Crandall and R. Vande Kopple for logistic support, and D. Budzinski, G. Dotski, and E. Riemann for permission to work on their properties. I thank C. M. Perrins, S. Haywood, J. Wright and P. W. Hicklin for stimulating discussions on avian reproductive strategies, and C. M. Perrins and the Edward Gray Institute of Field Ornithology, the Department of Zoology and Wolfson College, Oxford University for their gracious hospitality during my sabbatical stay at Oxford. I also thank an anonymous reviewer for many helpful suggestions. The University of Michigan Biological Station and McKendree College provided logistical support during the course of this study and during the preparation of the manuscript. Partial funding for this research was provided by an NSF-sponsored Research Experience for Undergraduates Program at UMBS (BMS-9100525).

#### LITERATURE CITED

- ANDERSON, T. R. 1989. Determinate vs. indeterminate laying in the House Sparrow. *Auk* 106:730-732.
- ANDERSON, T. R. 1994. Breeding biology of House Sparrows in northern lower Michigan. *Wilson Bull.* 106:537-548.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459-471.
- BOAG, P. T., AND A. J. VAN NOORDWIJK. 1987. Quantitative genetics, p. 45-78. *In* F. Cooke and P. A. Buckley [eds.], *Avian genetics: a population and ecological approach*. Academic Press, London.
- BRACKBILL, H. 1960. Determinate laying by House Sparrows. *Condor* 62:479.

- COLE, L. J. 1917. Determinate and indeterminate laying cycles in birds. *Anat. Rec.* 11:504-505.
- DAVIS, D. E. 1955. Determinate laying in Barn Swallows and Black-billed Magpies. *Condor* 57:81-87.
- DAWSON, D. G. 1972. The breeding biology of House Sparrows. Ph.D. diss., Oxford Univ., Oxford, U.K.
- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225-252.
- HAYWOOD, S. 1993. Sensory and hormonal control of clutch size in birds. *Quart. Rev. Biol.* 68:33-60.
- HOGSTEDT, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210:1148-1150.
- JONES, M. M. 1990. Muscle protein loss in laying House Sparrows *Passer domesticus*. *Ibis* 133:193-198.
- JONES, P. J., AND P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea *Quelea quelea*. *Ibis* 118:547-574.
- KENDRA, P. E., R. R. ROTH, AND D. W. TALLAMY. 1988. Conspecific brood parasitism in the House Sparrow. *Wilson Bull.* 100:80-90.
- KENNEDY, E. D. 1991. Determinate and indeterminate egg-laying patterns: a review. *Condor* 93:106-124.
- KLOMP, H. 1970. The determination of clutch-size in birds: a review. *Ardea* 58:1-124.
- KREMENTZ, D. G., AND C. D. ANKNEY. 1986. Bioenergetics of egg production by female House Sparrows. *Auk* 103:299-305.
- KREMENTZ, D. G., AND C. D. ANKNEY. 1988. Changes in lipid and protein reserves and in diet of breeding House Sparrows. *Can. J. Zool.* 66:950-956.
- LACK, D. 1947. The significance of clutch-size. *Ibis* 89:302-352.
- LOWTHER, P. E. 1988. Spotting pattern of the last laid egg of the House Sparrow. *J. Field Ornithol.* 59:51-54.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.* 18:453-487.
- MEAD, P. S., AND M. L. MORTON. 1985. Hatching asynchrony in the mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*): a selected or incidental trait? *Auk* 102:781-792.
- MEIJER, T. 1990. Incubation development and clutch size in the Starling. *Ornis Scand.* 21:163-168.
- MEIJER, T. 1993. Is the Starling *Sturnus vulgaris* a determinate layer? *Ibis* 135:315-319.
- MEIJER, T., S. DAAN, AND M. HALL. 1990. Family planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. *Behaviour* 114:117-136.
- MURPHY, E. C. 1978. Seasonal variation in reproductive output of House Sparrows: the determination of clutch size. *Ecology* 59:1189-1199.
- MURPHY, E. C., AND E. HAUKIOJA. 1986. Clutch-size in nidicolous birds. *Current Ornithol.* 4:141-180.
- NORTH, C. A. 1980. Attentiveness and nesting behavior of the male and female House Sparrow (*Passer domesticus*) in Wisconsin. *Acta XVII Intern. Ornithol. Congr.* 1122-1128.
- PERRINS, C. M., AND D. MOSS. 1975. Reproductive rates in the Great Tit. *J. Anim. Ecol.* 44:695-706.
- PETTIFOR, R. A., C. M. PERRINS, AND R. H. MCCLEERY. 1988. Individual optimization of clutch size in Great Tits. *Nature* 336:160-162.
- PINOWSKA, B. 1979. The effect of energy and building resources of females on the production of House Sparrow (*Passer domesticus* (L.)) populations. *Ekol. Polska* 27:363-396.
- PINOWSKA, B., AND K. KRASNICKI. 1985. Changes in the content of magnesium, copper, calcium, nitrogen and phosphorus in female House Sparrows during the breeding cycle. *Ardea* 73:175-182.
- RISING, J. D., AND K. M. SOMERS. 1989. The measurement of overall body size in birds. *Auk* 106:666-674.
- SCHIFFERLI, L. 1976. Factors affecting weight and condition in the House Sparrow particularly when breeding. Ph.D. diss., Oxford Univ., Oxford, U.K.
- SCHIFFERLI, L. 1980. Changes in the fat reserves of female House Sparrows, *Passer domesticus* during egg laying. *Acta XVII Congr. Intern. Ornithol.* 1129-1135.
- SEEL, D. C. 1968. Clutch-size, incubation and hatching success in the House Sparrow and Tree Sparrow *Passer* spp. at Oxford. *Ibis* 110:270-282.
- SUMMERS-SMITH, D. 1963. The House Sparrow. Collins, London.
- WITSCHI, E. 1935. Seasonal sex characters in birds and their hormonal control. *Wilson Bull.* 47:177-188.