VARIATIONS IN EGG CHARACTERISTICS OF THE HOUSE WREN

BY S. CHARLES KENDEIGH, THEODORE C. KRAMER, AND FRANCES HAMERSTROM

THERE are scattered records in the literature showing that the weights of consecutively laid fresh eggs or their measured lengths and maximum diameters may either decrease or increase in different species. In a statistical analysis of 20 clutches in the Laughing Gull (*Larus atricilla*), Preston and Preston (1953) showed that the length measurement did not differ significantly either among the eggs of the same clutch or between the eggs of different clutches. On the other hand, in three-egg clutches the third egg laid had a significantly smaller diameter than the first two. In two-egg clutches, the second egg appeared to resemble the third more than the second in the three-egg clutches, but the small number of measurements available did not permit definite conclusions.

Since a large series of data had been collected at the Baldwin Bird Research Laboratory, near Cleveland, Ohio, between 1925 and 1938, on the eggs of the House Wren (*Troglodytes aëdon*), we decided to determine whether or not there were any consistent changes in dimensions and weight with sequence of laying in this passerine species. Comparable data have been obtained for only one other passerine species, the Song Sparrow, *Melospiza melodia* (Nice, 1937).

S. C. Kendeigh of the University of Illinois is chiefly responsible for the statistics and for making the biological interpretations, T. C. Kramer of the University of Michigan collected much of the raw data, Frances Hamerstrom of the Wisconsin Conservation Department provided the original data for the experiments conducted by Dr. Leon J. Cole and for her own experiments in trying to force House Wrens to lay additional eggs. An early draft of the manuscript was read, important suggestions were offered, and help with the statistics was given by Dr. F. W. Preston and Mary E. Gemperle of the Preston Laboratories, Butler, Pennsylvania, by Dr. Alexis L. Romanoff of Cornell University, by Dr. H. M. Scott of the University of Illinois, and by Dr. David E. Davis of Johns Hopkins University. This paper is contribution number 45 of the Baldwin Bird Research Laboratory.

Materials and procedure.—The length and greatest diameter of the eggs were measured at the Baldwin Laboratory to 0.01 mm. with a Palo micrometer caliper equipped with a ratchet stop and adjustment screw. Each egg was numbered as laid so that the sequence of laying could be determined. All weights were obtained on the same day that the eggs were laid, usually within six hours. The eggs were weighed to 1 mg., generally on a chainomatic balance. Usable data are available on egg dimensions in sequence of normal laying for 29 clutches and on egg weights for 52 clutches. Egg measurements were obtained on 195 additional clutches where the sequence of laying was not known. Data are presented on forced laying experiments for eight females.

TABLE 1

AVERAGE LENGTH (IN MILLIMETERS) OF HOUSE WREN EGGS, WITH STANDARD DEVIATIONS

	Clutch Size			
	4	*5*	*6*	*7*
Position in sequence	(*2 clutches*)	(*11 clutches*)	(*13 clutches*)	(*3 clutches*)
1	16.08	16.80 ± 0.92	16.54 ± 1.10	16.08
2	15.95	16.75 ± 0.45	16.33 ± 0.68	16.82
3	16.31	16.83 ± 0.46	16.78 ± 0.57	16.59
4	16.58	17.03 ± 0.61	16.62 ± 0.52	16.96
5		17.12 ± 0.62	16.84 ± 0.47	16.60
6			17.12 ± 0.59	16.72
7				17.11
Total increase first to last egg	0.50	0.32	0.58	1.03
Average increase per egg	0.167	0.080	0.116	0.172
Per cent average increase per egg	1.03	0.47	0.69	1.03

Length.—Table 1 gives the average length of each egg according to its ordinal position in the clutch and according to the size of the clutch. Although there is some irregularity among the early eggs laid, the penultimate egg averages longer than the third from the last in each clutch and the last egg longer than the penultimate. There appear to be no statistically reliable differences between clutches in

TABLE 2

AVERAGE BREADTH (IN MILLIMETERS) OF HOUSE WREN EGGS, WITH STANDARD DEVIATIONS

	Clutch Size			
	4	*5*	*6*	*7*
Position in sequence	(*2 clutches*)	(*11 clutches*)	(*13 clutches*)	(*3 clutches*)
1	12.46	12.78 ± 0.49	12.54 ± 0.38	12.41
2	12.65	12.74 ± 0.31	12.58 ± 0.36	12.71
3	12.76	12.77 ± 0.22	12.73 ± 0.30	12.69
4	12.84	12.84 ± 0.29	12.81 ± 0.32	12.53
5		12.90 ± 0.31	12.85 ± 0.32	12.48
6			12.89 ± 0.32	12.76
7				12.94
Total increase first to last egg	0.38	0.12	0.35	0.53
Average increase per egg	0.127	0.030	0.070	0.088
Per cent average increase per egg	1.02	0.23	0.55	0.69

the total increase from first to last egg, the average increase per egg, or the per cent average increase per egg when all size clutches are included. However, if the four-egg clutches are excluded, all three calculations of increase from first to last egg become greater as the size of the clutch increases.

TABLE 3

RESULTS OF ANALYSES OF VARIANCE FOR LENGTH OF EGGS IN 24 COMBINED FIVE- AND SIX-EGG CLUTCHES

		First and third eggs	*First and last eggs*	*Third and last eggs*
Computed variance ratio	Sequence	0.64	4.80	17.7
	Parentage	2.29	1.56	7.86
F value for 1 per cent level	Sequence	7.88	7.88	7.88
	Parentage	2.72	2.72	2.72
F value for 5 per cent level	Sequence	4.28	4.28	4.28
	Parentage	2.01	2.01	2.01
Significance	Sequence	No	Barely	Yes
	Parentage	Barely	No	Yes
Variability	Sequence	—	1.0162	0.5768
	Parentage	0.0208	0.0124	0.0197
	Error	0.3869	0.5346	0.0689
	Total	0.4077	1.5632	0.6654
Partition of variability (per cent)	Sequence	—	65.0	86.7
	Parentage	5.1	0.8	3.0
	Error	94.8	34.2	10.3
Coefficient of variation (per cent)	Sequence	—	6.0	4.5
	Parentage	3.7	0.7	0.8
	Error	0.9	4.3	1.5
Mean value of characteristic for	First egg	16.66	16.66	—
	Third egg	16.80	—	16.80
	Last egg	—	17.12	17.12
	All eggs	16.73	16.89	16.96

Breadth.—Contrary to what was found in the Laughing Gull, the last egg in clutches of the House Wren is the largest in diameter (Table 2). As with length, there is some irregularity in the first eggs of each clutch, but the penultimate and last eggs average greater in breadth than the next preceding ones. If the four-egg clutches are excluded, there is an increase from five- to six- to seven-egg clutches in the total increase in breadth from first to last egg, in average increase per egg, and in per cent average increase per egg. However, if the four-egg clutches are included the differences are not significant.

Analysis of variance for length and breadth.—The standard deviations of both length and breadth as given in Tables 1 and 2 may be due in part to differences between individuals laying the eggs. An analysis of variance was therefore made according to (1) the bird that laid the egg or "parentage," (2) the position of the egg in the clutch sequence, and (3) a variety of other causes or "error." This is the same basis used by Preston and Preston (1953) for the eggs of the Laughing Gull, and both terminology and method of analysis are similar.

Considering only the 24 five- and six-egg clutches and only the first, third, and last egg, it was found that neither the length nor the breadth differed significantly at the one per cent level between the first and third egg in the sequence, but that the length and breadth of the third egg differed significantly from the last egg (Tables 3 and 4). The influence of parentage on length and breadth was relatively small.

TABLE 4

RESULTS OF ANALYSES OF VARIANCE FOR BREADTH OF EGGS IN 24 COMBINED FIVE- AND SIX-EGG CLUTCHES

		First and third eggs	*First and last eggs*	*Third and last eggs*
Computed variance ratio	Sequence	1.57	11.15	14.17
	Parentage	2.59	3.58	8.33
F value for 1 per cent level	Sequence	7.88	7.88	7.88
	Parentage	2.72	2.72	2.72
F value for 5 per cent level	Sequence	4.28	4.28	4.28
	Parentage	2.01	2.01	2.01
Significance	Sequence	No	Yes	Yes
	Parentage	Barely	Yes	Yes
Variability	Sequence	0.0213	0.3223	0.1159
	Parentage	0.0049	0.0121	0.0538
	Error	0.0745	0.0635	0.0176
	Total	0.1007	0.3979	0.1873
Partition of variability (per cent)	Sequence	21.0	81.0	61.9
	Parentage	5.0	3.0	28.7
	Error	74.0	16.0	9.4
Coefficient of variation (per cent)	Sequence	1.2	4.5	2.6
	Parentage	0.6	0.9	1.8
	Error	2.2	2.0	1.0
Mean value of characteristic for	First egg	12.65	12.65	—
	Third egg	12.75	—	12.75
	Last egg	—	12.89	12.89
	All eggs	12.70	12.77	12.82

Shape.—No detailed data are available on the shape of the eggs, but it will probably be near enough for our calculations to take them as being prolate ellipsoids, that is, spheres elongated along one axis. The only index of shape we have at our disposal is the ratio of maximum diameter to length. An increase in the value of this ratio indicates that the egg is relatively shorter and broader and a decrease in the index indicates that the egg is longer in proportion to its breadth. It appears from Table 5 that in all except the seven-egg clutches the second from the last and the last eggs show a progressively smaller index value. This means that although the last two eggs increase

TABLE 5

INDEX OF SHAPE ACCORDING TO THE FORMULA: $100 \cdot \frac{\text{breadth}}{\text{length}}$

Position in sequence	*Clutch size* 4 (*2 clutches*)	5 (*11 clutches*)	6 (*13 clutches*)	7 (*3 clutches*)
1	77.49	76.07	75.82	77.18
2	79.31	76.06	77.04	75.56
3	78.23	75.88	75.86	76.49
4	77.44	75.40	77.08	73.88
5		75.35	76.31	75.18
6			75.29	76.32
7				75.63

TABLE 6

AVERAGE WEIGHTS (IN GRAMS) OF NEW-LAID EGGS, WITH STANDARD DEVIATIONS

Position in sequence	*Clutch size* 4 (*6 clutches*)	5 (*16 clutches*)	6 (*20 clutches*)	7 (*10 clutches*)
1	1.393 ± 0.222	1.370 ± 0.086	1.416 ± 0.134	1.479 ± 0.129
2	1.417 ± 0.135	1.405 ± 0.074	1.436 ± 0.120	1.482 ± 0.098
3	1.456 ± 0.159	1.431 ± 0.094	1.442 ± 0.125	1.510 ± 0.105
4	1.481 ± 0.173	1.453 ± 0.103	1.452 ± 0.131	1.511 ± 0.102
5		1.498 ± 0.094	1.472 ± 0.129	1.512 ± 0.123
6			1.514 ± 0.124	1.520 ± 0.135
7				1.567 ± 0.151
Total increase first to last egg	0.088	0.128	0.098	0.088
Average increase per egg	0.0293	0.0320	0.0196	0.0147
Per cent average increase per egg	2.04	2.24	1.35	0.97

progressively in both length and breadth, the increase in length is proportionally greater than the increase in breadth.

Weight.—It is clear from Table 6 that in four- and five-egg clutches there is a progressive increase in the weight of eggs from the first to the last laid. In six- and seven-egg clutches the increase from egg to egg is small except for the last egg laid. In the five-, six-, and seven-egg clutches the increase from the penultimate to the last egg is greater than that between any other two eggs, being 3.10, 2.85, and 3.09 per cent of the penultimate egg respectively. In the four-egg clutches, the increase between the second and third is greater than between the last two eggs.

If the four-egg clutches are excluded, the total increase from first to last egg, the average increase per egg, and the per cent average increase all decrease in the larger clutches, which is just the opposite of what occurs with length and breadth.

Two clutches of eggs, not included in the above calculations, contained "runt" eggs. One was the fourth egg of a first clutch for the season, *viz.*, no. 1—1.401 gm., no. 2—1.458 gm., no. 3—1.518 gm., *no. 4—0.800 gm.*, no. 5—1.676 gm., no. 6—1.653 gm. The other was the first egg of a female's second clutch during the season, *viz.*, *no. 1—0.929 gm.*, no. 2—1.250 gm., no. 3—1.258 gm., no.4—1.338 gm., no. 5—1.360 gm. The first egg lacked a yolk, the second egg examined after the rest of the clutch had hatched had a yolk but was apparently infertile.

Analysis of variance for weight.—In order further to analyze the significance and reliability of the differences in egg weights, a three-by-three matrix of figures was composed representing the weights of the first, last, and middle eggs of clutches of five, six, and seven eggs. The "middle" egg of a clutch of six was considered the mean weight of the third and fourth eggs.

The analysis showed that both the position of the egg in its clutch and the clutch-size had a significant effect upon egg weight. The "partition of variability" expressed as percentages came out as follows:

variability as affected by clutch size	39.5 per cent
variability as affected by position in sequence	58.3 per cent
variability as affected by other causes	2.1 per cent
	99.9 per cent

The "coefficients of variation," expressed as percentages, are:

by clutch-size	2.9 per cent
by position in the sequence	3.6 per cent
by other causes	0.7 per cent

Still another analysis of significance by "Student's" *t*-test, has the advantage of incorporating not only the average figures shown in the matrix, but also the standard deviations of these figures, since they are derived from the weighings of many individual eggs, which are pooled to obtain the averages.

The *t*-test shows that in a five-egg clutch the difference between the first and last eggs is significant at the 99 per cent confidence level; in a six-egg clutch it is significant at the 95 per cent level; but in a seven-egg clutch, the difference is *not* significant at the 95 per cent level.

Comparing clutches of different sizes, the *t*-test reports that there is a significant difference, at the 95 per cent level, between the first egg of a clutch of five and of a clutch of seven. The same could *not* be established for the last egg of such clutches.

It is also possible to run various tests of "correlation." For instance, given the weight of the first egg of a clutch, can one prophesy the number of eggs that will be laid or their total weight? There is a positive correlation between these factors, but on account of the considerable scatter in weight of individual eggs, any prophecy is attended with a substantial risk. The coefficient of correlation is approximately +0.33. Curiously enough, when the first two eggs

TABLE 7

CHARACTERISTICS OF PARTICULAR EGGS

	Weight *grams*	*Length(l)* *millimeters*	*Breadth(b)* *millimeters*	*Volume(V)* *cubic centimeters*	*Specific* *Gravity*
Female 31917	1.358	16.28	12.49	1.330	1.02
(five-egg clutch)	1.405	16.80	12.57	1.390	1.01
	1.511	16.94	12.93	1.483	1.02
	1.574	17.40	13.04	1.549	1.02
	1.592	17.75	12.99	1.568	1.02
Female 183	1.312	16.55	12.32	1.315	1.00
(five-egg clutch)	1.379	16.61	12.52	1.363	1.01
	1.364	16.53	12.42	1.335	1.02
	1.359	16.51	14.43	1.336	1.02
	1.379	16.66	12.50	1.363	1.01
Female 167	1.440	16.20	12.92	1.416	1.02
(five-egg clutch)	1.395	16.76	12.57	1.387	1.01
	1.391		(egg too cracked to measure)		
	1.398	16.28	12.63	1.360	1.03
	1.430	16.55	12.86	1.433	1.00
Female 26551	1.420	16.02	12.72	1.357	1.05
(six-egg clutch)	1.402	15.87	12.74	1.349	1.04
	1.445	16.24	12.84	1.402	1.03
	1.552	16.29	13.26	1.500	1.03
	1.510	16.43	13.07	1.470	1.03
	1.598	16.30	13.44	1.542	1.04
Female 38479	1.290	16.40	12.10	1.257	1.03
(six-egg clutch)	1.322	16.30	12.34	1.300	1.02
	1.153[1]	16.65	12.32	1.323	0.87[1]
	1.163[1]	16.68	12.36	1.334	0.87[1]
	1.387	16.78	12.38	1.347	1.03
	1.361	16.99	12.26	1.337	1.02

[1] It appears that the weights and consequently the specific gravities of these two eggs were incorrectly determined.

are taken as a guide and not merely the first one, the correlation drops to about +0.25.

Volume, Mass, Density.—Both dimensions and weights were obtained on 26 eggs, which makes possible the determination of specific gravity when the volume is calculated. If the House Wren egg were a true prolate ellipsoid, its volume could be computed by the equation:

$$V = \frac{\pi}{6} \cdot l \cdot b^2$$

where V is the volume, l the length, and b the *equatorial* diameter.

The coefficient $\pi/6$ is approximately 0.5236. Since the maximum diameter is somewhat closer to the large than the small end, a small modification of this coefficient may be desirable. Actual measurements of volumes are more accurate than volumes calculated from the egg dimensions, but since such measurements are not available, the coefficient given must suffice. Worth (1940) found for eggs of the domestic fowl that volumes obtained by water displacement were 15 per cent less than those calculated by the ellipsoid formula, but the extent of this difference doubtless varies in differently shaped eggs laid by different species or even different individuals.

TABLE 8

DIFFERENCE IN AVERAGE CHARACTERISTICS OF THE FIRST AND LAST EGGS IN THE DIFFERENT SIZED CLUTCHES

	Four-, five-, six-, seven-egg clutches		*Five-, six-, seven-egg clutches only*	
	First egg	*Last egg*	*First egg*	*Last egg*
Average length (mm.)	16.38	16.98	16.47	17.12
Standard deviation	±0.31	±0.23	±0.30	±0.01
Coefficient of variation	1.89	1.35	1.82	0.06
Average breadth (mm.)	12.55	12.89	12.58	12.91
Standard deviation	±0.14	±0.04	±0.15	±0.02
Coefficient of variation	1.12	0.31	1.19	0.15
Average shape index	76.64	75.93	76.36	75.42
Standard deviation	±0.71	±0.88	±0.59	±0.15
Coefficient of variation	0.93	1.16	0.77	0.20
Average weight (gm.)	1.414	1.515	1.422	1.526
Standard deviation	±0.041	±0.032	±0.045	±0.030
Coefficient of variation	2.90	2.11	3.16	1.97
Average volume (cc.)	1.351	1.468	1.365	1.480
Standard deviation	±0.056	±0.025	±0.057	±0.011
Coefficient of variation	4.15	1.70	4.18	0.74
Average specific gravity	1.05	1.03	1.04	1.03
Standard deviation	±0.068	±0.025	±0.078	±0.029
Coefficient of variation	6.48	2.43	7.50	2.82

Volumes of each of the 26 eggs are presented in Table 7 and weight divided by volume gives their density or specific gravity. In all cases, the volume of the last egg is greater than the volume of the first, but otherwise there is considerable irregularity with sequence of laying. There is no consistent trend in specific gravity within the various clutches.

Variability.—There may be physiological importance in knowing which egg in a sequence of laying is most variable in its physical characteristics and which is the most constant. Since the first and last eggs are at opposite extremes of clutch gradients in size and weight, the variability in their average characteristics between clutches of different sizes was analyzed statistically.

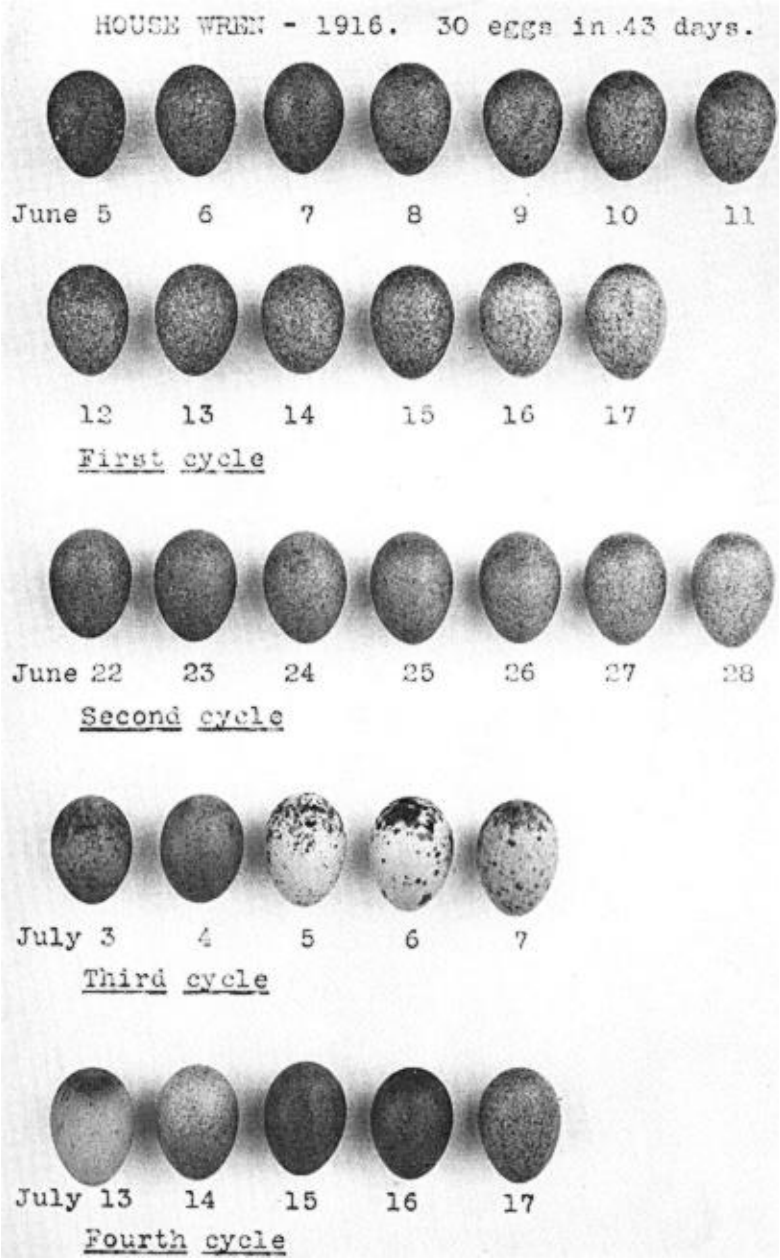
Coefficients of variation compiled in Table 8 are small in most instances, but, except for shape index when the four-egg clutches are included, they are significantly higher for first eggs than for last eggs. Considering the five-, six-, and seven-egg clutches only, the difference in variability between first and last eggs progressively declines for length, breadth, volume, shape index, specific gravity, and weight. The first egg is least variable in its shape index, the last egg in its length. The last eggs in five-, six-, and seven-egg clutches are remarkably uniform in length, weight, volume, and shape index, and while there is a tendency for weight to increase with the size of the clutch, there is less variation in the weight of the last eggs than of the first eggs. This is true also of specific gravity.

Color and markings.—Close observations were taken on the markings of five clutches of five-eggs each, one of a six-egg clutch, and one of a seven-egg clutch. The ground color of wren eggs is white or slightly grayish. The thick covering of markings is reddish brown or rufous or sometimes lavender. The markings are usually heaviest at or near the maximum diameter of the egg, forming a collar. Sometimes the entire large end is thickly pigmented, forming a cap. Rarely, the cap forms at the small end of the egg rather than the large end.

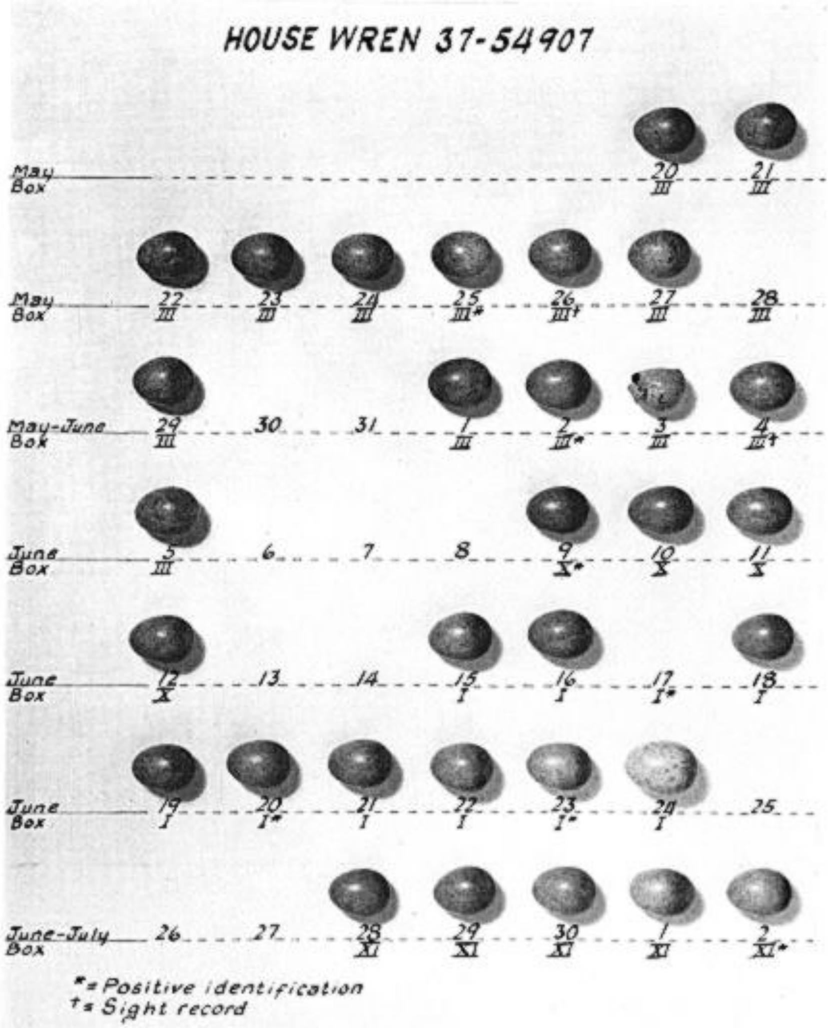
As a rule, the markings in five-egg clutches are fine and uniformly distributed in the first egg becoming progressively coarser and thicker on the subsequent eggs. In the six-egg clutch, the sixth egg had finer markings than the fifth. In the seven-egg clutch the sixth egg also had finer markings than the fifth, but the seventh egg had coarser markings. In this latter set, a day was skipped between the laying of the fifth and sixth eggs. It is also of interest that in this set the markings were reddish brown in the first five eggs but lavender in numbers 6 and 7. With the coarser markings in the later eggs, more ground color shows through so that the fifth egg is usually the lightest. A collar is scarcely perceptible in the first egg, but either a collar or a cap may become conspicuous in later eggs. One set of five eggs was exceptional in that the large irregular markings, together with a collar or cap, occurred on eggs numbers 1 and 5, while egg number 3 had the finest and most uniformly distributed markings.

The markings are seldom straight lines. Sometimes they run lengthwise of the egg although for only a few millimeters, but very often they take a spiral course around the egg. These markings indicate that the egg may make between one-eighth and one-third of a rotation, while a single line of pigment was being deposited. It is uncertain whether the direction of rotation is always the same.

Forced laying.—A preliminary experiment was made by Dr. Leon J.



House Wren eggs laid in the experiment conducted by Dr. L. J. Cole in 1916.



House Wren eggs laid in the experiment conducted by Frances Hamerstrom in 1938.

Cole in 1916 to discover whether the House Wren is a determinate or an indeterminate layer, *i.e.*, whether the number of eggs laid per clutch is controlled by internal physiological factors only or is influenced by external contact with a prescribed number of eggs already laid in the nest (Cole, 1930). The new egg laid each day was removed beginning with the second one laid, so that only one egg remained in the nest from one day to the next. The length and greatest breadth of each egg were measured (Figure 1). The bird began laying on June 5, and the first egg was removed on June 6. She continued to lay one egg each day for 13 days or until June 17. There was then a rest period of 4 days during which the female was occasionally found on the nest and the one "decoy" egg. Seven eggs were laid from June 22 through June 28 with the new one being removed each day.

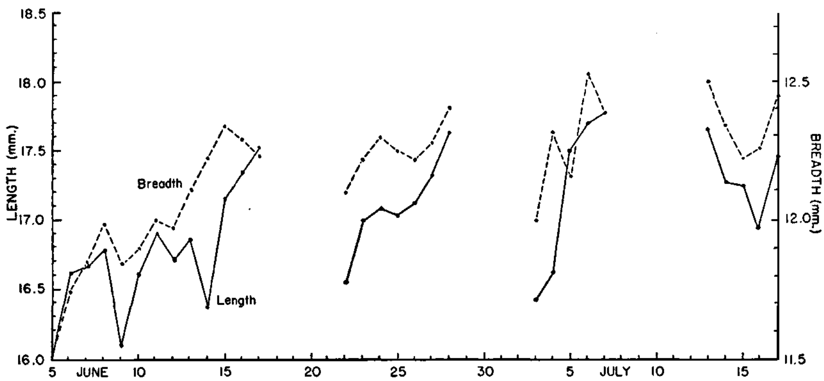


FIGURE 1. Variations in dimensions of eggs in a forced egg-laying experiment conducted by Dr. Leon J. Cole on an unbanded House Wren in 1916.

Another rest period of 4 days followed, after which 5 more eggs were deposited, July 3 through July 7. The rest period this time was 5 days, after which 5 more eggs were laid, July 13 through July 17. She then stopped laying entirely. Altogether she had laid a total of 30 eggs in 43 days.

An examination of the four egg-laying cycles shows that the last two or three eggs were larger than the preceding in three cycles but not in the fourth and last cycle where the first egg was the largest. Furthermore the first eggs of each new cycle, except the fourth, were smaller than the last eggs of the preceding cycle. This is in harmony with our other analyses.

There were also progressive changes in color (Plate 1). The first eggs of the first cycle were dark, but later eggs became gradually lighter. The second cycle began with eggs nearly as dark as the earliest ones of the first clutch and followed a similar color progression.

The third cycle showed greater variability with the first two eggs fairly normal but the last three eggs very different. The small dots became few, so the eggs were very light with large dark splotches. The fourth cycle began with somewhat irregular spotting, but the last three eggs had more normal coloration.

Four years later, Dr. Cole tried the reverse of the foregoing experiment; namely, presenting a full clutch to a wren on the first day of laying. On May 13, the first egg was laid early in the morning, and at 11:00 A.M. six eggs were added to make a total of seven. The following day the second egg was laid, raising the total to eight. Laying continued and on May 28, the nest was getting so full with

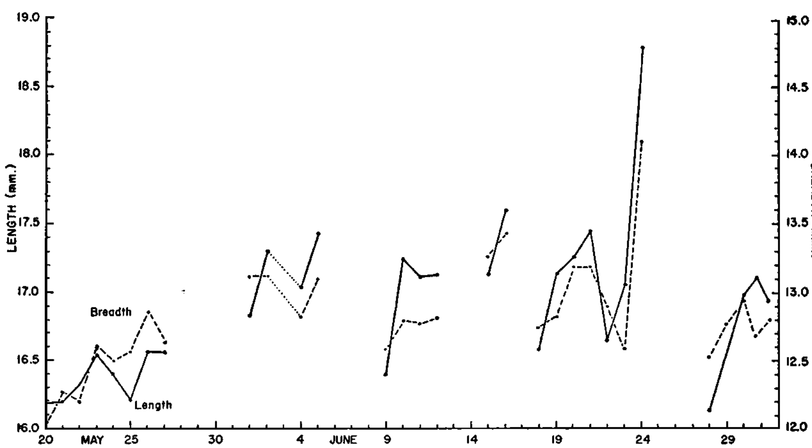


FIGURE 2. Variations in dimensions of eggs in a forced egg-laying experiment with female House Wren 37–54907, conducted by Frances Hamerstrom in 1938.

eleven eggs that three of the dummy eggs were removed and on the following day the other three dummy eggs were taken out. This left six of the birds own eggs. The seventh was laid on May 30 completing a normal set as incubation began. Six eggs hatched on June 11 and 12. The other egg was pipped but did not hatch.

The female wren in Cole's first experiment was not banded, hence it is not certain that the same individual was involved throughout. All evidence indicated, however, that it was. In 1938, Frances Hamerstrom repeated the experiment on several banded individuals in Wisconsin. The repeated trapping and handling of the birds for identification may have disturbed their laying cycle in some instances. Of the 12 experiments attempted, useful results were obtained for 7 females. One female laid 32 eggs in 44 days (Figure 2, Plate 2), other females laid 11 eggs in 13 days, 11 eggs in 15 days, 15 eggs in 30 days, 16 eggs in 25 days, 19 eggs in 29 days, and an unbanded female laid

14 eggs in 17 days. Intervals between successive series of eggs from banded females were: 1 day (2 times), 2 days (3), 3 days (2), 4 days (2), 6 days (1), 9 days (1), and 15 days (1). Normally an entire nesting cycle of four weeks or longer intervenes between laying of two clutches under natural conditions except when the first nest is destroyed, then laying often starts again in a few days.

Including Cole's experiment, 7 of the 8 birds began their first clutch during May or by June 9; the other record is for July and may represent a second clutch. The numbers of eggs laid in these seven first cycles are 13, 9, 9, 8, 8, 7, and 6. The numbers of eggs laid in 7 second cycles are 7, 7, 6, 6, 6, 5, and 5. The July female laid 6 eggs beginning the thirteenth, had a four-day interval, then laid 5 more.

Normal-sized clutches for wrens under natural conditions range from 3 to 9, with 5-, 6-, and 7-egg clutches most common. It appears that attempts to force extra laying resulted only in clutches of normal size after mid-June, but the number of clutches greater than 7 in the first laying cycles is unusual (71 per cent). The average of these seven sets is 8.6 ± 2.22 A compilation of data on all clutches laid under undisturbed natural conditions in northern Ohio during May and before mid-June, 1921 to 1938, gives the following distribution: 4 eggs, 1 clutch; 5 eggs, 7 clutches; 6 eggs, 52 clutches; 7 eggs, 32 clutches; 8 eggs, 4 clutches; and 9 eggs, 2 clutches. Clutches of 8 and 9 eggs constitute only 6 per cent of the total. The average of the 98 clutches is 6.4 ± 0.80. The difference between the two averages is 2.2 and this difference has a standard error of only 0.84 and hence is significant at least at the 95 per cent level. Unfortunately, comparable data for southern Wisconsin are not available.

Cole (1917) considered the House Wren to be an indeterminate layer, and this analysis indicates that the size of clutches laid by House Wrens early in the season is somewhat influenced by the number of eggs previously laid, *i.e.*, the bird shows a tendency toward indeterminism, which is lost after mid-June.

This ability to lay additional eggs has been demonstrated in our observations even when no experiment was intended. One such incident is described by Kendeigh (1952: 24) wherein the first four eggs were removed, probably by a wren itself, the fifth and sixth eggs were laid during the next two days, an interval of three days intervened, and then the seventh, eighth, and ninth eggs were laid. An even more interesting case occurred in 1922, when the first two eggs were laid on June 3 and 4 and the female banded on June 4. On June 5 eggs numbers 1 and 2 were gone but number 3 was present. Seven more eggs were laid on successive days, forming a sequence of eight eggs following the loss of the first two.

Another unusual record was obtained in 1924. The first two eggs were laid on June 12 and 13, but they were gone on June 14. Four more eggs were laid between June 15 and 18. A day was then skipped, and eggs numbers 7 and 8 were laid on June 20 and 21. On the latter day, four of the 6 eggs were then removed by the observer. No change was noted on June 22, but number 9 egg was found on June 23. None of these three records is included in the data averaged above to show number of eggs in normal clutches. There is, of course, an advantage to the species in being able to lay more eggs when part of a set is destroyed as it maintains a normal rate of reproduction.

Clutch size.—A much larger series of data is available for analyzing variations in egg dimensions between clutches of different size than for differences between consecutive eggs within the same clutch, since many clutches were measured where the order of laying the eggs was not known.

An irregular trend is evident (Table 9) for a decrease in average length, breadth, shape index, and calculated volume from four- to

TABLE 9

VARIATION OF EGG CHARACTERISTICS IN CLUTCHES OF DIFFERENT SIZES

	Four-egg clutches		*Five-egg clutches*		*Six-egg clutches*	
	Number	*Average*	*Number*	*Average*	*Number*	*Average*
Length (mm.)	11	16.85	51	16.63	103	16.70
Breadth (mm.)	11	12.95	51	12.79	103	12.76
Shape index		76.85		76.91		76.41
Volume (cc.)		1.480		1.424		1.424
Weight (gm.)	6	1.437 ± 0.022	16	1.431 ± 0.084	20	1.455 ± 0.115
Specific gravity		0.97		1.00		1.02

	Seven-egg clutches		*Eight-egg clutches*	
	Number	*Average*	*Number*	*Average*
Length (mm.)	53	16.55	6	16.55
Breadth (mm.)	53	12.61	6	12.71
Shape index		76.19		76.80
Volume (cc.)		1.378		1.400
Weight (gm.)	10	1.512 ± 0.115		
Specific gravity		1.10		

eight-egg clutches. However, statistical analysis does not give reliability to the differences indicated. It is of interest in this connection that Nice (1937: 114) found that eggs in 49 four-egg clutches of the Song Sparrow averaged 2 per cent longer and 0.6 per cent wider than eggs in 37 five-egg clutches. Using the "Student's" *t*-test, the increase in weight of House Wren eggs from the five-egg to the seven-egg clutches is statistically significant, but the increase from the five-egg to the six-egg clutches is not certainly so.

Special consideration needs to be made of the four-egg clutches.

Kendeigh (1941) stated that "7 eggs per set are common in May and early June, 6 eggs from early June to middle July, 5 eggs from early to late July, and 4 eggs from middle July to August." The laying of larger clutches and heavier eggs was associated with the cool temperatures of May and June and smaller clutches and lighter eggs with higher temperatures in July. In 5 of the 6 four-egg clutches used in analyzing egg weights, the first eggs were laid on July 5, 6, 6, 16, and 17. The odd clutch was laid from May 22 to 25 inclusive. It may be significant that the four days, May 20 to 23, were the warmest consecutive days during the entire month and this may have curtailed the laying of a large set (Kendeigh, 1941). The average weight of the four eggs in this May clutch is greater than the average in four-egg clutches laid normally in July. If this clutch is excluded, the average egg weight in four-egg clutches becomes 1.407 gm. instead of 1.437 gm. (Table 9) and adds to the strength of the conclusion that heavier eggs occur in the larger clutches.

If there is a decrease in the average volume of eggs in the larger clutches, or even if the volume remains the same but there is an increase in the average weight of the eggs, this necessitates a change in their density or specific gravity. Table 7 gives the specific gravity of a few eggs that were both measured and weighed. The average density of 14 eggs in the 3 five-egg clutches is 1.015 ± 0.008. If the two freak eggs are excluded, the average density of 10 eggs in the two six-egg clutches is 1.032 ± 0.009. The difference between these two averages is 0.017 and its probable error ± 0.004. Although the number of data is small the difference has statistical significance, indicating that the density or specific gravity of the six-egg clutches is greater than that of five-egg clutches.

In Table 9 the measured weights of one sample of eggs when divided by the calculated volumes of a *different* and larger sample of eggs shows an increase in specific gravity as the size of the clutch increases from 4 to 7.

Although an increase in specific gravity is indicated, the actual values for specific gravity given in Table 9 are not trustworthy. The value of 0.97 for the four-egg clutches is certainly too low and the value of 1.10 for the seven-egg clutches may be too high. Probably the excessive range of 0.13 between extreme values results from inaccurate determination of egg volumes, possibly augmented by some change in shape of the eggs in different sized clutches. What is needed is a large series of *direct* determinations of specific gravity. It is obvious, however, that when the specific gravity of an egg is not known, the weight of an egg cannot be accurately calculated from its dimensions or volume as has frequently been attempted.

Age of female.—Since the House Wrens were banded, their age can be approximated. New birds nesting in the area for the first time are considered one-year olds for reasons given elsewhere (Kendeigh and Baldwin, 1937) even though a few birds are known not to nest until they are two years old. After once nesting in the area and being banded, their subsequent careers are accurately followed.

TABLE 10

EFFECT OF AGE OF FEMALE ON SIZE OF EGGS

	1 year old	*2 years old*	*3 years old*
Five-egg clutches			
Number	31	9	7
Length (mm.)	16.59	16.81	16.61
Breadth (mm.)	12.75	12.86	12.85
Six-egg clutches			
Number	54	23	14
Length	16.64	16.65	16.84
Breadth	12.69	12.76	12.95
Seven-egg clutches			
Number	27	13	6
Length	16.44	16.69	16.83
Breadth	12.58	12.62	12.72
Weighted average			
Number	112	45	26
Length	16.58 ± 0.56	16.69 ± 0.63	16.78 ± 0.52
Breadth	12.68 ± 0.36	12.74 ± 0.35	12.88 ± 0.34
Shape index	76.18	76.33	76.76

Table 10 shows that with increasing age, birds lay eggs that are both longer and broader. The increase in length from the first to the third year is 1.21 per cent and in breadth 1.58 per cent. Statistically the differences between eggs of one- and two-year-old females are not significant. The differences in breadth of eggs between two- and three-year-old females and in length of eggs between one- and three-year-old females are significant at the 95 per cent level and the difference between breadth of eggs of one- and three-year-old females is significant at the 99 per cent level. In Song Sparrows (Nice, 1937: 115) the eggs of females two or more years of age average broader than do eggs of one-year-old females, but there is no consistent change in length.

The shape index, calculated from the weighted averages of length and breadth, shows a progressive increase with the age of the female. This means that the eggs increase in breadth to a greater extent than they do in length. This agrees with the data on Song Sparrows (Nice, 1937: 117).

Clutches and individuals.—General trends of variation in average egg characteristics have been indicated. Can these trends also be detected within single clutches of eggs or in the egg characteristics of the individual birds?

In 36 individual clutches where the sequence of laying is known, the last egg was the longest in 54 per cent of the cases, the second from the last in 8 per cent, the third from the last in 4 per cent, the first egg in 17 per cent, and intermediate eggs, that is, those between the first and the third from the last, in 17 per cent. In respect to maximum breadth, the percentages were: last—50, next to last—21, third from last—3, first—10, and intermediate—17. In 56 clutches, the last egg was the heaviest in 61 per cent, next to the last 7 per cent, third from the last 10 per cent, first 12 per cent, and intermediate 10 per cent. These data show that there is irregularity between clutches but verify the strong tendency for the last egg to be the longest, widest, and heaviest. Nice (1937: 113) found in 17 clutches of the Song Sparrow that the last egg was the heaviest in 41 per cent, the first egg in 29 per cent, an an intermediate egg in 29 per cent.

There are 26 comparisons on 25 females between the average egg characteristics of first and second clutches laid in a single year. In 69 per cent of the comparisons the second clutch was smaller than the first, in 23 per cent it was equal, in 8 per cent it was larger. Likewise in 65 per cent of the comparisons the average length of the eggs in second clutches was less than in first clutches, in 4 per cent it was equal, and in 31 per cent it was greater. In several instances, when the average length of eggs in second clutches decreased, the average breadth increased so that actually in 69 per cent of the second clutches the eggs averaged wider than in the first clutches, in 4 per cent they were equal, and in 27 per cent they were narrower. Thus, since there is a strong tendency for a decrease in length to be compensated for by an increase in width, a comparison of calculated volumes shows that in 58 per cent, the average volume of eggs in second clutches was greater, in 38 per cent it was smaller, and in 4 per cent it was equal. It is doubtful, therefore, if there is any significant difference in volume between eggs in first and second clutches.

In 17 comparisons of two clutches laid by the same Song Sparrow in the same year (Nice, 1937: 115), the dimensions of the egg decreased in 12 per cent of the cases, were the same in 6 per cent, and increased in 82 per cent. The eggs in the later clutches averaged 0.8 per cent longer and 2.5 per cent broader than the eggs in the early clutches. This shows a different relation from that in the House Wren.

The increase in average egg dimensions with aging of female House

Wrens is not supported by 14 comparisons of data obtained on eggs of birds one and two years old and 3 comparisons with birds three years old. In fact, in 11 of the 17 comparisons, the eggs are smaller in the older birds. The number of data available for individual birds is small, however, compared with the analysis presented in Table 10.

Records are available on 37 females where two to four clutches of eggs laid by the same individual either during the same year or in subsequent years were measured. These records make it possible to compare the amount of variation among eggs laid by the same female at different times and by different females. Since there is variation among individual eggs within a clutch, correlated with sequence of laying, comparisons are here made only between the average dimensions of whole clutches. The extreme range in average length and breadth measurements of eggs laid by different females is from 15.61 × 12.51 mm. to 18.09 × 13.20 mm. These ranges in length of 2.48 mm. and in breadth of 0.69 mm. are 14.9 and 5.4 per cent respectively of the mean dimensions of all the eggs. Nice (1937: 112) found in an analysis of 503 eggs of the Song Sparrow that the extreme range in length in percentage of the median was also greater than the extreme range in width. The *greatest* variations in average length and breadth of different clutches of one female House Wren were 4.0 and 4.5 per cent, respectively. The *average* extreme differences between different clutches laid by the same female are for length, 0.28 mm. and, for breadth, 0.21 mm., which are 1.7 and 1.6 per cent respectively of their average dimensions. Individual females, therefore, tend to lay eggs in different clutches of nearly the same average dimensions. The variability among different clutches of the same female is much less than among different females in the species.

Physiological interpretations.—The above primarily statistical treatment indicates that within a House Wren clutch, the last two eggs increase both in maximum breadth and length, but proportionately more in length than breadth. There is also an increase in weight and in coarseness of color markings in the egg sequence. The last eggs of clutches of different size are more alike in dimensions, shape, volume, weight, and specific gravity than are the first eggs. The bird can adjust for loss of eggs during the first laying cycle of the season by laying an average of two additional eggs, but this is not true in later cycles. Do these facts shed any light on the mechanism of egg formation?

Detailed information on the formation of eggs within the body of the bird is available only on the domestic fowl, and this information is by no means as complete as desired. The germ cell, yolk, and vitelline membrane are laid down in the ovary; all other parts of the egg are formed in the oviduct. There are several hundred ova in the ovary, but only a few mature, progressively one at a time. The ova, enclosed in individual follicles, initially consist largely of protoplasm and contain relatively high proportions of water and protein. Fats (phospholipids) are deposited from the blood as the ovum matures, and the percentage of water decreases. The increase in the size of the ovum is slow at first in all species studied but becomes very rapid two to eight days prior to ovulation.

The seasonal development of the ovary and ova is under control of follicle-stimulating and luteinizing hormones secreted by the anterior pituitary. The rapidly growing follicles and ova produce another hormone, estrin, which in turn stimulates the growth of the oviduct. Estrin is also responsible for increasing the mobilization of food substances needed for the formation of the egg and transported by the blood. As the laying of the clutch progresses, increasing amounts of prolactin are released from the pituitary gland, that decrease the production of gonad-stimulating hormones, bring about cessation in the development of ova, and induce incubating behavior (Riddle, 1938; Romanoff and Romanoff, 1949).

The chief regions of the oviduct are the infundibulum or funnel which receives the ovum when it erupts from the ovarian follicle (ovulation) and where fertilization occurs, the pars magnum where the chalazae and albumen are secreted around the yolk, the isthmus that secretes the two shell membranes, the uterus where the shell is formed and pigment is deposited, and the vagina which is involved only as a passageway when the egg is laid. The walls of the oviduct contain an outer longitudinal and an inner circular muscular layer. The outer layer controls the length of the oviduct, the inner layer controls its diameter, and coordination of muscular action in the two layers produces peristalsis that moves the egg mass onward through the oviduct. Ciliary action of the oviduct lining is probably also involved. The inner mucous membrane and ciliated epithelium are thrown into folds and contain many secretory glands. These glands are stimulated to secrete when exposed to contact pressure from the ovum and associated egg mass.

In the domestic fowl, the ovum enters the oviduct about 15 minutes after ovulation, passes through the infundibulum in 18 minutes, spends 3 hours in traversing the pars magnum, 1 hour in the isthmus, and the remainder of the time, usually 20 to 24 hours, in the uterus (Warren and Scott, 1935). Ovulation usually follows the laying of the previous egg within about 30 minutes, except when the previous egg is laid late in the afternoon, in which case ovulation is delayed until early the following morning. The interval between laying of successive eggs is usually greater than 24 hours, so that they are laid at progressively later hours until a day is skipped, after which egg-laying begins again in the early morning. Each series of eggs (usually 2 to 18) is called a clutch. The time interval between successive eggs in most song birds appears to be 24 hours, and much longer intervals of days separate successive clutches.

There is considerable uncertainty as to how the exact shape of the egg is determined (Pearl, 1909; Curtis, 1914: 322; Asmundson, 1931; Conrad and Scott, 1938; Harper and Marble, 1945), but there is general agreement that the shape is established by the time the egg leaves the isthmus. Factors involved are doubtless the size of the egg mass, the diameter of the pars magnum and isthmus, and the relative tension or action of the circular and longitudinal muscle layers in the walls of the oviduct. The small end of the egg is always directed caudalward in all parts of the oviduct anterior to the uterus, but in the uterus the egg is often rotated so that a large percentage are laid large end first.

It has been shown in two extensive studies of the domestic fowl that, outside of the shell, the weight of the yolk is the most variable characteristic of the egg (coefficient of variation: 11.31 ± 0.11, Curtis, 1914; 13.11 ± 0.24, Asmundson, 1931). A large yolk stimulates a greater production of albumen and shell and there results a good correlation between the weight of the yolk and the total weight of the egg ($+ 0.538 \pm 0.018$, Asmundson, 1931). The circular muscles in the walls of the oviduct would exert a greater pressure on a large than on a small egg mass and allow less albumen to remain around the equatorial region of the yolk. There is much less pressure restricting the lengthwise extension of the egg mass, and this may explain why large wren eggs in a clutch are proportionately longer than small eggs.

Each fine color mark is presumably produced by pigment deposition from a single gland in the uterus. With the smaller first eggs of the clutch this pigment is deposited evenly and uniformly, but with the larger later eggs in the clutch there may be exhaustion of pigment from many glands and, because of greater pressure against the walls the pigment, which is secreted is massed into coarser lines or splotches. Greater pressure from the large end may be responsible for the formation of a collar or a cap. The rotation of the egg in preparation for laying may account for the observed spiral direction of the markings.

Successive eggs in clutches of the domestic fowl, contrary to those in the House Wren, decrease in size and weight (Atwood and Weakly, 1917; Bennion and Warren, 1933). In two-egg clutches, the total decrease amounts to 2.2 per cent and in eight-egg clutches, 3.5 per cent. However, there is a decrease in per cent loss per egg in clutches of increasing size; in two-egg clutches this decrease is 2.2 per cent, in eight-egg clutches only 0.4 per cent. The decrease in weight has been explained as resulting from exhaustion of material available for elaborating into the various egg parts or to a fatigue of the organs involved so that less material is secreted. It may be significant that the greater the productive capacity of a hen, the larger are the clutches produced and the smaller is the average decrease in the weight of the eggs which are laid on consecutive days. Hormones may also be involved. Increased thyroid activity will induce a decrease in the size of the egg and in the amount of yolk produced (Asmundson, 1931a), and it is conceivable that variation in the action of estrin and prolactin may produce effects.

The increase in size and weight of consecutive eggs in the House Wren is more nearly comparable to what happens in mature domestic fowl after pauses in egg laying. Here it has been shown that the first eggs produced after pauses of 8 to 30 days were lighter in weight than the last eggs before the pause, but normal weight of the eggs was obtained with the laying of the second or third egg (Bennion and Warren, 1933). The egg weight of pullets also increases during the first three or four months of production (Jull, 1925). This may be correlated with the increase in size of the pullets and presumably with increasing ability to assimilate and mobilize various food elements, especially protein, necessary for egg production (Jull, 1924).

The fact that the first egg of clutches of different size in the House Wren are more variable in dimensions and weight than the last egg suggests that there may be a standard efficiency or procedure in egg formation which is not attained with the first egg but more closely as additional eggs are produced. Pearl (1909) cites a case in the domestic fowl where the first egg of a pullet was very abnormal in shape, but succeeding eggs changed progressively back to normal. Increased proficiency in mobilizing energy and in the mechanics of egg formation may also account for the larger eggs laid by the older birds.

There is a certain amount of irregular variation in the characteristics of the early eggs laid in the clutches of different size, but a consistent and marked increase in length, breadth, and weight from the third to the second from the last to the last egg. This is of special interest since it is correlated with an increase of incubating behavior with the third egg in five-egg clutches and the fourth egg in six-egg clutches (Kendeigh, 1952: 20). Environmental conditions, especially temperature during the two or three days preceding the laying of the eggs, have been shown to affect the weight and the number of eggs laid in the clutch (Kendeigh, 1941). It would appear that changes of some sort are being set into action at this stage in egg-laying that anticipate the normal termination of the clutch within an interval of two more days. The present study gives no hint of what these factors may be, although the hypothesis suggested by Kendeigh (1952: 24), that one or more hormones from the pituitary, particularly prolactin, may be associated with the changes, still appears likely.

If the size of the clutch is determined on the second day preceding the laying of the last egg, any other follicles or ova that had started to develop would stop or might even begin to atrophy. This might then explain the increase in size of the last two eggs in the clutch. Yolk material being brought to the ovary by the blood would not be divided among all the maturing ova but would be concentrated into the remaining two ova of the clutch and on the last day into the final ovum alone. It appears that the most rapid and critical growth period that affects the eventual size of the complete egg comes during the two or three days prior to its being laid.

The increase in the weight of eggs in the larger clutches without an increase in volume is obviously correlated with an increase in specific gravity, but why the specific gravity should increase so markedly in the larger sets is not immediately obvious. The differences in specific gravity among different eggs in the House Wren are much larger than have been noted in the eggs of the domestic fowl, turkey, and duck where extreme limits are 1.056 and 1.116 and the most common range is 1.080 to 1.090 (Romanoff and Romanoff, 1949: 368).

It has also been established for the domestic fowl that the proportion of shell to the total weight of the egg remains the same in eggs of different sizes (Romanoff and Romanoff, 1949: 116). It appears, therefore, that the greater specific gravity of eggs in the larger clutches of the House Wren may result from a greater proportion of solids to water in the egg contents. This can only be determined by direct measurements.

Romanoff and Romanoff (1949: 323) have compiled data for 14 species of altricial birds, which indicate that the average water content of the eggs is 80.9 per cent. Although there is not a great deal of difference in the absolute amounts of solid matter in yolk and albumen, the albumen contains between five and six times more water than does the yolk. House Wrens feed almost entirely on insects and derive water from their body fluids and from oxidation of nutrients which they provide. They seldom drink water directly, but it is hardly conceivable that lack of water is a critical factor in regulating the specific gravity of the egg contents. The likelihood is much greater that the density of yolk and albumen depends on the amount of solid materials that are available.

TABLE 11
COMPOSITION AND ENERGY VALUE OF SOLID SUBSTANCES IN THE YOLK AND ALBUMEN OF AN AVERAGE SIZE (1.500 GM.) HOUSE WREN EGG, CALCULATED FROM DATA GIVEN FOR OTHER SPECIES BY ROMANOFF AND ROMANOFF (1949)

	Yolk solids		*Albumen solids*		*Total solids (exclusive of shell and membranes)*	
	Amount in grams	*Energy value in Calories*	*Amount in grams*	*Energy value in Calories*	*Amount in grams*	*Energy value in Calories*
Proteins	0.048	0.211	0.099	0.436	0.147	0.647
Fats (lipids)	0.093	0.879	0.000	0.000	0.093	0.879
Carbohydrates	0.003	0.013	0.008	0.034	0.011	0.046
Inorganic	0.003	—	0.006	—	0.009	—
Total	0.147	1.103	0.113	0.470	0.260	1.572

Aside from their water content, yolk is composed mostly of fats and albumen mostly of proteins (Table 11). If the energy value of proteins is taken as 4.40, carbohydrates as 4.20, and fats as 9.45 Cal. per gram, the total energy, except for that in the shell membranes, of an average-sized House Wren egg is calculated as 1.572 Cal. This is equivalent to 105 Cal. per 100 grams or reasonably close to the value of 116 given for the egg of the House Sparrow (*Passer domesticus*) (Tangl, 1903). This energy must be obtained from the food eaten and from body reserves in the female. Furthermore most of it is probably deposited in the various parts of the egg in the period beginning three days before the first egg is laid and lasting until the last egg is fully formed. Thus most of the energy in a six-egg clutch is acquired in about a nine-day period or at an average rate of about 1.048 Cal. per day.

The daily energy intake and requirements of the House Wren have not been measured, but using comparable data obtained during the summer months for the House Sparrow (Davis, 1955) and considering that the female House Wren weighs 11.5 grams, the average energy demands for existence would be at least 8.8 Cal. per day, and the bird would be potentially able to absorb an additional 3.2 Cal. per day for productive purposes. The amount required for egg production would take about one-third of this potential surplus. However, any variation in this energy balance, either in intake or outgo, would conceivably affect the amount of material available for egg formation and thereby modify its specific gravity, size, and other characteristics. It is well known that the start of egg-laying in altricial species is often delayed by cold rainy weather in the spring, and this doubtlessly results from an increase in energy demands for existence with the consequent decrease in the amount of surplus energy available for other purposes.

When the bird first returns at the beginning of the breeding season it is at a peak of activity and vigor. The cool weather stimulates maximum feeding and a high level of productive energy. A high energy balance permits not only heavier eggs but more of them per clutch. As the season progresses and brings higher temperatures, there is a decrease in the rate of feeding and the lighter eggs and smaller number per clutch may well be a result of a less favorable energy balance.

Summary and conclusions.—1. The last two eggs laid in clutches of the House Wren are longer and broader, have a greater calculated volume, and are heavier than the first ones laid. The increase in length is proportionately greater than the increase in breadth.

2. The physical characteristics of the first egg in clutches of different size are more variable than of the last egg in the clutches.

3. The first eggs of a clutch tend to be darker in color because the markings are finer and more evenly distributed.

4. During its first laying cycle of the season, the House Wren shows a tendency toward indeterminism in that it may lay an average of two additional eggs if early eggs in the clutch are lost. Later in the season this indeterminism is lost.

5. There are no certainly significant differences in average length, breadth, shape, or calculated volumes between eggs in different size clutches, but larger clutches contain heavier eggs.

6. A greater specific gravity for eggs in large clutches compared with small clutches is indicated, but more positive evidence is required to establish the point.

7. Birds in their first reproductive season tend to lay smaller eggs than older birds, but this is not true of all individuals.

8. There is less variation among different eggs laid by the same bird than among the average egg characteristics of different birds.

9. The hypothesis is developed that the physical characteristics of the egg are influenced in an important manner by the energy resources of the bird during the three days immediately preceding laying.

LITERATURE CITED

ASMUNDSON, V. S. 1931. The formation of the hen's egg. Sci. Agr. **11**: 1–50.

ASMUNDSON, V. S. 1931a. Effect of hormones on the formation of the hen's egg. Poult. Sci. **10**: 157–165.

ATWOOD, H., and C. E. WEAKLEY. 1917. Certain characteristics of hen eggs. West Virginia Univ., Agr. Exp. Sta., Bull. **166**: 1–35.

BENNION, N. L., and D. C. WARREN. 1933. Some factors affecting egg size in the domestic fowl. Poult. Sci. **12**: 362–367.

COLE, L. J. 1917. Determinate and indeterminate laying cycles in birds. Anat. Rec. **11**: 504–505.

COLE, L. J. 1930. The laying cycle in the House Wren. Wilson Bull. **42**: 78.

CONRAD, R. M., and H. M. SCOTT. 1938. The formation of the egg of the domestic fowl. Physiol. Rev. **18**: 481–494.

CURTIS, M. R. 1914. A biometrical study of egg production in the domestic fowl. IV. Factors influencing the size, shape, and physical constitution of eggs. Arch. Entwick. Org. **39**: 217–327.

DAVIS, E. A., JR. 1955. Seasonal changes in the energy balance of the English Sparrow. Auk, **72**: 385–411.

HARPER, J. A., and D. R. MARBLE. 1945. Egg shape. II. Muscular and other oviducal influences. Poult. Sci. **24**: 61–65.

JULL, M. A. 1924. Egg weight in relation to production. I. The relationship of the weight of the parts of the egg to the total weight. Poult. Sci. **3**: 77–88.

JULL. M. A. 1925. Increase in egg weight in relation to the time that laying commences. Amer. Nat. **59**: 521–528.

KENDEIGH, S. C. 1941. Length of day and energy requirements for gonad development and egg-laying in birds. Ecol. **22**: 237–248.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Illinois Biol. Mono. **22**: i–x, 1–343.

KENDEIGH, S. C., and S. P. BALDWIN. 1937. Factors affecting yearly abundance of passerine birds. Ecol. Mono. **7**: 91–124.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. I. Trans. Linnean Soc. **4**: i–vi, 1–247.

PEARL, R. 1909. Studies on the physiology of reproduction in the domestic fowl. 1. Regulation in the morphogenetic activity of the oviduct. Journ. Exp. Zool. **6**: 340–360.

PRESTON, F. W., and E. J. PRESTON. 1953. Variation of the shapes of birds' eggs within the clutch. Ann. Carnegie Mus. **33**: 129–139.

RIDDLE, O. 1938. Prolactin, a product of the anterior pituitary, and the part it plays in vital processes. Sci. Month. **47**: 97–113.

ROMANOFF, A. L., and A. J. ROMANOFF. 1949. The avian egg. John Wiley and Sons, New York: i–xiii, 1–918.

TANGL, F. 1903. Beiträge zur Energetik der Ontogenese. 1. Mittheilung. Die Entwicklungsarbeit im Vogelei. Arch. ges. Physiol. (Pflüger's) **93**: 327–376.

WARREN, D. C., and H. M. SCOTT. 1935. Physiological factors influencing the rate of egg formation in the domestic hen. Journ. Agr. Res. **51**: 565–572.

WORTH, C. B. 1940. Egg volumes and incubation periods. Auk, **57**: 44–60.

Department of Zoology, University of Illinois, Champaign; Department of Anatomy, University of Michigan, Ann Arbor; and Wisconsin Conservation Department, Plainfield; October, 1954.