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F. B. MUMFORD, *Director*

GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XLVIII. Relation Between Body Weight, Amount of Wool or Feathers, and Temperature Regulation

SAMUEL BRODY AND JOHN CAMPBELL

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FOREWORD

The special investigation on growth and development is a cooperative enterprise in which the departments of Animal Husbandry, Dairy Husbandry, Agricultural Chemistry, and Poultry Husbandry have each contributed a substantial part. The parts for the investigation in the beginning were inaugurated by a committee including A. C. Ragsdale, E. A. Trowbridge, H. L. Kempster, A. G. Hogan, and F. B. Mumford. Samuel Brody served as Chairman of this committee and has been chiefly responsible for the execution of the plans, interpretation of results and the preparation of the publications resulting from this enterprise.

The investigation has been made possible through a grant by the Herman Frasch Foundation, now represented by Dr. F. J. Sievers.

F. B. MUMFORD
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ABSTRACT

The purpose of this research was to find whether the "amount" of wool or feathers tends to be more nearly proportional to surface area or to body weight, and to indicate the bearing of these results on thermoregulation and on the concept of physiologic units.

In yearling sheep the wool weight was found to be nearly directly proportional to surface area (wool weight per unit area nearly constant). In older sheep, which include a wider age group, wool weight per unit area decreased with increasing weight. The difference in result between the yearlings and older group may be due to a differential effect of age on body weight growth and on wool-weight growth.

In growing domestic fowls total feather weight tends to be proportional not to surface area but to body weight (in males feather weight tends to vary with the 1.2 power of body weight, in females with the 1.0 power). In pigeons and geese, total feather weight tends to vary with the 0.9 power of body weight. In passeriformes of different species (age unknown probably mature), contour feather weight tends to vary directly with body weight as in the growing domestic fowls.

While the contour feather *weight* in passeriformes tends to vary directly with body weight, contour feather *number* tends to vary not with body weight (1st power of body weight) but with approximately the 0.2 power of body weight as previously reported by Hutt and Ball.

THIS IS PAPER 175 IN THE HERMAN FRASCH FOUNDATION SERIES.

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I. INTRODUCTION

1. Aims

Warm-blooded animals have a variety of thermoregulatory methods. A covering of hair or feathers is an obvious one. It is reasonable to assume that the extent of surface area of the body is a good index of the tendency to heat loss and that the amount of hair or feathers would for thermoregulatory reasons tend to be proportional to the surface area. The amount of wool, or feathers, would also be expected to be proportional to surface area on which it is grown just as the amount of grass would be expected to be proportional to the surface area of the field on which it grows. The purpose of this paper is to report results of an investigation on the quantitative relationship between the amount of wool or feathers and body size.

2. Data

This bulletin presents the results of analyses of data on the relation of: 1) wool weight to body weight in sheep, and 2) feather *weight* and feather *number* to body weight in birds.

The wool data were collected in this Station[1], supplemented by one set collected at the Montana Station[2].

The feather data were taken from the literature: the domestic fowl data from Mitchell, Card, and Hamilton[3]; pigeon data from Riddle[4];

[1]Trowbridge, E. A., Moffett, H. C., Brody, S., Predicting Wool Weight from Body Weight. Missouri Agr. Exp. Sta. Unpublished data.

[2]Joseph, W. E., Relation of Size of Grade Fine Wool Ewes to Their Production. Univ. Montana Agric. Expt. Station Bulletin 242, 1931.

[3]Mitchell, H. H., Card, L. E., and Hamilton, T. S., The Growth of White Plymouth Rock Chickens, Univ. Ill. Bul. 278, 1926; A Technical Study of the Growth of White Leghorn Chickens. Id., Bul. 367, 1931.

[4]Riddle, O., Data on Weights of Feathers of Pigeons and Doves, data published by Benedict and Lee[5], p. 36.

geese data from Benedict and Lee[5]; Passeriformes data from Wetmore[6]. Wetmore's data were called to our attention by Hutt[7]. Hutt thought that the relation between feather number and body weight is conditioned by thermoregulatory needs. Our analysis differs from Hutt's in that his paper is concerned with the relation of feather *number* to body size while ours is primarily concerned with the relation of wool *weight,* or feather *weight* to body size. Because Hutt's interesting paper called our attention to Wetmore's unique data on feather *number* which "were plucked a few at a time by means of fine tweezers," and because Hutt's result was so very unexpected, we added for comparative purposes the analysis and discussion of the feather *number* problem after the preceding work on the relation between wool and feather weight and body weight was completed.

II. THE RELATION BETWEEN WOOL WEIGHT AND BODY WEIGHT OF SHEEP

1. Wool Weight vs. Body Weight

Figures 1a (Missouri data) and 1b (Montana data) present the results of our analysis of the relation between wool weight and body weight in sheep. The wool weights were plotted against the body weights on logarithmically divided paper on the assumption that wool weight, like the surface area on which the wool grows, will be directly proportional not to body weight, but to some fractional power of body weight as represented by the logarithmic equation

$$\log Y = \log a + n \log X \qquad (1a)$$

or, what is the same

$$Y = aX^n \qquad (1b)$$

in which Y is wool weight and X is body weight.

While the distribution of the data in Figs. 1a and 1b is irregular, the approach of the distribution to linearity on the logarithmic grid is sufficiently satisfactory to indicate that no mistake was made in choosing equation (1) for representing the relation between wool weight and body weight.

The upper-left corner in Fig. 1a shows the wool weight for yearling Shropshires (crosses) and *average* of yearling Dorsets, Hamp-

[5]Benedict, F. G., and Lee, R. C., Lipogenesis in the Animal Body With Special Reference to the Physiology of the Goose. Carnegie Institution of Washington Publication 489, 1937.

[6]Wetmore, Alexander, The Number of Contour Feathers in Passeriform and Related Birds. The AUK, *53*, 159, 1936. See also Wetmore, A., A Study of the Body Temperature of Birds, Smithsonian Misc. Coll. *72*, 1, 1921; Amman, G., Number of Contour Feathers of Cygna and Xanthocephalus. The AUK, *54*, 201, 1937.

[7]Hutt, F. B., and Ball, L., Number of Feathers and Body Size in Passerine Birds. The AUK, *55*, No. 4, 1938.

shires and Southdowns (circles). These three breeds were averaged since the wool production at *given weights* is of the same order in these three breeds. The smooth curves represent equation (1) fitted to the data by the method of least squares.

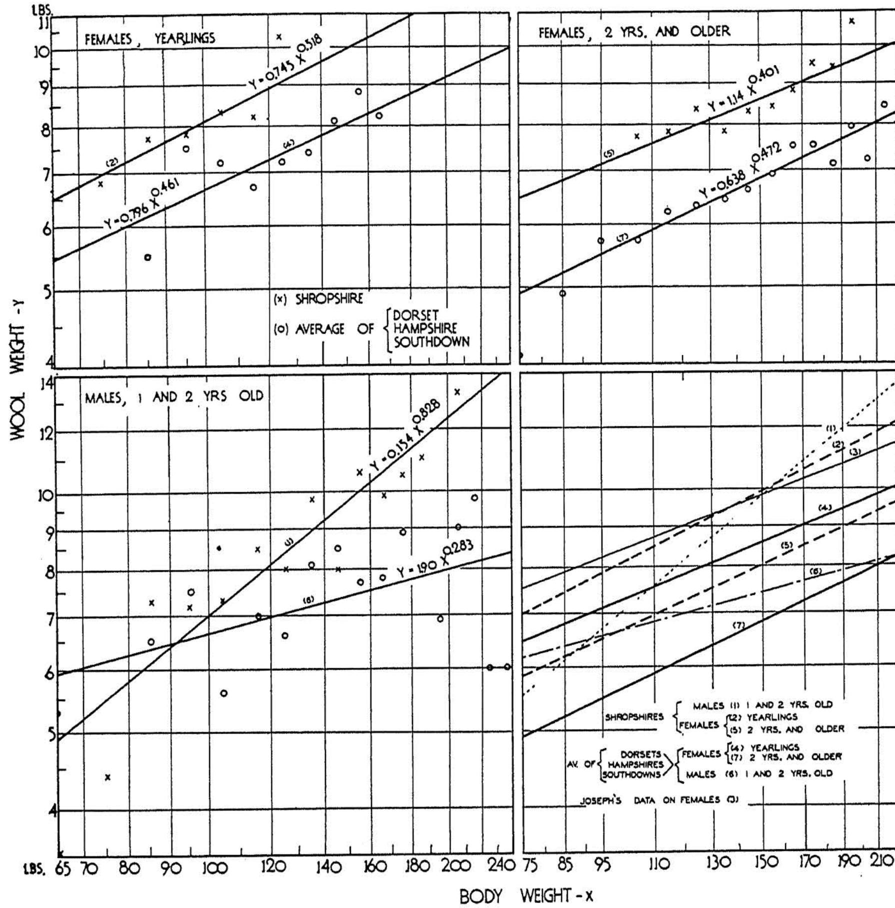

Fig. 1a.—The relation between wool production per sheep and live weight of sheep *plotted on logarithmically divided paper*. The data points (weighted averages by 10-pound live weight intervals) are shown as also the average curves and their equations. The crosses represent Shropshires, the circles represent average of the Dorsets, Hampshires, and Southdowns. The lower-right chart brings together all the fitted curves, including the curve we fitted to the data on grade fine wool sheep 3 years or over, published by W. E. Joseph, in Montana Agric. Expt. Station Bulletin 242, 1931, shown in Fig. 1b.

As the wool crop yielded by yearlings is considerably greater than that yielded by older animals, the data for the older animals were averaged separately from the yearlings and shown in the upper-right

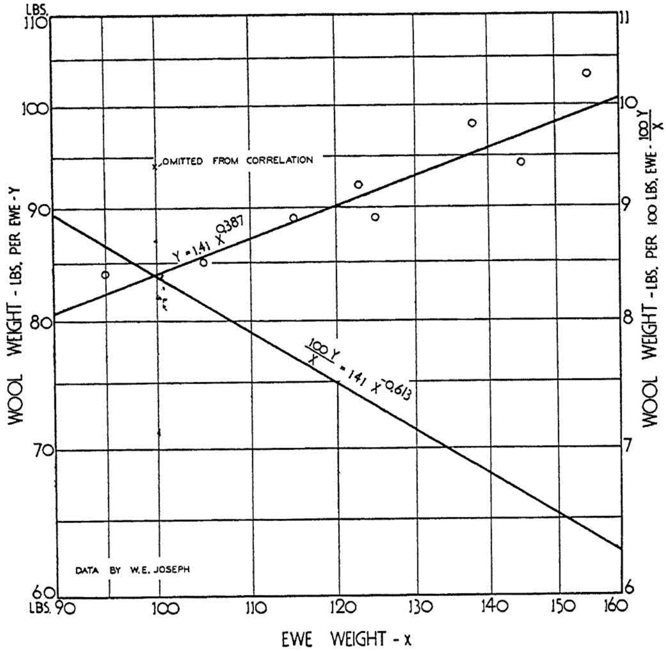

Fig. 1b.—The relation between wool weight per sheep (rising curve) and per 100-pounds live weight (declining curve) of Joseph's data.

corner of Fig. 1a. As before, crosses represent the Shropshire breed, and circles the average of the Dorset, Hampshire, and Southdown breeds.

The data for males are represented in the lower-left corner of Fig. 1a. These data are irregular not only because of the smallness of the populations but also because many of the rams were "stubble-sheared" for exhibition purposes.

In the lower-right corner in Fig. 1a are brought together the fitted curves of all the groups, including Joseph's data shown in Fig. 1b.

Figures 1a and 1b show that the slope (exponents in equation (1b)) of the curves relating wool weight to body weight in female sheep is between 0.46 and 0.52 for yearlings, and 0.40 to 0.47 for the older age group. This means that increasing body weight by 100% is associated with an increase in wool production not of 100% but of the order of 32% to 43%. That is, a 200-pound sheep produces not twice, but from 32% to 43% more wool than a 100-pound sheep. The relation between the value of n in equation (1) and the percentage increase in wool production when body weight is doubled, that is increased by 100%, is shown in Fig. A.

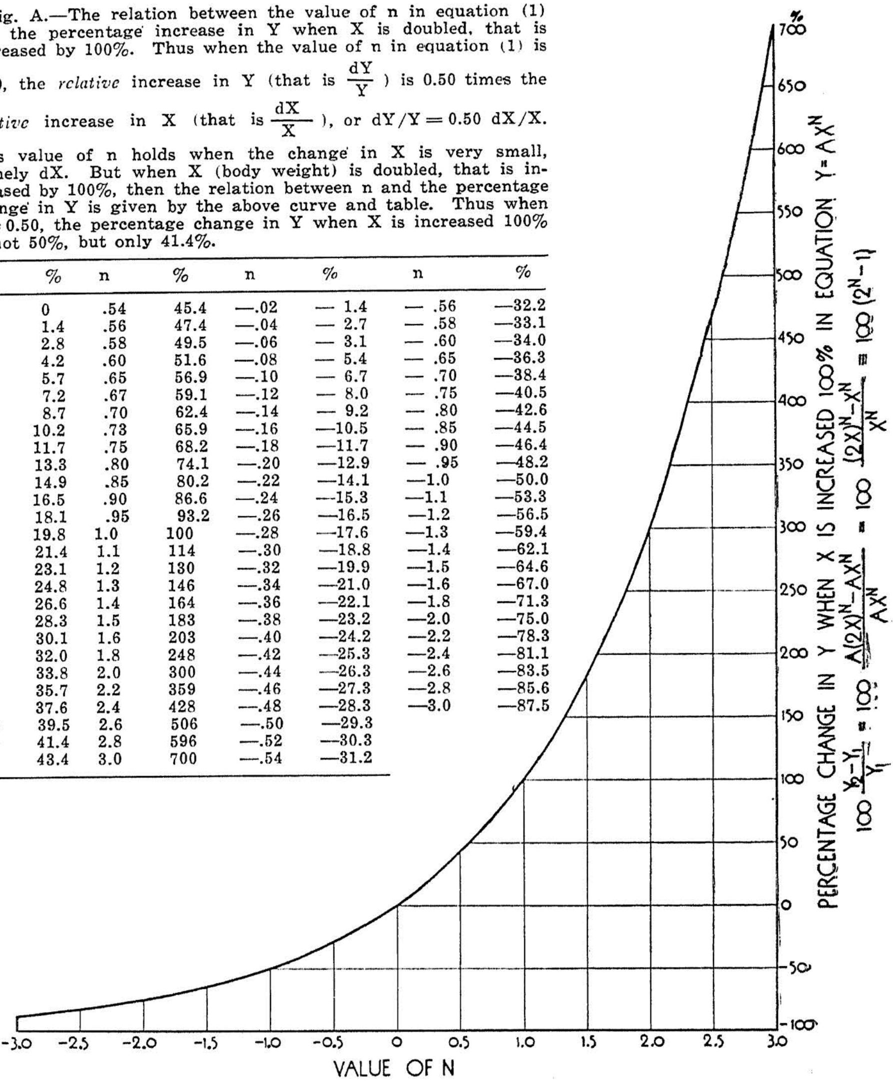

Fig. A.—The relation between the value of n in equation (1) and the percentage increase in Y when X is doubled, that is increased by 100%. Thus when the value of n in equation (1) is 0.50, the *relative* increase in Y (that is $\frac{dY}{Y}$) is 0.50 times the *relative* increase in X (that is $\frac{dX}{X}$), or $dY/Y = 0.50\ dX/X$. This value of n holds when the change in X is very small, namely dX. But when X (body weight) is doubled, that is increased by 100%, then the relation between n and the percentage change in Y is given by the above curve and table. Thus when n = 0.50, the percentage change in Y when X is increased 100% is not 50%, but only 41.4%.

n	%	n	%	n	%	n	%
0	0	.54	45.4	—.02	— 1.4	— .56	—32.2
.02	1.4	.56	47.4	—.04	— 2.7	— .58	—33.1
.04	2.8	.58	49.5	—.06	— 3.1	— .60	—34.0
.06	4.2	.60	51.6	—.08	— 5.4	— .65	—36.3
.08	5.7	.65	56.9	—.10	— 6.7	— .70	—38.4
.10	7.2	.67	59.1	—.12	— 8.0	— .75	—40.5
.12	8.7	.70	62.4	—.14	— 9.2	— .80	—42.6
.14	10.2	.73	65.9	—.16	—10.5	— .85	—44.5
.16	11.7	.75	68.2	—.18	—11.7	— .90	—46.4
.18	13.3	.80	74.1	—.20	—12.9	— .95	—48.2
.20	14.9	.85	80.2	—.22	—14.1	—1.0	—50.0
.22	16.5	.90	86.6	—.24	—15.3	—1.1	—53.3
.24	18.1	.95	93.2	—.26	—16.5	—1.2	—56.5
.26	19.8	1.0	100	—.28	—17.6	—1.3	—59.4
.28	21.4	1.1	114	—.30	—18.8	—1.4	—62.1
.30	23.1	1.2	130	—.32	—19.9	—1.5	—64.6
.32	24.8	1.3	146	—.34	—21.0	—1.6	—67.0
.34	26.6	1.4	164	—.36	—22.1	—1.8	—71.3
.36	28.3	1.5	183	—.38	—23.2	—2.0	—75.0
.38	30.1	1.6	203	—.40	—24.2	—2.2	—78.3
.40	32.0	1.8	248	—.42	—25.3	—2.4	—81.1
.42	33.8	2.0	300	—.44	—26.3	—2.6	—83.5
.44	35.7	2.2	359	—.46	—27.3	—2.8	—85.6
.46	37.6	2.4	428	—.48	—28.3	—3.0	—87.5
.48	39.5	2.6	506	—.50	—29.3		
.50	41.4	2.8	596	—.52	—30.3		
.52	43.4	3.0	700	—.54	—31.2		

Derivation of equation relating percentage change with the exponent n. Let $Y_1 = aX^n_1$, and $Y_2 = aX^n_2$, therefore the increase in Y expressed in per cent of Y_1 is $100\frac{Y_2-Y_1}{Y_1} = 100\frac{aX^n_2-aX^n_1}{aX^n_1} = 100\frac{X^n_2-X^n_1}{X^n_1} = 100\left(\frac{X_2}{X_1}\right)^n - 100$. When X_2 is twice X_1, $X_2 = 2X_1$, and percentage change is given by $100\left(\frac{2X_1}{X_1}\right)^n - 100 = 100\ (2^n-1)$.

2. Wool Weight Per Unit Body Weight vs. Body Weight

It is evident from the constants in Fig. 1 that the increase in wool weight does not keep up with the increase in body weight. This is particularly true of the age group following the yearling stage. The value of the exponent n in the age group following the yearling is between 0.40 and 0.47 which means, as indicated in Fig. A, that doubling body weight, does not double the wool weight, but only increases it 31% to 39% (see Fig. A). In yearlings the value of the exponent n is higher for reasons which will be presently discussed.

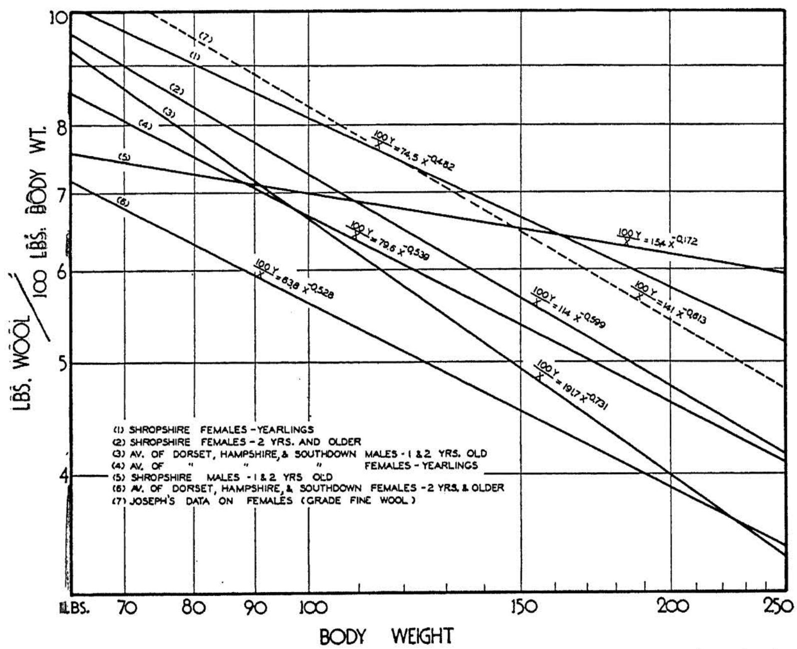

Fig. 2.—Curves (with their equations) showing the relation between *wool production per 100 pounds* live weight and body weight, plotted on logarithmically divided paper.

The ratios of wool weight, Y, per unit body weight, X, are presented in Fig. 2. The ratios, $\frac{Y}{X}$, are of course related to body weight, X, by the equation

$$\frac{Y}{X} = aX^{n-1} \qquad (2)$$

They are seen in Fig. 2 to decline rapidly with increasing live weight.

3. Wool Weight Per Unit Surface Area vs. Body Weight

According to the conventional Rubner or Meeh surface-area formula, the surface area of animals increases with the 2/3 or 0.67 power of body weight. According to Ritzman and Colovos,[8] the surface area of sheep based on "surface-integrator" *measurements* varies with the 0.50 to .56 power of body weight (for 32 yearlings, $S = 0.147\ W^{.520}$; for 60 adults, $S = 0.126\ W^{.556}$; for 23 lambs, $S = 0.139\ W^{0.501}$; for the 115 flock, $S = 0.124\ W^{.561}$. S represents area in sq. meters, W weight in kg.).

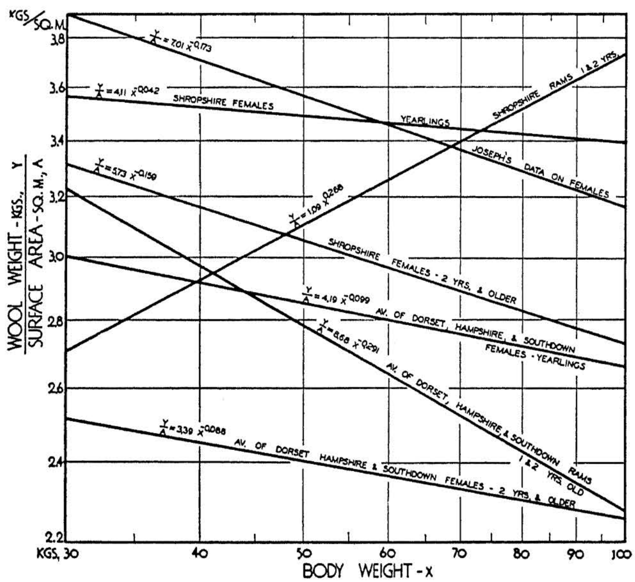

Fig. 3.—The ratio of wool weight (Kg.) to surface area (Sq. meter) as function of body weight.

Since the wool production of our sheep increased not with the 0.67 power (Meeh or Rubner formula), nor with the 0.52-.56 power (Ritzman and Colovos' formula), but varied, from the 0.5 power (yearlings) to 0.4 power (2 years and over), it is obvious that the wool production per unit surface area tends to decrease with increasing body weight. This is illustrated by the curves in Fig. 3 in which the wool production, Y, in Kg., per unit surface area, A, in square meters, was plotted against body weight, X, in Kg. The surface area, A, was computed from the Ritzman and Colovos yearling 0.520 power formula, and those above this age from the same authors'

[8]Ritzman, E. G., and Colovos, N. F., Surface Area of Sheep, Univ. of New Hampshire, Agric. Expt. Sta. Circular 32, 1930; or see S. Brody, Annual Review Biochem., 3, 324, 1934.

0.556 power formula. The declining slopes in Fig. 3 would of course be much steeper if Meeh's 0.67 power surface-area formula were used.

Fig. 3 shows that for yearlings, the decline of wool weight per unit area with increasing body size is slight (the slope is only 0.04 for the Shropshires and —0.1 for the average of the other 3 breeds). But for the average of the ages above yearlings, the decline of wool weight per unit area with increasing body weight is considerable (—0.16 for the Shropshires, —0.29 for the others). The reason for the greater decline in this ratio following the yearling stage is discussed in the following section.

4. Relative Age Effects on Body Weight, Wool Weight and on the Interrelations

Because of the relatively slight influence of age on wool production and fewness and variability of data following the yearling stage, the data were subdivided into two age classes only: 1) yearlings, and 2) the average of all ages above the yearling class, and thus far the discussion was confined to these two age classes. Before closing this section it seems desirable to get a somewhat closer view, with the aid of Figs. 4 and 5 of the influence of age on body weight, wool production, and on the wool-body relation. The data in Fig. 4 were plotted on arithlog (semi-log) paper in order to represent the *relative* changes in slopes

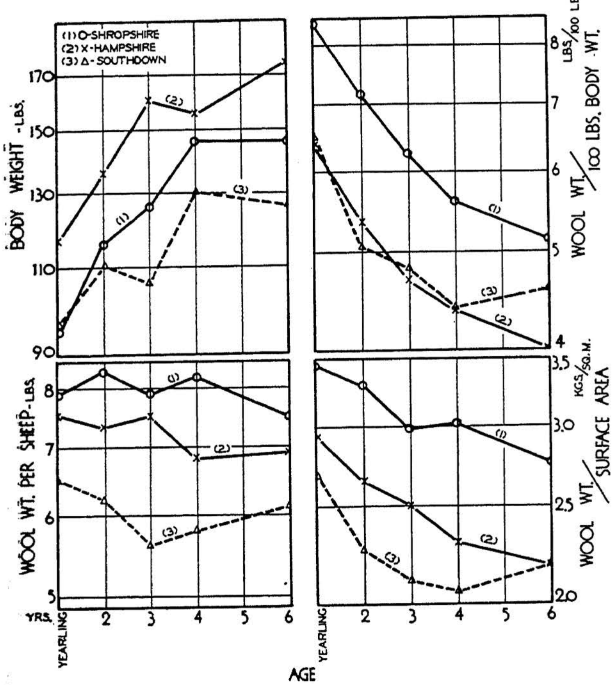

Fig. 4.—Age curves of body weight, wool weight, wool weight per unit surface area, and wool weight per unit body weight plotted on arithlog grid to indicate the *relative* influence of age on body weight and wool weight. Body weight increases up to about 4 years, while wool weight tends to decline following the yearling age.

of the curves (or when multiplied by 100, percentage changes).

The upper-left curves in Fig. 4 show that, on the average, body weight increases up to 4 years. The lower-left curves show that in spite of increasing body weight, the wool crop per animal does not increase, indeed tends to decrease somewhat, with increasing age following the yearling stage. In other words, following the yearling

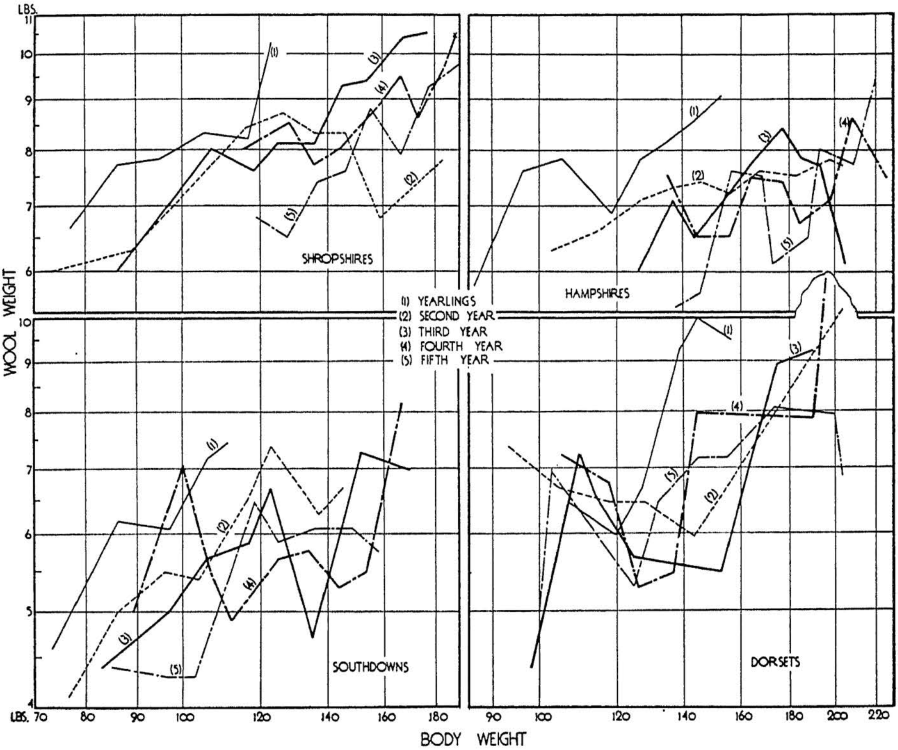

Fig. 5.—Relation between wool weight and body weight plotted on a logarithmic grid for each of the 5-age groups separately and for each of the 4 breeds to indicate the *relative* influence of age on the slopes of the curves, and variability of the data.

stage, wool growth lags behind increase in body weight with increasing age. This lag of wool weight behind body weight with increasing age may explain the fact previously discussed that not only the ratio of wool weight to body weight decreases with increasing body weight (upper-right in Fig. 4), but that even the ratio of wool weight to surface area (lower-right in Fig. 4) decreases with increasing body weight. In other words, the decrease of wool weight per unit surface area with increasing body weight following the yearling stage may be accounted for in part by a differential age effect on the two types of growth, body weight and wool weight, namely increasing age up to 4 years is associated with increasing body weight but not with increasing wool production. We are not prepared to discuss the failure of the wool weight to keep up with body weight. All we can say is that in this particular group of sheep under the given conditions, the body weight increases up to 4 years of age while the wool crop remains constant or even decreases, with the result that both ratios, wool weight to body weight and wool weight to surface area decrease with increasing body weight or with increasing age.

Figure 5 representing the relation between wool weight and body weight of the five age groups on a *logarithmic grid,* indicates the variability of the data and the relative influence of age on the slopes of each of the 5 wool-body curves. The yearlings appear to have the steepest slopes even though age is constant.

5. Discussion

We began this work with the expectation that the ratio of wool weight to surface area would be the same for all body weights because: 1) the function of the wool is to regulate the heat loss from the *surface;* 2) the heat dissipation is mostly by way of the surface area, and the *surface* area of the body is the soil, so to speak, on which the wool grows.

Analysis of the data has shown that in yearlings this expectation was nearly, but not quite, fulfilled. But for the combined ages following the yearling stage, the expectation that the ratio of wool weight to surface area is constant was not materialized. The ratio of wool weight to surface area decreased very substantially with increasing live weight. The fact that the yearlings wool represents the first crop while the later wool growth was preceded by shearing may be a factor in the situation. But the main reason for this decrease appears to be due to the fact that the older age group contains animals of widely differing ages, and that while body weight increases to about 4 years, wool does not increase following the first year. The reasons for this differential influence of age on wool growth and body-weight increase may be anatomical (the *number* of hairs may not increase after a certain age) or physiologic (the *length* or *thickness* of hair decreases with age). The combination of all age groups following the yearling stage instead separating them by 1-year classes, was made necessary by the fact that the data following the yearling age were too few and too variable, as shown in Fig. 5, when separated by yearly intervals and by breeds.

The reason for the tendency for decrease of wool production per unit area with increasing body weight may also be due to the assumption that gravitational wool *weight* is a directly simple measure of functional or physiologic "amount" of wool, an assumption which may be erroneous.[9] In other words, the discrepancy between observed and expected results may be due in part to the fact that we have not found a proper physiologic unit of "amount" of wool.

III. INTERRELATIONS BETWEEN FEATHER WEIGHT, FEATHER NUMBER AND BODY WEIGHT IN BIRDS

1. Introduction

Feathers are more complex and heterogeneous than hair or wool—especially in that feathers are burdened with heavy supporting structures, such as quills, which are in themselves of uncertain thermoregulatory significance. Unit *feather weight* is thus likely to have a different absolute and relative thermoregulatory significance than unit *wool-weight* in animals of different sizes.

Similar objections might be raised against adopting *feather number* as representing thermoregulatory unit of amount of feather. It is generally known that feathers differ enormously in structure, length, width, function: flight feathers, ornamental feathers, contour feathers, nest-forming feathers, brooding feathers, oil-gland feathers, ranging all the way from eyelash feathers, bristles, powder-down, down feathers, plumules, filoplumes, to contour feathers. Each feather is moreover very complex. The contour feather, for example, is made up of the heavy supporting structure, the quill or shaft, which supports two rows of barbs which together make up the web or wane of the feather. Each barb has in turn two rows of barbules—a barb is a small feather in its own right—and a contour feather is basically a population of smaller feathers. As previously noted, the quill which is gravimetrically, volumetrically, and morphologically a very important part of the feather, may be very unimportant from the thermoregulatory viewpoint.

If therefore we adopt feather *weight* as unit of "amount" of feathers, we shall include purely supporting structures, as quills, which may be devoid of thermoregulatory function; if we adopt feather *number* as unit of "amount" of feathers we have the problem of de-

[9]Cf. Brody, S., Relativity of Physiologic Time and Physiologic Weight. GROWTH, 1, 60, 1937.

ciding what constitutes a feather and how to "weight" each feather so as to reduce it to some standard thermoregulatory level. There may be qualitatively similar although quantitatively less striking difficulties as regards wool, such as differences in hair length, diameter, wall thickness, hair numbers, amount of inseparable grease and so on. The most difficult aspects of this investigation are thus concerned with choice of rational units of *amount* of feathers and to a less extent *amount* of wool. What shall the biological unit of *amount* be?

2. Feather Weight vs. Body Weight During Growth in Domestic Fowls

As pointed out in connection with the wool problem, it is exceedingly desirable to hold age constant because age probably has a different influence on body weight growth and feather (or wool) growth. Unfortunately, in spite of the assistance of Dr. Walter Landauer[10] who generously sent us a large amount of unpublished data on feathers of birds of constant age, the body-weight range was too narrow in comparison to the variability of the data to justify formulating any generalization relating feather weight to body weight for narrow age classes. We were therefore obliged to confine our examination to the feather-body relation of the domestic fowl *during growth,* disregarding the possible differential influence of age on feather and body growth.

The result of the analysis in Fig. 6, based on the data by Mitchell, Card and Hamilton (l.c.), shows that feather *weight* tends to vary directly with body weight rather than with surface area. In males, feather weight increases even more rapidly than body weight, no doubt due to the greater increase in ornamental feathers with increasing age (and therefore weight) in males than in females or in capons.

The significance of the fact that feather weight is proportional to body weight rather than to surface area may be no more than that feather weight is not a measure of the *biologic* (thermoregulatory) unit of feathers, and that the direct proportionality between feather weight and body weight is the result of certain mechanical (rather than thermoregulatory) necessities involving a heavy structural frame work (quill, etc.).

[10]Cf. Landauer, W., and Upham, E., Weight and Size of Organs in Frizzle Fowl. A study concerning organ adjustment following excessive loss of body heat and accelerated metabolism. Storrs Agric. Expt. Sta. Bulletin 210, April, 1936.

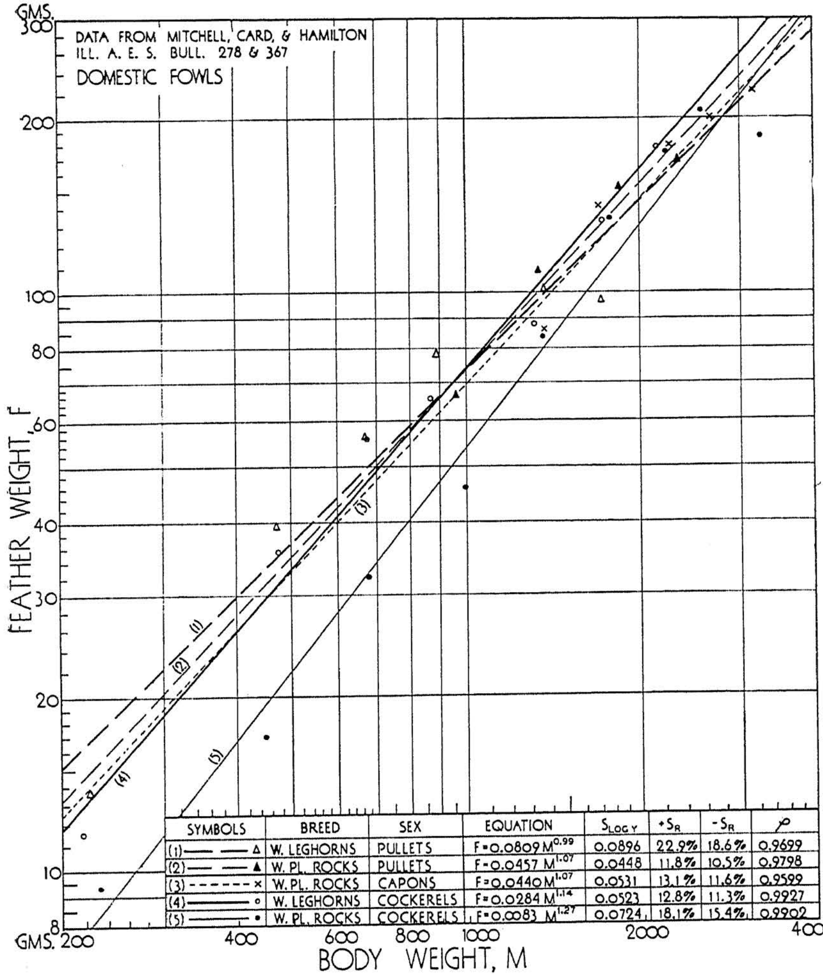

Fig. 6.—Relation between feather weight and body weight in domestic fowls.

3. Feather Weight vs. Body Weight in Pigeons and Geese

Figure 7 shows that: 1) the relation between feather weight and body weight is the same in pigeons and geese; 2) the total feather weight in these two species varies with the 0.9 power of body weight (increasing body weight by 100% increases feather weight by 86.6%) contrasted with the expected 0.67 power if feather weight were proportional to surface area and with the 1.0 power if it were proportional to body weight.

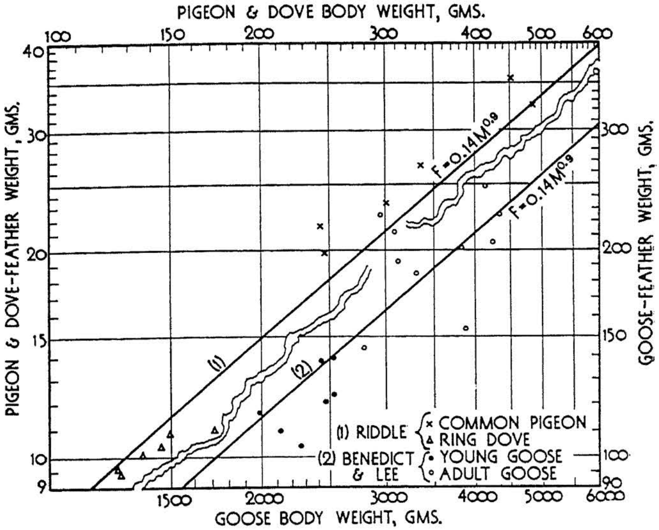

Fig. 7.—Relation between feather weight and body weight in pigeons and doves (upper line) and geese (lower line).

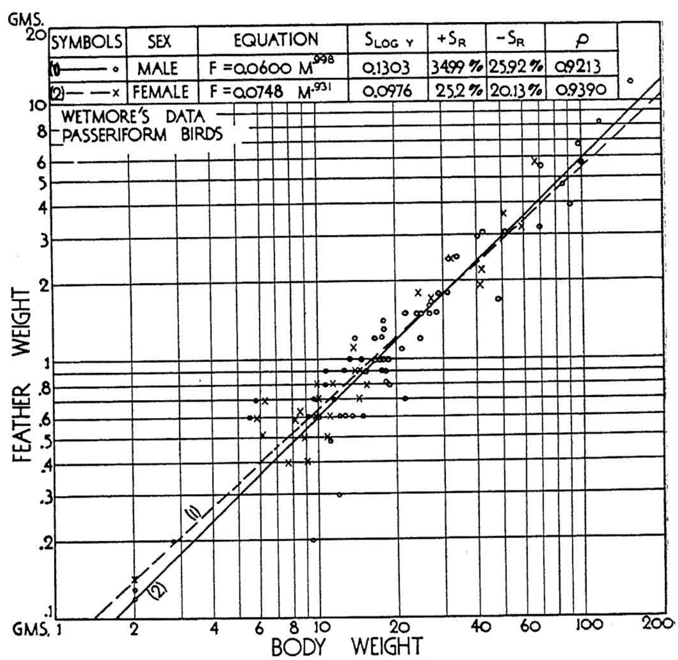

Fig. 8.—Relation between feather weight and body weight in Passeriform birds. The equations with their statistical constants are tabulated on the chart.

4. Feather Weight vs. Body Weight in Passeriform Birds

Wetmore's (l.c.) Passeriformes data in Fig. 8 are not concerned with the weight of all the feathers, as was the case with the data in Figs. 6 and 7, but with the contour feathers alone, the downs and filoplumes being disregarded. The Passeriformes data differ in two other respects from those in Figs. 6 and 7: 1) the data include many species (among others, goldfinches, woodpeckers, chickadees, mourning doves, robins, thrushes, warblers, bluebirds, juncos, grackles, tanagers, cardinals, grosbeaks, red-wings, cowbirds, catbirds, buntings, sparrows, night hawks, creepers, mocking birds, humming birds, kingbirds, fly catchers, phoebes, bluejays, wrens, vireos); 2) they were obtained on apparently mature birds.

Figure 8 indicates that in these birds as in domestic fowls the contour-feather weight tends to vary directly with body weight (with the .998 power of body weight in males and with the 0.93 power of body weight in females) and the feather weight in males increases more rapidly than in females with increasing body weight.

5. Feather Number vs. Body Weight and Feather Number vs. Feather Weight

The lower half of Fig. 9 represents the relation between feather *number*, N, and body weight of the same birds shown in Fig. 8 for the relation between feather *weight*, F, and body weight. The rising curves represent feather number, N, plotted against body weight, M; the declining curves represent the ratio $\frac{\text{Feather number}}{\text{Body Weight}}, \frac{N}{M}$, plotted against body weight.

The equations in the lower-right indicate that in the males the feather *number* increases with the 0.222 power of body weight, as contrasted to the feather *weight*, shown in Fig. 8 which increases with the 0.998 power of body weight; in the females the feather *number* increases with the 0.153 power of body weight as contrasted to the feather *weight*, shown in Fig. 8, which increases with the 0.930 power of body weight. (Increasing body weight by 100% increases feathers by 17% when $n = 0.222$; by 11% when $n = 0.153$; 91% when $n = 0.93$; by 100% when $n = 0.998$.)

Thus we find that with increasing body weight, feather weight increases more rapidly than surface area, and feather number increases much less rapidly than surface area. This fact is illustrated in more direct fashion in Fig. 10. The ratio of feather *weight*, F, to surface

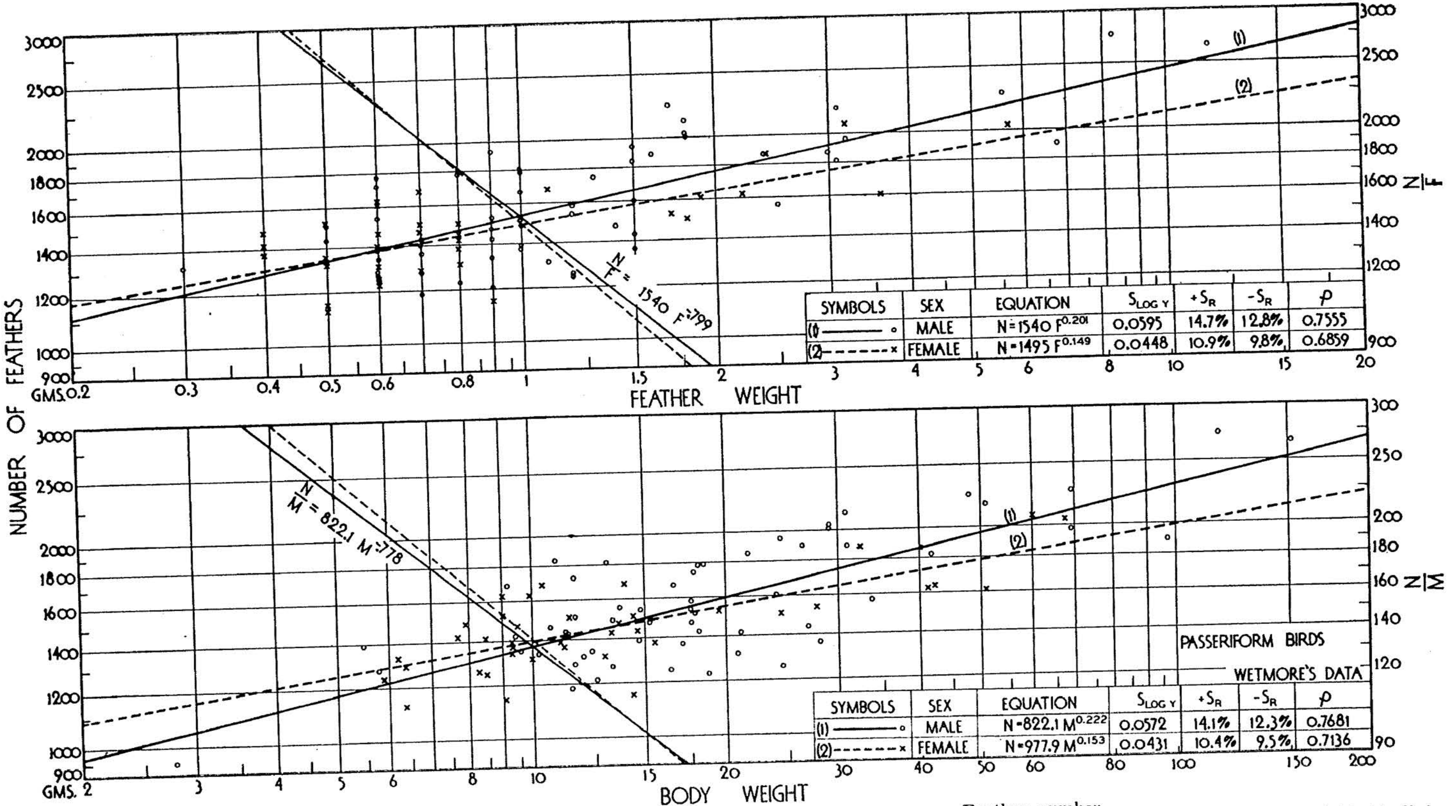

Fig. 9.—*Lower half*: Contour feather *number* plotted against body weight (rising curve) and the ratio $\frac{\text{Feather number}}{\text{Body Weight}}$ plotted against body weight (declining curve). Continuous curves and circles represent males, broken curves and crosses represent females. *Upper half*: Feather *numbers* plotted against feather *weight* (rising curves) and the ratio $\frac{\text{Feather number}}{\text{Feather weight}}$ plotted against body weight (declining curves). The values of the exponents (n in equation (1)) are nearly the same as for the relation of feather number and body weight.

area, A, *rises* with increasing body weight, and the ratio of feather *number*, N, to surface area, A, *declines* with increasing body weight. *Neither feather number nor feather weight is proportional to surface area.* Increasing body weight by 100% increases feather *weight* by 90 to 100% and feather *number* by 11% to 17%. In other words, the larger the bird the less the *number* of feathers or the smaller the bird the more the number of feathers it has in proportion to its size.

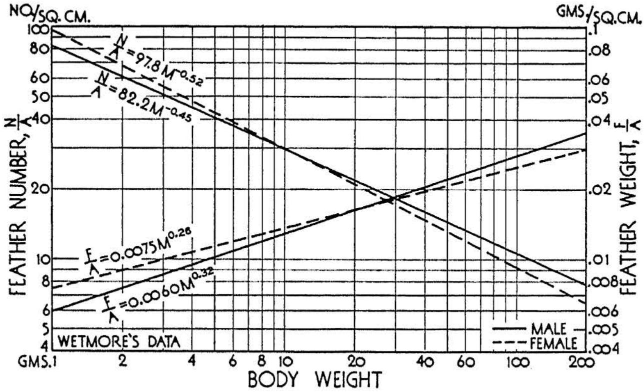

Fig. 10.—The radio of feather *number*, N, to surface area, A, decreases with increasing body weight (or increases with decreasing body weight), while the ratio of feather *weight*, F, to surface area, A, increases with increasing body weight.

IV. GENERAL SUMMARY AND CONCLUSIONS

The problem of interrelation between amount of body covering (hair, feathers) and body size is one aspect of the quantitative interrelation between structure and function which we have been investigating for years.[11]

Assuming that 1) the major function of body covering of hair, wool and feathers is regulation of heat loss from the body, and that 2) heat loss is proportional to surface area, and 3) considering that hair and feathers have their anchorage in the surface area of the body, it is logical to expect that the *amount* of wool and feathers would be proportional not to body weight but to the surface area of the body. Unfortunately there is some uncertainty as to what biological unit of *amount* of hair or feathers one should adopt. Should it be the *number* of hairs or feathers? There are objections against the *number* as unit of covering, because the length and structure of the individual hairs or feathers vary. There are, likewise, objections against adopting

[11]Cf. *inter alia.* Univ. Mo. Agric. Exp. Sta. Res. Buls. 89, 1926; 115, 1928; 166, 1932; 220, 1934; 238, 1936; 244, 1936; 262, 1937.

weight as unit of covering because, especially in feathers, the structural part, such as the quill, is a very substantial part of the feather weight, yet its heat-regulating function is probably slight.

Lacking rational units of "amounts" of hairy or feathery covering, *wool weight, feather weight,* and also *feather number* were related to *body weight* and also to *surface area* by the logarithmic equation $Y = aX^n$ and the values of the slopes, n, investigated.

In *yearling* Shropshire sheep, wool weight is practically proportional to surface area. We assumed with Ritzman and Colovos that the surface area of yearling sheep varies with the 0.52 power of body weight and we found that the wool weight varies with the 0.518 power of body weight, so that the ratio $\frac{\text{wool weight}}{\text{surface area}}$ is independent of body weight.

However, in another group of *yearling* sheep composed of averages of 3 breeds (Dorsets, Hampshires, Southdowns) the wool weight increased not with the 0.52 power, but with the 0.46 power.

There were not enough data for relating wool weight to body weight for each subsequent year separately; all the data following the yearling stage were therefore combined into one, "adult", stage. In adult sheep, the surface area was assumed to increase with the 0.556 power of body weight while the wool weight increased with the 0.40 power in the case of Shropshires, and with the 0.47 power in the case of the average of the other three breeds. In other words, the larger animals had less wool per unit area than the small. There is, however, the possibility that the apparently smaller wool per unit area in large animals as compared to small is due to a differential age effect on body weight and wool production: while the body weight increases up to 4 years of age the wool weight appeared to remain at nearly the same level between ages 1 and 4 years.

Unlike wool weight, feather weight is practically directly proportional to body weight. Feather *number* on the other hand, increases less rapidly than surface area with increasing body weight. Feather weight increases with the 1st power of body weight, while feather number increases approximately with the 0.2 power of body weight. Increasing body weight by 100% increases feather *weight* by near 100% (90 to 100%) and feather *number* by only 14% (11 to 17%).

In other words, the ratio $\frac{\text{feather number}}{\text{surface area}}$ decreases rapidly with increasing body weight, while the ratio $\frac{\text{feather weight}}{\text{surface area}}$ increases with increasing body weight.

The significance of the above results will remain uncertain until a "physiologic unit" of wool or feather is discovered. The fact that feather *number* and feather *weight* increase at such widely different relative rates (0.2 and 1.0 power of body weight) suggests that probably neither feather *number* nor feather *weight* is a satisfactory index of insulating or thermoregulatory capacity of feathers, and that a mechanical necessity enters the observed relationships. Thus the weight of the supporting quill must, for mechanical reasons, increase more rapidly than the weight of the insulating waynes. These mechanical reasons may be inferred from Thompson's discussion of such problems[12] as the "comparative *anatomy* of bridges", the "principle of similitude", and of such questions as to why the ostrich or moa can not fly, and why a flea can jump so much higher in *comparison to body weight* than can an elephant. These are problems in strength of materials and related aspects of constructional engineering as they occur in the animal body.

[12]Thompson, D'Arcy W., Growth and Form, Cambridge, 1917.

V. APPENDIX: PREDICTION TABLES AND DATA

The following tables present prediction values for 1) wool weight from body weight; 2) feather weight and feather number from body weight. The wool and feather data are presented for convenient body-weight intervals of the animals as computed from the corresponding equations fitted to by the method of least squares to the weighted data.

TABLE 1.—PREDICTING WOOL WEIGHT FROM BODY WEIGHT.

Wool Production: pounds per head and per 100 lbs. live weight—Females

	Yearlings				Over one year					
	(1) Shropshires		(2) Av. of Hampshires, Southdown & Dorsets		(3) Shropshires		(4) Av. of Hampshires, Southdown and Dorsets		Joseph's grade fine wool ewes 3 years and over	
Live Weight lbs.	per head	per 100 lbs.	per head	per 100 lbs.	per head	per 100 lbs.	per head	per 100 lbs.	per head	per 100 lbs.
70	6.7	9.6	5.6	8.0	6.3	9.0	4.7	6.7	7.3	10.4
80	7.2	9.0	6.0	7.5	6.6	8.3	5.0	6.3	7.7	9.6
90	7.7	8.6	6.3	7.0	6.9	7.7	5.3	5.9	8.0	8.9
100	8.1	8.1	6.7	6.7	7.2	7.2	5.6	5.6	8.4	8.4
110	8.5	7.7	7.0	6.4	7.5	6.8	5.9	5.4	8.7	7.9
120	8.9	7.4	7.2	6.0	7.8	6.5	6.1	5.1	9.0	7.5
130	9.3	7.2	7.5	5.8	8.0	6.2	6.3	4.8	9.3	7.2
140	9.6	6.9	7.8	5.6	8.3	5.9	6.6	4.7	9.5	6.8
150	10.0	6.7	8.0	5.3	8.5	5.7	6.8	4.5	9.8	6.5
160	10.3	6.4	8.3	5.2	8.7	5.4	7.0	4.4	10.1	6.3
170	10.7	6.3	8.5	5.0	8.9	5.2	7.2	4.2	10.3	6.1
180	11.0	6.1	8.7	4.8	9.1	5.1	7.4	4.1	10.5	5.8
190	11.3	5.9	8.9	4.7	9.3	4.9	7.6	4.0	10.7	5.6
200	11.6	5.8	9.2	4.6	9.5	4.8	7.8	3.9	11.0	5.5
210	11.9	5.7	9.4	4.5	9.7	4.6	8.0	3.8	11.2	5.3
220	12.2	5.5	9.6	4.4	9.9	4.5	8.1	3.7	11.4	5.2
230	12.5	5.4	9.8	4.3	10.1	4.4	8.3	3.6	11.6	5.0
240	12.7	5.3	10.0	4.2	10.3	4.3	8.5	3.5	11.8	4.9
250	13.0	5.2	10.1	4.0	10.4	4.2	8.6	3.4	11.9	4.8

(1) Computed from equation $Y = .745\ X^{.518}$ and $\frac{100\ Y}{X} = 74.5\ X^{-0.482}$

(2) " " " $Y = .796\ X^{.461}$ and $\frac{100\ Y}{X} = 79.6\ X^{-0.539}$

(3) " " " $Y = 1.14\ X^{.401}$ and $\frac{100\ Y}{X} = 114\ X^{-0.599}$

(4) " " " $Y = .638\ X^{.472}$ and $\frac{100\ Y}{X} = 63.8\ X^{-0.528}$

(5) " " " $Y = 1.41\ X^{0.387}$ and $\frac{100\ Y}{X} = 141\ X^{-0.613}$

TABLE 2.—PREDICTING FEATHER WEIGHT AND FEATHER NUMBER FROM BODY WEIGHT.

PASSERINE BIRDS

Body Wt. gms.	Feather weight grams		Feather number		Feather number per sq. cm. surface area		Feather weight per sq. cm. surface area	
	Males (1)	Females (2)	Males (3)	Females (4)	Males (5)	Females (6)	Males (7)	Females (8)
2	0.1198	0.1426	959	1087	60.2	68.2	0.0075	0.0090
3	0.1796	0.2080	1049	1157	50.1	55.2	0.0085	0.0100
4	0.2394	0.2719	1118	1209	44.1	47.6	0.0094	0.0108
5	0.2991	0.3347	1175	1251	39.8	42.3	0.0100	0.0114
6	0.3588	0.3967	1224	1286	36.7	38.5	0.0106	0.0120
7	0.4184	0.4578	1266	1317	34.2	35.6	0.0112	0.0124
8	0.4781	0.5184	1305	1344	32.2	33.2	0.0117	0.0129
9	0.5376	0.5784	1339	1369	30.8	31.2	0.0121	0.0133
10	0.5973	0.6381	1371	1391	29.2	29.5	0.0125	0.0136
12	0.7165	0.7562	1427	1430	26.9	26.9	0.0133	0.0143
14	0.8356	0.8740	1477	1464	25.1	24.8	0.0140	0.0149
16	0.9548	0.9884	1522	1495	23.6	23.1	0.0146	0.0154
18	1.074	1.103	1562	1522	22.4	21.8	0.0151	0.0159
20	1.193	1.217	1599	1547	21.4	20.6	0.0157	0.0163
22	1.312	1.329	1633	1569	20.5	19.6	0.0161	0.0168
24	1.431	1.442	1665	1590	19.7	18.7	0.0166	0.0171
26	1.550	1.553	1695	1610	19.0	18.0	0.0170	0.0175
28	1.669	1.664	1723	1628	18.4	17.3	0.0174	0.0178
30	1.788	1.775	1749	1645	17.8	16.7	0.0178	0.0182
40	2.383	2.320	1865	1720	15.6	14.4	0.0195	0.0196
50	2.977	2.855	1959	1779	14.1	12.8	0.0210	0.0207
60	3.571	3.384	2040	1830	13.0	11.6	0.0222	0.0217
70	4.165	3.906	2111	1873	12.2	10.7	0.0234	0.0226
80	4.769	4.423	2175	1912	11.4	10.0	0.0244	0.0234
90	5.352	4.935	2232	1947	10.9	9.4	0.0253	0.0241
100	5.946	5.444	2285	1978	10.3	8.9	0.0262	0.0248
110	6.54	5.95	2334	2007	9.9	8.5	0.0270	0.0255
120	7.13	6.45	2380	2034	9.5	8.1	0.0278	0.0260
130	7.72	6.95	2422	2059	9.2	7.8	0.0285	0.0266
140	8.32		2463		8.9		0.0292	
160	9.50		2537		8.4		0.0304	
180	10.69		2604		7.9		0.0316	
200	11.87		2666		7.6		0.0327	

TABLE 2.—PREDICTING FEATHER WEIGHT AND FEATHER NUMBER FROM BODY WEIGHT.—(CONTINUED)

DOMESTIC FOWLS DURING GROWTH

Body	Feather weight, gms. Leghorns		Feather weight, gms./bird White Plymouth Rocks			Feather wt., gms./sq. cm. surface area White Leghorns		Feather wt., gms./sq. cm. surface area White Plymouth Rocks		
Wt.	Males	Females	Males	Females	Capons	Males	Females	Males	Females	Capons
gms.	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)
200	11.9	15.3	6.9	13.2	12.8	.0338	.0441	.0199	.0383	.0366
300	18.9	22.9	11.6	20.4	19.7	.0409	.0503	.0254	.0450	.0431
400	26.3	30.5	16.7	27.8	26.8	.0468	.0551	.0302	.0505	.0483
500	33.9	38.0	22.2	35.3	35.0	.0520	.0592	.0346	.0553	.0529
600	41.7	45.5	28.0	42.9	41.3	.0566	.0627	0386	.0594	.0569
700	49.7	53.0	34.1	50.6	48.7	.0609	.0659	.0423	.0632	.0605
800	57.9	60.5	40.4	58.4	56.2	.0648	.0688	.0458	.0667	.0638
900	66.2	68.0	46.9	66.2	63.8	.0685	.0714	0492	.0699	.0669
1000	74.7	75.5	53.6	74.1	71.4	.0720	.0739	.0524	.0729	.0697
1200	92.0	90.4	67.6	90.1	86.7	.0784	.0783	.0584	.0784	.0750
1400	109	105	82.2	106	102	.0832	.0823	.0641	.0834	.0798
1600	128	120	96.2	123	118	.0898	.0859	.0694	.0880	.0842
1800	146	135	113	139	134	.0949	.0892	.0745	.0922	.0882
2000	165	150	129	156	150	.0985	.0922	.0794	.0962	.0910
2200	184	165	146	172	166	.1043	.0951	.0840	.0999	.0956
2400	203	180	163	189	182	.1086	.0978	.0886	.1035	.0990
2600	222	194	180	206	198	.1128	.1003	.0929	.1069	.1022
2800	242		198		215	.1168	.1027	.0971	.1101	.1053
3000	261		216		231	.1206	.1050	.1012	.1132	.1082
3500	312		263		273	.1297	.1103	.1111	.1204	.1151

TABLE 2.—PREDICTING FEATHER WEIGHT AND FEATHER NUMBER FROM BODY WEIGHT.—(CONTINUED)

PIGEONS AND DOVES

Body Wt. gms.	Feather Weight, gms. Per Bird (19)	Per Sq. cm. Surface Area (20)
100	8.8	.0404
110	9.6	.0413
120	10.4	.0421
130	11.2	.0429
140	12.0	.0436
160	13.5	.0450
180	15.0	.0462
200	16.5	.0474
300	23.7	.0520
400	30.8	.0555
500	37.6	.0585
600	44.3	.0610

GEESE

Body Wt. gms.	Feather Weight, gms. Per Bird (21)	Per Sq. cm. Surface Area (22)
1600	107.1	.0764
1800	119.1	.0785
2000	130.9	.0804
2200	142.6	.0822
2400	154.3	.0839
2600	165.8	.0854
2800	177.2	.0869
3000	188.6	.0883
3500	216.7	.0915
4000	244.3	.0943
4500	271.6	.0969
5000	298.7	.0993
5500	325.4	.1015
6000	352.0	.1035

Computed from the following equations:

(1) $F = .06\ M^{.998}$

(2) $F = .0748\ M^{.931}$

(3) $N = 822.1\ M^{.222}$

(4) $N = 977.9\ M^{.153}$

(5) $\frac{N}{A} = 82.2\ M^{-.45}$

(6) $\frac{N}{A} = 97.8\ M^{-.52}$

(7) $\frac{F}{A} = .006\ M^{.32}$

(8) $\frac{F}{A} = .0075\ M^{.26}$

(9) $F = .0284\ M^{1.14}$

(10) $F = .0809\ M^{.99}$

(11) $F = .0083\ M^{1.27}$

(12) $F = .0457\ M^{1.07}$

(13) $F = .044\ M^{1.07}$

(14) $\frac{F}{A} = .0028\ M^{.47}$

(15) $\frac{F}{A} = .0081\ M^{.32}$

(16) $\frac{F}{A} = .00083\ M^{.6}$

(17) $\frac{F}{A} = .0046\ M^{.4}$

(18) $\frac{F}{A} = .0044\ M^{.4}$

(19 & 21) $F = .14\ M^{.9}$

(20 & 22) $\frac{F}{A} = .014\ M^{.23}$