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The Metabolism of the Honeybee Colony During Winter

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The Metabolism of the Honeybee Colony During Winter

By C. L. Corkins

Associate Research Entomologist and Apiculturist

INTRODUCTION

In order to obtain a sound basis upon which methods of wintering bees successfully in cold climates can be founded, it becomes necessary to understand the fundamental principles of the metabolism of their winter cluster in relation to outside temperatures. The present accepted theory states that as the outside temperatures decline below about 55° to 57° F. the bees are forced to the production of heat by an increase in muscular activity. As the temperature of the air immediately surrounding the bees reaches this level, a definite winter cluster is formed. Also, the temperature at the periphery of this cluster is maintained at about this temperature level, insofar as possible. In order to maintain this peripheral temperature as outside temperatures decline, it is assumed that the bees inside this cluster increase their muscular activity and consequently consume greater amounts of their carbohydrate food, honey, the end products of the metabolism of which are heat, carbon dioxide and water vapor. Thus, according to this theory, as outside temperatures become greatly depressed the consumption of stores and muscular activity by the bees are greatly increased, though the extent and rate of such induced metabolic processes have not been definitely determined.

The practical application which has been made of this theory has resulted in the belief that bees wintered in cold climates must be given a great amount of protection by insulation and windbreaks from excessively low outside temperatures and strong winter winds. Hence, the practice of “packing” the colonies of bees with such insulation materials as sawdust or straw to a thickness of from 2 to 14 inches has developed.

However, there are many successful commercial beekeepers in Wyoming, Colorado, Utah, Idaho and other mountain states, as
well as other areas of the northern states, who have not practiced winter insulation of their colonies of bees or have given but little protection in addition to the ordinary hive body. Many of these beekeepers have tried heavy insulation of their bees during the winter but do not find that the results justify the practice. Windbreaks are pretty generally used, regardless of other protection.

Furthermore, it has often been observed that neglected colonies of bees, sometimes in make-shift hives opened by many cracks to the weather, may come through rather severe winter conditions in good strength, though occasionally there are severe losses of such colonies. Although details for the analysis of these situations are obviously lacking, their history is so often repeated that it is difficult to completely ignore their importance or attempt to explain away their significance.

The end results of the two greatly divergent types of outdoor wintering of bees in cold climates creates a paradox which cannot be explained entirely by the above stated theory of the winter activity of bees. It leads one to wonder if there may be other facts concerning the fundamental metabolism of the winter cluster of bees which may not have been disclosed by the work of previous investigators. It was with this thought in mind that the research herein reported was prosecuted.

A REVIEW OF THE LITERATURE

The results to be given in this paper tend not to bear out some of the statements made by previous investigators of this problem. Hence, attention is called to the more important contributions on the subject and to a summary of the results given.

Gates (1)* pioneered in the investigation of the winter activity of bees, studying daily loss in weight and temperature reactions by the use of precision mercury thermometers. His findings were: (a) The rate of consumption of stores exhibited a relatively constant decrease from month to month; (b) the amplitude of variation in cluster temperature varied between 20° C. and 28° C.;

*Numbers in parenthesis refer to "Literature Cited" at the end of this bulletin.
(c) the maximum cluster temperature occurred practically simultaneously with the minimum outside, and the minimum cluster temperature \textit{vice versa}; (d) cluster expansion and contraction was noted in relation to warm and cold weather, respectively; and (e) an interchange of bees from the outside to the inside of the cluster and back was observed in the cluster. The minimum outside temperature during these experiments was $14^\circ$ F.

Phillips and Demuth (2) continued this work on temperature reactions, replacing mercury thermometers with thermo-couples. They stressed as their most important conclusion the fact that as outside temperatures fall below the clustering temperature, which is approximately $57^\circ$ F., the bees begin to generate heat by extra-normal activity, which activity increases to an alarming degree as low temperatures are reached. They observed this activity as a moving of the abdomen from side to side and the fanning of the wings. Their published data covered a period of three days' experimentation with a minimum outside temperature of $39^\circ$ F.

Milner and Demuth (3) measured the rate of metabolism of bees while clustered at temperatures ranging between $42.8^\circ$ F. and $48.5^\circ$ F. by means of a respiration calorimeter. Their important contribution is a demonstration of the fact that bees under these conditions perform an amount of work comparable with that done by a man at hard labor, pound for pound. However, they also reached the hypothetical conclusion that the energy output under cold weather conditions must be enormous, presumably much greater than that which they actually observed.

Phillips and Demuth, (4), (5) and (6), later made practical application of their previous investigations and call attention to the following points: (a) Unless bees are well protected by insulation during the winter, the colony will generate a great amount of heat and burn itself out; (b) it is impossible to insulate bees too heavily during winter; and (c) a temperature of $40^\circ$ to $45^\circ$ F. is best for bee cellars, whereas a temperature below $40^\circ$ F. is invariably bad for the bees, and a cellar in which the temperature goes as low as freezing is not a fit place for bees.
Wilson and Milum (7) diagramatically called attention to cluster expansion and contraction, but did not set forth the significance of this phenomenon. They agree with previous authors that “As the temperature outside the cluster becomes lower, the temperature within the cluster becomes higher up to a variable limit.” This statement is not clearly demonstrated by their data. During the coldest period (−15°F.), the high point in the cluster was 84°F., whereas it fluctuates both ways from this point during both warm and cold periods. Because they plotted a curve for each thermo-couple in chronological order, their data are difficult to analyze and interpret. They made this very significant statement, which is hardly compatible with the foregoing conclusion, “That, regardless of the amount of insulation provided the colonies, they maintain about the same high temperature and about the same average temperature of the cluster.”

Hess (8) confirms the findings of other investigators on the inverse temperature relationship of the cluster to outside temperature. His observed normal amplitude of variation is between 68°F. and 86°F.

Himmer (9) is also in agreement upon this same point of temperature relationships. He also cited a variation in the winter cluster between 68°F. and 86°F. A study of the loss in weight coincident with temperature records proved unsatisfactory, but the conclusion was drawn that on the whole the more severe winter caused a larger consumption of stores than the mild winter, but the difference was so small that it was not significant.

He further found that continued cold weather had a smaller influence on consumption than frequent and large temperature fluctuations. This author is the first to point out the great significance of the conservation of normal metabolic heat by the mere fact of the clustering of cold-blooded organisms, which he indicated may amount to 30°F. to 35°F. in the case of a cluster of bees. Himmer did not find an interchange of the bees from the surface to the center of the cluster and concluded that such an activity did not take place. Consequently, he advanced the theory that the inner bees are induced to activity by a mechanical impulse imparted by the surface bees.
In summing up the review of the literature it appears that all of the authors are in agreement upon the following points:

1. That as the outside winter temperature declines, the temperature in the center of the cluster rises, and vice versa.
2. That as outdoor temperatures decline below the clustering temperature greater metabolism within the cluster is induced.

TECHNIQUE

Determination of Daily Loss in Weight. There are four possible methods by which an index to the metabolism of the winter cluster of bees may be obtained. These, in the order of their importance and precision, are:

1. The determination of the carbon dioxide output. At the time the investigations herein reported were begun, the only possible method of measuring the carbon dioxide output of the colony was by means of the respiration calorimeter. This apparatus is obviously not adaptable to a study of this problem when it is desirable to handle the colonies normally out of doors. Hence, this most precise of all of the methods of measuring the rate of metabolism of the bees could not be used.

2. The determination of the daily consumption of honey by means of recording the daily loss in weight of the colony. If this method would provide a precise measure of the daily net consumption of honey it would be more simple and as accurate as the measure of the carbon dioxide output. However, four variables are involved which are difficult of absolute control and proper mathematical analysis. First, there is the possibility of the condensation upon the inner parts of the hive and the hygroscopic absorption by honey of the metabolic water produced. Second, the accumulation of feces due to certain undigestible materials in the honey which are retained within the rectum during cold weather and expelled outside of the hive when warm weather makes flight possible, must be considered. Third, bees which die during cold weather may be dragged out of the hives during periods of flight. Fourth, there is the possibility of absorption of moisture from
normal precipitation, as well as from the atmosphere, primarily by the external parts of the housing, and secondly by the inner portions of the hive and by the hygroscopic honey. These disturbing variable factors must be reduced to insignificance or mathematically measured if this method is to be employed with precision.

3. Temperature measurements of the winter cluster of bees in relation to external temperature. Although this method is the one which has been most extensively used by previous investigators, it is open to criticism. The variable of greatest importance involved is the effect of contraction and expansion of the winter cluster upon varying degrees of retention of metabolic heat by the increased or decreased radiation and insulation produced. Previous investigators have pointed out the fact that such insulation and retention of heat is accomplished by the winter cluster of bees, but none has taken into serious consideration the variable involved in the correlation of metabolic rate with cluster temperatures in relation to outside temperatures. It is the opinion of the writer that this variable is of much greater importance than has previously been considered and that temperature studies alone are misleading as a measure of metabolic rate.

4. The direct observation of the activity of the bees within the winter cluster. That this method does not permit of very extended or detailed investigation is perfectly obvious. In order to see what any of the bees are actually doing, except upon the periphery of the cluster, one must create artificially disturbing conditions. That the method is seriously questionable is evidenced by the fact of the greatly divergent observations and opinions given in the works of the authors reviewed.

In the investigation here reported the second and third methods were used in order to check the one against the other.

Under the climatic conditions obtaining and with the apparatus used the variables involved in the determination of the daily honey consumption were either reduced to comparative insignificance or their effect upon the analysis of the data calculated. The effect of the expulsion of condensed metabolic water within the hive, the cleansing of accumulated feces and the expulsion of dead
bees is measured during an extended warm period immediately following a cold wave. The relative humidity in our climate at Laramie, Wyoming, is so low that if the coldest part of the hive is at the entrance, the carrying off of metabolic water vapor is greatly expedited. The top of the uninsulated colony was given protection in addition to the ordinary cover by the use of an inner cover and a pad of tar paper.

As evidence of the dryness of the climate, 1.46 inches of precipitation fell during December, January and February of 1927-28, which was the maximum for the four years involved. This point is further emphasized by the fact that the mean free water surface evaporation for Laramie is 73 inches per year.

The variable induced by precipitation was, in the work reported, of no significance whatsoever. The hives and packing cases were given two coats of paint to prevent absorption of water. All cracks were sealed with a water-proof material. The small amount of precipitation which did occur fell in the form of cold snow, which was immediately removed from all parts of the hive and the scales. The total precipitation for each three months' period involved was as follows: 1927-28, 1.46 inches; 1928-29, 0.60 inches, and 1929-1930, 0.97 inches. The maximum amount of precipitation for any one day during 1927-28 was 0.28 inch. Ordinarily no weight records were taken during a stormy period, particularly when ice or snow accumulated on the hive so that it could not be removed. One period of 27 days with only 0.01 inches of precipitation upon one day was available for study. Weight records taken during some stormy days contrasted with those of the storm-free days did not reveal any serious experimental error.

As to the variable introduced by the accumulation of feces, it is important to point out the fact that the honey used for stores was white and water-white sweet clover honey. Sweet clover honeys may run as high as 0.5 per cent dextrin. Figuring waste material upon a basis of 1 per cent for the maximum period of confinement studied, a maximum experimental error of $\pm 0.00034$ ounces of daily loss in weight per ounce of bees is possible.
The removal of dead bees was of less consequence than the factor of accumulated feces. During the periods studied, few dead bees were taken out of the hives, as the weather was not ordinarily sufficiently warm to facilitate such activity.

The scales used in the experiment were graduated to \( \frac{1}{4} \)th of an ounce and broke readily with this amount of change in weight. Records were taken from each colony daily at 8 a.m. No disturbances detected by temperature increases within the cluster were noted because of the taking of these weight records.

**Temperature Measurements.** All temperature measurements taken inside the colonies were electro-thermically made by the use of thermo-couples. The thermo-couples were made of number 30 gauge copper and constantan wire. A Leeds-Northrup precision mirror galvonometer and a potentiometer sensitive to \( \frac{1}{20} \)th of a degree thermol differential measured the flow of electrical current. The cold junction of the thermo-couple circuit was standardized to \( 0^\circ \) C. by immersion in cracked ice and water contained within a thermos bottle. The rapid reading of the 84 to 126 different thermo-couples used was facilitated by means of 24-point double-contact Leeds-Northrup rotary switches. The potentiometer was calibrated to degrees of temperature at the factory. At the beginning and at the end of each experiment the thermo-couples were tested and none was ever found to be giving an inaccurate reading.

Twenty-one thermo-couples were introduced into each colony and arranged according to Figures 14 to 16. All spaces between combs in both the horizontal and vertical planes within the hive body occupied by the bees were thus covered. The arrangement was such that the greater proportion of the thermo-couples would be within the winter cluster most of the time.

Each thermo-couple was protected inside of the colony with a thin sheath of pyralin tubing. This assured the fixation of the location of each couple at a definitely pre-arranged point. The pyralin tubes were imbedded vertically in a sheet of pyralin which was placed upon the top of the hive body much as an inner cover. Thus, all of the couples were introduced into the hive body between the combs at one operation. The relative transparency of
the pyralin sheeting made it possible to observe any abnormal activity which might be induced by the introduction of the pyralin tubes. No abnormal reactions were observed.

The wires coming from each pyralin tube were imbedded in the pyralin sheeting with a heavy coating of beeswax and resin. Finally, all of the lead wires were consolidated for each hive at the edge of the sheeting and carried into the instrument laboratory through rubber conduits.

For this particular study it was desirable to have only the temperature readings following the period of minimum outdoor temperature. As a consequence, for the most part only the temperatures taken at 8 a.m. daily are taken into consideration, although readings were taken at all periods of the day and occasionally the night during the winter of 1926-27. This was also done during some of the cold periods of the winters of 1927-28 and 1929-30. Such temperature records correlated with the time of day have been well studied and analyzed by previous investigators and will be largely omitted from this paper.

The Construction of the Winter Protecting Cases. In order to give a further check upon the relation of the metabolism of the winter cluster of bees to outside temperature, the colonies were given varying degrees of protection from outside temperature influences. During the winter of 1926-27, Colony Number One was placed inside of a single packing case and given 6 inches of sawdust insulation on the sides and the top. Only the 7/8-inch pine board flooring protected it from the bottom, and the case rested upon the platform of the scales in such a way as to allow free access of the wind to it. Colony Number Two had no protection from the cold in addition to the ordinary 10-frame summer hive, except the top protection of the pyralin sheet, an inner cover and a pad of tar paper. Colony Number Three was protected with several thicknesses of newspaper and finally wrapped in tar paper. Upward ventilation was given, i.e., a one-inch auger hole entrance was bored in the lower hive body near the normal entrance position, and another midway up on the upper hive body. Colony Number Four was insulated in exactly the same manner as Number Three, but the upward ventilation was omitted.
During the winter of 1927-28, Colony Number One was insulated the same as Number One of the previous year, except that six inches of sawdust were added to the bottom of the packing case. This additional protection seems to have a significance which will be pointed out later. These methods of protection were followed out from year to year according to the following chart:

**COLONY NUMBERS WITH REFERENCE TO DEGREES OF INSULATION**

<table>
<thead>
<tr>
<th>Year</th>
<th>Single Packing Cases without Bottom Packing</th>
<th>Single Packing Cases with Bottom Packing</th>
<th>No. Packing</th>
<th>Tar Paper Packing with Normal Ventilation</th>
<th>Tar Paper Packing with Upward Ventilation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1926-27</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>1927-28</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1928-29</td>
<td>2</td>
<td>3-4</td>
<td>5</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>1929-30</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Two standard-depth hive bodies were provided for each colony. During the period studied the normal entrances were reduced to the size of a one-inch auger hole.

**The Kind and Amount of Bees.** The bees used during 1926-27 were Italians and during 1927-28 they were Caucasians. In each case they were from 3-pound packages established the previous spring. The queens had all passed through but one honey flow. During the winter of 1928-29 Caucasian bees were again used, with the exception of Colony Number Four, the bees in which were Italians. This colony, unprotected, was placed beside the unprotected Caucasian colony in order that any differences in racial reaction to winter temperatures might be noted.

Caucasian bees were used in all of the colonies in the 1929-30 experiment.

These colonies were afforded excellent protection from winds. They stood within a few feet of a four-story building, which protected them on the west. On the east a group of evergreen trees further broke the effect of winds.

Table I gives the weights of the various lots of bees at the beginning and close of each winter period.


**TABLE I.**

<table>
<thead>
<tr>
<th>Colony Number</th>
<th>Fall Weight of Bees in Ounces</th>
<th>Spring Weight of Bees in Ounces</th>
<th>Winter Loss of Bees in Ounces</th>
<th>Per Cent Winter Loss of Bees</th>
</tr>
</thead>
<tbody>
<tr>
<td>1926-27</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>121</td>
<td>57 1/2</td>
<td>63 1/2</td>
<td>52.4</td>
</tr>
<tr>
<td>2</td>
<td>131</td>
<td>89</td>
<td>51</td>
<td>38.9</td>
</tr>
<tr>
<td>3</td>
<td>116</td>
<td>69</td>
<td>47</td>
<td>40.5</td>
</tr>
<tr>
<td>4</td>
<td>101</td>
<td>54</td>
<td>47</td>
<td>46.5</td>
</tr>
<tr>
<td>1927-28</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>90 1/4</td>
<td>58 1/2</td>
<td>31 1/4</td>
<td>35.1</td>
</tr>
<tr>
<td>2</td>
<td>73 1/4</td>
<td>69</td>
<td>4 1/2</td>
<td>5.8</td>
</tr>
<tr>
<td>3</td>
<td>81 1/4</td>
<td>79</td>
<td>2 1/2</td>
<td>2.7</td>
</tr>
<tr>
<td>1928-29</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>105</td>
<td>53</td>
<td>52</td>
<td>49.5</td>
</tr>
<tr>
<td>2</td>
<td>108</td>
<td>52</td>
<td>56</td>
<td>51.8</td>
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<tr>
<td>3</td>
<td>114</td>
<td>68</td>
<td>46</td>
<td>40.3</td>
</tr>
<tr>
<td>4</td>
<td>114</td>
<td>68</td>
<td>46</td>
<td>40.3</td>
</tr>
<tr>
<td>5</td>
<td>113</td>
<td>76</td>
<td>37</td>
<td>32.7</td>
</tr>
<tr>
<td>6</td>
<td>117</td>
<td>104 1/4</td>
<td>12 1/4</td>
<td>10.9</td>
</tr>
<tr>
<td>1929-30</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>93</td>
<td>52</td>
<td>41</td>
<td>44.0</td>
</tr>
<tr>
<td>2</td>
<td>85</td>
<td>38</td>
<td>47</td>
<td>55.3</td>
</tr>
<tr>
<td>3</td>
<td>118</td>
<td>48</td>
<td>70</td>
<td>59.3</td>
</tr>
</tbody>
</table>

Fall weight record 1926 taken Oct. 26; Spring, May 7, 1927.
Fall weight record 1927 taken Oct. 19; Spring, May 22, 1928.
Fall weight record 1928 taken Oct. 22; Spring, May 21, 1929.
Fall weight record 1929 taken Oct. 16; Spring, April 28, 1930.

THE MEAN DAILY LOSS IN WEIGHT CORRELATED WITH COLD VERSUS WARM PERIODS

In order to bring about a clear-cut differentiation between the metabolic rate of the winter cluster of bees and external temperatures, the data for definite cold and warm periods were selected, computed and analyzed. These periods varied in length from 5 to 10 days, but for the most part are for 5 or 6 days. In all cases the coldest and warmest periods obtaining during the months studied are included and, in certain instances, also periods of intermediate temperatures.

It is, of course, apparent that during the warm periods flights occurred which would, presumably, increase the metabolism above that of a cluster at ideal temperatures. However, for the most part, these flights were of short duration due to the fact that the hives were shaded during the afternoon. Furthermore, the evening, night and early morning temperatures during this time were those considered most ideal for minimum activity.
The daily loss in weight of each colony is reduced to a common factor by its computation in terms of ounces per ounce of bees. By reference to Table I it will be seen that for each series of experiments the difference in the amount of bees in each colony is so minimized by selection of colonies of similar strength, or by the addition of bees to the lighter ones, as to prevent distortion of the significance of this data in the comparison of the various colonies. Although this computation is based upon the late fall weights, in all but three instances the progressive loss during the winter is so similar that subsequent reduction in the number of bees would not seriously distort the data. Further, the maximum loss of bees, naturally, occurred after the time the records were taken.

The data presented in the tables and graphs are placed in the order of the coldest to the warmest mean outdoor temperatures for the periods selected rather than in their chronological position. The daily loss in weight of each colony of bees, together with the temperature data, is presented in Table II and in Figures 4 to 9, inclusive. The detailed discussion of the temperature relationships will occur later in this paper.
<table>
<thead>
<tr>
<th>Date of Periods</th>
<th>Mean Outdoor Temperature</th>
<th>Mean Hive Temperature</th>
<th>Mean Cluster Temperature</th>
<th>Mean Maximum Cluster Temperature</th>
<th>Daily Loss in Weight in Ounces Per Ounce of Bees</th>
</tr>
</thead>
<tbody>
<tr>
<td>1926-27</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12-23 to 28</td>
<td>7.5</td>
<td>45.4</td>
<td>79.3</td>
<td>85.0</td>
<td>0.014</td>
</tr>
<tr>
<td>1-21 to 25</td>
<td>14.4</td>
<td>47.4</td>
<td>81.3</td>
<td>86.2</td>
<td>0.011</td>
</tr>
<tr>
<td>1-15 to 20</td>
<td>28.1</td>
<td>51.6</td>
<td>81.8</td>
<td>87.3</td>
<td>0.026</td>
</tr>
<tr>
<td>2-7 to 12</td>
<td>32.4</td>
<td>61.2</td>
<td>84.5</td>
<td>87.9</td>
<td>0.038</td>
</tr>
<tr>
<td>1-1 to 6</td>
<td>37.6</td>
<td>61.2</td>
<td>82.8</td>
<td>86.1</td>
<td>0.047</td>
</tr>
<tr>
<td>1927-28</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12-29 to 1-3</td>
<td>11.9</td>
<td>6.2</td>
<td>87.1</td>
<td>92.9</td>
<td>0.015</td>
</tr>
<tr>
<td>2-22 to 26</td>
<td>12.3</td>
<td>6.2</td>
<td>88.5</td>
<td>90.9</td>
<td>0.029</td>
</tr>
<tr>
<td>1-16 to 25</td>
<td>15.7</td>
<td>75.0</td>
<td>90.0</td>
<td>90.2</td>
<td>0.042</td>
</tr>
<tr>
<td>12-24 to 28</td>
<td>23.6</td>
<td>34.2</td>
<td>89.0</td>
<td>92.0</td>
<td>0.055</td>
</tr>
<tr>
<td>1-2 to 6</td>
<td>35.5</td>
<td>78.1</td>
<td>88.9</td>
<td>90.2</td>
<td>0.059</td>
</tr>
<tr>
<td>1-6 to 15</td>
<td>36.2</td>
<td>75.5</td>
<td>88.6</td>
<td>91.6</td>
<td></td>
</tr>
<tr>
<td>1928-29</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-6 to 10</td>
<td>0.4</td>
<td>33.2</td>
<td>72.6</td>
<td>90.1</td>
<td>*0.025</td>
</tr>
<tr>
<td>1-23 to 27</td>
<td>8.9</td>
<td>37.4</td>
<td>66.0</td>
<td>82.2</td>
<td>0.025</td>
</tr>
<tr>
<td>1-15 to 19</td>
<td>10.9</td>
<td>49.6</td>
<td>68.9</td>
<td>79.7</td>
<td>0.034</td>
</tr>
<tr>
<td>2-24 to 3-1</td>
<td>11.2</td>
<td>40.1</td>
<td>73.8</td>
<td>91.4</td>
<td>0.035</td>
</tr>
<tr>
<td>1-18 to 22</td>
<td>17.9</td>
<td>29.1</td>
<td>78.4</td>
<td>81.8</td>
<td>0.036</td>
</tr>
<tr>
<td>1-31 to 2-4</td>
<td>39.1</td>
<td>41.3</td>
<td>86.5</td>
<td>86.8</td>
<td>0.037</td>
</tr>
<tr>
<td>1-27 to 25</td>
<td>31.7</td>
<td>42.9</td>
<td>86.9</td>
<td>83.1</td>
<td>0.038</td>
</tr>
<tr>
<td>1-12 to 31</td>
<td>32.3</td>
<td>51.8</td>
<td>85.6</td>
<td>83.1</td>
<td>0.039</td>
</tr>
<tr>
<td>3-4 to 11</td>
<td>37.3</td>
<td>66.0</td>
<td>88.7</td>
<td>93.7</td>
<td></td>
</tr>
<tr>
<td>1929-30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-13 to 24</td>
<td>-2.0</td>
<td>28.2</td>
<td>83.3</td>
<td>90.3</td>
<td>0.023</td>
</tr>
<tr>
<td>12-18 to 22</td>
<td>8.5</td>
<td>32.7</td>
<td>82.2</td>
<td>84.9</td>
<td>0.010</td>
</tr>
<tr>
<td>1-7 to 12</td>
<td>12.2</td>
<td>32.7</td>
<td>89.9</td>
<td>89.9</td>
<td>0.019</td>
</tr>
<tr>
<td>1-25 to 30</td>
<td>19.3</td>
<td>35.6</td>
<td>87.0</td>
<td>89.9</td>
<td>0.025</td>
</tr>
<tr>
<td>1-2 to 6</td>
<td>27.4</td>
<td>39.0</td>
<td>80.0</td>
<td>90.7</td>
<td>0.017</td>
</tr>
<tr>
<td>2-5 to 11</td>
<td>34.6</td>
<td>48.4</td>
<td>90.7</td>
<td>93.9</td>
<td>0.046</td>
</tr>
<tr>
<td>1-16 to 23</td>
<td>38.3</td>
<td>51.8</td>
<td>90.8</td>
<td>94.1</td>
<td>0.000</td>
</tr>
<tr>
<td>9-12 to 16</td>
<td>41.4</td>
<td>49.8</td>
<td>92.2</td>
<td>89.2</td>
<td>0.034</td>
</tr>
</tbody>
</table>

*This is Colony No. 6 for 1928-29.
The outstanding fact shown by all tables, and even more apparent in the graphs, is the definite increase of the daily loss in weight in every colony during every year in a progression from the cold to the warm periods. Some few slight variations in this upward trend of the curves appear, but none of any great significance occur. A comparison of the maximum variation in daily loss in weight for the various types of protection is shown in Table III.
Figure 5. Temperature and loss in weight relations for Colony No. 2, 1926-28. Curves as in Figure 4.

TABLE III.
COMPARISON OF THE MAXIMUM VARIATION IN DAILY LOSS OF WEIGHT FOR VARIOUS TYPES OF PROTECTION

<table>
<thead>
<tr>
<th>Type of Protection</th>
<th>Year</th>
<th>Minimum Daily Loss in Weight Per Ounce of Bees</th>
<th>Maximum Daily Loss in Weight Per Ounce of Bees</th>
<th>Per Cent of Increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>Packed</td>
<td>1926-27</td>
<td>0.011</td>
<td>0.047</td>
<td>330.6</td>
</tr>
<tr>
<td></td>
<td>1927-28</td>
<td>0.015</td>
<td>0.059</td>
<td>285.8</td>
</tr>
<tr>
<td></td>
<td>1928-29</td>
<td>0.021</td>
<td>0.078</td>
<td>263.4</td>
</tr>
<tr>
<td></td>
<td>1929-30</td>
<td>0.013</td>
<td>0.064</td>
<td>332.4</td>
</tr>
<tr>
<td>Unprotected</td>
<td>1926-27</td>
<td>0.018</td>
<td>0.049</td>
<td>263.2</td>
</tr>
<tr>
<td></td>
<td>1927-28</td>
<td>0.013</td>
<td>0.040</td>
<td>167.4</td>
</tr>
<tr>
<td></td>
<td>1928-29</td>
<td>0.015</td>
<td>0.040</td>
<td>112.6</td>
</tr>
<tr>
<td></td>
<td>1929-30</td>
<td>0.013</td>
<td>0.053</td>
<td>391.9</td>
</tr>
<tr>
<td>Tar-Paper Normal</td>
<td>1926-27</td>
<td>0.022</td>
<td>0.053</td>
<td>133.9</td>
</tr>
<tr>
<td></td>
<td>1928-29</td>
<td>0.014</td>
<td>0.060</td>
<td>329.1</td>
</tr>
<tr>
<td></td>
<td>1929-30</td>
<td>0.010</td>
<td>0.060</td>
<td>469.1</td>
</tr>
<tr>
<td>Tar-Paper</td>
<td>1926-27</td>
<td>0.015</td>
<td>0.049</td>
<td>230.0</td>
</tr>
<tr>
<td>With Upward</td>
<td>1927-28</td>
<td>0.014</td>
<td>0.044</td>
<td>201.3</td>
</tr>
<tr>
<td>Ventilation</td>
<td>1928-29</td>
<td>0.021</td>
<td>0.039</td>
<td>86.4</td>
</tr>
<tr>
<td></td>
<td>1929-30</td>
<td>0.021</td>
<td>0.062</td>
<td>198.1</td>
</tr>
</tbody>
</table>
The details of the packed colonies will first be considered. An interesting and perhaps significant difference in the daily loss in weight of the three packed colonies is apparent. The loss during 1926-27 was markedly less than for either 1927-28 or 1928-29. During the first year bottom packing was omitted, whereas it was added during the next two years with the assumption that possibly insufficient protection for best results had been given during 1926-27. As a consequence, by reference to the mean hive temperatures it will be seen that during 1926-27 a definite cluster was formed. With the added bottom packing during 1927-28, the mean hive temperature was not low enough to cause the formation of a definite cluster at any time, though it was low enough, presumably, to bring about comparative inactivity during the cold periods. The hive temperatures during 1928-29 were slightly be-
low the clustering temperature, but it should be noted that one of the five couples included in this mean temperature for the first time this year was at the inside entrance of the hive, whereas the coldest couple was previously removed from the entrance by the depth of one hive body. This fact, therefore, would make the hive temperatures for 1928-29 comparable with those of 1927-28, and it is unlikely that there was a definite cluster formed for any great amount of time. As a matter of fact, the hive temperatures during the latter two years were those at or near the temperature levels previously considered productive of the minimum metabolic rate by the bees. The former period should have increased it. However, the reverse relationship here occurs.
According to the old theory previously stated, the greatest daily loss in weight of all colonies should have taken place in the unprotected colonies during the cold periods. Such was not the case, and here again, as in the packed colonies, the loss in weight curve rose in a progression from the cold to the warm periods.

Referring again to Table II, the following facts are evident:

During the years 1926-27 and 1929-30 there was a much greater increase in the percentage of variation from the cold to the warm periods than during any other years. In the first instance there appeared the only record of evidence of the condensation of moisture within the hive as a serious variable factor. Water was seen dripping from this hive during this period of extraordinarily

\[\text{Figure 8. Temperature and loss in weight relations for Colony No. 2, 1929-30. Curves as in Figure 4.}\]
high loss in weight. In the second instance, the great loss in weight for the unpacked colony during the winter of 1929-30 from February 16 to 23 can only be explained by excessive activities due to flights, as every day had very high maximum temperatures. No cold period immediately preceded it. In fact, it followed a period of weather having temperatures nearly as high as during this period.

Again, with the tar paper packed colonies the same increase of daily loss in weight was exhibited. There seems to be some difference in the reaction of the colonies with upward ventilation and those without.
It will be noted that the colony packed in tar paper with upward ventilation during 1927-28 exhibits a drop in the curve for the warmest period down to the level of the curve for the second coldest period. One other similar discrepancy occurs in this same series during the winter of 1929-30. In the first case the mean hive temperature dropped slightly more than during the preceding warm period, but this fact alone does not offer adequate explanation for the great drop in the loss-in-weight curve. It remains unexplained. In the second case, this slight drop in the mean hive temperature also occurs, but it is not sufficient to be of any consequence. However, it will be noted that all colonies for this period of December 9 to 16, 1929, show a marked decrease over the preceding warm periods, which would seem significant. It is possible that because this period came early in the winter and was not preceded by such cold periods as were the other two, the bees did not fly so freely even though the outdoor temperatures were more favorable. However, this surmise does not adequately explain this situation. Since these discrepancies are so few in the entire series, they do not seem to be of any great significance, and in no case does the daily loss in weight for a warm period fall below the minimum for a cold period for a given colony.

A summary of all the records of daily loss in weight for all of the colonies for all four years contrasting those when the mean outside temperatures were below 15° F. with those when the mean outside temperatures were above 28° F. shows an average loss of 0.023 ounces and 0.042 ounces, respectively, an increase of 84.4 per cent. If it were assumed that all of this difference was caused by condensation of metabolic water in the hive during cold periods and its release during warm periods, it would amount on the average to 2.047 ounces per day. This amount accumulating daily during a period of cold weather lasting from 5 to 10 days, and in some cases longer, would cause a stream of water to run from the hives during warm periods when it was released. Such a situation was noted only in one case for one colony, and as previously noted at this time the daily loss in weight was markedly greater for this colony than for any other colony at any time during the entire experiment. Furthermore, it would require the total condensa-
tion within the hive of all the metabolic water produced by a daily average consumption of 0.0293 ounces of honey per ounce of bees to bring about such a condition. Taking these two facts into consideration and allowing for the possible condensation of metabolic water within the hives, which undoubtedly took place at times, it would still seem impossible to deduct that the daily store consumption was greater during the cold periods than during the warm. It would seem to have been much less.

A summary of the daily loss in weight in ounces per ounce of bees for the various types of protection for the three months' winter period, shown in Table Number IV, also tends to bear out the conclusion that cold weather does not materially induce increased activity of the winter cluster. For such a long period as this the possibility of distortion of the data by the condensation of metabolic water within the hive is minimized to comparative insignificance. If excessive cold did greatly increase activity, as previously assumed, then the unprotected colonies should show a much greater daily loss in weight than the packed colonies. Only in one case was it greater, and in all others it was less. In the single case where the packed colony lost less than the unpacked it was without the bottom packing, whereas the other packed colonies had this added protection. Even in this one case, the difference was manifest largely during the warm periods, and would seem likely to be due to more frequent making and breaking of the cluster when weather was favorable. Likewise, if the old theory were correct, the colonies with upward ventilation should

**TABLE IV.**

<table>
<thead>
<tr>
<th>Year</th>
<th>Packed Top and Sides</th>
<th>Packed Top, Sides and Bottom</th>
<th>Unpacked</th>
<th>Tar Paper Without Upward Ventilation</th>
<th>Tar Paper with Upward Ventilation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1926-27</td>
<td>0.0221</td>
<td>0.0472</td>
<td></td>
<td>0.0428</td>
<td>0.0371</td>
</tr>
<tr>
<td>1927-28</td>
<td>0.0340</td>
<td>0.0310</td>
<td></td>
<td>0.0295</td>
<td>0.0265</td>
</tr>
<tr>
<td>1928-29</td>
<td>0.0418</td>
<td>0.0316 0.0301</td>
<td></td>
<td>0.0295</td>
<td>0.0305</td>
</tr>
<tr>
<td>1929-30</td>
<td>0.0311</td>
<td></td>
<td></td>
<td>0.0268</td>
<td>0.0427</td>
</tr>
</tbody>
</table>
have fared worst of all. Upward ventilation has been generally considered one of the most ill-advised of wintering practices. Only in one instance out of four is the rate high for such a colony, and in this case it is only 0.0009 ounces greater than for the packed colony during 1928-29. During 1927-28 the colony with upward ventilation showed the lowest stores consumption of any, and during the other two years they compared very favorably with those without upward ventilation.

During the winters of 1927-28 and 1929-30 there was a great contrast in the mean monthly temperatures. The relationship of the daily loss in weight by monthly periods is shown in Figures 1 and 2. Here again is found the striking correlation of low daily loss in weight with the cold periods, and the high daily loss in weight with the warm periods.

Figure 3 is constructed to measure the possibility of the variables, previously mentioned in detail, in affecting the use of the daily loss in weight of the hives as an index to metabolic activity. It is to be assumed that if the expulsion of possible condensed metabolic water, accumulated feces and dead bees were important disturbing factors, that the greater summation of their effect upon
an exaggerated daily loss in weight would occur during the first part, rather than the second part, of a protracted warm period. One long warm period with similar mean outdoor temperatures each day immediately following a cold period, upon which to base an analysis of the potentialities of these disturbing factors is, fortunately, available. It is of twelve days' duration. No greater daily loss in weight, which might be caused by the greater summa-
tion of these factors, occurs during the first part of this period, except in the case of Colony Number One, packed, where it is least to be expected.

The data on the daily loss in weight presents no facts which would lead to the conclusion that as outdoor temperatures subside below the clustering temperature the metabolic rate is materially increased. On the other hand, it is certain that too frequent and unnecessary making and breaking of the cluster coincident with flight activities during warm periods is far more harmful to the bees because of an increased metabolic rate than the effect of any of the cold periods recorded.
TEMPERATURE LEVELS WITHIN THE CLUSTER IN RELATION TO SURROUNDING TEMPERATURES AS AN INDEX TO METABOLIC RATE

Previous investigators have based their conclusions that the metabolic rate is greatly increased as outside temperatures decline below the clustering temperature largely upon an inversion of temperature relationships under such conditions. They have found that as the temperature surrounding the cluster goes down, the temperature in the so-called heat-producing portion of the cluster goes up. Their reported amplitude of this variation, however, is greatly different. Of course, the temperature ranges with which the various investigators dealt were markedly divergent, which may explain the difference in the results obtained. None worked with as many different types of protection or for so long a period or with such wide ranges of temperature as are herein recorded. The minimum temperature obtaining during the course of these investigations was 41° F. below zero.

As previously stated, the mean cluster temperature data were obtained by averaging the temperatures of the five couples giving the maximum temperature records. Since these correlate very closely with the mean maximum cluster temperature, it would indicate that such a method gives a true picture of the temperature relations within the so-called heat-producing portion of the cluster. It is true that the recording of the mean cluster temperatures at from seven to eight o'clock a. m., only, tends to flatten out the curves and reduce the amplitude of variation. However, certain curves showing hourly and bi-hourly temperature relationships and other data for frequent temperature records taken throughout the day, but not here recorded because of their lack of importance, indicate that the method of analysis used is not in error. Likewise, since these records were taken for periods of maximum and minimum outside temperatures of great divergence, there can
be no serious objection raised to the method. The data on the total amplitude of variation at the point of maximum heat supports this point.

It should also be noted at this time that the recording of the temperature reactions of the cluster at this morning period catches the cluster under the most severe outside temperature conditions during cold weather and under its most ideal outside temperature conditions during warm weather. During the cold weather the cluster has just passed through or is still contending with the severity of the minimum temperatures obtaining at these times. On the other hand, the temperatures during the warm weather are ideally just below the clustering temperature. It would be impossible to bring about the desired comparison if the temperature records were taken during the warm period when the cluster was loosely formed or broken for activity. Under the circumstances, the contrast in the temperature relationships of the cluster at its top temperature range of formation and the minimum range obtainable is brought about. This condition should display the maximum amplitude of variation and inversion of temperature relationships.

**Temperature Relationships of Colonies Wintered Outdoors.** Some of the typical temperature relationships of the colonies wintered outdoors for four years are shown in Figures 4 to 9, inclusive. The surprising feature of these curves is the fact that the amplitude of variation of the cluster temperature is so very low when it is so great in outside temperatures, as shown in Table V.

The figures presented in Table V do not contrast the temperatures for the periods of minimum and maximum outdoor temperature. They are for the maximum amplitude of variation in each colony at whatever time the high and low cluster temperatures happen to obtain. A comparison of the amplitude of variation between the periods of minimum and maximum outdoor temperatures presents a much lower amplitude of variation, and minimizes the importance of the larger degrees of variation as exhibited in Table V. It was previously supposed that the maximum
cluster temperature occurred when the outside temperature was the lowest. Hence the amplitude of variation between the points of minimum and maximum outdoor temperature when inversion occurs is expressed as a positive variation and when reversed as a negative variation.

Upon this basis the mean amplitude of variation for all packed colonies is $-5.1^\circ F$; for all unpacked colonies, $-0.3^\circ F$; for all tar-paper packed colonies without upward ventilation, $1.7^\circ F$; and for all tar-paper packed colonies with upward ventilation, $3.0^\circ F$.

It is, therefore, to be noted that the periods of maximum amplitude of variation are very divergent in their occurrence in relationship to outside temperature. They cannot be correlated with the periods of minimum and maximum outside temperatures. In fact, the amplitude for these periods is so low as to be negligible and does not show an inversion of the temperature levels within the cluster as compared to the temperature of the air surrounding the cluster.

The analysis of the amplitude of variation of the cluster temperatures does not indicate that the metabolic rate materially in-
creases as outdoor temperatures decline below the clustering temperature.

The contention of previous investigators that the metabolic rate did increase materially during declining outdoor temperatures has been based almost entirely upon the inversion of the temperature levels of the so-called heat-producing portion of the cluster in relation to the temperature of the air surrounding the cluster. By reference to Figures 4 to 9, inclusive, and Table II, it will be seen that there is very little in the data here presented to support such a conclusion. In eleven colonies there is no indication of such an inversion, and in the other four the inversion is so slight that it is not of material significance. The most important fact presented is that the cluster temperature remains so nearly constant and the curves tend far more towards a straight line in their mean than towards a declining line as should be the case if an inversion of importance occurred.

This fact becomes more evident if the mean cluster temperatures for all colonies during all four years are averaged, contrasting those which are recorded when the mean outdoor temperature was 15° F. or below and those when the mean outdoor temperature was 28° F. or above. The differential in the mean outdoor temperature is 24.9° F.; in the mean cluster temperature it is 0.4° F., and in the mean maximum cluster temperature it is 0.7° F. An inversion of 0.4° F. and 0.7° F. is not significant as an index to an increased metabolic rate, but rather indicates little or no mean change in the rate. The only appreciable mean inversion which occurs for any one year is 5.7° F. for 1928-29.

This situation is also made strikingly apparent by the computation of a correlation showing the relationship between the mean cluster temperature and the mean outdoor temperature. In so doing all of these temperatures for all colonies during all four years have been calculated and the coefficient of correlation is 0.053±0.026. This plainly shows that there is very little relationship between the mean cluster temperature and the mean hive temperature, even though the latter has a range varying from -2° F. to 40° F. The mean outdoor temperatures for these periods ranged from a minimum of -11.0° F. to 47.0° F. In figuring
this coefficient of correlation the colony-period population is 105, and the colony-day population is 687.

A strikingly apparent difference between the mean cluster temperatures in 1926-27 and in 1927-28 needs explanation. It is much lower for the first year. Two different races of bees were used in the experiment, which induced a variable. Later these two races were studied under exactly similar conditions, and this variable was not found to account for any possible differences in temperature reactions. No satisfactory explanation for this phenomenon was discovered until the location of the clusters with reference to the position of the thermo-couples was plotted for the two years. It then became clear that during 1926-27 the clusters were lower with reference to the couples than during 1927-28. In fact, during the first winter, records were being taken only in the upper portions of the clusters, and, therefore, do not give a true mean of either the cluster temperature or the maximum cluster temperatures. This, apparently, explains the lower tempera-

Figure 10. Hourly temperature relations for Colony No. 3, Jan. 14-15, 1930.
Curves as in Figure 4.
ture level during 1926-27. Such differences in the position of the cluster in reference to the couples was not always avoidable during the course of the experiments. However, such differences do not distort the significance of the data.

Figure 10 presents the hourly temperature relationships for the unprotected colony for a 24-hour period during a cold day in 1930. This curve is plotted to show the unlikelihood of variations occurring at certain short intervals which might be missed when the records were taken only once daily. The curves of the mean cluster temperature are exceedingly flat with only one variation of note, which indicates that major fluctuations in the cluster temperature at short intervals are not apt to occur. Many other similar records have been examined and other curves constructed with similar results and need not be included. This tends to show the reliability of the temperature records taken once daily which have been used for analysis in this report.

Temperature Relationships in Colonies Under Controlled Temperature Conditions. In order to study the temperature reactions of the winter cluster of bees under predetermined conditions, two colonies were placed in controlled temperature cabinets, which could be reduced to a minimum of 6° F. when unoccupied by any heat-producing body. The temperature in the cabinet was reduced by a thermostatically controlled Frigidaire unit, and an even level of temperature obtained by opposing this control with a bank of thermostatically controlled lights. Fresh air was maintained in the cabinet by means of a small forced draft through it.

Each colony was placed in an eight-frame observation hive, one hive body in depth. The bees were confined to the hive as the entrance was closed. Both sides of the hive were screened and the blocks removed so that so far as temperature and air conditions were concerned, the cluster was really confined in the cabinet rather than in a hive body, giving protection from external temperature conditions. In some cases the mean hive temperature was actually slightly lower than the mean cabinet temperature due to the fact that the top of the hive was very close to the cooling unit in the cabinet.
The relative humidity in the cabinet was held as constant as possible under the circumstances by means of a large pan of concentrated solution of NaCl. This could only be done, of course, as long as the mean hive temperature remained above the freezing point. During the periods of the run when the temperatures were above 32° F. the maximum variation in relative humidity was from 24 per cent to 40 per cent. For the greater share of the time the relative humidity was 32 per cent with only a 5 per cent variation. This was determined by means of a recording hygrothermograph.

Series 1 was run from November 2 to November 11, 1928. Series 2 was run from December 27, 1928, to January 30, 1929. In both cases Caucasian bees were used. Also, both clusters were small and their reactions to temperature faster than in the normal sized colonies in the outdoor experiment. In series 1 the number of bees by actual count was 17,437, and in series 2, 11,700. The bees were not placed in the cabinet until they had enjoyed two days of good cleansing flight activities just prior to their confinement.

The temperature records were taken and analyzed in the same manner as previously described for the colonies wintered under natural conditions. In series 1 the records were taken hourly.
The records for this run were such that they obviated the necessity of such frequent reading so that in series 2 they were taken every three hours.

Figure 11 presents the essential temperature data for series 1. The cluster temperature curve shows a striking positive correlation with the mean hive temperature curve, though its pitch is not so steep. This condition is the very opposite of temperature inversion, previously discussed. The couples in this series were not well centered so that the means are undoubtedly low, but this fact does not preclude the accuracy of comparisons.

It will be noted that both the mean cluster and the mean maximum cluster temperature for the coldest period are very low as compared to similar mean hive temperature conditions in the colonies wintered outdoors. They are 60° F. and 65.3° F., respectively. There are two possible explanations for this fact: first, the clusters were much smaller; second, cold air currents circulated freely about the bees contained in the cabinet.

Three major fluctuations from the mean temperature level of the cluster in this series should be noted. In chronological period 1, two sudden rises in the cluster temperature of a 2 to 3 hour duration occurred, running the maximum to 874.4° F. and 84.3° F., respectively, when the mean maximum cluster temperature for this period was 72.5° F. Again in the 6th period the maximum cluster temperature rose to 86.4° F. for two hours when the mean maximum cluster temperature for the period was 65.3° F. Otherwise the temperature levels were on a very even line for any given period.

It was observed that during these periods when the temperature of the cluster fluctuated suddenly upward, bees on the periphery of the cluster were active. In the 6th period, when the mean hive temperature stood at 22.1° F. some bees would leave the cluster, wander about aimlessly and excitedly, a few of them getting so far away that they could not return to it, and in a few minutes they would begin to stiffen and fall to the bottom of the hive in a condition of cold rigor.

On November 10th at 10 o'clock a.m. the cooling unit was started on a constant run and the heating elements turned off. By
5 o'clock, November 11th, there appeared to be live bees between only three frames. The live bees were pumping their abdomens vigorously in the same manner as bees which left the cluster and were subjected to extreme cold. Otherwise there was no apparent sign of extraordinary activity. All temperatures at this time were below $50.9^\circ$ F., and only two couples showed temperatures above that of stiffening. At 11:30 o'clock p. m. this same day no activity could be observed, and the cooling apparatus was shut off, though the cabinet remained closed.

The following morning the cabinet was opened at 7:30 o'clock and the hive removed. The cabinet temperature stood at $45^\circ$ F. Live bees were found between two frames, and as the hive warmed up to room temperature practically all of the bees revived and had to be killed with hydrocyanic acid gas in order that they might be counted.

![Figure 12. Temperature relations under controlled external temperature conditions, Series No. 2, curves as in Figure 11.](image)

The temperature data for series 2 are presented in Figure 12. In general, the curves are very similar to those of the previous series. The only difference noted is that the cluster temperatures are lower for the cold periods and higher for the warm periods.
This cluster was much smaller, which probably accounts for the first difference. The cluster was better centered with reference to the couples, which probably accounts for the second difference.

Three periods of upward rise from the mean cluster temperature are also noted in this series, which are generally similar to those previously described.

The exact chronological history of the mean cluster temperature of this colony in relation to the mean hive temperature is given in Figure 13. In general, this curve also shows a positive correlation of the mean cluster temperature with the mean hive temperature.

At noon on January 7th the cooling unit was set for constant operation and the heating element turned off. It was desired to determine the exact length of time this small cluster could withstand the minimum temperature of the cabinet under such a condition of exposure. For 19 days the mean hive temperature stood at a minimum of 15° F. and a maximum of 22° F., the usual temperature being about 18° F. At the end of this time the colony was still alive and the experiment was closed. It will be noted, however, that the mean cluster temperature on January 27th dropped to the stiffening temperature, about 45° F., and then gradually rose above it to 57° F. on January 29th. It is thought that possibly a period of excitement and activity just prior to cold rigor accounts for this rise in temperature, and that the end of the colony was not far off. Such an activity just prior to cold rigor has been observed in other insects.

It is concluded from the data here presented that within certain temperature limits below that at which the cluster forms, the mean cluster temperature is maintained on a fairly even level. This is undoubtedly possible due to the change in the rate of radiation effected by the contraction of the cluster as temperatures decline, as will be explained in detail later. However, there are certain limits to such cluster contraction, and when the temperature of the air surrounding the cluster subsides to the point that radiation, together with loss of heat by convection currents and conduction, removes the normal metabolic heat from the cluster faster than it can be produced the cluster temperature declines. This is
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Figure 11: Temperature relations under controlled external temperature conditions. Series No. 1, in chronological order of records taken. Upper curve, mean daily temperature; and lower curve, mean hive temperature. Every 3 hours.
Figure 14. Cluster contraction in relation to weather, Colony No. 1, 1927-28. Small cluster when mean outside temperature was 7.5°F. Large cluster when mean outside temperature was 31.7°F. Vertical lines represent thermo-couples seen in oblique vertical plane.

Figure 15. Cluster contraction in relation to weather, Colony No. 1, 1927-28, differentiated at 65°F, rather than 57°F. Smaller cluster when mean outside temperature was 12.3°F. Large cluster when mean outside temperature was 36.2°F.
undoubtedly true at the periphery of the cluster as well as in the so-called heat-producing portion of the cluster, here expressed in terms of mean cluster temperature. With small clusters open to a ready flow of convection currents of air, such as obtained in this experiment, this condition is reached at a comparatively high mean hive temperature and is not analogous to normal conditions outdoors with clusters of normal size, as used in the experiments previously described.

In these temperature experiments conducted with colonies placed under controlled temperature conditions, there are no data which tend to show an increase of metabolic rate as external temperature declines below the clustering temperature.
CLUSTER EXPANSION AND CONTRACTION IN RELATION TO EXTERNAL TEMPERATURES

The fact that after the winter cluster of bees has formed it contracts as outside temperatures decline and again expands as the weather warms up is well known. However, the great significance of this phenomenon apparently has not been determined, and its importance to the economy in the preservation of normal metabolic heat during extremely cold weather has not been established. By the use of the term “normal metabolic heat” here, I refer to the amount of heat energy released by normal bees which are comparatively inactive in a loosely formed cluster, just at or just below the temperature of its formation, without the previously supposed induced activity brought about by declining external temperatures.

The loss of normal metabolic heat from a cluster may be brought about in three ways, namely, conduction, convection and radiation. Conduction is not an important factor as the bees are clustered upon beeswax, a material of notably low conductivity. The rate of the loss of heat by this means under divergent temperature conditions is negligible. Likewise, the rate of loss by convection under different ranges of temperature is negligible when we consider that the method of the aeration of the hive is exactly the same at all times, and the colonies are well protected from wind, as was the case in these experiments. On the other hand, the loss of heat by radiation is the important variable factor under different external temperature conditions and is the factor to be considered in connection with cluster contraction and expansion.

The rate of radiation from a body as expressed by Boyle’s Law is: $W = sa \left(T_1^4 - T_2^4\right)$, where $W$ is the rate, $s$, the constant for the particular radiating body being dealt with, $a$, the area of the radiating body, $T_1$, absolute temperature plus the temperature of the surface of the radiating body, and $T_2$, absolute temperature plus the temperature towards which radiation is taking place.
In the application of this equation to the winter cluster of bees in a given hive, there are only two variables present. The area of the cluster is one and the temperature toward which radiation is taking place is the other. The value of constant, s, for bees is unknown, but since the same bees in the same hive are under consideration at all times it is not a variable and, for purposes of comparison rather than for the establishment of the exact rate, it may be omitted from the equation. \( T_1^4 \) remains constant if we consider that the periphery of the cluster is maintained at or near 57° F. It therefore, becomes 460 + 57 or 517 raised to the 4th power.

For purposes of comparing the ratio of the rate of radiation of a given cluster of bees under different external temperature conditions certain variable errors are apparent which it has been impossible, thus far, to measure. In the first place, the area of the cluster cannot be determined to any great degree of accuracy. It is assumed that the shape of the cluster is more or less spherical so that its area may be expressed as \( 4\pi R^2 \). However, the surface of the cluster may be somewhat irregular and its shape at times somewhat ellipsoid in general. For purposes of comparison it is assumed that it is a sphere and the area computed as \( 4\pi R^2 \). Even then the exact value of \( R \) is difficult to determine and must arbitrarily be established by the plotting of the couples that show a temperature of 57° F. or greater.

The exact value of \( T_2^4 \) is also difficult to ascertain. It is here determined by taking the mean of the couples within the hive which give the five coldest records. These couples are at the edge of the inside of the hive body and should establish this factor fairly accurately.

The assumption that the periphery of the cluster remains at 57° F. also induces a possible error as there is reason to believe that at times a slight departure from this temperature occurs, although this undoubtedly is not of any great importance for the temperature limits here considered.

In the application of this equation to the rate of radiation from the winter cluster of bees, it will be seen that as external temperatures decline \( a \) becomes rapidly less while \( (T_1^4 - T_2^4) \) in-
creases. If the decrease of $a$ is exactly compensated by the increase of $(T_1^4 - T_2^4)$, $W$, or the rate of radiation, would be the same under the two different external temperature conditions. This would mean that the contraction of the cluster during a decline in external temperatures is an adjustment to conserve the normal metabolic heat by the maintenance of a constant rate of radiation regardless of the drop in temperature toward which radiation is taking place. There is also an additional factor in the conservation of heat present brought about during periods of contraction. As the bees tighten the cluster, the closer intermingling of the branched hairs of the body creates a greater insulation value for the entire cluster by means of the smaller dead-air spaces produced. The exact value of this factor seems beyond computation, but it should here be pointed out that if the decrease of $a$ is not entirely compensated by the increase of $(T_1^4 - T_2^4)$ and $W$ is somewhat greater during cold periods, yet the internal areas of the cluster may still remain at a fairly constant temperature without the assumption of increased metabolic activity.

In view of the errors which obviously creep into the computation of the two varying factors in the equation, should $W$ in two instances of great external temperature range be within 20 per cent to 25 per cent of one another, it would seem safe to assume that cluster contraction brings about a fairly constant rate of radiation within a certain range of temperature below the cluster temperature.

In computing $W$ from the data for the years 1926, 1927 and 1928, the ratio of radiation was so nearly alike for a given cluster that a more detailed study seemed justifiable. As a consequence, the number of couples in an unpacked colony, Number 3, during the winter of 1920-30 was increased to 33, as shown in Figure 16. This facilitated the more accurate determination of both the radius of the cluster and the temperature towards which radiation was taking place.

A summary of the ratio of the rate of radiation of the cluster in this colony during cold as opposed to warm periods is presented in Table 6. All possible situations where an appreciable degree
of contrast could be brought about during four winter months have been computed. The difference in time between each cold and warm period computed was reduced to the greatest possible minimum that would still bring about an appreciable contrast. The radius of the cluster was figured in the horizontal plane only, as shown in Figure 16 for January 17, 1930, and February 19, 1930.
### TABLE VI. RATIO OF RATE OF RADIATION DURING COLD VERSUS WARM PERIODS

<table>
<thead>
<tr>
<th>Date</th>
<th>Minimum Outside Temperature °F</th>
<th>Outside Temperature when Recorded °F</th>
<th>Mean Hive Temperature °F</th>
<th>Radius of Cluster in inches</th>
<th>Rate of Radiation</th>
<th>Date</th>
<th>Minimum Outside Temperature °F</th>
<th>Outside Temperature when Recorded °F</th>
<th>Mean Hive Temperatures °F</th>
<th>Radius of Cluster in inches</th>
<th>Rate of Radiation</th>
<th>Ratio</th>
<th>Per Cent of Difference</th>
<th>Period of Maximum Rate of Radiation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-17-30</td>
<td>-41</td>
<td>-25.8</td>
<td>3½</td>
<td>428+</td>
<td>2-19-30</td>
<td>35</td>
<td>39.2</td>
<td>46.0</td>
<td>6-3/8</td>
<td>300+</td>
<td>428</td>
<td>487</td>
<td>42.66</td>
<td>Cold</td>
</tr>
<tr>
<td>1-23-30</td>
<td>-8</td>
<td>14.4</td>
<td>4½</td>
<td>457+</td>
<td>2-11-30</td>
<td>27</td>
<td>32.9</td>
<td>40.5</td>
<td>6-1/4</td>
<td>426+</td>
<td>469</td>
<td>455</td>
<td>14.31</td>
<td>Cold</td>
</tr>
<tr>
<td>12-21-29</td>
<td>-7</td>
<td>7.2</td>
<td>4½</td>
<td>455+</td>
<td>12-13-29</td>
<td>36</td>
<td>41.0</td>
<td>42.6</td>
<td>7</td>
<td>469+</td>
<td>469</td>
<td>514</td>
<td>3.07</td>
<td>Warm</td>
</tr>
<tr>
<td>11-22-29</td>
<td>-17</td>
<td>8.1</td>
<td>5</td>
<td>514+</td>
<td>11-27-29</td>
<td>26</td>
<td>39.2</td>
<td>45.0</td>
<td>8</td>
<td>389+</td>
<td>389</td>
<td>459</td>
<td>32.13</td>
<td>Cold</td>
</tr>
<tr>
<td>12-2-29</td>
<td>-7</td>
<td>15.3</td>
<td>5</td>
<td>459+</td>
<td>12-9-29</td>
<td>33</td>
<td>62.6</td>
<td>46.6</td>
<td>7-1/2</td>
<td>394+</td>
<td>394</td>
<td>627</td>
<td>16.49</td>
<td>Cold</td>
</tr>
<tr>
<td>1-30-30</td>
<td>5</td>
<td>12.1</td>
<td>5-7/10</td>
<td>627+</td>
<td>2-2-30</td>
<td>28</td>
<td>33.4</td>
<td>37.7</td>
<td>6-4/10</td>
<td>550+</td>
<td>550</td>
<td>422</td>
<td>14.00</td>
<td>Cold</td>
</tr>
<tr>
<td>1-21-30</td>
<td>-31</td>
<td>-18.0</td>
<td>4-3/10</td>
<td>422+</td>
<td>2-6-30</td>
<td>30</td>
<td>34.5</td>
<td>43.0</td>
<td>7</td>
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<td>457</td>
<td>584</td>
<td>8.29</td>
<td>Warm</td>
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<tr>
<td>11-13-29</td>
<td>-2</td>
<td>9.5</td>
<td>5-1/2</td>
<td>584+</td>
<td>11-17-29</td>
<td>20</td>
<td>47.8</td>
<td>42.4</td>
<td>8</td>
<td>621+</td>
<td>621</td>
<td>547</td>
<td>6.33</td>
<td>Warm</td>
</tr>
<tr>
<td>1-9-30</td>
<td>-8</td>
<td>0.5</td>
<td>4-8/10</td>
<td>547+</td>
<td>12-30-29</td>
<td>32</td>
<td>46.9</td>
<td>41.2</td>
<td>6-1/10</td>
<td>389+</td>
<td>389</td>
<td>541</td>
<td>40.61</td>
<td>Cold</td>
</tr>
<tr>
<td>11-29-30</td>
<td>-21</td>
<td>-0.4</td>
<td>4-8/10</td>
<td>541+</td>
<td>11-23-29</td>
<td>24</td>
<td>39.2</td>
<td>48.0</td>
<td>8</td>
<td>389+</td>
<td>389</td>
<td>18.158</td>
<td>39.07</td>
<td>Cold</td>
</tr>
</tbody>
</table>

**Mean**: 18.158 Cold
Since the ratio of radiation under the different temperature situations, rather than the exact rate, was desired, $W$ is here expressed in 3 figures plus. The greatest difference in the ratio of any two periods computed is 42.66 per cent and the least 3.07 per cent. However, since the rate in 3 instances was greater for the warm periods, and in 7 greater for the cold periods, the mean difference shows 18.158 per cent greater radiation during the cold situations. The probable error of this mean is $\pm 3.425$ per cent.

If the mean hive temperatures during the 10 cold and 10 warm periods are figured with the assumption that the cluster would not contract during cold weather, the ratio of the rate of radiation would become $\frac{1.133}{439}$, or an increase in radiation during the cold periods of 158.08 per cent. This would be 8.70 times the percentage of increase shown in Table VI, which, with a probable error of only $\pm 3.425$ per cent, points out the great importance of the conservation of normal metabolic heat by the decrease of radiation by means of cluster contraction.

These preliminary data on this problem are presented as supporting evidence to the temperature studies, and further intensive studies will be made on it.

These figures suggest that a natural law may be involved which may be stated as follows: As external temperatures decline below the clustering temperature the cluster of bees contracts, thereby reducing the surface area from which loss of heat takes place, bringing about a fairly constant rate of radiation, down to the point of minimum cluster contraction.

Naturally, there is a limit to which the contraction can progress. When this limit is reached the rate of the loss of heat by radiation will materially increase. Such a situation was evident in both series of experiments conducted under controlled temperature conditions. It was evidenced by an extreme lowering of the mean cluster temperature. It has not been apparent in any of the colonies with nominal-sized clusters studied under outdoor conditions.

Some of the differences in the various clusters under cold and warm external temperature conditions are shown in Figures
14, 15 and 16. Three minor points of some significance are noteworthy. First, very little contraction and expansion is evident in the packed colonies. Second, a definite cluster never formed in packed Colony Number 1 during 1927-28, whereas a contracted cluster was evident in the companion Colony Number 1 during two cold periods of 1926-27. In order to depict any difference in the size of the space occupied by the bees in the packed colony during 1927-28, it was necessary to differentiate at a temperature of 65° F. rather than 57° F. During the entire winter period all of the couples within the upper hive body of this colony stood at 57° F. or above, yet it used more stores than any other colony and showed a 35.1 per cent loss of bees in the spring as compared with 5.8 per cent for the unpacked colony and 2.7 per cent for the tar-paper packed colony with upward ventilation. The failure of this colony to form a definite winter cluster is explained by the fact that it was provided with 8 inches of bottom packing, whereas this was omitted from the packed colony during 1926-27, as previously explained. Third, all clusters were lower during 1926-27 with reference to the position of the couples than during 1927-28. This accounts for the difference in the cluster temperatures of the two years, which has previously been discussed.

The data on the rate of radiation from the winter cluster of bees as affected by the contraction and expansion of the cluster also lend weight to the proposition that as external temperatures decline below the clustering temperature there is no material increase in the metabolic rate. Previously it has been noted that the mean cluster temperature remains on a fairly constant level under very wide temperature conditions externally. If the area of the surface remained constant it would be evident that the maintenance of such a level during cold periods could not obtain without an increase in metabolic rate due to increased consumption of honey and extra-normal activity. However, the contraction of the cluster obviates such a necessity within certain limits, and when these limits are passed the mean cluster temperature declines without any apparent increase in metabolic rate.
GENERAL DISCUSSION

Flight Periods. Possible condensation of metabolic water within the hives during cold periods as a variable factor in the analysis of the daily loss in weight data has been taken into consideration. It must also be recognized that flight activities during the warm periods increase the metabolic rate. Just what the extent of this increase amounts to is difficult to determine. It is evident, however, that the flight activity of bees, even though the hive temperatures are below 57° F., greatly increases their metabolism. This would seem to be of more importance in the expenditure of the physiological reserve of bees during the winter than the effect of the cold periods studied. In the practical application of the data herein presented, the prevention of excessive and unnecessary flights by insulation or otherwise must not be overlooked.

The flight activities of the colonies in this experiment during the last three years were recorded. In general, they show, first, that bees in all types of protection had flights at about the same time, though the reaction each day in the single packing cases was slower and less general and, second, generally good cleansing flights occurred over periods with a mean temperature of 35° F. or above, with flights of a lesser degree down to about 30° F.

Winter Protection. It is not to be concluded that it is wise to dispense with all winter protection to the bee colonies in cold climates. Recognition should be given to the fact that if there are protracted periods of sub-zero weather the bees will use up their reserve supply of honey within the cluster. Because the external temperatures during such a period may be below the minimum critical temperature for life, which is 30.25° F. according to Pirsch (10), the bees cannot leave the cluster which has contracted away from their food supply and replenish their stores. Likewise, regardless of this fact, there will be periods when the loss of heat from the cluster cannot be further reduced by the contraction of the cluster, and its loss will be greater than its compensation by the activity of the bees. Consequently they perish.
However, no such periods of weather were available during the course of these experiments. The apparent resistance to cold which the bees displayed was, indeed, remarkable. One unpacked colony out of the entire series died during January 7, 1930. Another unpacked colony beside it, and presumed to be generally similar to it, showed no ill effects of the cold. It is not clear whether the long, cold period, alone, caused the demise of this colony, or if there were other contributing factors. It is likely, however, that there was real danger to unpacked colonies at this time, although none was lost out of the general apiary under similar conditions. During this critical period of 16 days' duration all but three days had sub-zero minimums, one of which dropped to $-41^\circ$ F. The mean minimum temperature for this period was $-12.2^\circ$ F. and the mean maximum $18.3^\circ$ F. One day remained sub-zero for 24 hours. The highest temperature reached during the period was $30^\circ$ F. That all but one of the unpacked colonies survived such a severe and long period of cold weather was truly astounding.

The different understanding of the reaction of the winter cluster to cold weather resulting from these data harmonizes with practical experience in wintering bees in the intermountain region. In relatively few instances have the commercial beekeepers packed their bees in accordance with the standards generally recommended. On the whole, they have used far less winter insulation, and in some instances none at all, than has been advised in the majority of publications upon the wintering of bees. Each commercial beekeeper has arrived at his own requirements by trial and error, and from the standpoint of protection from cold alone the beekeepers have doubtless come closer to the ideal than some of the published recommendations.

These data also intensify the importance of other recognized standards essential to the successful wintering of bees. It is certain that too much stress cannot be placed upon the supply of a sufficient quantity of the best quality of stores from the standpoint of freedom from dextrine and the propensity to granulate, properly placed in the hives; the provision of young queens; the establishment of a normal colony of good strength containing both old
and young bees; sufficient ventilation of the colony at all times; and protection by a good windbreak from the prevailing winds. In addition to these, there is indication that attention should be given to the prevention of unnecessary flights, especially during the fall and early spring periods. This point needs further investigation and an inquiry into practical ways and means.
SUMMARY

The data from four years experimentation upon the metabolism of the honeybee colony during winter indicate that as external temperatures decline below the clustering temperature, the metabolic rate is not materially increased or possibly is not increased at all. There are three reasons for this conclusion:

1. The daily loss in weight of colonies with all types of protection is less for the cold periods than for the warm periods of the winter. A summary of all colonies during all periods studied when the mean outside temperature was above 28°F shows a daily loss in weight 84.4 per cent greater than during all cold periods when the mean outside temperature was 15°F or below.

2. The mean cluster temperatures in the so-called heat-producing region remained remarkably constant regardless of outside weather. In eleven out of fifteen colonies there was no inversion of the cluster temperature in relation to the outside temperature during the coldest periods of four winters, and the four cases of inversion are so slight as to be insignificant. The coefficient of correlation between the mean cluster temperature and the mean outside temperature is only $0.053 \pm 0.026$. It should be noted that this slight correlation is positive, whereas marked inversion should show a high negative correlation.

3. Cluster contraction during cold weather permits of the conservation of normal metabolic heat down to a variable limit. In the colony critically studied, the rate of radiation from the surface of the cluster during the coldest weather was increased only 18.15 per cent $\pm$ 3.45 per cent, contrasted to periods of so-called ideal clustering temperatures. The difference in the mean outdoor temperature for these periods of differentiation was 40.4°F. Had there been no contraction of the cluster, the rate of radiation would have increased 158.08 per cent.
ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the cooperation of two assistants in the department in the prosecution of this research. My sincere thanks are due Mr. C. H. Gilbert, Assistant Research Apiculturist, for his assistance and suggestions in setting up the equipment and in the taking of records. During the winter of 1929-30 he was wholly responsible for this part of the work. I am also grateful for the help of Mr. H. L. Sweetman, Assistant Research Entomologist, in securing the records and their tabulation for the first two years.
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The following bulletins of the Wyoming Experiment Station may be had upon request. (Revised list, November, 1930.)

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