A relationship between the character of the diet and the water content of the body has been recognized for nearly two centuries, but its quantitative aspects are still to be finally determined. A portion of the shift in body water, observed when the composition of the diet is changed, has been attributed to the water accompanying the variation in the quantity of liver glycogen. We have accordingly reinvestigated this question and were preparing to publish our results when the recent paper by Bridge and Bridges (1) appeared.

In 1906, Zuntz, Loewy, Müller, and Caspari (2), basing their calculations on data reported by Pavy (3), concluded that the deposition of 1 gm. of glycogen in the liver was accompanied by the storage of 3 gm. of water. This figure has been in use since, regardless of the fact that the methods employed by Pavy had not reached their present degree of perfection.

EXPERIMENTAL

In our experiments, albino rats have been subjected to various dietary procedures in order to vary the glycogen content of the liver. In one case, after prolonged fasting, strychnine convulsions were induced to reduce the glycogen to a minimum. The rats were killed, bled, the liver removed immediately, placed in a tared weighing bottle with a ground glass top, and weighed. A portion of the liver was removed and placed in a 60 per cent solution of potassium hydroxide. Glycogen was isolated from this aliquot.

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by a modification of Pflüger's method (4), the glycogen hydrolyzed with hydrochloric acid, and the glucose determined by the method of Hagedorn and Jensen (5). The weighing bottle and the remainder of the liver were again weighed to ascertain the weight of the aliquot taken for the glycogen determination, then placed in the freezing unit of a mechanical refrigerator until thoroughly frozen, and dried in a vacuum desiccator to constant weight.

**Table I**

*Water and Glycogen Content of Livers of Rats in Various States of Nutrition*

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Fresh liver</th>
<th>State of nutrition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>H₂O per cent</td>
<td>Glycogen per cent</td>
</tr>
<tr>
<td>1</td>
<td>71.1</td>
<td>0.0</td>
</tr>
<tr>
<td>2</td>
<td>70.6</td>
<td>0.02</td>
</tr>
<tr>
<td>3</td>
<td>70.5</td>
<td>0.18</td>
</tr>
<tr>
<td>4</td>
<td>69.9</td>
<td>0.23</td>
</tr>
<tr>
<td>5</td>
<td>70.0</td>
<td>0.38</td>
</tr>
<tr>
<td>6</td>
<td>70.1</td>
<td>0.93</td>
</tr>
<tr>
<td>7</td>
<td>70.1</td>
<td>2.14</td>
</tr>
<tr>
<td>8</td>
<td>70.3</td>
<td>3.54</td>
</tr>
<tr>
<td>9</td>
<td>69.7</td>
<td>6.11</td>
</tr>
<tr>
<td>10</td>
<td>70.4</td>
<td>6.15</td>
</tr>
<tr>
<td>11</td>
<td>63.9</td>
<td>7.62</td>
</tr>
</tbody>
</table>

**48 hr. fast + 0.9 mg. strychnine**

**56 hr. fast**

**40 " "**

**24 " "**

**24 " "**

**12 " "**

**Undernourished**

**Moderately obese; weight 450 gm.**

**Maintenance diet**

**Extremely obese; weight 700 gm.**

**Results**

Table I contains the percentile values for water and glycogen of the livers of rats on various dietary régimes. In all cases, with the exception of Experiment 11, the water content of the livers was very constant. In this exceptional case, the low water content may well be explained by the presence of striking quantities of fat in the liver. If this one value is omitted, the average water content of the livers was 70.3 per cent, with maximum deviations of +0.8 and -0.6 per cent. The glycogen content of the livers varied from 0 to 7.62 per cent.
DISCUSSION

In a recent article by Bridge and Bridges (1), the analyses of a number of rabbit livers are reported. It is to be understood from the introduction of the article that they were concerned in proving or disproving the statement that every gm. of glycogen stores 3 gm. of water. In the discussion of their results, however, they deal not with the relationship between the glycogen content and the water stored with it, but with the ratio of the glycogen to the total water of the liver. It is not difficult to understand the reason for the wide divergence of these ratios, since if the ratios were constant, a glycogen-free liver would necessarily be absolutely dry. The presence of a dry liver in a living organism is beyond imagination.

The data on the protein content of the livers can hardly be as valuable as they intimate, since these values were calculated from the total nitrogen content of an organ which is likely to contain considerable and varying amounts of non-protein nitrogen. They also appear to be slightly inconsistent in first showing that there is no relationship between the weight of the liver and the body weight and then computing their data in gm. of each component of the liver per kilo of body weight.

The data obtained by these authors and the data presented in this paper show a remarkable degree of consistency when the differences in technique and animals used are considered. In both cases the percentile water content of the livers was practically constant regardless of the amount of glycogen present. Thus, except in the presence of large quantities of fats, there is a constant ratio between the total water and the total solids of the liver. The average value for this ratio, calculated from our data, is 2.4, or, for each gm. of solids, there are 2.4 gm. of water in the liver. We have varied the percentile value of the glycogen present from 6.15 to 0 without changing the value of this ratio. This seems to indicate a rather constant ratio between the amount of glycogen in the liver and the weight of water held by it. If liver glycogen held more water per gm. than the other solids present, a decrease in the glycogen content would cause a decrease in the ratio of total water to total solids remaining and vice versa. But this is not the case. This appears to be ample proof that a gm. of
glycogen stores the same amount of water in the liver as that held by a gm. of the other solids. Thus, when 1 gm. of glycogen is deposited in the liver, 2.4 gm. of water accompany it, and when 1 gm. of liver glycogen is destroyed, 2.4 gm. of water are liberated. This value is remarkably close to that originally proposed by Zuntz, Loewy, Müller, and Caspari (2) when the methods by which their data were obtained are considered.

It is not our contention that all of the shift in body water on varying diets may be accounted for in this manner. Benedict and Milner (6) placed a subject on a very constant physical régime, so that the transformation of energy would be constant from day to day. He was first placed on a diet high in carbohydrate and gained a small amount of weight for 3 days. This gain was nearly entirely due to the retention of water. When this subject was given a high fat diet, isocaloric with the first, he lost over 2700 gm. of water from the body in 3 days. If all of the liver glycogen had been consumed in that period, it could not have accounted for more than 600 to 700 gm. of this water. However, if the source of the water is to be studied, certainly that arising from the destruction of liver glycogen must be recognized, and, as previously stated, both the data from this laboratory and those reported by Bridge and Bridges indicate that this value varies directly with the amount of liver glycogen consumed. We do not care to enter into the question of whether this is "bound water" or "free water."

**SUMMARY**

Glycogen and water have been determined on a number of rat livers. The percentile water content was found to be constant regardless of the glycogen present, except in one case in which the fat content of the liver was high. Thus it is evident that, per unit of weight, the glycogen contains an amount of water equal to that held by the non-carbohydrate solids. This value was found to be 2.4 gm. of water per gm. of glycogen. Any changes in the glycogen content of the liver should be considered, in the study of water balance, as a possible site for the retention of water, or as a source of water to be excreted when liberated by the destruction of glycogen.
H. L. Puckett and F. H. Wiley

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THE RELATION OF GLYCOGEN TO WATER STORAGE IN THE LIVER
Howard L. Puckett and Frank H. Wiley


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