THE RATE OF OVULATION IN THE DOMESTIC FOWL DURING THE PULLET YEAR.

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It is well known among poultrymen that ovulation in the hen is an orderly process with a fairly predictable average production of eggs for each month of the year. The object of this paper is to contribute an idea toward the formulation of an hypothesis concerning the principles underlying this orderly process of ovulation. This idea is based on a suggestion of Loeb[1] that growth, or at any rate the limiting factor of growth, is in the nature of an autocatalytic monomolecular reaction. The rate of ovulation may reasonably be taken as an index of growth of the eggs, and if the limiting factor of growth of eggs is an autocatalytic reaction, then the rate of ovulation should be expressible by the equation of such a reaction.

The application of this equation to experimental data is familiar to the chemist.[2] Robertson[3] and Ostwald[4] were the first to apply the equation to the phenomena of growth. In the formulation of the equation it is assumed that the velocity of reaction at any moment is proportional to the quantity of the reacting substance $(A - x)$ at that moment, and also to the quantity of the product of the reaction

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[1] Loeb, J., *Biochem. Z.*, 1907, ii, 34; *7th Internat. Zool. Cong.*, 1907; The dynamics of living matter, New York, 1906; *Univ. California Pub., Physiol.*, 1905–10, iii, 61.

[2] Ostwald, W., Lehrbuch der allgemeinen Chemie, Leipsic, 1903, i. Lewis, G. N., *Z. physikal.Chem.*, 1905, lii, 310; *Dept. Interior, Bureau Gov. Labor., Chem. Lab., No. 30*, 1905.

[3] Robertson, T. B., *Arch. Entwcklngsmechn. Organ.*, 1908, xxv, 581; *Am. J. Physiol.*, 1915, xxxvii, 1, 74; Principles of biochemistry, for students of medicine, agriculture and related sciences, Philadelphia, 1920.

[4] Ostwald, W., Vorträge und Aufsätze über Entwicklungsmechanik Organismen, Leipsic, 1908, v.

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x, present at that moment, which acts as the catalyst of the reaction; that is

$$\frac{dx}{dt} = K_1x\,(A - x) \qquad (1)$$

where $\frac{dx}{dt}$ stands for the momentary velocity or rate of reaction, and K_1 is the velocity constant. Equation (1) cannot be applied to experimental data since the momentary velocity of the reaction is not known, and since the velocity is not expressed as a function of time. It is therefore first integrated obtaining

$$\log \frac{x}{A - x} = K_1At + C \qquad (2)$$

where C is the integration constant. The value of the integration constant C is found by an analysis of the meaning of t in equation (2) above. Equation (1) represents a curve of a rising and falling type, the maximum or turning point occurring when $x = A - x$; that is, when the reaction is half way completed, and when the reaction is at the maximum velocity. At that point, therefore, $\log \frac{x}{A - x} = 0$. It is most convenient to count the time from this maximum or turning point, that is t at this point is just equal to zero; therefore, $K_1At = 0$ and also $C = 0$; if it is agreed to count time from the maximum velocity, then $C = 0$, and equation (2) becomes

$$\log \frac{x}{A - x} = K_1At \qquad (3)$$

t in equation (3) is then the time on either side of the maximum point, counted from that point as zero. Equation (3) may be more conveniently written

$$\log \frac{x}{A - x} = K_1A\,(t - t_1) \qquad (4)$$

where t_1 is the time from the beginning of the reaction to the maximum point; t is any time from the beginning of the reaction chosen for discussion; and $(t - t_1)$ is therefore the difference of time from the maximum point to the chosen time t. The minus sign between t and t_1 indicates difference in time between the maximum and

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any chosen time t, anywhere along the reaction curve, on either side of the maximum, rather than that t_1 is negative. Equation (4) may be still further simplified by writing it

$$\log \frac{x}{A - x} = K\,(t - t_1) \qquad (5)$$

where K is written for K_1A. Equation (5), used by Robertson[3] in the study of growth, may now be applied to the study of data on ovulation.

A large amount of data on ovulation of the domestic fowl is found in the work of the several Agricultural Experiment stations in this country. The best known published records are undoubtedly those prepared by Pearl[5] on the weighted mean monthly egg production of barred Plymouth Rock pullets representing 4,210 birds covering the records kept from 1899 to 1907 at the Maine Agricultural Station, and the results of the international egg laying contests conducted by the Storrs Experiment Station.[6] The average monthly production of 1,000 White Leghorn pullets during the seventh international contest[6] will be taken as the second example for computation.

It might be well before applying equation (5) to these data to redefine them in terms of ovulation during the pullet year. x = number of eggs laid from November 1 of the pullet year up to the end of any month, t. A = total number of eggs laid in the *natural laying season* which lasts very nearly 1 year, November 1 of pullet year to Novem- 1 of the succeeding year. Some eggs may be, and in fact are, laid outside this arbitrarily defined limit of 1 year. However, all published records adhere to this arbitrary year, and hence A is tentatively defined as eggs laid from November 1 to November 1 of the succeeding year. t_1 = time in month when $x = A - x$ = time required to lay half of the total number of eggs laid in 1 year = time when the monthly rate of laying is at its maximum. K = velocity constant found by substituting values for x, A, t, and t_1, and solving for K. Substituting the values of A, K, t, and t_1, and solving for x, we obtain the following calculated values for the two examples chosen,

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[5] Pearl, R., *U. S. Bureau Animal Industry, Bull. 110*, 1910, pt. 2.

[6] Card, L. E., and Kirkpatrick, W. F., *Storrs Agric. Exp. Station, Bull. 100*, 1919, pt. 2, 35.

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which are tabulated with the experimental values. Robertson's tables[7] are helpful in solving for x, the calculated number of eggs laid.

Month.	No. of month. t	Barred Plymouth Rock.		White Leghorn.	
		Experimental values.	Calculated values.	Experimental values.	Calculated values.
Nov.	1	4.63	10.8	6.5	7.3
Dec.	2	13.54	16.8	13.1	12.2
Jan.	3	25.25	25.2	20.2	19.9
Feb.	4	36.12	36.7	30.7	31.5
Mar.	5	52.23	50.6	48.4	47.5
Apr.	6	68.08	66.1	66.9	67.5
May.	7	82.00	81.5	89.5	89.5
June.	8	94.46	95.0	109.2	110.1
July.	9	105.53	105.8	127.2	127.5
Aug.	10	115.17	113.7	143.8	140.2
Sept.	11	123.36	119.2	156.8	149.0
Oct.	12	128.86	123.0	162.8	154.8

Similar results are obtained with the other principal breeds of birds, the equation for Plymouth Rocks being

$$\log \frac{x}{129 - x} = 0.212\ (t - 5.9)$$

and the equation for White Leghorns

$$\log \frac{x}{163 - x} = 0.235\ (t - 6.64)$$

In the equation for White Leghorns, 163 is the value of A since the total number of eggs laid in the year is in round numbers 163 eggs. It takes 6.64 months to lay half this number of eggs. 0.235 is the constant of the reaction.

It is clear from the tabulation that the agreement between the experimental and calculated values of x (eggs laid) is very good for three-quarters of the laying season—January to August. On the other hand the per cent deviation in the first 2 months (November and December) and the last 2 months (September and October) is very great. The deviations in the last 2 months (September and

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[7] Robertson, T. B., *Univ. California Pub., Physiol.*, 1910–15, iv, 211.

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October) can be easily corrected by assuming the value of A to be slightly larger than the recorded number of eggs laid during the arbitrarily defined laying year of November 1 to the following November 1. Thus, instead of taking the value of A to be 163 eggs for the White Leghorns, 175 eggs are taken, an increase of only 12 eggs over the recorded value, a number which will probably be laid by this breed outside the arbitrary, conventional year; then an excellent agreement is obtained as shown in the following tabulation and in Fig. 1.

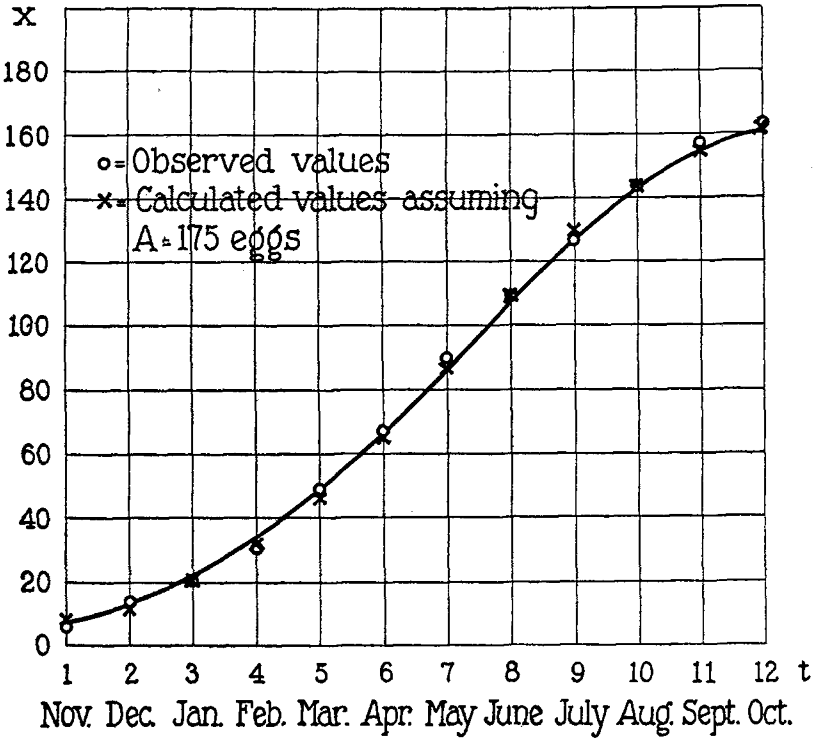

FIG. 1. Curve showing the average number of eggs laid by the White Leghorn fowl at the Storrs Seventh International Egg Laying Contest. Ordinates represent the number of eggs laid (x) for the time t; abscissæ represent the time t from Nov. 1, the beginning of the observation, to any time of the year.

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Assume then $A = 175$; t_1 is shifted to 7 months and the equation becomes

$$\log \frac{x}{175 - x} = 0.222\ (t - 7)$$

obtaining the following values for x for the White Leghorns.

Month.	No. of month. t	White Leghorn.	
		Experimental value.	Calculated value.
Nov.	1	6.5	7.9
Dec.	2	13.1	12.6
Jan.	3	20.2	20.1
Feb.	4	30.7	31.0
Mar.	5	48.4	46.4
Apr.	6	66.9	65.6
May.	7	89.5	87.5
June.	8	109.2	109.2
July.	9	127.2	129.0
Aug.	10	143.8	144.0
Sept.	11	156.8	155.0
Oct.	12	162.8	162.4

The agreement is seen to be excellent except during the first 2 months (November and December). The discrepancy during the first 2 months cannot, however, be considered serious, in view of the fact that the initiation of chemical processes even *in vitro* is in many cases irregular and does not follow the mathematical expressions for the rate of reaction. The initiation of processes in living organisms, especially in the case of ovulation, may be attended in addition by purely mechanical difficulties and irregularities. The discrepancy might also be explained on evolutionary grounds following the argument of Pearl.[5] Pearl calls attention to the fact that the wild *Gallus*, the ancestor of the domestic fowl, does not lay during the winter months, and that the winter laying period is not a part of the natural or normal reproductive cycle of the hen. The high variability of egg production during this period is explained by Pearl on this basis.

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SUMMARY.

The rate of ovulation of the domestic fowl may be expressed by the equation of an autocatalytic chemical reaction. This is not surprising in view of the fact that the rate of growth may also be expressed by such an equation, and that the rate of ovulation is probably an index of the growth of the eggs. This brings the phenomenon of ovulation in the hen under the general subject of growth, and substantiates the generality and the probability of the hypothesis that growth, or at any rate the limiting factor of growth, is an autocatalytic reaction.

The idea of applying the equation of growth to the rate of ovulation in the fowl suggested itself while studying the rate of growth of the dairy cow with Mr. A. C. Ragsdale, Chairman of the Department of Dairy Husbandry. I take pleasure in expressing my appreciation to Mr. Ragsdale, and Mr. H. L. Kempster, Chairman of the Department of Poultry Husbandry in this station, for their encouragement.

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