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Breeding biology of House Sparrows: Patterns of intra-clutch variation in egg size

ABSTRACT

In general, House Sparrows [*Passer domesticus* (L.)] show a "brood survival strategy" with regard to intra-clutch variation in egg size. Within a clutch, eggs hatch asynchronously and last-laid eggs are larger than first-laid eggs. The increase in egg size with laying order becomes greater for late season clutches. Early season clutches suggest the contrasting "brood reduction strategy" since eggs show only a slight increase in size with laying order. During the middle – and supposedly optimum – portion of the breeding season, survival of eggs, clutch size and food reserves are greatest; also during this time, within clutch egg size shows its greatest rate of increase.

KEY WORDS: *Passer domesticus*, clutch-size, egg size, brood reduction.

1. INTRODUCTION

There are several hypotheses that purport to explain reproductive strategies of birds with regard to the quantity and quality of eggs that should be produced in order to maximize fledgling production. The chances of survival of particular eggs or young throughout a nesting attempt may depend on number of eggs, egg mass, laying order and time of initiation of incubation (and subsequent degree of

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hatching synchrony), and environmental conditions (e. g., amount and predictability of food resources; predation pressures) (LACK 1954, 1966, O'CONNOR 1978, CLARK and WILSON 1981, 1985, SLAGSVOLD 1982, 1986, RICHTER 1982). Comparisons of breeding biologies, both inter- and intraspecific, have provided ideas to aid understanding of adaptations for successful reproduction. Recently, SLAGSVOLD et al. (1984) examined the adaptive value of within-clutch egg-size variation. They proposed two contrasting patterns of egg-size variation: the "brood reduction strategy" and the "brood survival strategy". Within a "brood reduction" clutch the last egg laid is smaller than the others. Young hatched from small eggs are small in relation to nestmates which, of course, hatched from larger eggs. Coupled with any hatching asynchrony (which is usual among passerines; CLARK and WILSON 1981, p. 265), the last hatched young may be 1 to 2 days younger than its sibs, and these small individuals ("runts"; RICKLEFS 1965) die quickly if food is not abundant. By producing a small last egg, parents thus minimize their total investment in those young most likely to die. In contrast, within a "brood survival" clutch the last laid egg is larger than others in the clutch; these last eggs are "provisioned" with more yolk than others in the clutch. The last egg's larger size counteracts the effects of hatching asynchrony by increasing the short-term survival of last hatched young in the presence of older nestmates (demonstrated for Great Tits *Parus major* L., SCHIFFERLI 1973) until, perhaps, better food conditions appear later in the season. There have been many studies showing brood reduction occurring in passerines, and more recently several studies have documented regular patterns of within-clutch egg size variation (e.g., see OJANEN et al. 1981: 104).

House Sparrows [*Passer domesticus* (L.)] begin incubation on the penultimate egg (SUMMERS-SMITH 1963, SEEL 1968) and as a consequence exhibit asynchronous hatching; eggs may hatch over a 2 or 3 day period. In addition, as I show here, within a clutch, egg size (on average) increases through the laying sequence (see also MURPHY 1978a). House Sparrows then would appear to fit this "brood survival" model of SLAGSVOLD et al. (1984).

2. MATERIALS AND METHODS

The data I examined were obtained during a 4 year study (1975–1978) of House Sparrow population ecology and breeding biology at 9 farms in Leavenworth County, northeastern Kansas, USA. Other reports provide more detail of this sparrow population (MURPHY 1978a, b, LOWTHER 1979a, b, 1983, FLEISCHER 1983, FLEISCHER et al. 1984). Nests were checked, for the most part, every 3 days and new eggs numbered. Egg mass was measured for all eggs to the nearest 0.1 g with a Pesola spring scale. Egg length and width were measured to the nearest 0.1 mm with vernier calipers for all eggs in 1975 and 1976 and at 2 study farms in 1978. Data I use here are from eggs with all 3 measurements. In all, measurements of 764 completed clutches provide data for this analysis. I will emphasize data from 4-, 5-, and 6-egg clutches; these clutch sizes comprise 90% of the sample. I use the variable "volume" to indicate egg size; I calculated volume as (0.512) (length) $(\text{width})^2$.

I use the following definitions. A "FIRST" egg is an egg known to be first in the laying sequence; it was the only egg in the nest after a new clutch was initiated. A "first" egg is the egg numbered "1", when 2 or more eggs present in the nest on the first visit after clutch initiation. A "LAST" egg is an egg sometimes known to be last laid in the clutch (only new egg added to clutch and no others added later) or identified as last due to spotting pattern (LAST eggs could be easily separated from others in the clutch because of their larger spot size and less dense spotting pattern; more than 90% of completed clutches contained a LAST egg in this study; see also DAWSON 1964, SEEL 1968, MURPHY 1978a, LOWTHER 1983, 1988). A "completed clutch" is a clutch containing a LAST egg or known to have been incubated or from which young had hatched. "Egg survivorship" is the proportion of eggs in completed clutches which produce young that leave the nest. The "date of clutch initiation" is the date the first egg was laid. The breeding season was divided into approximate fourths by dates of clutch initiation: "April clutches" were initiated on or before 30 April and as early as 7 March (= days 65 to 120); "May clutches" were initiated between 1 May and 30 May (= days 121 to 150); "June clutches" were initiated between 31 May and 29 June (= days 151 to 180); and "July clutches" were initiated on or after 30 June and as late as 25 August (= days 181 to 237).

Nest visits every 3 days did not permit determination of the exact laying sequencing of all eggs. However, since House Sparrows lay 1 egg/day, eggs could be properly assigned to segments of the laying sequence depending on how many eggs were present on the first visit after clutch initiation. Below I show the precision of laying order for 5- and 6-egg clutches. The first visit after clutch initiation may have 1, 2 or 3 new eggs, which would be numbered (with no relationship necessarily existing between laying order and egg number). Later visits, at 3 day intervals, will add, at most, 3 new eggs which would also be numbered. Thus, considering visits to the nest during egg laying, the laying order of eggs would be known with varying precision (see below).

	First visit	Second visit	Third visit
5-egg clutch:	(1)	2, 3, 4	5
	1, 2	3, 4, (5)	
	1, 2, 3	4, (5)	
6-egg clutch:	(1)	2, 3, 4	5, (6)
	1, 2	3, 4, 5	6
	1, 2, 3	4, 5, (6)	

The (5) and (6) above indicate LAST eggs known by their spotting pattern; (1) indicates a FIRST egg.

3. RESULTS

Egg volume increases during the laying sequence (Fig. 1). Table I compares measures of FIRST and LAST eggs. LAST eggs are larger in all measurements but differences are statistically significant only for egg width and egg volume.

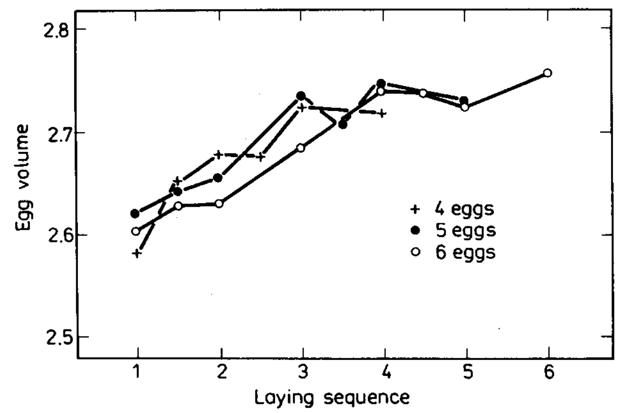

Fig. 1. Egg volume in relation to laying sequence for House Sparrow populations in Kansas, USA

In this figure, eggs that were, for example, numbered "1" and "2" when two eggs were found on the first visit would be combined and placed ys "1.5" in the laying sequence. See text discussion of nest checking frequency and Table V

TABLE I

Comparison of FIRST and LAST eggs from 4-, 5-, and 6-egg clutches

Variable	Clutch size	n	FIRST egg		LAST egg		*t*
			mean	variance	mean	variance	
Width (cm)	4	30	1.521	0.003	1.556	0.003	2.475*
	5	80	1.547	0.004	1.577	0.033	3.207**
	6	66	1.535	0.004	1.570	0.002	3.671***
Length (cm)	4	30	2.165	0.017	2.178	0.012	0.418 ns
	5	80	2.163	0.012	2.173	0.009	0.617 ns
	6	66	2.157	0.012	2.177	0.008	1.149 ns
Volume (cm^3)	4	30	2.575	0.094	2.709	0.080	1.759 ns
	5	80	2.658	0.072	2.773	0.061	2.820**
	6	66	2.613	0.083	2.754	0.051	3.129**
Mass (g)	4	29	2.734	0.104	2.841	0.079	1.347 ns
	5	80	2.799	0.082	2.873	0.066	1.720 ns
	6	65	2.737	0.086	2.851	0.068	2.342*

ns – not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

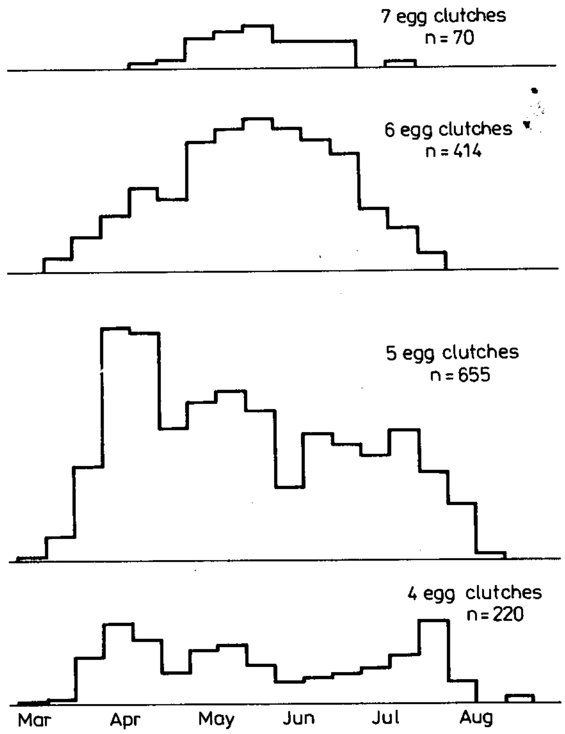

Fig. 2. Seasonal distribution, at 10-day intervals, of 4-, 5-, 6- and 7-egg clutches of House Sparrows in northeastern Kansas, USA (1975–1978)

Mean clutch size increases to a maximum in mid-season; 7-egg clutches appeared only in the middle of the breeding season; 6-egg clutches show a greater spread of laying dates; 5-egg clutches greater still; and 4-egg clutches are most common early and late in the nesting season (MURPHY 1978b, LOWTHER 1979a, Fig. 2). In 4-egg clutches, survival rates are lowest early in the season and highest during late season; for 5-egg clutches, survival is lowest at season's end and highest during mid-season; survival in 6-egg clutches is low during both early and late season and highest during mid-season. Survivorship values varied between 38 and 53% (Table II).

The only instance where average egg volume for a clutch size differed from the grand mean for all eggs is for April 6-egg clutches which have a small average volume (2.64 cm^3 versus the overall mean of 2.68 cm^3 based on 4573 eggs; Table III). Difference in total clutch volume (that is, the summed volume of all eggs in the clutch) between April 5-egg and 4-egg clutches (2.53 cm^3) and between April 6-egg and 5-egg clutches (2.55 cm^3) are small in comparison to other periods of the nesting season (Table IV). In other words, eggs from large clutches are slightly

TABLE II

Measures of egg survivorship partitioned by clutch size and by portion of the nesting season. Data are from those clutches from which all eggs were measured

Season	Clutch size	Young reared							Young/nest	Egg survivor-ship* %
		0	1	2	3	4	5	6		
April	4	20	2	10	8	7			1.57	39
	5	60	3	19	13	38	18		2.13	43
	6	28	0	5	4	12	8	6	2.32	39
May	4	11	4	8	7	5			1.74	44
	5	37	2	10	7	21	13		2.13	43
	6	33	2	4	10	18	14	8	2.58	43
June	4	7	2	1	3	2			1.40	47
	5	18	1	3	14	13	8		2.47	49
	6	27	1	2	8	12	16	8	2.77	46
July	4	12	0	6	12	8			2.11	53
	5	31	1	5	7	14	9		1.93	39
	6	8	1	1	1	4	3	1	2.26	38

* Egg survival within July shows significant differences between clutch sizes ($\chi^2 = 25.7$, df = 2). Within other months, rate of egg survival for 4-, 5-, and 6-egg clutches are not significantly different.

Within clutch sizes, all comparisons of rates of egg survival among months show significant χ^2 values: for 4-egg clutches, $\chi^2 = 8.23$, df = 3; for 5-egg clutches, $\chi^2 = 66.26$, df = 3; and for 6-egg clutches, $\chi^2 = 24.25$, df = 3.

TABLE III

Mean volume of eggs from clutches of 4-, 5- and 6-eggs partitioned by season. Within clutch sizes, rows show means, variances and sample sizes (total eggs)

Clutch size	Portion of breeding season			
	April	May	June	July
4	2.684	2.711	2.659	2.660
	0.067	0.061	0.065	0.089
	181	136	60	144
5	2.660	2.708	2.712	2.688
	0.057	0.062	0.060	0.064
	736	443	276	335
6	2.645	2.711	2.700	2.734
	0.070	0.061	0.086	0.098
	353	514	434	113

TABLE IV

Mean values for total clutch volume (= summed volume of all eggs in clutch). Within clutch sizes, rows show means, variances and sample sizes (total clutches)

Clutch size	Portion of breeding season			
	April	May	June	July
4	10.765	10.877	10.635	10.648
	0.877	0.746	0.533	1.215
	46	32	15	35
Difference between total volume of 4- and 5-egg clutches	2.528	2.653	2.980	2.770
5	13.293	13.530	13.615	13.418
	1.032	1.184	1.119	1.140
	142	86	54	66
Difference between total volume of 5- and 6-egg clutches	2.548	2.721	2.627	3.032
6	15.841	16.251	16.242	16.450
	2.145	1.626	2.412	2.964
	48	79	71	18

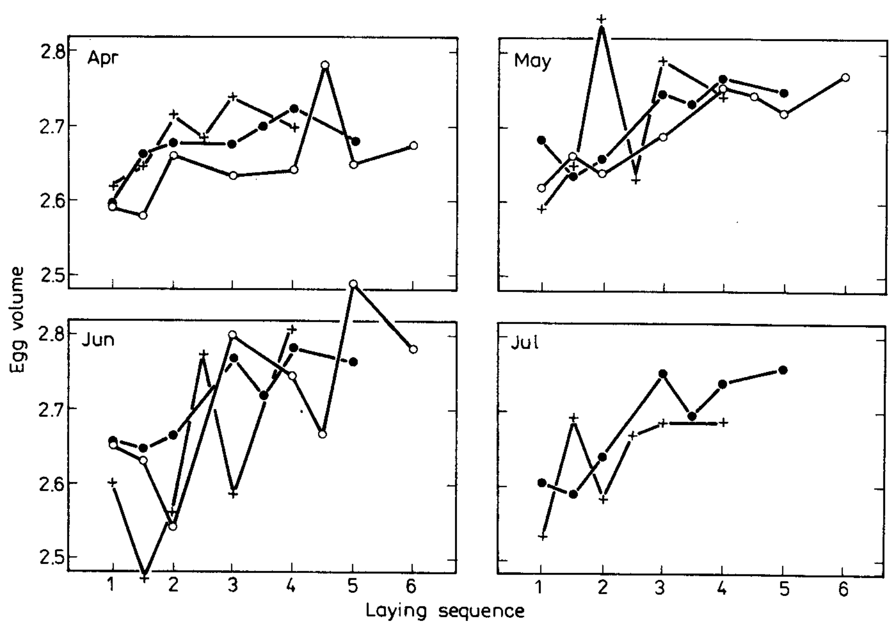

Fig. 3. Egg volume in relation to laying sequence partitioned by portion of the breeding season for House Sparrow populations in Kansas, USA

See also Fig. 1, Table V. + 4-egg clutches; • 5-egg clutches; o 6-egg clutches smaller than those from small clutches early in the breeding season but this difference disappears in mid- and late-season time periods.

Seasonal comparisons of known FIRST egg and known LAST egg volumes show a similar pattern for all clutch sizes – April clutches show a small difference between volumes of FIRST and LAST eggs; later in the breeding season this difference is larger. April clutches show the lowest rate of increase in egg volume with regression slopes of about 0.02 as compared to slopes of 0.03 or 0.04 later in the nesting season (Fig. 3, Table V).

TABLE V

Mean volumes of eggs of House Sparrows. Season designations are defined in the text. Position in laying sequence is indicated as accurately as possible. Within each clutch-season category, rows of values are means, variances, and sample sizes. Value of regression slope, b, describes least squares regression of egg volume on laying sequence; statistical significance is shown by t-test value

Clutch size	Season	Position in laying sequence						*b*	*t*
		1	1–2	1–2–3	2–3	3	4		
4	April	2.622	2.654	2.718	2.680	2.739	2.693	0.025	1.254
		0.090	0.046	0.031	0.083	0.030	0.063		
		14	28	27	26	14	36		
	May	2.591	2.657	2.850	2.627	2.790	2.748	0.044	1.075
		0.080	0.059	0.041	0.090	0.023	0.049		
		12	18	27	24	8	28		
	June	2.599	2.465	2.552	2.778	2.586	2.819	0.088	1.942
		0.064	0.017	0.040	0.065	0.104	0.084		
		6	4	15	12	2	13		
	July	2.539	2.690	2.578	2.670	2.685	2.686	0.039	1.645
		0.102	0.121	0.106	0.039	0.146	0.067		
		13	22	32	24	11	35		
Overall		2.587	2.655	2.684	2.676	2.725	2.719	0.041	3.62*
		0.083	0.071	0.071	0.070	0.065	0.063		
		45	72	101	86	35	112		

Clutch size	Season	1	1–2	1–2–3	2–3–4	3–4	4	5	*b*	*t*
5	April	2.599	2.666	2.674	2.679	2.700	2.723	2.679	0.019	2.25
		0.062	0.058	0.047	0.045	0.058	0.041	0.053		
		43	98	72	129	92	24	111		
	May	2.648	2.635	2.656	2.743	2.730	2.761	2.743	0.033	4.37**
		0.078	0.062	0.046	0.073	0.053	0.042	0.068		
		32	54	68	96	52	22	80		
	June	2.645	2.643	2.662	2.769	2.717	2.782	2.754	0.036	3.68*
		0.060	0.052	0.045	0.069	0.076	0.029	0.065		
		24	28	48	72	28	14	51		
	July	2.603	2.588	2.639	2.756	2.692	2.735	2.756	0.044	4.30**
		0.135	0.055	0.072	0.091	0.037	0.054	0.062		
		17	34	63	51	34	21	55		
Overall		2.623	2.643	2.658	2.727	2.709	2.747	2.723	0.030	4.46**
		0.075	0.058	0.052	0.065	0.055	0.042	0.061		
		116	214	251	348	206	81	297		

Table V (*continued*)

	1	1–2	1–2–3	2–3–4	3–4–5	4–5	5	6	*b*	*t*
6 April	2.590	2.583	2.664	2.633	2.641	2.786	2.647	2.677	0.021	1.81
	0.078	0.111	0.040	0.068	0.075	0.037	0.056	0.074		
	22	30	30	73	44	22	25	48		
May	2.622	2.656	2.636	2.686	2.750	2.740	2.716	2.770	0.029	6.35***
	0.087	0.085	0.052	0.046	0.084	0.025	0.031	0.045		
	35	56	39	108	81	26	33	73		
June	2.654	2.629	2.540	2.802	2.745	2.667	2.877	2.786	0.041	2.26*
	0.074	0.067	0.090	0.078	0.052	0.119	0.067	0.067		
	21	48	54	63	72	38	21	63		
July	2.411	2.614	2.936	2.568	2.917	2.955	2.597	2.840	0.053	1.28
	0.178	0.112	0.023	0.071	0.052	0.026	0.074	0.100		
	7	12	12	24	18	8	8	18		
Overall	2.604	2.629	2.630	2.688	2.740	2.740	2.724	2.759	0.032	8.21***
	0.089	0.085	0.073	0.066	0.073	0.071	0.058	0.065		
	85	146	135	268	215	94	87	202		

ns – not significant; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

4. DISCUSSION

House Sparrows do lay eggs that show an increase in size through the laying sequence. As summarized in Figure 1, eggs become larger in volume within a clutch. This is true for other species as well (Pikula 1971, Howe 1976, Ryden 1978, Mead and Morton 1985, Weatherhead 1985). This increased size is a result of additional food reserves present in later eggs, indirectly evidenced here, but more directly measured by Krementz and Ankney (1986), who found yolk reserves in last-laid eggs of House Sparrows to be larger. House Sparrows provision their eggs least during the early nesting season when food resources for egg production are low. From this "brood reduction mode" of April clutches, birds switch to a "brood survival mode". Within later clutches, last eggs show a greater degree of provisioning and egg survivorship is higher.

Otto (1979) noted a positive association between food resources (biomass of earthworms at feeding areas) and changes in average egg mass among several colonies of Fieldfare (*Turdus pilaris* L.). For another thrush, Blackbird (*Turdus merula* L.), Ryden (1978) showed that food resources do influence the pattern of within clutch variation in egg mass. The first half of the breeding season is most favorable for earthworm populations which form a major portion of the birds' diet, at least of the young, and egg mass increases with the order of laying sequence. For the second half of the breeding season, when earthworm populations gradually decline, egg mass of all eggs in a clutch are near the same.

Ojanen et al. (1981) found a relatively small proportion of the total egg size variation within a population to be attributed to laying sequence. They did find slight, but statistically significant, correlations with temperatures prior to egg laying. They relate this association to the availability of food levels during the period females build their fat and protein reserves prior to clutch initiation and the time of rapid yolk growth the few days before an egg is finally laid. Temperatures prior to clutch initiation have a direct influence on insect egg and pupae development, a major source of proteins for many passerines in the breeding season. OJANEN et al. (1981) found that egg size of FIRST eggs to be most influenced by temperatures one week prior to egg laying, when females are building their reserves; these reserves become depleted as the clutch is laid (especially larger clutch sizes – see PINOWSKA 1979) and the size of the LAST egg is correlated with temperatures 1–3 days prior to egg laying – the time yolk formation occurs (SCHIFFERLI 1980).

JÄRVINEN and YLIMAUNU (1986) critique the paper of SLAGSVOLD et al. (1984) and offer data to show that breeding birds are laying eggs of a size and number of which they are physiologically capable under constraints imposed by the environment. From their work with Pied Flycatcher [*Ficedula hypoleuca* (Pallas)], they suggest that temperatures prior to egg laying influence the condition of females and female condition determines the size of eggs. Presumably ambient temperatures have an impact on insect populations; cold temperatures would reduce the availability of food for this insectivorous flycatcher. This relationship between temperature and egg size is also evidenced in comparing good (warm) and bad (cold) breeding seasons (JÄRVINEN and VÄISÄNEN 1984). Although a direct relationship between temperature and egg size is not strikingly evident for House Sparrows such an association is likely valid also. Environmental conditions can influence the availability of food resources; food resource levels may affect a female's condition which, in turn, affects the quantity and quality of eggs she can lay. Such environmental influences will vary between and within breeding seasons. Early ("April") clutches in this study were more often comprised of 4 and 5 eggs (Fig. 2) and the rate of increase in egg size within a clutch was lower than at other times of the breeding season (Table V).

PINOWSKI and MYRCHA (1977) found within clutch egg mass to decline through the laying sequence for an Indian population of House Sparrows. This finding is not necessarily inconsistent with the interpretation I give to my Kansas data. In this tropical population, the breeding season was very long (February to October), clutch size was small (3.5 eggs) and egg survivorship was low (25%). Temperate breeding cycles exhibit a sudden surge of food availability which is not as evident in tropical areas. In tropical populations females may not, or can not, accumulate sufficient fat and protein reserves from available food resources for provisioning eggs or for larger clutches. As a result a "brood reduction" mode constantly exists in these populations. Similar differences in pattern of egg size variation exist among geographically separated populations of other species also (e.g., *Tyrannus tyrannus* (L.), MURPHY 1983).

Nesting House Sparrows show a flexible response to environmental conditions. Females lay the largest clutch possible as dictated by environmental and individual condition. Constraints imposed by changing levels of food resources produce changes in individual responses (a change in "strategy") which appear to maximize fledgling production while reducing overall initial reproductive effort by egg-laying females.

5. SUMMARY

Many species of birds show asynchronous hatching, an adaptation thought to enhance brood reduction. Some of these species also "provision" the last-laid (and last-to-hatch) eggs to enhance the initial survival of these chicks and to slow down the speed of brood reduction. House sparrows (*Passer domesticus*) show both traits – asynchronous hatching and provisioning last-laid eggs – attributes which together describe a "brood survival" strategy (Slagsvold et al. 1984). During a 4 year breeding biology study in northeastern Kansas, USA, eggs from 764 clutches were measured (length, width, and mass). These data are examined to show trends in egg size variation. Last-laid eggs are larger than first eggs in most measures of size (width, volume, mass; no difference in length). Egg volume increases in the laying sequence. Differences between first and last eggs are greatest later in the season for 4-, 5- and 6-egg clutches. Egg volume decreases with increasing clutch size at the start of the nesting season. During mid-season, eggs in 5-egg clutches have the largest volumes. Both 5- and 6-egg clutches have their largest egg volumes mid-season. Females of early season nestings have a "brood reduction" strategy with clutches showing only slight increases in volume during the laying sequence. As food reserves and availability increases later in the breeding season, survival of eggs to fledging and mean clutch size increases; also, birds adopt a "brood survival" mode in which egg size increases at a greater rate.

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