During the past 25 years much attention has been given to methods of estimating the chemical composition of the body, especially in the living animal. The methods to be examined in this report have seemed, at least until recently, to have potential utility. The degree of validity of the following methods has been appraised in comparisons with body composition determined by direct chemical analysis: (a) antipyrine (AP), (b) N-acetyl-4 aminoantipyrine (NAAP), (c) urinary creatinine excretion rate, (d) tritium (TOH) dilution, (e) deuterium (D₂O) dilution, (f) body density, and (g) potassium. As a further index of the validity of these methods, the extent to which they improve upon the estimation of body composition from body weight alone has been determined.

In many studies of indirect methods, a correlation coefficient (r) of 0.9 or higher between the estimated and measured components has been tacitly accepted as an index of the validity of a method. However, a conclusion based on this criterion alone can be a delusion. In some instances in which the "r" value has met this standard, the coefficient of variation (C.V.) between the measured and estimated component has exceeded 10%. In fact, in some of the same instances, body weight alone has been a more effective predictor of body composition than has the indirect method being studied.

Most of the pigs, sheep and cattle used for meat in the United States are slaughtered while they are somewhat immature and following a management scheme that results in rapid growth. Body composition of immature animals is much more rigidly associated with linear body size than is that of mature animals (47). As will be documented in this report, some indirect methods do not result in an improvement in the precision with which body composition is predicted over that from body weight alone (3). In some experimental situations or for certain purposes, the additional precision provided by certain indirect methods may not be sufficiently greater to warrant the expense. For these reasons, some attention will be given in this report to the relationships between body weight and the...
weight of chemical components or of the physically separated parts of the body, especially from the standpoint of application to the usual meat animal, i.e., the relatively immature animal.

Premises on Which Indirect Methods are Based

In general, indirect methods are employed to estimate the concentration or weight of one chemical component (e.g., water or fat) from which the amounts of the other components are derived. Thus, the inherent assumption in the application of an indirect method is that the quantities of the chemical components of the body are predictively interrelated and that the total composition of the body can be resolved from the knowledge of the amount of either water or fat.

Recently it was established by employing the data obtained with large populations of pigs, sheep and cattle that the within-species coefficient of variation between the fat concentration determined by direct chemical analysis and that predicted from the concentration of water in the body is of the order of 3 to 7% (47). For the same populations, the intra-species protein concentration in the fat-free, dry matter was found to be constant, with C.V. values between 2.1 and 2.8%. Although these relationships are different for the three species, they do not vary with breed or sex within species (47). Thus, if either the concentration of water or of fat can be estimated accurately by an indirect method, the total proximate chemical composition of the body can be resolved.

Another premise sometimes applied when an indirect method (especially density or specific gravity) is employed is that the composition of the fat-free body is constant and known. Although values have been determined for a number of animal species, the value most commonly employed is 72.4% as derived for headless, eviscerated, depilated guinea pigs by Pace and Rathbun (40).

The following table summarizes the mean and range of water concentration in the fat-free body which we have determined or computed from the data reported by other workers for four species of animals. Not only is the water concentration different among species, but the concentration within species decreases markedly as the fat concentration in the whole animal increases.

Table 1. Concentration of Water in the Fat-free Body of Animals.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of animals</th>
<th>Range in total body fat (%)</th>
<th>Water (%) in fat-free body</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
<td></td>
</tr>
<tr>
<td>Guinea Pig</td>
<td>32</td>
<td>0.9 to 15.0</td>
<td>73.6</td>
</tr>
<tr>
<td>Pig</td>
<td>714</td>
<td>1.0 to 61.5</td>
<td>77.0</td>
</tr>
<tr>
<td>Sheep</td>
<td>300</td>
<td>4.1 to 47.7</td>
<td>74.9</td>
</tr>
<tr>
<td>Cattle</td>
<td>256</td>
<td>1.8 to 44.6</td>
<td>72.9</td>
</tr>
</tbody>
</table>
A premise on which certain methods of estimating body water is based is that the luminal water of the gastrointestinal tract is either nil or at least estimable. Naturally, the problem involving luminal water is greater in ruminants than in simple-gutted animals. However, as has been shown by Panaretto (42) and Panaretto and Till (43) using the tritium dilution method and by Besadaoun et al. (3) using various other methods, it is possible to predict the empty-body water from dilution spaces in the whole body (including gut water).

Results Obtained with Various Methods

Antipyrine (AP), N-acetyl-4-aminoantipyrine (NAAP) and Creatinine Excretion. Certain features of body composition were determined simultaneously by means of these three methods (3). Body composition estimated by these methods was compared with that determined directly in 125 sheep representing the range of composition shown in Table 2.

Table 2. Composition of 125 Sheep

<table>
<thead>
<tr>
<th>Constituents</th>
<th>Concentration (%)</th>
<th>Components (Kg.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>Water</td>
<td>60.0</td>
<td>39.6 to 73.9</td>
</tr>
<tr>
<td>Fat</td>
<td>19.8</td>
<td>4.1 to 46.6</td>
</tr>
<tr>
<td>Protein</td>
<td>16.0</td>
<td>11.2 to 19.2</td>
</tr>
<tr>
<td>Ash</td>
<td>4.0</td>
<td>1.7 to 5.8</td>
</tr>
</tbody>
</table>

1/ Data expressed on ingesta-free, wool-free basis.

Table 3 summarizes some statistics reflecting the predictability of body water by the AP, NAAP, and urinary-creatinine methods. These data indicate that 88 to 93% of the variability in body water is associated with the variability in the AP or NAAP space or in the urinary output of creatinine. However, in this population of sheep, shrunk body weight (SBW) alone as a linear predictor was more effective (C.V. = 7.0%).

It was noted (47) that the weights of the chemical components in bodies of sheep increase linearly as body weight increases until the concentration of fat in the body exceeds approximately 31%. Above this concentration, the weights of chemical components increase as a curvilinear function of body weight. When the data for 29 sheep containing more than 31% of fat were excluded from the population, the C.V. between the measured body water and the body water predicted from linear SBW was reduced appreciably (i.e., to 5.1%).

A marked improvement in the use of body weight as a predictor resulted from $\log_{10}: \log_{10}$ transformations (viz., $Y = a X^b$). As shown in Table 3, the logarithm of the weight of water was highly predictable from
the logarithm of the empty-body weight (EBW). The C.V. between the body water so predicted and the measured water content was only 2.5%.

These data show that the AP and NAAP spaces and the creatinine-excretion rate are only mediocre predictors of body composition, with the latter method having an advantage over linear body weight as a predictor only in very fat (i.e. above 31% fat) animals. These data also indicate that body weight alone can be an effective predictor of body composition in those species for which body composition-body weight relationships have been quantified and for which the knowledge of the biology of body composition is well developed.

Table 3. Estimation of Body Water in Sheep.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>r²</th>
<th>C.V. ²/</th>
</tr>
</thead>
<tbody>
<tr>
<td>AP space</td>
<td>0.884</td>
<td>9.6</td>
</tr>
<tr>
<td>NAAP space</td>
<td>0.908</td>
<td>8.5</td>
</tr>
<tr>
<td>Creatinine output</td>
<td>0.931</td>
<td>7.4</td>
</tr>
<tr>
<td>Linear SEBW ³/ (4.1 to 46.6% Fat)</td>
<td>0.939</td>
<td>7.0</td>
</tr>
<tr>
<td>Linear SEBW ³/ (4.1 to 31.0% Fat)</td>
<td>0.947</td>
<td>5.1</td>
</tr>
<tr>
<td>Log EBW ⁴/ (4.1 to 46.6% Fat)</td>
<td>0.951</td>
<td>2.5</td>
</tr>
</tbody>
</table>

1/ Where the predictand is body water determined by desiccation.
2/ C.V. = coefficient of variation between volume of body water determined by desiccation and that estimated by indirect means.
3/ SEBW = shrunk body weight employed in a linear relationship.

In the present studies most of the sheep were immature and would qualify for common use in the meat trade. However, the populations studied did include other sheep as old as 895 days and weighing as much as 150 lbs. empty. Also, the sheep in these studies were wethers.

In subsequent work with sheep, we have observed that the Southdown intact female contains 30 to 35% more fat than the intact male at any body weight, ranging from 10 to 50 kg. The intact males contained somewhat more water and protein than the intact females of the same breed. Thus, the equations we have developed for the prediction of body composition in the wether (See Table 4) do not apply to the intact female or male. The equations in Table 4 represent 221 wethers of 6 breed populations. However, we have observed decided breed differences in body composition (47). Southdowns, Shropshires and Corriedales contain more fat and energy and less protein and water at the same body weights than the other breeds studied. Suffolks, on the other hand, contained more water and protein and less fat
and energy than the other sheep, while Hampshires and two crossbred populations (Rambouillet x Columbia and Hampshire x Suffolk x Shropshire) were intermediate in composition.

Table 4. Some General Relationships between the Body Composition and Body Weight of Sheep.

<table>
<thead>
<tr>
<th>Component</th>
<th>Prediction equation</th>
<th>Correlation coefficient</th>
<th>Sy [\times] x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water</td>
<td>[Y = 0.73976 \times X + 0.15466]</td>
<td>0.975</td>
<td>2.22</td>
</tr>
<tr>
<td>Protein</td>
<td>[Y = 0.80148 \times X - 0.50283]</td>
<td>0.974</td>
<td>4.55</td>
</tr>
<tr>
<td>Energy</td>
<td>[Y = 1.58937 \times X - 0.43499]</td>
<td>0.970</td>
<td>3.45</td>
</tr>
</tbody>
</table>

\[1/\] Based on composition of 221 sheep representing 6 breed populations; 
\[Y = \log\] component (kg. or Meal.) and \[X = \log\] EBW (Kg.).

Later in this report body composition - body weight relationships will be considered in further detail.

Carcass density and body composition. The oldest and perhaps the most widely used indirect method of estimating body composition is the density or specific gravity method. These methods are based on the considerable differential in density between the body fat and lean portions. As applied to meat-producing animals, the concentration of fat is usually predicted from the specific gravity of the carcass determined by weighing in water and in air. (For historical details and for an account of the variety of methods employed to determine density or specific gravity the reader's attention is called to the reports of Pearson (44) and Garrett (12)).

Some of the statistics derived from the data obtained in various studies of pigs, sheep and cattle in which the concentration of fat in the carcass was regressed on the specific gravity of the carcass, are summarized in Table 5. Some of these data were tabulated by Garrett (12) and others were computed by us from the data reported by various workers.

It will be noted in Table 5 that the regression coefficients for sheep vary considerably from study to study. Also, the coefficient of variation between the measured fat percentage and the fat percentage predicted from specific gravity in sheep is of the general order of 10 to 11%. Despite giving careful attention to controlling the temperature of the immersion water, to the removal of the pelt without forming air pockets in the fascia, and to spraying the carcass surfaces with a mono-molecular film of silicone to prevent the formation of air bubbles, we obtained data with sheep carcasses that were only slightly more organized than a random arrangement. The data summarized in Table 5 indicate that specific gravity is decidedly inferior to body weight as a predictor of body composition in sheep (See Table 3).
Table 5. Relationships between Carcass Fat (%) and Specific Gravity.

<table>
<thead>
<tr>
<th>No. of animals</th>
<th>Range in Fat (%)</th>
<th>Slope</th>
<th>$R^2$ (%)</th>
<th>C.V. (%)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>SHEEP</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>57</td>
<td>7.1 - 61.7</td>
<td>0.78</td>
<td>11.0</td>
<td>0.79</td>
<td>Kirton &amp; Barton (30)</td>
</tr>
<tr>
<td>20</td>
<td>14.3 - 37.5</td>
<td>0.81</td>
<td>11.1</td>
<td>0.79</td>
<td>Garrett et al. (13)</td>
</tr>
<tr>
<td>29</td>
<td>15.2 - 32.0</td>
<td>0.71</td>
<td>10.2</td>
<td>0.71</td>
<td>Meyer (36)</td>
</tr>
<tr>
<td>20</td>
<td>25.2 - 40.6</td>
<td>0.31</td>
<td>10.2</td>
<td>0.31</td>
<td>Kirton &amp; Barton (31)</td>
</tr>
<tr>
<td>30</td>
<td>15.6 - 37.9</td>
<td>0.79</td>
<td>13.0</td>
<td>0.79</td>
<td>Spurlock &amp; Bradford (48)</td>
</tr>
<tr>
<td>65</td>
<td>34.1 - 40.0</td>
<td>0.24</td>
<td>10.3</td>
<td>0.24</td>
<td>Field et al. (9)</td>
</tr>
<tr>
<td>35</td>
<td>14.2 - 49.6</td>
<td>0.90</td>
<td>7.6</td>
<td>0.90</td>
<td>Garrett (12)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CATTLE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>48</td>
<td>15.1 - 38.8</td>
<td>-530.4</td>
<td>0.90</td>
<td>7.0</td>
<td>Garrett (12)</td>
</tr>
<tr>
<td>51</td>
<td>13.6 - 39.6</td>
<td>-425.1</td>
<td>0.91</td>
<td>6.0</td>
<td>Guenther et al. (20)</td>
</tr>
<tr>
<td>56</td>
<td>2.5 - 9.9%</td>
<td>-127.4</td>
<td>0.21</td>
<td>41.8</td>
<td>Kelly et al. (28)</td>
</tr>
<tr>
<td>57</td>
<td>10.0 - 19.9%</td>
<td>-53.8</td>
<td>0.04</td>
<td>18.5</td>
<td>&quot;</td>
</tr>
<tr>
<td>35</td>
<td>20.0 - 29.9%</td>
<td>-276.2</td>
<td>0.32</td>
<td>10.7</td>
<td>&quot;</td>
</tr>
<tr>
<td>20</td>
<td>30.0 - 39.9%</td>
<td>-181.2</td>
<td>0.25</td>
<td>7.1</td>
<td>&quot;</td>
</tr>
<tr>
<td>5</td>
<td>40.0 - 49.9%</td>
<td>-302.7</td>
<td>0.62</td>
<td>5.9</td>
<td>&quot;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PIGS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>66</td>
<td>54.6 - 4.1</td>
<td>0.56</td>
<td>Brown et al. (5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>332</td>
<td>30.6 - 47.2</td>
<td>0.75</td>
<td>Whiteman et al. (21)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>35.8 - 48.9</td>
<td>0.85</td>
<td>Hornick (29)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>40.4 - 4.7</td>
<td>0.90</td>
<td>2.6</td>
<td>Dornenbal et al. (7)</td>
<td></td>
</tr>
<tr>
<td>52</td>
<td>36.9 - 5.9</td>
<td>0.90</td>
<td>4.7</td>
<td>&quot;</td>
<td></td>
</tr>
<tr>
<td>42</td>
<td>35.5 - 4.4</td>
<td>0.90</td>
<td>3.5</td>
<td>Jöcklin (29)</td>
<td></td>
</tr>
<tr>
<td>64</td>
<td>35.0 - 4.4</td>
<td>0.85</td>
<td>5.0</td>
<td>&quot;</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>33.2 - 50.3</td>
<td>0.90</td>
<td>4.0</td>
<td>Hintz (21)</td>
<td></td>
</tr>
<tr>
<td>Composite 4/</td>
<td>40</td>
<td>613.5</td>
<td>4.3</td>
<td>Garrett (12)</td>
<td></td>
</tr>
</tbody>
</table>

1/ Dissectable fat in half-carcass.

2/ Separable fat based on physical analysis of 9-11 rib cut and the use of Hopper's (24) equations to estimate carcass fat.

3/ Fat based on chemical analysis of meat (lean + fat), but does not include bone.

4/ Excluding data of Dornenbal et al. (7) and those for Adam and Smith's 24 pigs (1) for which a slope of -237.4 was computed.
Relatively few studies have been made with cattle of the validity of the specific gravity method as determined in a half or whole carcass. The data of Kraybill et al. (32) are based on the fat concentration of the carcass as estimated from the amount of fat separated from 9-11 rib cut and converted by means of Hopper's equations (24).

Although bone fat was not included in the fat concentration that was regressed on specific gravity in the experiments of Kelly et al. (28), these studies appear to be the most extensive ones conducted to date. They studied the carcasses of 156 steers which had been exposed to various nutritional regimens for various periods of time and were killed at various ages. During each of two years, steer calves were begun in drylot where they were provided one of four energy levels. Some steers were slaughtered at the beginning and others after they had been on the various regimens for 5, 10, 16, or 23 months. Some animals were put on pasture after they had been on one of the drylot regimens for 5 or 17 months, and then slaughtered at the end of the grazing season. As a consequence, the meat separated from bone contained from 2.5 to 50% of fat.

Kelly et al. (28) found that the predictability of fat from specific gravity determined in 128 carcasses in which the meat contained less than 30% of fat was very low (C.V. ranging from 10.7 to 41.8% for various fat levels). When the fat concentration of the meat ranged from 30 to 50%, the coefficient of variation between the measured and estimated fat concentrations was less than 10.7%, reaching 3.9% when the fat concentration was 40 to 50%.

Based on additional data provided to us by the Virginia workers (Fontenot, personal communication), we have examined the relationships between carcass weight and the weights of protein and fat in the carcass meat of the same groups of animals employed in their study of the specific gravity method. These calculations resulted in the statistics shown in Table 6.

Table 6. Relationship between Carcass Weight and Weights of Protein and Fat in Carcass Meat of Cattle.

<table>
<thead>
<tr>
<th>Predictand</th>
<th>Prediction equations 1/</th>
<th>( R^2 )</th>
<th>C.V. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein</td>
<td>( Y = 0.835483 X - 0.435439 )</td>
<td>0.977</td>
<td>1.26</td>
</tr>
<tr>
<td>Fat 2/</td>
<td>( Y = 2.907194 X - 5.948013 )</td>
<td>0.931</td>
<td>8.13</td>
</tr>
<tr>
<td>Fat 3/</td>
<td>( Y = 2.487151 X - 4.730833 )</td>
<td>0.956</td>
<td>4.35</td>
</tr>
</tbody>
</table>

1/ \( Y = \log \) protein or fat (in pounds) and \( X = \log \) carcass weight (in pounds).
2/ Data represent all 24 groups of cattle, irrespective of fat concentration.
3/ Data represent the 20 groups of cattle whose carcass meat contained more than 5.5% of fat, as the group average.
The data in Tables 5 and 6 show that the coefficient of variation between the measured and estimated fat was lower for the total population when the predictor was carcass weight than when it was specific gravity of the carcass. Table 6 contains data for two populations in which fat is the predictand. A plot of the data showed that 4 groups of the animals, all fed the lowest energy level, contained somewhat less of fat per unit of carcass weight than the other 20 groups. These 4 groups accounted for almost half of the total variation in fat weight associated with carcass weight. It will be recalled that Kelly et al. (28) observed a coefficient of variation of 41.8% between the measured fat concentration and the fat concentration predicted from specific gravity in carcasses containing less than 9.99% of fat.

In other studies (4, 6, 39) involving certain carcass parts, such as specific muscle or cut or ground samples of certain carcass cuts, specific gravity has been only a mediocre predictor of the fat concentration. Most of the $R^2$ values were between 0.55 and 0.65, with an overall range of 0.12 to 0.85.

On the other hand, Guenther et al. (20) reported data which gave an $R^2$ value of 0.86 between carcass fat determined chemically and carcass fat estimated from specific gravity. Garrett (12) also estimated carcass fat reasonably accurately in 48 steers by means of body density. The $R^2$ value was 0.92 and the coefficient of variation between the measured and estimated concentration of fat was 7.0% (Table 5).

However, the degree of success, experienced to date in the use of specific gravity to estimate the fatness of the carcass or of its parts in cattle, has been variable. The majority of the data reported indicate that specific gravity measurements do not improve upon the accuracy of body fat estimates made from body weight alone in this species. Future technical refinements may improve the prediction value of the method.

Specific gravity of the carcass has been a much more effective predictor of fatness in the pig than in cattle or sheep. As shown in Table 5, 85 to 90% of the variation in the fat concentration of pigs is consistently associated with the variation in specific gravity, and the coefficient of variation between the measured and estimated (specific gravity) fat concentration is of the order of 4 to 5%. However, in one study (27) of 8 male and 8 female pigs killed at body weights of 27, 55, and 90 kg., the correlation coefficient between the fat content and body density was only - 0.57. In 11 of the same pigs body water was accurately estimated from the tritium-dilution space.

Although no comparisons were made between specific gravity and the body or carcass weights as fat predictors, it seems unlikely that the latter criteria would be superior to specific gravity as a predictor of fatness in the pig.
Although, at the present time, the specific gravity method must be applied to the carcass, eventually methods for the measurement of body density by other means may evolve to permit measurements to be made in the living animal. Air and water displacement and helium dilution techniques for the determination of density or specific gravity of living animals have been explored (2, 11, 17, 22, 23, 34). Despite certain recent modifications in technique, very poor results have been obtained. Thus, at the present time when the experimenter uses specific gravity for this purpose, he ends up with a slaughtered animal and this constitutes a major defect of the method for many pursuits (e.g., certain kinds of genetic research).

Potassium. Underlying the use of potassium, whether by the whole-body counting of K\(^{40}\) emissions or by the use of the short-half life isotope, K\(^{42}\), is the assumption that all of the potassium is located within the cells. Since almost all cells contribute to the lean-body mass, it is assumed that potassium is highly related to the protein mass and to intracellular water and other features of body composition.

Although Pfau and Kallistratos (45) observed that the potassium content of the fat-free, dry matter was essentially the same in all muscles of the one pig they studied, others have found marked inter-muscle differences in the potassium content. That the potassium content is variable was shown in pigs by Lawrie and Pomeroy (33) and by Gillett et al. (15); in man by Flear et al. (10); in cattle by Gillett et al. (14); and in sheep by Gillett et al. (16). Even the potassium content per unit of protein in the muscles of cattle varied significantly, according to the latter workers (14). The variation observed constitutes a potential source of error in the use of K\(^{40}\) as an index of body composition.

It is not the intent in the present report to deal with the merits and disadvantages of the indirect methods based upon potassium. Rather, it is our objective to report on an experiment (3) in which we determined the theoretical limit of accuracy in the prediction of body protein from total body potassium.

In this experiment 46 sheep fed a variety of diets and ranging in body-fat concentration from 4.1 to 36.8%, were employed. The total body minus ingesta and wool was minced and homogenized 6 times and 4 subsamples representing 15 to 25% of the total mass were freeze-dried. Subsequently the freeze-dried matter was ground with dry ice to form a finely pulverized sample. For each sheep, 4 replicates were analyzed for protein and 8 replicates were analyzed for potassium, the latter by means of atomic absorption spectrometry. As shown in Table 7, neither the predictor (potassium) nor the predictand (protein) is determined without error.

<table>
<thead>
<tr>
<th>Body constituent</th>
<th>Replicates</th>
<th>C.V. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>Protein</td>
<td>4</td>
<td>0.8</td>
</tr>
<tr>
<td>Potassium</td>
<td>1</td>
<td>7.0</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>2.5</td>
</tr>
</tbody>
</table>

Table 7. Analytical Errors Associated with Protein and Potassium Determinations.
In this population of sheep the mean potassium concentration was 14.22 mg. per gm of protein. The potassium concentration decreased slightly with increasing body size; in 20- to 30- kg. lambs, the concentration was of the order of 14.5 mg./1 gm of protein and in an animal of 73 kg. of body weight, the concentration was about 14.0 mg. For this population, having a considerable range in composition and body size, the correlation coefficient between body potassium and protein was 0.973 and the coefficient of variation between the measured protein and that estimated from body potassium was 5.9%. However, when shrunk (20-hour fast) body weight alone was employed as the predictor, these statistics were 0.976 and 5.5%, respectively.

The variance in body protein and potassium was partitioned into components associated with the variation among sheep and that of the analytical errors of determination. The minimum standard error of estimate associated with the prediction of body protein from potassium was computed after the effect of the analytical errors had been nullified. This value (i.e., $\bar{y}$. $\sigma_x$) provides a measure of the theoretical limit of accuracy in the prediction of protein when body potassium is determined by such a method as whole-body $K^{40}$ counting. Using the variance components computed, the correlation coefficient between protein and potassium and the standard error of estimate of protein were expressed as a function of the number of replicates analyzed for potassium and protein. When 4 replicates were analyzed for protein and the number of potassium replicates was increased, the asymptotic standard error of estimate was found to be 310 gm of protein. For this population, the coefficient of variation between the measured protein content of the body and that predicted from body potassium was 5.4%. This is the limit of accuracy that can be achieved when body potassium is determined by an indirect method. (The asymptotic correlation coefficient between body potassium and protein was 0.977.) Thus, since analytical errors are additional to the minimum error measured in this study, it remains to be determined to what extent, if any, the methods based on body potassium will improve upon the estimation of body composition in immature animals conventionally employed as meat producers.

**Hydrogen Isotopes (Tritium and Deuterium).** Of all indirect methods of estimating body composition, the most effective found to date are those based on tritium and deuterium dilution (18, 27, 42, 43, 47). Both deuterium and tritium distribute into gut luminal water, a defect common to all dilution methods, but one that is more severe in ruminants than in simple-gutted animals because of the volume of gut water. In addition, tritium represents a human health hazard although with present-day counting devices the dose required can be quite small, but the meat of experimental animals cannot be used for human consumption. Deuterium is very expensive, especially in the quantities needed for dosing large animals.

In one experiment (47) with 36 sheep containing from 12 to 38 kg. of total body water (i.e., including gut water), we observed a coefficient of variation of 2.1% between the water volume determined by desiccation and that predicted from the tritium dilution space. The mean overestimation of body water was 2.65%, largely the result of tritium exchanging with hydrogen in non-water substances.
Some of the sheep employed in this study were maintained in a steadily increasing positive energy balance. Another group of sheep were fed a sub-maintenance level of the same diet to result in a mean loss of 0.44 lbs. per day during a 26-day period, at the end of which some of the animals were slaughtered. The remaining sub-maintenance sheep then were fed ad libitum for a subsequent period of 52 days during which the average body weight gain per day was 0.57 lbs. At given body weights, the sheep kept in a state of continuous, positive energy balance contained more fat and less water and protein than the starved-refed sheep. The composition of the sheep which lost an average of 0.44 lbs. per day resembled that of sheep of the same body size, but steadily gaining energy.

These observations indicate that a prolonged submaintenance intake of energy followed by ad libitum feeding deranged the composition of the body. Of many greatly different dietary treatments that we have imposed on sheep, this is the only one we have encountered to date that disturbs the mass-related homeostatic nature of body composition in sheep, as described by the equations in Table 4 for animals kept continuously in positive energy balance. Obviously in this experiment, body weight was an inadequate predictor of body composition and decidedly inferior to tritium dilution.

In a subsequent experiment with sheep for which the data are not yet completely analyzed, the results we have obtained appear to be considerably inferior to those obtained in the first experiment, however.

Groves and Wood (18), employing the deuterium dilution method in pigs weighing 2 to 48 lbs., found a coefficient of variation of only 4.77% between the water volume determined by desiccation and that predicted from deuterium dilution. The mean underestimation of body water by the indirect method was 1.65% of the measured water volume. These workers determined deuterium by the falling-drop method. Fig. 1 shows the relationship they observed between body water determined by desiccation and that predicted from deuterium dilution, as well as certain related statistics.

Fig. 2 shows the relationship between body water determined by desiccation and the linear body weights of the same population of pigs. Although these were very immature pigs, with the largest weighing only 48 lbs., it is of interest that the coefficient of variation (3.21%) between the water content determined by desiccation and that predicted by body weight was a little less than that (4.77%) between the measured water volume and that predicted from deuterium dilution.

As explained in the "premises of indirect methods", the resolution of the total composition of the body requires the prediction of the other components from the body water estimates derived by either the tritium or deuterium method. Of the indirect methods whose validity has been examined by comparison with direct chemical analysis of the body, the methods based on the use of the hydrogen isotopes are the only ones for which the prediction errors are consistently less than 5%.
Relationship of Body Weight to Body Composition

As an index of animal response to nutritional or other environmental or biological treatments, body weight changes, though greatly used, have been denigrated for many years. However, in our own studies of indirect methods of estimating body composition, we have employed body weight as a "baseline predictor" or as a reference base with which to determine the effectiveness of indirect methods (3).

There are numerous published claims that body composition differences have been effected by certain dietary treatments. In some cases the conclusions have been correct, but in other cases it is clear that the treatments imposed did not affect body composition in a manner that was independent of the effects exerted upon total body mass. In certain cases, animals were fatter and therefore, contained different quantities of other chemical components than the animals to which they were compared, chiefly because they were larger. In such cases, the nutritive effect is one exerted upon total mass and the apparent effect upon composition is coincident to the mass changes. However, it is becoming clear that the body composition of certain species of animals is more pliant to nutritional treatment than is that of others, i.e., body composition yields to changes independently of the changes in body mass.

It is indicated that in future studies of body composition, increased emphasis should be given to body weight as a reference baseline to which various biological things and events might be related (e.g., sex and interspecific peculiarities, and nutritional, other environmental, and hormonal effects). That this approach would be fruitful is borne out by some of the examples cited previously as well as by the subsequent ones in this report. In the remainder of this report, attention will be given to the relationships between certain criteria of body composition (either determined chemically or by physical separation) and a parameter of body size (either body weight or carcass weight).

Pigs. In the very young animal, body composition appears to conform rigidly with body size. An example of this in the pig may be seen in the data of Wood and Groves (55) as summarized in Fig. 3. (Twenty-six of the 37 pigs in this population are the ones these workers employed in their study of the deuterium method.) The Landrace x Yorkshire pigs used in this study consisted of 18 intact males and 19 intact females ranging from 2 to 66 lbs. in body weight. It will be noted that the relationship between the weight of body water and linear body weight was not different for the males and females and that the pooled relationship has a very low error of prediction. (In a study of published data on the chemical composition of 714 pigs representing a variety of breeds and a great range in body size, we (47) noted that intact female pigs contain more fat than male castrates from birth to the time they reach 70 kg., at which body weight, they contain the same amount of fat. Above a body weight of 70 kg. castrate males are fatter than intact females.) Also plotted in Fig. 3 are 5 points, each representing the data for 3 pigs of the Large White x Wessex breeds as reported by Manners and McCrea (35).
The dissection data obtained by the Cambridge school led to various concepts concerning the development of the animal body and especially to the view that the plane of nutrition imposed at certain times influences the development of the various body parts differently depending upon their nutrient priorities and needs and when their greatest growth intensity exists. Studies with the pig contributing to these viewpoints were conducted by McMeekan (38) and Pomeroy (46). As the result of experiments in which he imposed two planes of nutrition until 16 weeks of age and combinations of these (4 to them) from 16 weeks to 200 lbs. body weight, McMeekan concluded that the relative development of different tissues and organs in the pig is greatly influenced by nutritional plane. Wallace (53) who studied the effects of level of nutrition on the growth of sheep, challenged McMeekan's conclusions by suggesting that the apparent differential influence of nutritional level on the relationships within tissues is in fact an artefact resulting from the means of expression. According to Wallace, the proportion of each tissue in the various carcass cuts relative to the total weight of that tissue in each animal in McMeekan's experiments was quite normal and therefore not different in a way attributable to the plane of nutrition imposed at certain times. More recently Elsley et al. (9) reanalyzed the data of McMeekan for pigs and those of Pålsson and Verge (41) for sheep by eliminating the effects of variation in fat content, and concluded that a large part of the apparent differences in body proportions observed by those workers is attributable to the effects of level of nutrition on fat deposition. They (8) demonstrated especially that plane of nutrition did not exert a differential effect on the total weight of bone or of muscle relative to the sum of the total weights of muscle and bone together.

We propose to examine the McMeekan (38) and Pomeroy (46) data from the standpoint of the relationships between the logarithms of the weights of the separated muscle and fat fractions and the logarithm of the empty body weight. Fig. 4 and 5 show the treatments imposed and the slaughter plans of the two studies relative to time and body size. Both workers employed the same highly inbred strain of Large White pigs and the same technicians carried out the dissections. Intermuscular fat was carved away from the muscle; if the fat entered a muscle, it was cut on the same plane as the muscle contour. Pomeroy's experiment (46) involved 5 pigs reared on a high plane of nutrition until they reached an empty body weight of 327 to 331 lbs. At that weight, one pig was slaughtered and the other 4 were given a diet of wheat straw and water. As they lost weight, one-by-one, the pigs were slaughtered.

Fig. 6 and 7 show the log-log relationships between empty body weight and the weight of fat and muscle, respectively. The regression equations were computed from McMeekan's group-average data and the Pomeroy data were merely plotted in the figures. The two most discrepant points for fat (Fig. 6) represent a group of 4-week old pigs reared on the high plane and a group of 16-week old pigs reared on the low plane of nutrition. Approximately 75% of the total variation was contributed by these two values. It will be noted in Fig. 7 that almost all of the variation in the logarithm of muscle weight was ascribable to the variation in the logarithm of the
empty body weight. These observations suggest that plane of nutrition had very little effect upon the amount of fat or muscle that was independent of the effect upon total body mass. It is cautioned that the rates of increase (i.e., the slope) of physically separated fat and muscle should not be interpreted to mean the rates of increase of chemically determined fat and protein, respectively. Since the fat entering muscles was not separated, it is expected that the slope for physically separated fat would be lower than that for chemically determined fat, and the slope for muscle would be greater than that for chemically determined protein.

In a recent experiment conducted by Stant et al. (49), 6 barrows each of Yorkshire x Chester Whites (Y-CW) and of Yorkshire x Durocs (Y-D) were slaughtered at each of four body weights ranging from 23 to 91 kg. All pigs were fed the same diet ad libitum. The carcasses were separated physically into muscle, fat, and bone and these parts after grinding were then analyzed chemically for water, protein and fat. The Purdue workers (49) observed that the physically separated components expressed as a percentage of the carcass were significantly (P< 0.05) different for the two breed populations. The carcasses of Yorkshire x Duroc pigs contained more of muscle and bone and less of fat than those of the Yorkshire x Chester Whites. However, the concentrations of water, protein and chemically determined fat in the total carcass were not different for the two breed populations. Obviously the pigs of the two populations were different in their distribution of the chemical components among the physically separated parts. The Y-CW pigs contained more protein and water in the muscle fraction and more water and less chemically determined fat in the physically separated fat fraction than did the Y-D pigs. On the other hand, the Y-D pigs contained considerably more fat in the bone than did the Y-CW pigs.

These observations emphasize that it is hazardous to translate physically determined components into terms of chemical constituents and vice versa. Also, these data emphasize the variable nature of the distribution of chemical components among the body tissues.

Using the group-average data reported by the Purdue workers (49) we have examined in log: log transformations the relationships between the weights of the chemically determined components and body weight, ignoring breed. The statistics resulting from these calculations are shown in Table 8.

| Component | Prediction equation 1/ | R²  | C.V.  
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Y = log weight</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water</td>
<td>Y = 0.82697 X - 0.24967</td>
<td>0.997</td>
<td>0.99</td>
</tr>
<tr>
<td>Fat</td>
<td>Y = 1.76096 X - 1.98874</td>
<td>0.996</td>
<td>2.76</td>
</tr>
<tr>
<td>Protein</td>
<td>Y = 0.90424 X - 0.84547</td>
<td>0.994</td>
<td>2.39</td>
</tr>
</tbody>
</table>

1/ Y = log weight of component and X = log body weight.
It is expected that future studies will show that the slopes of the relationships between body components and body weight will reflect the maturing rate. Especially, the slope for fat is expected to be greater for rapid maturing breeds and strains than for slower maturing ones.

In extensive experiments concerned with the energy and protein requirements of the growing pig Mitchell and Hamilton (37) analyzed the whole bodies (minus ingesta) of 141 Poland China pigs representing three distinct body types (viz., chuffy, intermediate, and range). From their data for pigs weighing between 90 and 100 kg. empty, we have adjusted by covariance analysis the weights of body components to a common empty-body weight of 100 kg. The results of this analysis are summarized in Table 9.

### Table 9. Chemical Composition of Poland China Pigs of Three Body Types.

<table>
<thead>
<tr>
<th>Body Type</th>
<th>No. of Animals</th>
<th>Uncorrected Mean Weight (Kg.) of Empty Body Fat</th>
<th>Weight of Components (Kg.) in 100-kg. EBW:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chuffy</td>
<td>15</td>
<td>91.69 34.88</td>
<td>45.2 40.9 12.9 2.3</td>
</tr>
<tr>
<td>Intermediate</td>
<td>26</td>
<td>93.32 37.42</td>
<td>44.8 41.5 12.4 2.2</td>
</tr>
<tr>
<td>Range</td>
<td>20</td>
<td>93.75 34.61</td>
<td>47.1 38.1 13.1 2.4</td>
</tr>
</tbody>
</table>

1/ Weight of components adjusted by covariance analysis to the EBW of 100 Kg., using data for population ranging from 90 to 100 Kg.

Mitchell and Hamilton (37) stated: "The carcass analyses revealed only inappreciable differences between types in spite of large differences in their market finish. The dressed carcasses of pigs of distinctly different type slaughtered at the same weight, altho differing distinctly in market finish, analyzed very nearly the same. Apparently these carcasses differed in the distribution of fat, but not in the content of fat." These statements are borne out by the data in Table 9.

The results of this study emphasize again the significance of the distribution of the chemical components in the body. Further, these data suggest the possibility that although the "meat-type" hog has less back fat, certain separable muscles which are larger, or cuts containing muscles which are larger, and which possibly have less separable fat, he may not necessarily have less total chemically determined fat than his lard-type predecessor of the same body weight. The possibility exists that in breeding the meat-type pig, body fat, though possibly unchanged in total quantity in the body, might have become more intensely concentrated intra- and inter-muscularly. If so, this represents a defect from the standpoint of fat consumption by man, for the fat would be located where it cannot be readily cut
off. On the other hand, the intensification of intra- and inter-muscular fat may represent an economic advantage for it might improve such characteristics as flavor and cookability of meat. The fact remains, however, that the commonly assumed more favorable chemical composition of the meat-type pig has not been based on direct chemical analysis of the total body or carcass. Rather, it has been based mainly on partial separations of body tissues and largely upon subjective visual analysis.

Sheep. In previous parts of this report (viz., those concerned with the AP, NAAP and the creatinine-excretion methods, with the tritium-dilution method, and in Table 4), we have dealt with certain aspects of the relationships between the chemical components of the body and body weight of sheep. In those sections it was shown that: (a) The equation of the model, \( Y = aX^b \), fits body components-body weight relationships quite well, (b) the weight of chemical components at a given body weight varies with breed, (c) intact females are fatter than intact males at all weights ranging from 10 to 50 kg., (d) however, within sex and within breed, the predictability of body components from the body weight of animals maintained in continuous positive energy balance was quite high, but (e) body composition relative to body weight of sheep that have been starved and refed is quite different from that of sheep in continuously increasing body energy.

During the past 11 years, we have imposed a variety of nutritional treatments on sheep to study the effects on body composition and energetic efficiency. These have consisted of (a) various protein to energy inputs, (b) various planes of nutrition imposed continuously or alternately at certain times, (c) various proportions of concentrates to forage, (d) various physical forms, (e) various frequencies of meals, and (f) supplementation with specific metabolites such as acetic acid. Despite marked differences in energetic efficiency between certain treatments, the body composition of sheep has not varied in a manner independent of the effects of the treatments on total body mass - when sheep have maintained at least a continuously positive energy balance.

An example of one experiment (47) which contributed to these viewpoints is that in which we varied body weight independently of age of sheep by manipulating the energy input. The basic experimental unit consisted of 3 sheep of the same age and body weight at the beginning. One member of the trio was provided a high level of energy and the remaining members received a low level of energy. When the high-level animal reached a pre-set weight, he was killed, and one of his low-level mates was killed on the same day. The remaining low-level animal was allowed to grow until he reached the same weight as that at which his high-level mate was slaughtered; at that time, he was killed. Thus, in each trio, one low-level animal was killed at the same age, and the other at the same body weight, as the high-level animal. In this study 6 trios + 1 odd animal were employed with high-level animals being killed at pre-set, full-body weights ranging from 25 to 65 kg. Data for three such trios of sheep are summarized in Table 10.
Table 10. Relative Dependence of Body Composition on Body Weight and Age of Sheep as Modified by Level of Energy Input.

<table>
<thead>
<tr>
<th>Anim. No.</th>
<th>Level of intake 1/</th>
<th>Age (days)</th>
<th>EBW 2/ (Kg.)</th>
<th>Composition of empty, shorn body</th>
<th>Water (%)</th>
<th>Fat (%)</th>
<th>Protein (%)</th>
<th>Ash (%)</th>
<th>Energy (kcal./gm.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>88</td>
<td>270</td>
<td>28.19</td>
<td>57.4 24.4 15.0 2.9 3.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>63</td>
<td>270</td>
<td>19.89</td>
<td>61.5 18.5 15.6 3.9 2.61</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>63</td>
<td>343</td>
<td>28.73</td>
<td>56.6 23.9 15.8 4.0 3.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>97</td>
<td>381</td>
<td>49.56</td>
<td>46.1 38.1 13.1 2.6 4.30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>67</td>
<td>381</td>
<td>27.69</td>
<td>54.5 27.7 14.3 2.8 3.38</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>62</td>
<td>583</td>
<td>47.50</td>
<td>46.1 38.5 12.6 2.7 4.32</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>97</td>
<td>374</td>
<td>58.3</td>
<td>46.2 38.4 12.8 2.4 4.38</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>65</td>
<td>374</td>
<td>31.8</td>
<td>56.3 24.1 15.8 3.3 3.13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>63</td>
<td>613</td>
<td>56.0</td>
<td>46.0 38.5 12.7 2.8 4.42</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1/ Level of intake expressed as grams of dry matter ingested per kilogram of metabolic weight per day, adjusted at weekly intervals; the mean energy gains (including wool)/1 kg. MBS/day were: lower level, 31.3; and higher level, 58.3.

2/ EBW = Ingesta-free body weight.

A comparison of the standard partial regression coefficients of the chemical components on empty-body weight with the corresponding coefficients for the regression of the same components on age revealed that those for empty-body weight were 7 to 10 times as large as those for age. In addition, the inclusion of age with body weight as predictors of body composition increased the $R^2$ for empty-body weight alone by only 0.003 to 0.005 for a given chemical component. The $R^2$ values between empty-body weight alone and the various proximate chemical components ranged from 0.961 to 0.975.

These observations as well as those made in other experiments support the viewpoint that the body composition of healthy sheep (especially those which have not reached maturity) which have been maintained in a state of increasing energy retention is rigidly associated with body weight and is relatively impervious to nutritional pliancy. Further, these observations are consistent with the conclusions of Tulloh (52) who examined data for
Pigs, sheep and cattle published by various workers. His study of the data of Pálsson and Vergés (41) showed that the weights of certain carcass cuts as well as the weights of muscle and fat dissected from the cuts of sheep were very little related to age or nutritional history, but were strongly related to the empty-body weight. Also, he found the following proportions of the variance in the logarithms of the weights of bone, muscle and fat in the total sheep carcass to be associated with the variability in the logarithm of the empty-body weight: 96.1, 98.0, and 88.3%, respectively. These values, based on physically separated body parts, are of the same order of magnitude as our \( R^2 \) values (47) based on chemically determined components. It will be recalled that the Pálsson and Vergés experiments (41) involved the feeding of high and low planes of nutrition until 6 weeks of age and then the high and low levels were superimposed upon the previous high- and low-level animals until they reached various slaughter ages and weights. None of these animals experienced a prolonged period of body weight loss or was older than 11 months at slaughter.

Cattle. The relationships between the body or carcass weight and the weights of chemical components in the body or carcass have been studied very little in cattle. In this report under "carcass density and body composition", and in Table 6, we have considered certain of these relationships in cattle based on the extensive experiment of Kelly et al. (28). Tulloh (52), studying published data for 64 cattle, observed the following proportions of the variance in the logarithm of the weights of dissected carcass bone, muscle and fat to be ascribable to the variability in the logarithm of empty-body weight: 93.3, 98.2, and 94.0%, respectively. The data with which Tulloh (52) worked represented cattle on which various nutritional regimens had been imposed mainly by early Missouri workers.

In addition, we have examined the data of Guenther et al. (19) produced in a study of growth and development of the major carcass tissues of beef steers. Their experiment involved the separation of the lean-fat tissues from bone and the chemical analysis of the bone-free tissue. One group of calves was killed at weaning. The remaining calves were fed a high level of energy (to produce a daily gain in excess of 2.0 lbs. per day) or a medium plane of nutrition intended to produce a gain of approximately 1.7 lbs. per day. The high-level steers were killed at 10.8 or 14.3 months of age, and the medium-level animals at 10.8, 14.3 or 15.6 months of age.

The Oklahoma workers (19) observed that, at a given age, the high-level steers contained considerably more lean and fat than did the medium-level steers. Bone content at a given age was not different for the two feeding level groups. We have plotted in Fig. 8 their data for lean (i.e., sum of chemically determined protein, water and ash), protein and chemically determined fat, against age. This shows the segregation of data in accordance with nutritional plane. However, as shown in Fig. 9 nutritional plane was without effect on the weights of the same components per unit of slaughter weight. The data shown in Fig. 9 were derived by means of log: log transformations.

Based on the limited studies made of cattle, it appears that in this species, as in sheep, the chemical components of the body are rigidly associated with body mass. As shown by the Oklahoma (19), and Virginia (28) studies and by that of Tulloh (52), the nutritional treatments imposed on
cattle to date have not had much effect upon the body components independently of the effect upon total body or carcass weight.

Other animals. Present evidence indicates that the body composition of certain animals is more pliant to nutritional manipulation than is that of pigs, sheep, or cattle. For example, body composition in the rat and chicken has been influenced independently of body mass by the imposition of certain dietary treatments.

In an experiment with the chick, Thomas (50) fed diets containing 6.3, 12.6, 18.9 and 25.2% of protein, each at 4 levels of metabolizable energy input. Three groups of 8 male White Rock chicks were allotted to each of the 16 dietary treatments at 10 days of age and fed during a 15-day period. At the end of the feeding period, one-half of the chicks were killed and analyzed chemically. From Thomas' data (50), we have computed the body energy value and plotted these against the final body weights, in Fig. 10. It will be noted that body energy (as an index of composition) was quite different at the same body weight for the chickens receiving the various dietary treatments.

In an experiment (47) with rats, we examined the effects of meal frequency on body composition. The rats were pair-fed the same diet. One rat was allowed to eat ad libitum. During the subsequent 24-hr. period, his mate was fed in 2 meals precisely the same amount of food. After feeding periods of 2, 4, 6, and 8 days, 3 pairs of rats were killed and analyzed, and after 14 days, 11 pairs were analyzed. The data obtained were condensed in Table 11 for three slaughter periods. It will be observed that the body weight gain was about the same for the two treatments; however, body composition changes were decidedly different. The rats fed 2 meals per day for 14 days weighed 266.5 gm. and contained 43.4 gm. of fat, on the average.

Table 11. Influence of Frequency of Meals on Body Gain and Composition of Rats.

<table>
<thead>
<tr>
<th>Dietary treatment</th>
<th>Feeding period (days)</th>
<th>Total gain in:</th>
<th>Composition of empty body</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Body Wt. (gm.)</td>
<td>Energy (kcal.)</td>
</tr>
<tr>
<td>Ad lib 4</td>
<td>0</td>
<td>26.2</td>
<td>69</td>
</tr>
<tr>
<td>2 meals 4</td>
<td>4</td>
<td>22.6</td>
<td>83</td>
</tr>
<tr>
<td>Ad lib 6</td>
<td>6</td>
<td>35.5</td>
<td>106</td>
</tr>
<tr>
<td>2 meals 6</td>
<td>6</td>
<td>33.5</td>
<td>126</td>
</tr>
<tr>
<td>Ad lib 14</td>
<td>14</td>
<td>85.8</td>
<td>235</td>
</tr>
<tr>
<td>2 meals 14</td>
<td>14</td>
<td>82.4</td>
<td>354</td>
</tr>
</tbody>
</table>

1/ Same amount of feed ingested by pair-fed mates.
Those fed ad libitum weighed 265.6 gm., but contained only 26.4 gm. of fat. Obviously, frequency of meals disturbed body composition independently of the effects on body weight in these rats. Also, it is known that other dietary treatments influence body composition in the rat.

In contrast to these responses in the rat, body composition in the sheep was not affected independently of body size by different meal frequencies.

**SUMMARY**

1. The validity of body composition estimated by several indirect methods has been examined in comparisons with body composition determined by direct chemical analysis. The extent to which body composition estimated by means of an indirect method improves upon the accuracy of prediction from body weight alone has been employed as a further criterion.

   (a) Body water estimates made in sheep by means of the antipyrine (C.V. = 9.6%) and N-acetyl-4-aminoantipyrine (C.V. = 8.5%) dilution methods, and of the method based on urinary creatinine excretion (7.4%) were not as accurate as those predicted from linear shrunk-body weight alone (C.V. = 7.0%). The indirect methods were more effective than linear body weight as predictors in very fat animals; however, they were not as effective in very fat animals as body weight employed in log: log transformations.

   (b) The effectiveness of specific gravity of the carcass as a predictor of fatness varies among species. In sheep, the coefficient of variation between measured fat and fat predicted from specific gravity is of the order of 10 to 11%. In pigs, the C.V. value between these variables is only 4 to 5%. The data for cattle vary according to the fat concentration in the carcass. The coefficients of variation observed in the most extensive study made to date are as follows within various ranges of fat concentration: below 10% of fat, 41.8%; from 10 to 20% of fat, 18.8%; from 20 to 30% of fat, 10.7%; from 30 to 40% of fat, 7.1%; and from 40 to 50% of fat, 3.9%.

   Thus, over the range of cattle and sheep slaughtered for meat, specific gravity is not as effective as body weight alone as a predictor of body composition. Although they were not compared directly in pigs, it seems unlikely that body weight is as effective as specific gravity as a predictor in this species.

   (c) The most effective indirect methods studied to date are the deuterium and tritium dilution methods. The coefficients of variation between body water determined by desiccation and that estimated by deuterium or tritium dilution have been consistently less than 5%.

   (d) As the result of nullifying the variance associated with the chemical determination of nitrogen and potassium, the asymptotic standard error of estimate of body protein predicted from the
potassium content of the sheep body was found to be 310 gm. This is equivalent to a coefficient of variation of 5.4% between the measured protein and the protein estimated from body potassium. Thus, this Sy. x value represents the limit of accuracy with which body protein can be determined from body potassium as measured by an indirect method such as whole-body counting.

2. Some relationships between body weight and the weight of the chemical or physically separated components of the body were examined in several animal species.

(a) The model, $Y = a X^b$, provided a good fit of such relationships in pigs, sheep and cattle, ranging in maturity from that of the very young animal to that represented by animals in usual slaughter stages, and on which a variety of nutritional treatments had been imposed.

(b) A relatively rigid relationship was observed between body weight and the weight of the chemical components in pigs, sheep, and cattle. Thus, in these animals the nutritional treatments imposed to date have had very little effect upon chemical composition that is independent of the effect on total body mass. The only known exception is, that prolonged submaintenance inputs of energy followed by ad libitum feeding result in sheep having a markedly different chemical composition at the same body weights from their controls kept in continuously increasing energy balance.

However, evidence was presented which indicates that body composition in the rat and chicken may be decidedly more pliant to nutritional treatment. Certain regimens have produced great changes in body composition of these animals quite independent of the changes in total body weight. Some of the same treatments are without effect in the sheep.

Based on present evidence, body composition appears to be rigidly associated with body weight in ruminants that have been maintained in continuous, positive energy balance. Although currently available evidence suggests unexpectedly the same conclusion for the pig, it is difficult to reconcile this observation with the relatively more plastic response of the rat. Further study may reveal other treatments, however, that will disturb the body composition: body weight relationships in pigs, sheep and cattle.

(c) Although studied only in sheep, the weights of chemical components in animals of given body weights were different among breeds and between sexes.

(d) It is expected that the relationships between chemical composition and body weight may not hold rigidly in animals much more mature than the usual slaughter stage.
Although body weight: bone weight relationships were not examined, it is expected that the predictability of bone from body weight might be considerably less than that of other body components.

3. The present data suggest that animals of the same body weight, sex, strain or breed, and species have similar amounts of chemical components irrespective of age (prior to maturity). Yet the same animals may have decidedly different amounts of subcutaneous, visceral, intra-muscular, inter-muscular, and bone fat. Obviously, the distribution of chemical components in the body may be quite variable among animals.

In some studies in which the amounts of physically separated bone, muscle and fat have been different between body types within breed or between breeds, the amounts of chemically determined water, fat and protein were the same. Thus, the amounts of chemically determined components are not reliable indices of the dissected components and vice versa.

The changes in carcass composition associated with genetic improvement and nutritional treatments have been monitored chiefly on the basis of visual criteria, back-fat thickness, partial dissections, or the chemical analysis of several carcass cuts rather than on the basis of chemical analysis of half or total carcass or body. As a consequence, the modern animal and production methods might be producing a carcass in which there is, for example, less back fat, but more of intra- and inter-muscular fat, with no net gain of protein or loss in total fat. Although this may have an economic advantage and might result in certain desirable characteristics in the carcass, it represents a disadvantage from the standpoint of human nutrition.

The data examined in this report, including the chemical analyses of the whole bodies of 714 pigs, 256 cattle and over 350 sheep, strongly suggest that the amounts of the chemical components in the bodies of animals of the same sex, breed and species are similar at the same body weights, but that the major difference between animals is the distribution of fat. To a lesser degree, the same is true ignoring breed. Naturally, all generalizations are associated with some degree of variation; those set forth in this report are not unique in this respect. It is emphasized that it is not being argued in this report that small changes cannot be effected in the amounts of the chemical components relative to body weight of meat-producing animals by genetic or nutritional means, but rather that the rate or degree of change expected will be slow or small, respectively.
REFERENCES


40. Pace, N. and Rathbun, E. N. Jour. Biol. Chem. 150: 685. 1945


Fig. 1. Relationship between Measured Body Water and Deuterium-Water Spaces in Pigs. (Data adapted from those of Groves and Wood (18).)

Body $H_2O = 0.9937 \ D_2O \ Space + 0.128$

Sy.$x = 0.344 \ Kg.$

C.$V. = 4.77\%$

$r^2 = 0.995$

Mean underestimation = 1.65\%

Fig. 2. Relationship between Measured Body Water and Body Weight of Pigs. (Data adapted from those of Groves and Wood (18).)

$Y = 0.6298 \ X + 0.249$

Sy.$x = 0.232 \ Kg.$

C.$V. = 3.21\%$

$r^2 = 0.997$
Wood and Groves

- MALES
- FEMALES
- Manners & McCrea

Data of Wood & Groves:

\[ Y = 0.6277X + 0.294 \]
\[ \text{Sy.X} = 0.168 \text{ Kg.} \]
\[ \text{C.V.} = 2.55\% \]

Fig. 3. Relationship between Body Water and Body Weight of Male and Female Pigs. (Data adapted from those of Wood and Groves (55) and of Manners and McCrea (35).)
Fig. 4. Slaughter Plan and Treatments Employed by McMeekan (38).

Fig. 5. Slaughter Plan and Treatments Employed by Pomerooy (46).
Data of McMeekan:

\[ Y = 1.365977X - 1.252578 \]

\[ r^2 = 0.956 \]

C.V. = 12.63%

Fig. 6. Relationship between log Empty-Body Weight and log Weight of Dissected Fat in Pigs. (Data adapted from those of McMeekan (38) and Pomeroy (46).)
Fig. 7. Relationship between log Empty-Body Weight and log Weight of Dissected Muscle. (Data adapted from those of McMeekan [38] and Pomeroy [46].)

\[ Y = 0.990394 X - 0.458972 \]

\[ r^2 = 0.991 \]

C.V. = 3.51%
Fig. 8 Effect of Plane of Nutrition on Relationship between Carcass Composition and Age of Cattle. (Data computed from those of Guenther et al. (19).)
Identity: W

Age (mos.): 7.0

M1   H1   M2   H2   M3
10.8 10.8 14.3 14.3 15.6

"LEAN" = \( \frac{\text{H}_{2}O}{H_{1} + M_{1} + H_{2} + M_{2} + M_{3}} \), Ash, Protein.

\[
\log Y = 0.86835 \log X - 0.42125 \\
C.V. = 0.33\%; \quad r^2 = 0.996
\]

FAT (Bone-free carcass)

\[
\log Y = 1.81626 \log X - 3.18816 \\
C.V. = 2.50\%; \quad r^2 = 0.969
\]

PROTEIN (Bone-free carcass)

\[
\log Y = 0.83748 \log X - 1.00694 \\
C.V. = 0.39\%; \quad r^2 = 0.998
\]

Fig. 9. Effect of Age and Plane of Nutrition on Relationship between Carcass Composition and Body Weight of Cattle. (Data computed from those of Guenther et al. (19).)
Fig. 10. Effect of Protein-Energy Input on Relationship between Body Energy and Body Weight of Chickens. (Data adapted from those of Thomas (50).)

L. E. WALTERS: Now this afternoon substituting for Dr. Brungardt who could not be with us today is Richard Waldman. He is currently working with Dr. Brungardt and is with us today to present the next paper.

Richard is a native Ohioan, was on Bob Saffle's 1956 meat team, has the BS degree from Ohio State University. Following his BS degree program, he spent seven years in industry, two years, I am told, on his own—running his own meat processing business—after which time he became associated with a super market chain and dealt in the area of meat merchandising. Richard told me last night that after September 1, he hopes to be associated with Union Carbide in their Food Science Institute in Chicago.

We are sorry that our friend Val couldn't be with us, but we are real happy that you could be here to present the paper "Changes in Body Composition During Maturation."