THE EFFECT OF ADVANCE IN LACTATION AND GESTATION ON MAMMARY ACTIVITY.

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This study is based on certain of the records of Guernsey cows as published in the Advanced Register of the American Guernsey Cattle Club.[1] This extract is presented in the interest of the physiological bearing of the data on the problems of milk secretion. The records are unique in comparison with the natural course of events in the wild state, in that the rate of mammary activity has been artificially developed to a point far in excess of the requirements of the young. Also, in many cases, the recurrence of pregnancy is unusually delayed and lactation is greatly protracted under the stimulation of artificial milking and liberal feeding. Similar data have been studied by Brody, Ragsdale, and Turner in this journal.[2] Other literature references are here omitted.

By appropriate statistical treatment a series of eleven observed values was obtained for farrow cows, each value representing the yield for a month, the mid-point of which was 1, 2, ... or 11 months after calving. Twelve additional similar series were calculated, one each for cows conceiving .5, 1.5, ... and 11.5 months after calving.

Milk yield is regarded as the result of the rate of milk secretion. The rate of milk secretion is treated as continually decreasing at a

[1] The results are being published in detail as a bulletin of the Illinois Agricultural Experiment Station (Gaines, W. L., and Davidson, F. A., *Illinois Agric. Exp. Station, Bull. 272*, 1926 (in press).

[2] Brody, S., Ragsdale, A. C., and Turner, C. W., *J. Gen. Physiol.*, 1922–23, v, 441, 777. Brody, S., Turner, C. W., and Ragsdale, A. C., *J. Gen. Physiol.*, 1923–24, vi, 541.

rate proportional to its momentary value, in accordance with the equation:

$$\frac{dy}{dt} = ae^{-kt} \tag{1}$$

in which y = yield in pounds, t = time in months from calving, a is a constant representing the initial rate of yield in pounds per month, and k is a constant representing the rate of decrease per month in the rate of yield per month.

Equation (1) was applied to the observed values as:

$$y_m = Ae^{-kt} \tag{2}$$

in which y_m is the yield for a month, time being reckoned to the middle of the month; and $A = a\frac{e^{.5k} - e^{-.5k}}{k}$. Practically, for the values of k at present involved, A and a may be considered as equal.

Cows Farrow or in Early Pregnancy.

The data for farrow cows and the curves from equation (2) fitted by the method of least squares are shown in Fig. 1. The lower series of observations and curve relate to milk yield. The upper series of observations and curve relate to fat yield. The middle series needs a word of explanation. It is an estimate of the energy value of the milk solids yield, expressed in terms of normal milk of 4 per cent fat content, and designated F.C.M., fat corrected milk. The values are derived from the milk (M) and fat (F) by the equation $F.C.M. = .4M + 15F$ (1 pound $F.C.M.$ = 331 large calories.) As a quantitative measure of mammary activity, energy yield has several biological arguments in its favor.

It is evident from Fig. 1, that the theoretical curves correspond well with the observed values. The root mean square errors are: *fat corrected milk*, 5.23; *fat*, .303; *milk*, 7.14. Weighting the errors by their respective $1/A$'s and taking the weighted F.C.M. error as 100, the fat error is 138, and milk, 147.

Equation (2) was found applicable to the groups bred 11.5, 10.5, 9.5, 8.5, 7.5, and 6.5 months after calving. Data for the latter group are presented in Fig. 2. Pregnancy is 4.5 months advanced at the last observation in this group. It appears, therefore, that for the first 5 months of the gestation period pregnancy does not appreciably affect the rate of milk secretion. Both the A and k constants of

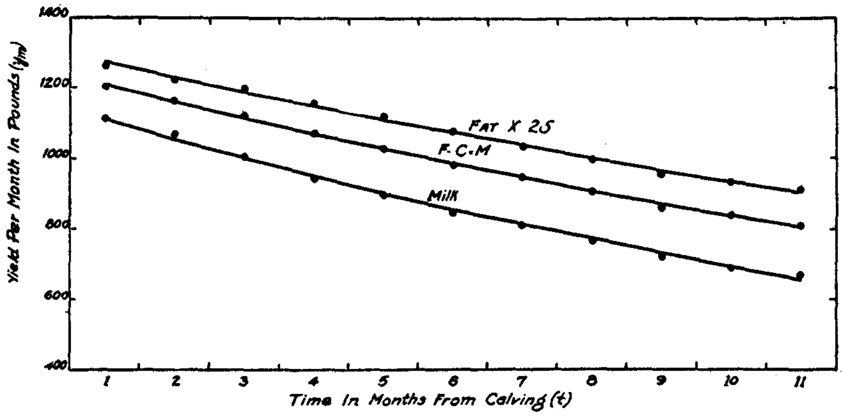

FIG. 1. Rate of activity of the mammary gland in farrow cows as measured by fat yield ($y_m = 52.575e^{-.034202t}$); milk yield ($y_m = 1167.6e^{-.052347t}$); and F.C.M. yield ($y_m = 1254.7e^{-.040524t}$).

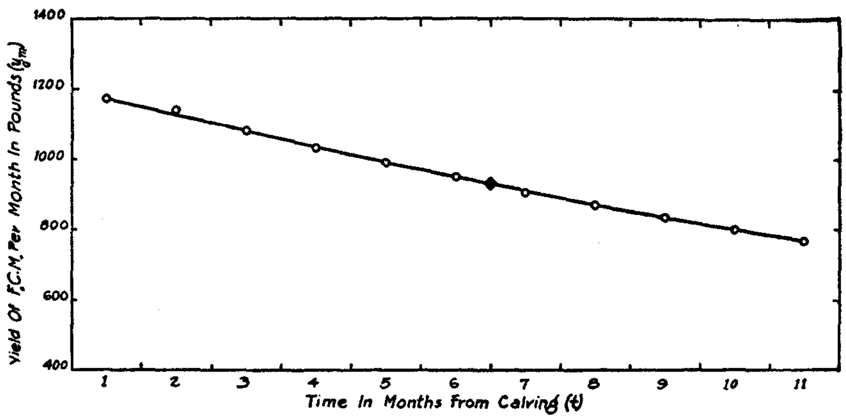

FIG. 2. Rate of activity of the mammary gland in pregnant cows as measured by F.C.M. yield ($y_m = 1220e^{-.04232t}$). Time of conception is marked by ◆ on the curve. Up to 5 months pregnancy does not appreciably affect the rate of milk secretion.

Fig. 2 differ from those of Fig. 1 in the direction of a decrease in yield, but there is no apparent reason to connect this decrease in yield with the occurrence of pregnancy in Fig. 2.

Equation (1) furnishes a ready means of computing the relative yields for various portions of the lactation. The ratio between any two portions is a function of k. The average value found for k was .04412. Breeders of dairy cattle are particularly interested in the relation between the yield for 305 days and 365 days. Starting at the same time after calving the 305 day yield is 86.97 per cent of the 365 day yield, for the value of k given.

Cows in Advanced Pregnancy.

When pregnancy becomes further advanced in the observed lactation, equation (1) is not sufficient to describe the rate of milk secretion throughout. It is necessary to add a term to take care of the effect of pregnancy. The equation used for the groups bred 5.5, 4.5, 3.5, 2.5, 1.5, and .5 months after calving in its differential form is:

$$\frac{dy}{dt} = ae^{-kt} - be^{K(t-c)} \quad (3)$$

and as applied to the observed values:

$$y_m = Ae^{-kt} - Be^{K(t-c)} \quad (4)$$

In equations (3) and (4) the minus term measures the effect of pregnancy on milk secretion; b is a constant representing the initial rate of inhibition of the rate of milk secretion; $B = b\,\frac{e^{.5K} - e^{-.5K}}{K}$; K is a constant representing the rate of change per month in the rate of inhibition; c is the number of months from calving to conception, and $t - c$ is time in months from conception.

Fig. 3 shows the observed values and fitted curve of equation (4) for the group of cows bred 1.5 months after calving. In the six groups for which equation (4) was used the K constant is the same (1.09861) in each case. The B constant is also the same (.01206) in five of the six cases. Representing the inhibition of milk secretion in pounds per month by i, and time in months of pregnancy by p we have $\frac{di}{dp} = .01147e^{1.09861p}$. The gestation period in the cow is 9.2 months and integration between the limits 0 and 9.2 gives 256 pounds F.C.M.

as representing the average total decrease in yield due to carrying the calf full term.

The groups of cows bred 1.5 and 2.5 months after calving were each further separated into four age classes. Equation (4) applied to these age data led to the same constant value of K. The values of B varied, however, and were roughly proportional to A. That is, the decrease in yield associated with pregnancy tends to be proportional to the productive level.

Inhibition of Milk Secretion Due to Pregnancy.

Two explanations have been offered for the decrease in milk yield associated with pregnancy: one, that it is due to the demands of

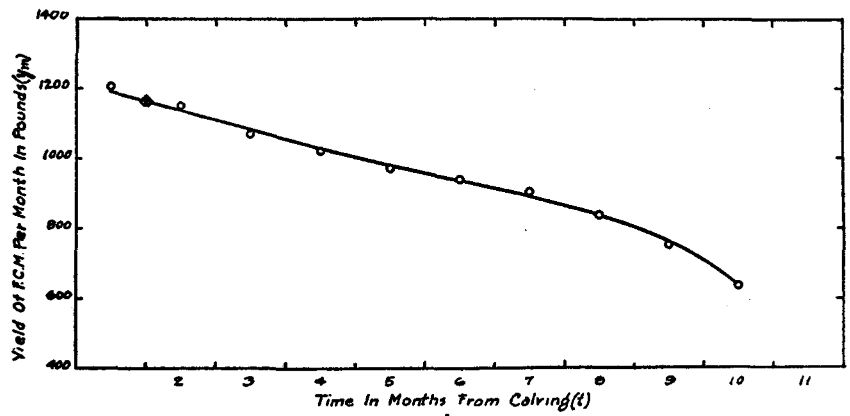

FIG. 3. Rate of activity of the mammary gland in pregnant cows as measured by F.C.M. yield ($y_m = 1250e^{-.04796t} - .01206e^{1.09861\ (t\ -\ 1.5)}$). Time of conception is marked by ◆ on the curve. Advanced pregnancy occasions a marked decrease in the rate of milk secretion, measured by the minus term of the equation.

the growing fetus for nutrients; the other, that it is due to a hormone thrown into the circulation during pregnancy and acting as an inhibitor to milk secretion. The latter view seems to have the most adherents and seems to be better supported by experimental evidence. The inhibition theory leads also to a possible explanation of the increasing rate of milk secretion for a short time following parturition.

It is known that the rate of milk secretion increases following parturition for a period of 10 to 30 days, or longer in individual cases. Brody, Turner, and Ragsdale have applied the equation

$$M = Ae^{-k_1t} - Be^{-k_2t} \quad (5)$$

to observed daily milk yields following parturition and obtained a satisfactory agreement (M = milk yield, t = time from parturition).

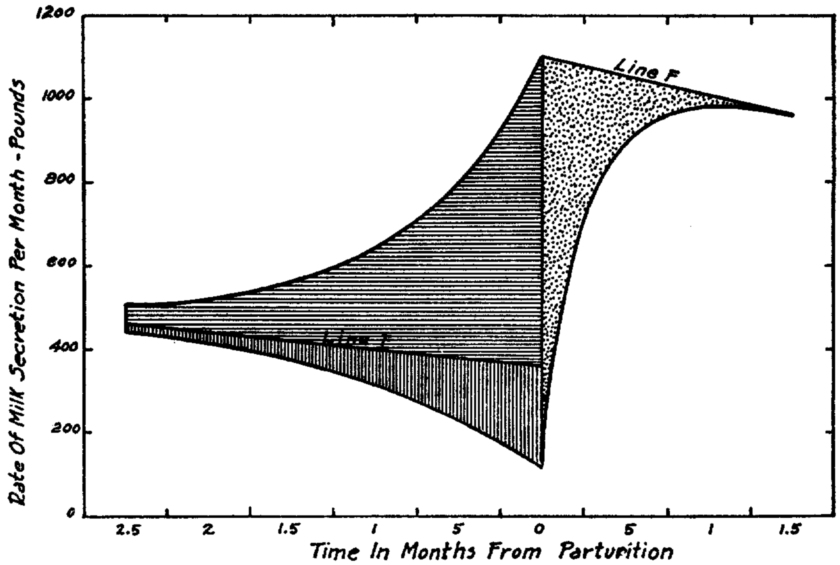

FIG. 4. Diagram illustrating the potential rate of milk secretion (upper line) and the realized rate of milk secretion (lower line) shortly preceding and following parturition. The area under the upper curve represents potential yield; the shaded area, the inhibition of pregnancy; and the area under the lower curve, the realized yield.

If pregnancy is terminated before full term the maximum rate of milk secretion following would be lowered according to the degree of prematurity. This is in accord with observed milk yields following abortion. The higher the maximum realized rate of milk secretion following parturition, the more delayed its appearance. This also is in accord with observations.

Further explanation of diagram in text.

They have interpreted their results as indicating an underlying consecutive chemical reaction as directly or indirectly responsible for the rate of milk secretion.

An alternative interpretation of the data is suggested by the inhibition hypothesis. This is illustrated diagrammatically in Fig. 4. The figure covers a period from 2.5 months preceding to 1.5 months following parturition. The ordinates of the lines F, represent the rate of milk secretion outside the influence of pregnancy according to equation (1). The vertically shaded portions of the ordinates represent the observed decrease in rate of yield of pregnant cows as compared with farrow cows. The horizontally shaded portions represent an assumed increase in the potential capacity for milk secretion of the pregnant cow as compared with the farrow cow. The vertically and horizontally shaded portions together represent the prepartum rate of inhibition of milk secretion due to pregnancy.

It is assumed that the source of the inhibitor is removed with the birth of the fetus so that the supply to the maternal circulation is cut off abruptly at parturition. A certain amount of inhibitor is at that time left in the maternal body and gradually disappears. The stippled portions of the ordinates represent the postpartum rate of inhibition of milk secretion due to this residue.

It is evident that if this residue is destroyed or eliminated at a rate proportional to its concentration the postpartum rate of inhibition may be represented by be^{-kt}, which subtracted from equation (1) would lead precisely to equation (5). There is some experimental evidence of the presence of an inhibitor to milk secretion in the maternal circulation both preceding and following parturition, and the considerations presented diagrammatically in Fig. 4 offer an alternative interpretation of equation (5).

Teleologically, one might say that gestation provides a mechanism which insures the preparation of the mammary gland for the secretion of milk for the postnatal nourishment of the young; which inhibits the secretion, almost or quite entirely, preceding parturition; and which by the gradual removal of the inhibitor following parturition provides for some time an increasing milk supply to meet the increasing needs of the growing young.

SUMMARY.

The rate of milk secretion in farrow cows may be expressed as $\frac{dy}{dt} = ae^{-kt}$, in which y = yield and t = time from calving. Preg-

nancy causes a decrease in yield which may be expressed as $\frac{di}{dp} = be^{Kp}$, in which i = inhibition or decrease in yield and p = time from conception. The constant K appears to be the same for various groups but b is roughly proportional to a. The decrease in yield associated with pregnancy is interpreted as due to a hormone. The hormone hypothesis also affords an interpretation of the increasing rate of milk secretion which occurs for a short time following parturition.