PHYSIOLOGY OF THE TEMPERATURE OF BIRDS

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By

S. Prentiss Baldwin

and

S. Charles Kendeigh

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VOLUME III

PUBLICATIONS OF THE CLEVELAND MUSEUM OF NATURAL HISTORY

The publications of the Cleveland Museum of Natural History appear in six series, as follows:

1. *Scientific Publications,* consisting of natural history and anthropological papers of technical character, of varying length and appearing at irregular intervals.

   Of this series, all of Volume I, containing numbers 1-5, issued, 1928–1931; Volume II, issued in one number, 1931; and Volume IV, number 1, issued, 1932, have already been published. The present contribution constitutes Volume III complete.

2. *Popular Publications,* which are non-technical articles of general natural history or anthropological interest, issued also at irregular intervals.

   Of this series, numbers 1-2 of Volume I have appeared, 1928-1931.

3. *Bulletin,* containing short popular, educational, or semi-technical articles on natural history and anthropology; notes on the Museum's activities; and the Museum's announcements. It is published monthly, except in July and August.

   Of this publication, numbers 1-54 have been issued, 1922-1931.

4. *Pocket Natural Histories,* consisting of popular pocket educational manuals for the information of students in natural history and anthropology, including keys and illustrations for the ready identification of species.

   Of this series the following have been published:

   No. 1—Trees of Ohio, 1922.
   No. 2—Indian Homes, 1925.
   No. 3—Mound Builders, 1925.

5. *Annual Report,* containing the report of the Director and the reports of the different departments of the Museum, setting forth their activities during the preceding year.

   Two of these have been published, those for 1929 and 1930.

6. *Miscellaneous Publications,* comprising educational leaflets; and such other publications of local or temporary interest as descriptions of the Museum and its work, post cards, cards for games, lecture and other programs, and announcements of other Museum activities.

   A considerable number (about 100) of such publications have already appeared.

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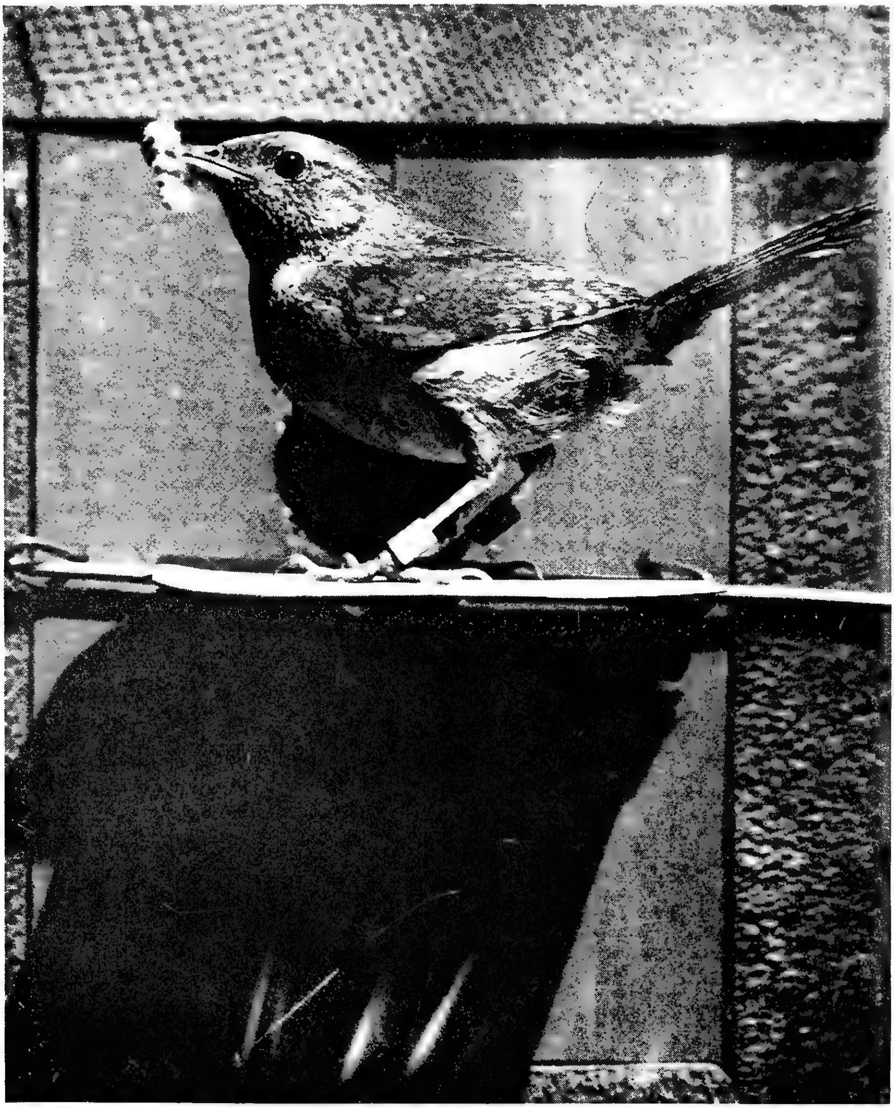
Physiology of the Temperature of Birds



Eastern House Wren *(Troglodytes aedon aedon).*

The bird is standing on the trap-perch of its nesting box. Note the numbered aluminum band for identification around the left leg, and the colored celluloid band indicating sex around the right leg. *(Natural size.)*

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Vol. III | Issued, October 15, 1932 | Vol. III

PHYSIOLOGY OF THE TEMPERATURE OF BIRDS

BY

S. Prentiss Baldwin and S. Charles Kendeigh

Contribution No. 21
from The Baldwin Bird Research Laboratory
Gates Mills, Ohio

OCT 20 1932

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INTRODUCTION

HISTORICAL ACCOUNT

Temperature is a factor of primary importance in both the physiology and ecology of animals. The rate at which most physiological processes function is determined largely by temperature. In fact, the maintenance of a certain degree or range of temperature within the body is essential for the proper functioning and coordination of physiological processes in most warm-blooded (homoiothermic) animals. If this temperature is not maintained, dormancy, improper functioning of organs, or even death may result. This subject of the temperature of animals long ago attracted the attention of investigators.

An extensive general account of animal temperatures is given by Edwards (1839) and this contains much on the temperature of birds. Gavarret's account, coming at a somewhat later date (1855), is excellent for those interested in following the history of this subject. Pembrey (1898) summarized most of the literature up to near the end of the 19th century, not only on mammalian and human temperatures, but also on the physiology of bird temperature. The best modern accounts of animal temperature are those of Pütter (1911), Lusk (1921), Barbour (1921), Starling (1926), and Bazett (1927). These texts, however, deal only incidentally with birds.

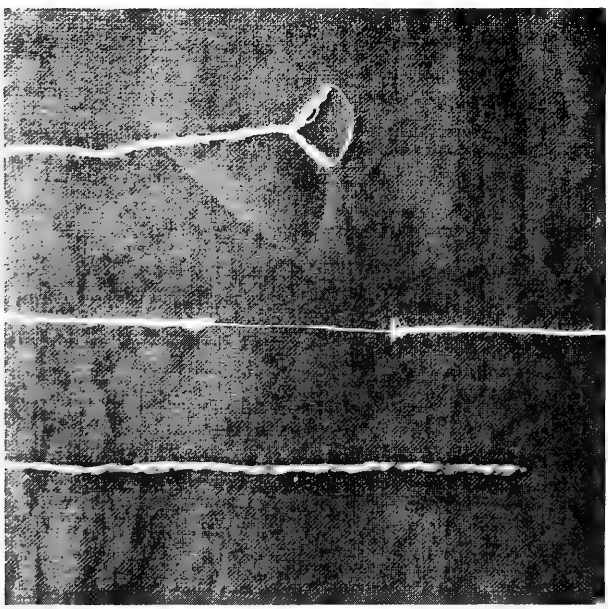
The chief students of the temperature of birds in the twentieth century have been Simpson (1905-1912), Hildén and Stenbäck (1916), Bergtold (1917), and Wetmore (1921), although others have done valuable work along more restricted lines. Groebbel's work (1920-1928) on the metabolism of birds is important for a satisfactory understanding of the factors influencing temperature.

Our first work on this study of the physiology of the temperature of birds was done in 1926. Aside from a brief description of method (Baldwin and Kendeigh, 1927), and a short report describing the development of temperature control in nestling house wrens (Kendeigh and Baldwin, 1928), we have published nothing on bird temperature up to this time (1932). The present contribution is intended to serve for a preliminary survey of the whole field and for the presentation of results thus far obtained. Final results and conclusions have not been obtained on any one phase of the general problem. Each item in the physiology of bird temperature is now ready for more detailed and analytical investigation. The survey here presented will aid in orienting and correlating such special studies in the problem of bird temperature. We have ready for publication by Kendeigh such a concentrated study on the resistance of birds to environmental cold and heat, and have started a detailed study of temperature and other factors involved in incubation.

Much is to be learned from the correlation of physiology and behavior in birds. Bird behavior is determined as much by physiological "urges" as by nervous reactions to external stimuli. In this report, stress is placed more on working out the physiological side than on correlation with behavior, although a beginning has been made in the latter. An interpretation of some of these data with respect to the abundance, migration, and distribution of birds will follow in the paper by Kendeigh to which reference has already been made.

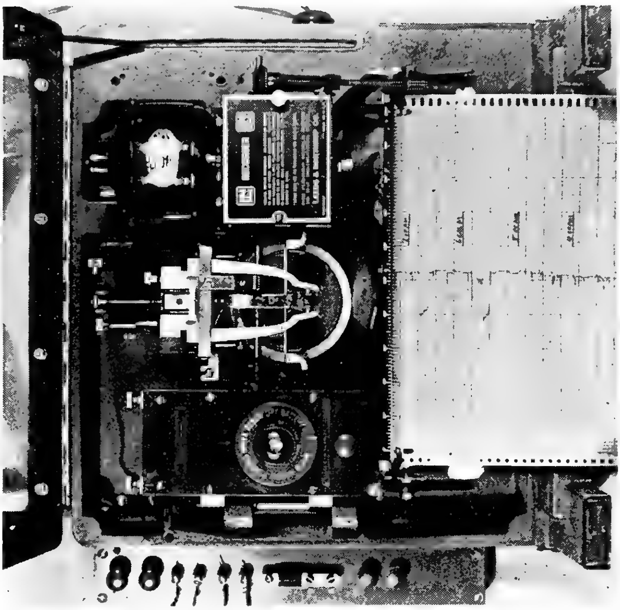
ACKNOWLEDGMENTS

Acknowledgments are due several persons who have aided more or less directly in this study. We are constantly under obligation to Dr. C. Baldwin Sawyer, president of the Brush Laboratories in Cleveland, Ohio, who has assisted by suggesting and constructing useful instruments and apparatus as well as aiding us in the mechanics of their use. The manuscript was read for criticism in whole or in part by Dr. Victor E. Shelford, Dr. Leon J. Cole, Dr. Harry C. Oberholser, and Dr. C. J. Wiggars. The following assistants at the Baldwin Bird Research Laboratory, Gates Mills, Ohio, have aided in various ways: Rudyerd Boulton, W. W. Bowen, C. H. Johnson, T. C. Kramer, James Stevenson, and L. G. Worley.



A.—TYPES OF THERMOCOUPLES.

The one on the left is for internal body temperature (thermocouple thermometer); the one in the center is for nest temperature (thread thermocouple); and the one on the right is for skin temperature (loop thermocouple).



B.—RECORDING POTENTIOMETER.

PURPOSE OF THE STUDY

Variation in body temperature may be produced both by internal and external factors. The main source of heat in the body lies in the general metabolism of the tissues and particularly of the muscles. Anything that disturbs the metabolism of the body is very likely to modify the body temperature unless proper compensation is made.

External factors may affect the temperature of the body through increasing or decreasing heat loss from the organism, and through modifying internal heat production. Low environmental temperature greatly lowers the body temperature of cold-blooded (poikilothermic) animals. In warm-blooded organisms, this depressing action is compensated for by increased heat production and decreased heat loss. Some organisms are able to adjust to changes in environmental temperature more than others, while some species withstand certain degrees of temperature which others cannot. Temperature is thus a factor in the distribution of organisms, and plays an important role in the activities of most species.

Birds have the highest constantly maintained body temperature of all animals, except for those few forms of low organization occurring in hot springs or under certain peculiar conditions in the tropics. Mammals have a lower temperature than birds, and their temperature usually varies only within comparatively narrow limits. Monotremes and hibernating mammals form exceptions to this rule. The body temperature of at least the higher species of birds is variable over a wide range. As a result of this, the influence of external and internal factors on body temperature may be profitably studied in these forms.

The purpose of the present study then is partly to learn the physiology of bird temperature, and partly to discover the relation existing between these temperatures and the environmental conditions under which the bird lives.

PHYSIOLOGICAL POINT OF VIEW

Very little is known about the physiology of bird temperature, except in a general way. This is due to the previous difficulty of obtaining living wild birds in sufficient number and variety with which to work, to the difficulty of obtaining the right sort of instruments with which temperature may be properly taken, and to the easier use of mammals and man in studies of body heat and metabolism. With proper methods of capturing and handling birds, however, they offer subjects for a wide range of experimental purposes, and are of considerable value in studies of such physiological problems as temperature.

The temperature of birds was studied in this work under both laboratory and field conditions. Attempt was made to study all phases of the problem both under controlled conditions, for the purpose of analyzing the reactions more closely; and under natural conditions, where the relation between the normal behavior of the bird and natural environmental conditions could more easily be observed. One set of experiments served as a check and control for the other, and so the advantages of both methods were obtained.

Most of this study and experimentation was carried out on the Ohio subspecies of the house wren, the eastern house wren, *Troglodytes aedon aedon*.[1] Other species are considered, but no extensive comparative work was done on them. This was due partly to the limitations of equipment and time, and partly to the desire for analyzing the factors involved in the physiology of one bird as fully as possible before special effort was applied to other forms. We are reasonably sure, however, that the reactions of this species are typical of at least the large order of Passeriformes.

ECOLOGICAL POINT OF VIEW

All living organisms are affected by external conditions to a greater or less extent. To meet changes in the environmental factors which occur regularly during different seasons of the year, between different localities, and during different activities, there must be internal physiological adjustments. The physiological processes of an organism are in large part conditioned by the external environment in which it finds itself. This is true with temperature fully as much as with oxygen supply, available food and drink, and barometric pressure. It is necessary, then, when one undertakes to study the physiology of such sensitive and responsive organisms as birds, to consider the ecological conditions in which the organisms live and to interpret his findings in rela-

[1]See footnote on page 10.

tion to these conditions. The physiology of bird temperature is probably different and the bird's activities and responses to environmental conditions much changed in the tropics from what they are on the Arctic tundra, or on the deserts of the southwestern United States from what they are in the mild temperate eastern portion.

The subspecies with which we are most concerned here, the eastern house wren, *Troglodytes aedon aedon*,[2] is a seasonal member (socies) of two ecological communities in the eastern part of the United States and Canada—the Acer-Fagus (hard maple-beech) Association, and the Quercus-Castanea (oak-chestnut) Association. It remains as a constituent member in these biotic communities from the last of April to the first of October. Within these associations, the species may be found most commonly in subclimax plant and animal communities developing after fires or lumbering operations, or around human habitations. Its presence in any particular locality within these habitats is determined largely by the availability of nesting sites. During the winter season, it is found rarely in the climax Quercus-Castanea (oak-chestnut) Association, more commonly southward in the subclimax southern pine forest (Pinus Associes), and rather abundantly in Florida where it enters the magnolia-bay forest (Magnolia-Tamala Association) in the northern part of the state, and the sub-tropics in the southern part. It migrates in the spring and fall between these two areas. In its ecological relationships, this species appears to be more or less typical of a large portion of the avifauna of these ecological communities.

SCIENTIFIC NAMES OF BIRDS INCLUDED IN THIS STUDY

In the use of names we here follow the American Ornithologists' Union Check-List of North American Birds, Fourth Edition, 1931.

Eastern Bob-white, *Colinus virginianus virginianus* (Linnaeus).
Killdeer, *Oxyechus vociferus vociferus* (Linnaeus).
Eastern Mourning Dove, *Zenaidura macroura carolinensis* (Linnaeus).
Ruby-throated Hummingbird, *Archilochus colubris* (Linnaeus).

[2]See footnote on page 10.

Northern Flicker, *Colaptes auratus luteus* Bangs.
Red-bellied Woodpecker, *Centurus carolinus* (Linnaeus).
Eastern Hairy Woodpecker, *Dryobates villosus villosus* (Linnaeus).
Northern Downy Woodpecker, *Dryobates pubescens medianus* (Swainson).
Northern Crested Flycatcher, *Myiarchus crinitus boreus* Bangs.
Eastern Phoebe, *Sayornis phoebe* (Latham).
Eastern Wood Pewee, *Myiochanes virens* (Linnaeus).
Purple Martin, *Progne subis subis* (Linnaeus).
Eastern Crow, *Corvus brachyrhynchos brachyrhynchos* Brehm.
White-breasted Nuthatch, *Sitta carolinensis carolinensis* Latham.
Eastern House Wren, *Troglodytes aedon aedon* Vieillot.[3]
Catbird, *Dumetella carolinensis* (Linnaeus).
Brown Thrasher, *Toxostoma rufum* (Linnaeus).
Eastern Robin, *Turdus migratorius migratorius* Linnaeus.
Wood Thrush, *Hylocichla mustelina* (Gmelin).
Eastern Bluebird, *Sialia sialis sialis* (Linnaeus).
Cedar Waxwing, *Bombycilla cedrorum* Vieillot.
Starling, *Sturnus vulgaris vulgaris* Linnaeus.
Eastern Yellow Warbler, *Dendroica aestiva aestiva* (Gmelin).
Northern Yellow-throat, *Geothlypis trichas brachidactyla* (Swainson).
English Sparrow, *Passer domesticus domesticus* (Linnaeus).
Eastern Cowbird, *Molothrus ater ater* (Boddaert).
Eastern Cardinal, *Richmondena cardinalis cardinalis* (Linnaeus).
Red-eyed Towhee, *Pipilo erythrophthalmus erythrophthalmus* (Linnaeus).
Eastern Chipping Sparrow, *Spizella passerina passerina* (Bechstein).
Eastern Field Sparrow, *Spizella pusilla pusilla* (Wilson).
Eastern Song Sparrow, *Melospiza melodia melodia* (Wilson).

[3]The subspecific status of the Ohio house wren is at present under investigation; but pending any necessary change in name, we are following current usage in calling this bird the eastern house wren.

METHODS OF STUDY

RESEARCH FACILITIES

The Baldwin Bird Research Laboratory is the only biological laboratory either in this country or abroad that is devoted chiefly to the physiological and ecological life-history studies of wild birds. As a result, new methods of attack and new approaches to problems have had to be worked out independently.

A building of ample size, conveniently situated, and well supplied with instruments and other equipment, makes possible the carrying out of all manner of experiments with the birds available.

Around the laboratory building there is a bird sanctuary of 15 acres where approximately 125 nests are studied each season. Of these nests, about 16 belong to eastern house wrens, involving 8 to 10 pairs of birds. The proximity of the nests allows intensive study of these birds.

Numerous traps of various sorts are available in this sanctuary for capturing many species of birds. Some 2000 birds are handled in the active living condition each season. They are handled not only once but many times during the year without disturbing their normal nesting behavior in any material way. In the case of the eastern house wren, the birds are captured at their nests. All these nests are in boxes (Frontispiece; Plate IV–B) so that the bird must enter or leave through a narrow entrance hole. A trap perch on the outside of the entrance, pulled shut over the hole by a string, permits the bird to be captured in the box at will.

In addition, numerous birds for experimental use are brought in from outside this immediate area around the laboratory. These are mostly house wrens. Some 400 nest boxes have been located on various neighboring estates, and constant record is kept of all activities. About 150 adult house wrens and 800 young birds are handled each year, making available a large number of individuals for physiological study. It is with these resources that the study of the temperature of birds is conducted.

The modern methods of bird banding originated at this laboratory (Baldwin, 1919). This is mentioned because the exact and continuous identification of the individual bird furnishes the basis for this study as well as all lines of research at the laboratory. Each bird is identified by a numbered aluminum band placed around its leg. The bands are issued by the Bureau of Biological Survey, Washington, D. C., and all work is done under permit issued by the Biological Survey.

INSTRUMENTS USED

Mercury thermometer.—Thermometers at first, and thermocouples later, were used in this investigation. The thermometer has been the standard instrument in clinical diagnosis since the days of Boerhaave, 1668–1738. It has been and is still being used in much physiological work. Wetmore (1921) used the thermometer entirely in his study of bird temperature.

All the mercury thermometers used at this laboratory were especially adapted and constructed for our purposes. They were fashioned after the ordinary clinical thermometer commonly used by physicians. However, they differ from the clinical thermometer in registering temperatures from 90° to 115° F., instead of to 110° F. only. The thermometers are self-registering like the clinical type, but their diameters are smaller and their bulbs in some cases are longer.

After experimenting with readings down the throat, through the anal opening, under the wing, and on the belly, it has been found that the most accurate method of obtaining the bird's temperature is to thrust the thermometer down the throat of the bird until it has penetrated well down next to the body cavity, which means usually that the bulb is down the gullet as far as the proventriculus. It is then left several seconds until the mercury ceases to rise, when it is removed and read. All the thermometers have a certified accuracy of one-tenth of a degree, Fahrenheit scale. In this way several temperatures were taken of different species of birds. Table I illustrates the type of results that is obtained by this method.

TABLE I.—*Body Temperature of Adult Birds Taken with a Mercury Thermometer*

Species	Sex	Number of Records	Average Body Temperature
Eastern bob-white	Male	1	111.2° F. (44.0° C.)
Eastern mourning dove	?	4	108.8° F. (42.7° C.)
Ruby-throated hummingbird	Female	1	108.0° F. (42.2° C.)
Red-bellied woodpecker	Female	1	109.8° F. (43.2° C.)
Northern downy woodpecker	Male	1	108.1° F. (42.3° C.)
" " "	Female	2	108.4° F. (42.4° C.)
Northern flicker	Male	1	109.2° F. (42.9° C.)
" "	Female	1	107.5° F. (42.0° C.)
Eastern phoebe	Male	1	110.0° F. (43.3° C.)
" "	Female	1	110.9° F. (43.8° C.)
Northern crested flycatcher	Female	2	111.4° F. (44.1° C.)
Purple martin	Male	1	108.2° F. (42.3° C.)
" "	Female	1	110.4° F. (43.6° C.)
Eastern yellow warbler	Male	1	108.0° F. (42.2° C.)
" " "	Female	1	110.2° F. (43.4° C.)
Eastern crow	Male	1	106.0° F. (41.1° C.)
Eastern bluebird	Male	1	107.1° F. (41.7° C.)
" "	Female	2	110.0° F. (43.3° C.)
Eastern robin	Male	3	109.6° F. (43.1° C.)
" "	Female	2	109.5° F. (43.1° C.)
Catbird	?	1	108.4° F. (42.4° C.)
Eastern house wren	Male	18	108.6° F. (42.6° C.)
" " "	Female	21	108.2° F. (42.3° C.)

These records have a certain amount of value since they give an approximate idea of what the temperature of the bird may be at any one instant. However, as will be shown later, the temperature of birds, at least in the higher Passeriformes, is exceedingly variable, and these variations cannot well be followed by this type of thermometer. No one temperature observation is of great significance. After any one reading is taken the thermometer must be removed and the mercury shaken down before a new reading can be taken. As the bird is usually excited and agitated when first captured and handled, the temperature, if taken at once, will not have the same significance as when the bird has later become quiet and at ease. Also, as we have shown in a previous paper (Kendeigh and Baldwin, 1928), the thrusting of a cold thermometer into a young bird may cause an appreciable lowering of its body temperature, even to several tenths of a degree. Later additional determinations on juvenal English sparrows verify this effect even to the extent of four-tenths or five-tenths of a degree Fahrenheit. This depressing effect on body temperature was determined by taking first a reading of the body temperature by means of a thermocouple (Plate I–A) thrust through the anal opening into the rectum, then inserting the mercury thermometer down the throat, and then taking another reading of the body temperature with the thermocouple in the rectum. The two readings of the thermocouple could then be compared with that of the mercury thermometer. Due to these disadvantages and to the fact that another and better method of obtaining temperatures was developed, the use of the thermometer, in this study, was discarded at the end of the second season's work. Aside from one or two phases of the work, all this study is based on records obtained by the use of the thermocouple. Using thermocouples, the bird's temperature may be followed continuously over almost indefinite lengths of time.

Thermocouple.—According to Kimball (1917), knowledge of the principle of thermoelectricity dates back to 1821, when Seebeck, of Berlin, discovered that "in a circuit made of two different metals if one junction is hotter than the other there is an electromotive force which causes an electric current." Thus if two different

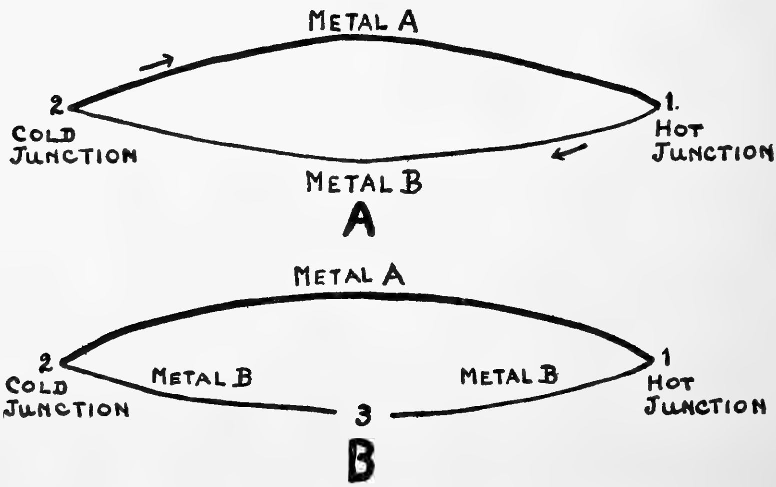


FIGURE 1.—THERMOELECTRIC CIRCUIT (THERMOCOUPLE).

metals, designated A and B above (Figure 1–A), be joined together at points 1 and 2, and point 1 heated to a temperature higher than point 2, a current will flow around the circuit. The direction of the current depends on the character of the metals used. If the thermoelectric circuit be broken at any point, as at point 3 in the diagram (Figure 1–B), the current, of course, will cease flowing, and a difference of potential or electromotive force will appear.

The magnitude of this electromotive force depends on the temperature difference between points 1 and 2, and furnishes a means of measuring this temperature difference. If one of the junctions, for example the cold junction at point 2, be maintained at a constant temperature, the temperature at point 1 is determined when the electromotive force is known. This, in brief, is the principle and basic nature of the thermocouple.

Becquerel and Breschet in 1838 appear to have been the first to make serious use of the thermocouple in physiological work. Using thermocouples of copper and steel they investigated the temperature of the mouth and certain of the tissues and internal organs of the body in man and some of the lower animals. The history of the use of thermocouples has been reviewed by Gamgee (1908) and Karrer and Estabrook (1930). Thermocouples are now being used rather generally by physiologists.

We first used thermocouples and a recording potentiometer to obtain continuous day and night records of bird activities at the nest (Baldwin and Kendeigh, 1927), but we have since developed the instrument to do accurate temperature work.

All the thermocouples that we have used have been made of copper and constantan (an alloy of copper and nickel). All the wires are silk insulated, and the warm junction is made by soldering together the ends of the two metals.

The thermocouple junction may be prepared in various ways, dependent on the purpose to be served (Plate I–A). For obtaining internal body temperatures the wires back of the junction are twisted around each other so that a *thermocouple thermometer* is formed. The wires are well insulated except at the soldered tip, so this is the only point effective in taking temperatures, since it is the only point where the two metals are in contact. To insure further protection and insulation, a coating of collodion is given the wires for three or four inches back of the junction; this, when dried, forms a firm, flexible, waterproof covering. For obtaining body temperatures, this thermometer is thrust down the gullet of the bird so that the junction is usually as far as the proventriculus. It was found that unless the junction were inserted this far a difference of two or three degrees would result, since the temperature of the upper neck and mouth is lower than that of the body proper. There was no evidence from the results obtained or from the actions of the bird that, except in a few unusual cases, there was any local congestion or irritation as the result of the presence of the thermocouple. In fact, at times, the birds actually went to sleep with the thermocouple two or three inches down their throats. The thermocouple could be left in the bird as long as desired and numerous readings taken.

For obtaining skin temperatures a modification of the thermocouple thermometer is used. In this, a loop is left just back of the junction before the wires are twisted around each other. This permits the junction to lie flat on the skin and to be thrust up underneath the feathers. Also, collodion is not used to coat these wires. This we call our *loop thermocouple* (Plate I–A).

The *thread thermocouple* (Plate I–A) is best for getting nest temperatures. This is made simply by soldering the tips of the two metals to each other and not twisting them together. The thermocouple can then be stretched either above or below the eggs as a continuous thread or wire extending from one side of the nest to the other.

Recording potentiometer.—Owing to the small magnitude of the electromotive forces involved in the use of thermocouples (generally less than .002 volt in the work to be described), only the most delicate and sensitive instruments can be employed for their measurement. We have used both recording and indicator instruments. When a continuous record of temperature variations is to be made, the recording instrument must be designed not only for great sensitiveness, but also for strength enough to make the record. The Leeds and Northrup Company have developed such a recorder (Plate I–B). Their instrument is operated in conjunction with a thermocouple composed of the two metals, copper and constantan. The two thermocouple wires are run directly to the recorder, which is therefore at the same temperature as the cold junction. An electrically compensating device, embodied in the instrument, automatically corrects for external temperature variations at the recorder and gives as true an indication of temperature at the warm junction, as though the cold junction were maintained constant at zero.

The recorder operates on the potentiometer system, by which a small sensitive galvanometer needle is caused to swing to the right or left whenever the warm junction is at a temperature higher or lower than that indicated on the recorder (Figure 2). At once,

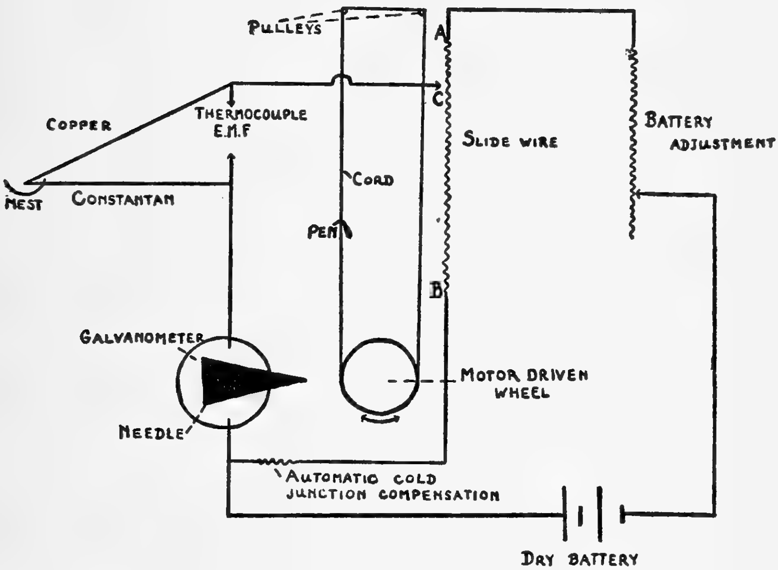


Figure 2.—Electrical Connections in a Recording Potentiometer.

through the agency of levers, cams, etc., a small electric motor causes a wheel, attached by a cord to the recording pen, to rotate one way or the other until the temperature indicated by the recorder is again the same as that at the warm junction. At this point the galvanometer needle is again in its neutral position and the recording pen is at rest.

When at rest, the electromotive force of the thermocouple is exactly balanced with a potential produced by two dry cells. The potential of the dry cell current is greater at A than at B and passes gradually from the first extreme to the second because of the increasing resistance in the slide wire. Thus by varying the location of point C, through the revolving of the wheel mentioned in the paragraph above, any thermocouple potential may be balanced against an equal potential in the dry cell circuit. The two potentials are of opposite polarity, and so oppose each other. Hence, when the two potentials are equal, no current flows around the thermocouple and a uniform temperature record is produced. When the thermocouple potential becomes greater or less than the potential of the dry cell circuit at point C, a current flows around the thermocouple until C is shifted to a point between A and B which will make the two potentials again equal.

The recording pen attached to the cord bears on a paper rolled past at a constant speed by means of the same small motor above mentioned. Thus there is furnished a paper and ink record of temperature variations with the time of each. This paper is marked in degrees of temperature, and the instrument can be adjusted to use either the Centigrade or Fahrenheit scale. We have given some thought to the question of which scale should be used for the temperature studies in our laboratory, and finally decided to use Fahrenheit, because it is in more general use in America, particularly by physicians, is better understood by most people, and its unit of measurement is smaller. However, in all the tables and figures given in this paper, the Centigrade equivalents are included in parenthesis immediately after the Fahrenheit temperatures.

The operation of the recorder requires a small amount of power from the electric light circuit and also the daily standardization of the current from the dry cells. The recorder is placed in the laboratory, and wires are run out to any nest near at hand. The warm junction end of the thermocouple is placed in the nest. The thermocouple wire at this point is thin and flexible, and is run from one side of the nest box through the nest just above the eggs (if it is eggs that happen to be in the nest) and then out on the other side (Plate IV–A). The junction of the two metals, copper and constantan, comes at the middle of the nest.

When the adult bird enters the box and settles down on the eggs, she, of course, applies heat to them and warms up the nest cavity. The increase in temperature causes an increase of electric potential at the recorder, and this is registered on the paper evolving from the recorder in the laboratory by a variation in the line drawn by the pen. Every time that the bird settles down in the nest there will be one kind of variation in the line, and every time that she leaves the nest there will be another kind of variation—because of the difference in the temperature of the nest. In fact, every time she stirs around in the nest to any extent, shifts her feet, gets up on the rim of the nest, or goes to the entrance of the box for an instant, the movement will be registered by characteristic marks in the record (Plate V). Since the recorder is in action day and night we have thus a fairly complete record of the activities of the adult bird at the nest. It is possible to get such records of the female from the beginning of the nest-building activities until the end of the brooding period.

The manufacturers guarantee an absolute accuracy of 0.5% of the temperature range of their instrument, which variation in the case of the recording potentiometers would be ± 1.0° F. (0.6° C.). The instruments were checked and calibrated at frequent intervals during the work by means of a standard thermometer. It was not unusual even after several days of continuous running for the recording instruments and the standard thermometer to read exactly alike. At other times the recorder would be a half degree or so too high or too low, never more. The recorder would be then corrected, and the error allowed for in the records obtained. Special care was taken to have the recording instrument read accurately between 100° F. (37.8° C.) and 112° F. (44.4° C.).

The long thermocouple wires (200 feet) used to connect the recording instrument to the nest caused no error in the readings of the potentiometer. These were checked against short thermocouple wires of about 4 feet in length, and identical temperatures were recorded.

The recording potentiometers are equipped, as already stated, with an automatic cold junction compensation coil which is supposed to compensate for all variations in room temperature where the instrument is placed, so that the cold junction is maintained constant. Extensive tests have been carried out to check this compensation.

The recording instrument was connected with a thermocouple placed in a water bath in a thermos bottle maintained at constant temperature. A standard thermometer was inserted into this thermos bottle, and the thermocouple wound around it so that the water temperature that the thermocouple was reading could be accurately determined. The recording instrument, placed in another room, was then subjected to air temperature changes of various degrees and varying rapidity of fluctuation. The temperatures recorded by the instrument at these different room temperatures were then compared with those obtained by means of the standard thermometer, with the results shown in Table II.

TABLE II.—*Influence of Room Temperature on Accuracy of Recording Potentiometer*

Degrees Change in Room Temperature	Number of Tests	Error in Record Made by Recording Potentiometer
Drop of 20°–30° F. (11.2°–16.8° C.)	5	+1.0° F. (0.6° C.)
Drop of 10°–20° F. (5.6°–11.2° C.)	5	+0.6° F. (0.3° C.)
Drop of 1°–10° F. (0.6°–5.6° C.)	4	0.0
Rise of 1°–10° F. (0.6°–5.6° C.)	5	0.0
Rise of 10°–20° F. (5.6°–11.2° C.)	6	—0.5° F. (0.3° C.)
Rise of 20°–30° F. (11.2°–16.8° C.)	5	—1.0° F. (0.6° C.)

These tests show that the recording instrument does not register absolutely the same at all room temperatures, but when the air temperature is low it registers high, and when the air temperature is high it registers low. For medium variations in room temperature, however, this error is negligible; that is, for fluctuations in room temperature of 10° F. (5.6° C.) or even 20° F. (11.2° C.) in either direction.

With this possible source of error in mind, special care was taken always to keep the recording instruments at temperatures as nearly constant as possible. This could be done rather easily by keeping them in basement rooms. Record kept of the daily variation of temperature in these rooms assured us that there was no appreciable error from this source, since in no case did the room temperature vary more than a very few degrees, while the extreme variation reached during the entire period of study was only 12° F. (6.7° C.), and this lasted for only a short time.

Frequent and varied testings of these recording instruments assure us, therefore, that the accuracy of ± 1.0° F. (0.6° C.) guaranteed by the manufacturers was obtained. Actually, however, since hundreds and in some cases thousands of records are averaged to obtain the figures quoted below, the plus and minus errors in recording tend to cancel each other and thus produce results that have an accuracy considerably greater than ± 1.0° F. (0.6° C.).

Indicator potentiometer.—The indicator potentiometer (Plate II–A) is based on exactly the same principles as the recording instrument except that it does not give a continuous automatic and permanent record. Each temperature must be read by eye from the scale. To compensate for this disadvantage the instrument is smaller, less cumbersome, readily portable, and more sensitive to changes in temperature at the warm junction of the thermocouple. For ordinary use, this instrument has a guaranteed accuracy of 0.45° F. (0.25° C.), but to make it even more accurate, a larger and more sensitive galvanometer than that which ordinarily comes with the instrument was used in this work. This increased the dependable accuracy of the records to one-tenth or two-tenths of a degree (F.) at ordinary room temperatures. The automatic cold-junction compensation for differences in room temperature is not perfect, and so a correction must be applied when the instrument is used at widely different air temperatures.

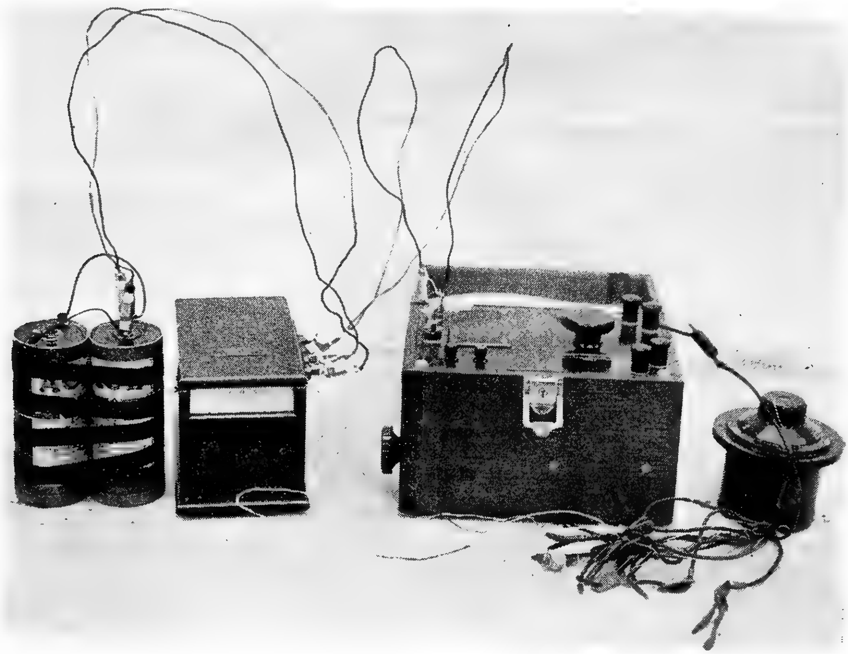
Sensitive galvanometer.—Still another instrument (Leeds and Northrup Company) was used in obtaining the temperature of eggs (Plate II–B). This consists of a galvanometer with reflecting mirror, scale, and telescope. Slight variations in the galvanometer are read through the microscope directed at the mirror which in turn reflects the scale. Two thermocouples were used; one placed in a thermos bottle with a standard thermometer, the other subjected to the temperature to be measured. Differences in potential between the two thermocouples were measured on the scale and calibrated into degrees of temperature. This, when added or subtracted from the reading of the standard thermometer, gave the temperature measured. This was our most accurate instrument for measuring temperatures, being accurate to better than 0.1° F., or with some further adjustments to a few hundredths of a degree.

BODY TEMPERATURE OF ADULT BIRDS

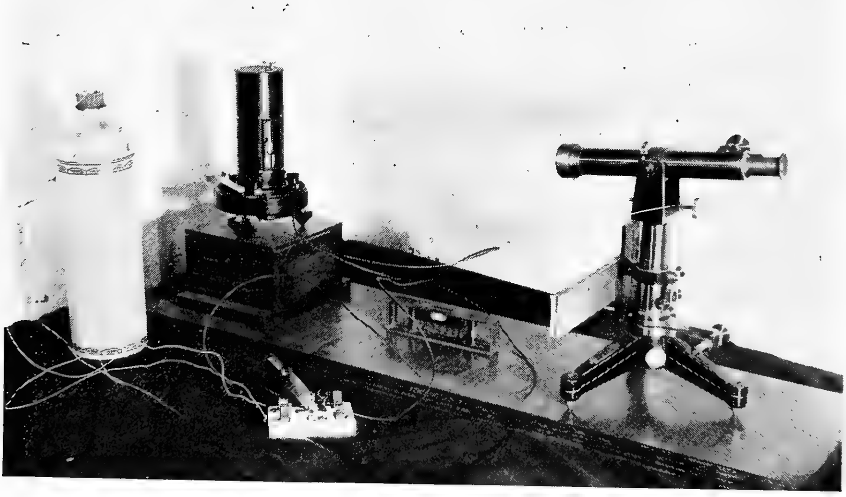
It seems in the past generally to have been assumed that birds have a definite and constant temperature. Only recently has it been pointed out that the body temperature of birds is subject to considerable fluctuation (Stoner, 1926; Kendeigh and Baldwin, 1928). Previous investigators, using mercury thermometers, have assumed that the readings obtained were characteristic. Care was not even taken, in many instances, to keep the bird quiet while the readings were made, so that muscular activities and excitement have caused inaccurate results. Sea birds were formerly caught for such purposes with baited hooks and lines. Some more recent investigators (Simpson, 1912–a; Wetmore, 1921) have taken the temperature of birds immediately after killing them. With the smaller active passeriform species, variations in the temperature of single adult individuals of as much as ten degrees are not unusual at different hours of the day. This is more variation than previous observers have obtained between many different species of birds, and is more than the averages obtained between such widely separated groups as *Apteryx* (100.2° F. [37.9° C.], Sutherland, 1899) and Turdidae (108.9° F. [42.7° C.], Wetmore, 1921). According to Simpson and Galbraith (1905), there is less temperature variation in large birds than in the smaller species. Such great fluctuations as occur in the house wren may not be typical for all birds; but, from some comparative work, we believe that they occur to some such extent in the great order Passeriformes, which makes up by far the larger part of our common land avifauna.

STANDARD TEMPERATURE

In spite of the general variability in the temperature of birds under normal living conditions, there is one temperature, the *standard temperature,* which is much more constant and which can be determined by experiment. That temperature is the temperature of standard or basal metabolism. The standard metabolism of an organism is its metabolism or energy exchange when at com-



A.—Indicator Potentiometer (Portable).



B.—Sensitive Galvanometer (Portable).

plete rest and at a sufficient time after the last meal to escape the stimulating effect of food (Krogh, 1916). Standard metabolism has been very generally confused with basal metabolism, but as Krogh points out the two are not strictly synonymous. Certain functional activities still operate even when the organism is at rest, such as the heart beat, respiratory movements, glandular action, muscle tone, etc., and these may account for a large percentage of the total standard metabolism and production of body heat. If these factors could be eliminated or corrected for, then basal metabolism would be determined, but as yet it has not been generally practicable to do this.

In this study no direct correlation of standard metabolism and standard temperature has been made. The temperature obtained has been assumed to be that of standard metabolism because it was obtained under conditions identical with those obtaining for standard metabolism. To determine the standard temperature of the birds, they were captured, taken to the laboratory, kept without food for a while, and their temperature taken while at complete rest.

Treatment of birds before determining standard temperature.—As most of the work of obtaining standard temperature was done with the eastern house wren, it will be considered first and the other species will be taken up later for comparison. All the house wrens used were captured at their nest boxes after they had entered to feed the young or to incubate the eggs. This was usually after a period of inattentiveness to nest duties when they had been absent from the box for a few minutes getting and ingesting food themselves. So at time of capture their stomachs were usually filled with recently obtained food.

The birds were removed from the box by means of a small gathering net placed over the entrance hole. This net is made of black mosquito netting sewed around a wire frame. The birds were driven out of the box into this net where they were easily taken in hand. If caught near the laboratory they were carried there immediately. If caught at one of the outlying boxes they were placed in darkened cages and brought to the laboratory later.

In the laboratory, the birds were first confined in small cages covered with one or two layers of black cloth so that they were in the dark. This was necessary in order to keep them quiet. Also, from the time of capture until release they were without food. From other experiments, we have evidence that 2.5 hours is sufficient time for all the food in the stomach to pass through the entire length of the alimentary tract and be voided. In all cases, therefore, it could be made certain that the birds were in a post-absorptive state before attempts at determining the standard temperature were made.

Special care had to be taken not to let the birds become too weak from lack of food, yet to keep them confined in the dark long enough to quiet them sufficiently. In some instances, the birds became too weak from lack of food, and in other cases the birds could not be quieted to complete rest, so that, in all, standard temperatures could be determined on only 65% of the birds obtained for this purpose. The average length of time that the birds, both male and female, were held without food before the standard temperature was determined was 4.7 hours. Of this time, 2.6 hours were spent in darkness.

After the birds had been allowed to remain in the darkened cages the allotted length of time, they were removed and held in the left hand of the investigator. A thermocouple thermometer was thrust down the throat well into the alimentary canal, and then the bird, still in the hand, was placed in another small, narrow, dark cage. The bird was thus removed from the dark where it had been at rest, and after a minute or two returned to the dark. It was necessary, whenever it was desired to keep the birds quiet, to put them in the dark, as they were continually active in the light. Complete darkness has an almost instantaneous effect in quieting some birds. The thermocouple wires ran out of the cage from the bird to the indicator potentiometer. This was manipulated and the records of temperature and time recorded with the free right hand.

The position of the bird in the left hand was a natural one. The bird's neck was held between the first and second fingers and its feet usually rested on the third. It was only at these points that the hand came into constant contact with the bird, although frequently the side of the bird was touching the palm of the hand and at other times the thumb was used to prevent excessive struggling by the bird.

There has been suggested the possibility that being in contact with another being, and a human being at that, may have some emotional effect upon the bird which would detract from the results. Actual experiments, however, do not justify this criticism. For a check, a few birds, mostly eastern chipping sparrows, were fastened by other means in the darkened cage, and their temperatures taken. The records obtained in this less convenient and less satisfactory manner were quite comparable with those obtained from the bird held in the hand. The warmth of the hand could not well affect the bird because of the insulating coat of feathers. As the bird was held loosely, free circulation of air around the bird was not appreciably handicapped.

Behavior of birds during the experiments.—Ordinarily the birds while in the darkened cage remained quiet or moved around only to a very limited extent. When the bird was removed for the insertion of the thermocouple, it had to be taken into the light for a minute or two, and this always caused the bird to become somewhat excited and active. It was, therefore, necessary to work

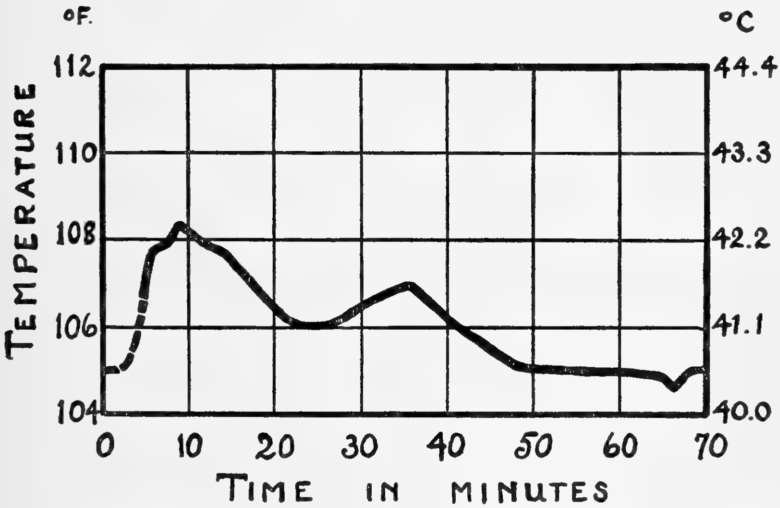


FIGURE 3.—FLUCTUATIONS IN THE BODY TEMPERATURE OF AN EASTERN HOUSE WREN WHILE ITS STANDARD TEMPERATURE (105° F. [40.6° C.]) WAS BEING DETERMINED. The temperature of the bird during the first few minutes before the thermocouple was inserted is interpolated and is shown by the broken line.

awhile with the bird in the hand when placed again in the dark before it became quiet the second time. This required on the average about 1.5 hours, although a few birds became quiet in half that length of time, and others required considerably longer. Nothing was done to pacify the birds except to hold them loosely in the hand in the dark, with external noises and commotion largely eliminated, and to prevent any excess body movements.

Figure 3 shows a typical temperature curve of a bird during the taking of a standard temperature. The first part is interpolated and represents the bird quiet in the dark cage with its body temperature at standard level. When removed from the cage for insertion of the thermocouple its temperature rises a few degrees, but when returned to the dark it begins to drop. The temperature drops until the low standard temperature level is again reached, and here it is maintained constant for several minutes. Usually it is possible to tell when the bird has reached this point, even without taking its temperature, by the feel of the bird in the hand. It is completely relaxed, absolutely motionless except for the movements caused by respiration and heart beat, its eyelids are closed, and the bird is undoubtedly as much asleep as it ever becomes. On the average, this complete relaxation was maintained for 10.2 minutes before a slight stirring or movement would cause its temperature and metabolism to increase again. In one instance it was maintained for 22 minutes, but this is unusual, even under natural conditions, with such active birds as the house wren. Another satisfactory criterion on the time when standard metabolism was attained was furnished by the rate of respiration which then reached a low steady uniform rate (pages 50–55).

Standard temperature determined.—In Table III there is given the standard temperature as determined on 31 birds of 5 species. The readings were taken with the indicator potentiometer.

It will be noticed that the standard temperatures for all 5 species lie within a few tenths of a degree of each other. The average of the 3 passeriform species (which excludes the woodpeckers), considering the figure for each species and sex of equal value, is 104.7° F. (40.4° C.). The number of records and species are too few to allow this figure to be considered the average of the order, but the probabilities are that, if such an average could be

TABLE III.—*Standard Temperature*

Band Number	Date (1928)	Time of Day	Standard Temperature	Duration
Eastern House Wren				
Male				
{45546	June 12	1:30 P. M.	103.7° F. (39.8° C.)	11 minutes
{45546	June 12	4:50 P. M.	103.7° F. (39.8° C.)	11 "
93573	June 15	4:20 P. M.	104.5° F. (40.3° C.)	12 "
664601	June 16	1:10 P. M.	105.0° F. (40.6° C.)	9 "
93433	June 17	3:25 P. M.	104.6° F. (40.3° C.)	16 "
35362	June 29	3:20 P. M.	104.3° F. (40.2° C.)	12 "
35363	June 30	2:05 P. M.	104.4° F. (40.2° C.)	5 "
664716	June 30	3:00 P. M.	104.4° F. (40.2° C.)	18 "
38398	July 19	1:30 P. M.	104.2° F. (40.1° C.)	12 "
93546	July 21	1:21 P. M.	104.2° F. (40.1° C.)	4 "
45320	August 1	12:50 P. M.	104.4° F. (40.2° C.)	14 "
		Average	104. 37° F. (40.2° C.)	11.3 minutes
		Probable error	±.07° F. (.04° C.)	
Female				
664708	June 17	5:05 P. M.	105.0° F. (40.6° C.)	5 minutes
45708	June 21	7:12 P. M.	105.0° F. (40.6° C.)	22 "
45350	June 22	1:10 P. M.	105.0° F. (40.6° C.)	11 "
45649	June 26	2:25 P. M.	105.0° F. (40.6° C.)	7 "
45536	June 30	11:35 P. M.	105.4° F. (40.8° C.)	15 "
45569	July 9	2:43 P. M.	104.7° F. (40.4° C.)	5 "
45348	July 26	3:35 P. M.	105.4° F. (40.8° C.)	2 "
664751	August 17	4:50 P. M.	104.9° F. (40.5° C.)	3 "
		Average	105.05° F. (40.6° C.)	8.8 minutes
		Probable error	±.05° F. (.03° C.)	
Eastern Chipping Sparrow				
Male				
45300	June 13	4:00 P. M.	105.1° F. (40.6° C.)	10 minutes
45305	June 13	5:05 P. M.	104.7° F. (40.4° C.)	10 "
45309	June 25	11:00 A. M.	104.5° F. (40.3° C.)	19 "
31900	July 14	2:00 A. M.	105.0° F. (40.6° C.)	53 "
56207	August 2	4:45 P. M.	104.9° F. (40.5° C.)	33 "
		Average	104.84° F. (40.5° C.)	25 minutes
		Probable error	±.07° F. (.04° C.)	
Female				
45314	June 9	11:30 A. M.	104.5° F. (40.3° C.)	16 minutes
38469	June 23	5:30 P. M.	105.4° F. (40.8° C.)	5 "
45315	June 27	11:30 A. M.	105.0° F. (40.6° C.)	23 "
93414	July 5	5:00 P. M.	104.8° F. (40.4° C.)	48 "
		Average	104.92° F. (40.5° C.)	23 minutes
		Probable error	±.11° F. (.06° C.)	
Eastern Robin				
Male 549420	June 6	2:40 P. M.	104.5° F. (40.3° C.)	6 minutes
Female 549425	June 20	7:35 P. M.	104.6° F. (40.3° C.)	6 "
Northern Downy Woodpecker				
Male 572414	June 11	8:30 P. M.	104.3° F. (40.2° C.)	19 minutes
Eastern Hairy Woodpecker				
Female 459740	June 3	7:45 A. M.	105.0° F. (40.6° C.)	5 minutes

obtained, it would not be far from this. Attention is called to the work of Benedict and Fox (1927), who obtained what were probably standard temperatures in many cases on several species of large wild birds under aviary conditions. The body temperatures that they obtained vary from 102.0° F. (38.9° C.) to 106.9° F. (41.6° C.), the average being 104.4° F. (40.2° C.).

Sex difference in standard temperature.—A difference between the two sexes in their standard temperatures is apparent from the above records. This difference amounts to 0.6° F. (0.4° C.), with the larger value for the female in the case of the house wren. This difference is a significant one, since it amounts to ten times the probable error. In the case of the eastern chipping sparrow and eastern robin, there is a tendency for the female to have a slightly higher temperature than the male, but the difference between the two sexes is so small that it is insignificant and within the limits of chance variation. The eastern chipping sparrow was found to be a rather difficult species with which to work, since it was not very resistant under controlled conditions and the mortality rate was greater than in any other species on which we have experimented. Possibly this greater frailty and more delicate vitality of the species was a factor in not permitting a possible difference between the two sexes to show more than it did. The single records for each sex in the eastern robin are insufficient for any serious consideration. The striking dissimilarity, however, between the two sexes in the house wren does warrant attention.

This difference between the sexes in the breeding season may possibly not persist throughout the year. Due to the functional and organic changes (Riddle and coworkers, 1925, 1927, 1928) that take place during the period of reproduction, direct comparison with other times of the year cannot be safely assumed. The reason for this discrepancy between the sexes is not clear, but appears to be bound in some way to the temperature regulating mechanism. In the ring dove, the male has been found to have a higher standard metabolism than the female (Riddle, Christman, and Benedict, 1930); and a higher metabolism has also been found in the mourning dove (Riddle, Smith, and Benedict, 1932). If this is true for the house wren also, then the rate of heat loss must be greater in the male to explain the lower body temperature.

Other observers (Martins, 1858; Simpson and Galbraith, 1905; Simpson, 1912–a) have also noted a difference in the temperature of the two sexes, with the female having the higher value, although one might question the reliability of the data with which they worked, as they were, in many cases, obviously not those of standard temperature. To Wetmore (1921) it appeared that in different groups of birds the difference in temperatures between the sexes favored the male in some cases, the female in others, while in many there was none. He attempts to correlate a higher temperature with the sex that does the major share of the duties pertaining to incubation and care of the young. In some instances his records appear to be those of standard temperature, but in the majority they are not. Where records are not those of standard temperature, any sex difference is largely obscured, at least in the higher species, by the normal variations in temperature under stress of internal and external factors, such as excitement, food, activity, etc., and any difference obtained represents more the influence of these factors on the two sexes than of any fundamental differences in metabolism. In the house wren, the higher standard temperature of the female is correlated with a slightly larger size of the body, as determined by length and breadth measurements of the thorax and abdomen, a greater total weight, and with a larger share in the nesting duties involved in reproduction.

Constancy of standard temperature.—Very little in a definite way can be said concerning the variation in the standard temperature at different hours of the day and night, as the records are not numerous enough or evenly enough distributed. Data of a little different character to be discussed in a later section (page 69) indicate that the standard temperature may be somewhat lower at night than during the day.

There is no appreciable variation in the standard temperature of either the eastern house wren or eastern chipping sparrow during the three summer months of June, July, and August (Table IV). What may occur during the winter cannot, of course, be predicted from the data available.

The average air temperature at which all the experiments with the house wren were performed was 73.8° F. (23.2° C.). Although there was some variation from this between the limits of

TABLE IV.—*Variation in Standard Temperature with Season*

Species	Sex	June		July		August	
		Number of Records	Average Standard Temperature	Number of Records	Average Standard Temperature	Number of Records	Average Standard Temperature
Eastern house wren...	Male	7	104.4° F. (40.2° C.)	2	104.2° F. (40.1° C.)	1	104.4° F. (40.2° C.)
" " " ...	Female	5	105.1° F. (40.6° C.)	2	105.1° F. (40.7° C.)	1	104.9° F. (40.5° C.)
Eastern chipping sparrow	Male	3	104.8° F. (40.4° C.)	1	105.0° F. (40.6° C.)	1	104.9° F. (40.5° C.)
" "	Female	3	105.0° F. (40.6° C.)	1	104.8° F. (40.4° C.)	..	....
		Average	104.8° F. (40.4° C.)		104.7° F. (40.4° C.)		

62.0° F. (16.7° C.) and 83.0° F. (28.3° C.) at which the standard temperatures were determined on different individuals, no definite correlation with air temperature can be stated.

From the above discussion it appears that the standard temperature is a value of some constancy in the physiology of bird temperatures, at least during the daytime. It thus furnishes a base from which the effect of various factors on body temperature may be determined.

NORMAL TEMPERATURE

By normal temperature is meant the actual temperature of the bird during the day and night. This is most typical while the bird is carrying on normal activities under natural conditions, but is difficult to obtain, since the taking of temperature usually interferes more or less with the natural course of events or the physiological behavior of the bird. Ordinarily the bird in nature does not stay quiet for a time long enough to allow its temperature to drop to the level of standard metabolism, and, therefore, the bird seldom comes down to standard temperature except at night. Action temperatures or temperatures of birds that are excited or frightened are included in this category of normal temperatures. Some of the different factors that affect the normal temperatures of birds will first be considered, then the temperature of birds under natural conditions.

Effect of emotional excitement.—One of the chief problems that students of bird temperatures have always had to face has been to get the temperature of the bird when it is as little excited as possible. Some investigators have attempted to do this by killing the bird as nearly instantaneously as possible while it was quiet, and then taking its temperature immediately after it was shot (Simpson, 1912–a; Wetmore, 1921). In taking the temperature of living birds, the objection has been that they are so excitable that the temperature of rest could not be obtained, because fear and excitement would cause the body temperature to rise. This, however, is not the case, as the following section on the effect of muscular activity upon the body temperature will clearly bring out. The temperature of the bird falls while it is held in the hand rather than rises, and, after a few minutes, rest temperatures may be obtained.

It is true that when house wrens are first captured at the nest or taken from the traps and their temperatures determined at once, high values are obtained because of the intense excitement and struggling at capture. This is indicated in the results shown in Table V.

TABLE V.—*Maximum Body Temperature of the Eastern House Wren*

Male		Female	
Band Number	Temperature	Band Number	Temperature
Obtained with mercury thermometer			
63824	110.0° F. (43.3° C.).........	34269	111.2° F. (44.0° C.)
38388	111.1° F. (44.0° C.).........	34271	110.0° F. (43.3° C.)
38389	111.1° F. (44.0° C.).........	63757	110.0° F. (43.4° C.)
38390	110.4° F. (43.6° C.).........	38387	110.1° F. (43.4° C.)
38394	111.3° F. (44.1° C.).........	38418	110.4° F. (43.6° C.)
Average	110.8° F. (43.8° C.)	....	110.5° F. (43.6° C.)
Obtained with thermocouple			
93573	110.6° F. (43.7° C.).........	45349	112.0° F. (44.4° C.)
93433	110.4° F. (43.6° C.).........	45350	110.7° F. (43.7° C.)
45320	111.5° F. (44.2° C.).........	45536	111.5° F. (44.2° C.)
94249	111.2° F. (44.0° C.).........	664751	111.6° F. (44.2° C.)
		C68978	112.0° F. (44.4° C.)
		F45745	112.3° F. (44.6° C.)
Average	110.9° F. (43.8° C.)	....	111.7° F. (44.3° C.)

The maximum temperature of other species is worthy of note. Records obtained from both mercury thermometers and thermocouples are here averaged together (Table VI).

The general average of the maxima of body temperatures for these various species, including the eastern house wren but excluding the two woodpeckers, which are non-passeriform species, is 111.5° F. (44.2° C.). The values for the two sexes are averaged to get a figure to represent those species in the few instances where records for both sexes are available. The highest normal record obtained from birds in the hand was 113.5° F. (45.3° C.), from a female eastern robin. The next highest record of 112.7° F.

TABLE VI.—*Maximum Body Temperature of Birds Other than House Wren*

Species	Sex	Number of Records from Different Individuals	Temperature
Eastern chipping sparrow.....	Male	5	111.3° F. (44.1° C.)
" " "	Female	1	112.7° F. (44.8° C.)
Eastern song sparrow.........	Female	1	111.8° F. (44.3° C.)
English sparrow.............	Male	1	111.1° F. (44.0° C.)
" "	Female	1	112.1° F. (44.5° C.)
Eastern robin...............	Male	3	111.1° F. (44.0° C.)
" "	Female	6	111.8° F. (44.3° C.)
Eastern bluebird............	Female	1	111.3° F. (44.1° C.)
Eastern yellow warbler.......	Female	1	111.6° F. (44.2° C.)
Purple martin...............	Female	1	110.4° F. (43.6° C.)
Eastern phoebe..............	Female	1	110.9° F. (43.8° C.)
Northern crested flycatcher...	Female	2	112.6° F. (44.8° C.)
Northern downy woodpecker..	Female	1	110.0° F. (43.3° C.)
Northern flicker............	Male	1	111.2° F. (44.0° C.)

(44.8° C.) was obtained from a female crested flycatcher and a female eastern chipping sparrow. A record of 112.6° F. (44.8° C.) was obtained once from another female eastern robin. In the eastern house wren, 112.3° F. (44.6° C.) has been the highest obtained, again from a female. There is evidence all through the records obtained from passeriform species that higher temperatures occur in the females than in the males. This is true with the standard temperatures, and these maximum temperatures furnish another instance. In Table VI this is apparent in the case of those species where records for both sexes are given. Where but one sex is recorded, it is in all but one instance the female. This does not always mean that no records were obtained for the male, but that they were so much lower that it was questionable that the maximum temperature of the individuals really was determined, and they were, therefore, omitted. These data, together with those on standard temperatures, would argue either that the whole level of metabolism in the female is slightly higher than that of the male during the season of reproduction, or that there is some difference in the temperature regulation.

Thus far, we have in this discussion attributed these high temperatures in birds to their excitability. This is true only in a broad sense when muscular, functional, and nervous activity are not closely distinguished. There is some question whether or not mental excitement or emotional states in themselves cause a fluctuation in the temperature of birds. In the functional activity of nervous tissue, it has only comparatively recently been demonstrated that heat of metabolism is given off (Downing, Gerard, and Hill, 1926). This metabolism would probably not be enough to affect body temperature, although Gesell (1925) presents some evidence that the metabolism of nervous tissue may be greater than formerly supposed.

Effect of muscular activity.—Muscular activity is closely bound up with nervous and mental activity. The nervousness and excitability of birds, when first captured, are expressed in flutterings and struggles to escape. Maximum temperatures are the result of these exertions plus the previous activities of the birds before capture.

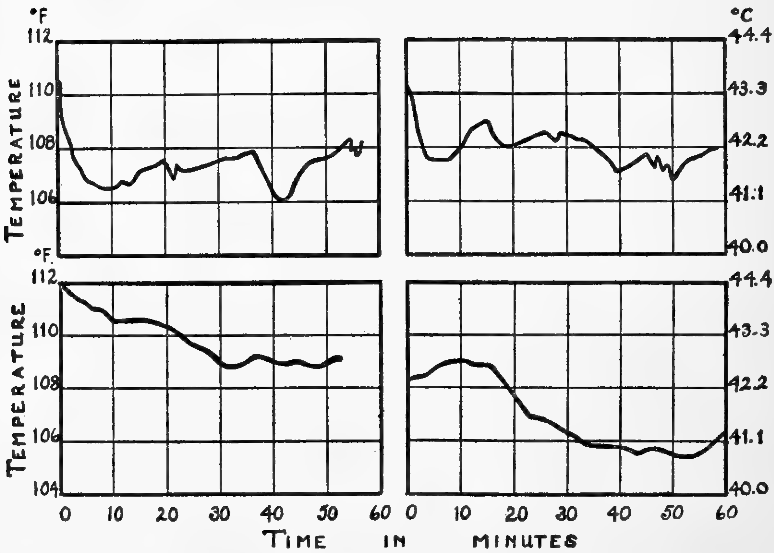


FIGURE 4.—FLUCTUATIONS IN THE BODY TEMPERATURE OF EASTERN HOUSE WRENS HELD IN THE HAND. In three instances, the unusually high initial temperatures are due to the activity of the birds after having just been captured; in the fourth, where the initial temperature is low, the bird had been kept quiet in a darkened cage several minutes before its temperature was taken.

Curiously enough, and quite opposite to what one might at first expect, the temperature of the bird after it is taken from the traps and held in the hand, or in other confinement, drops rather than rises (Table VII). The highest record one gets of the bird's temperature is usually the one first made. This drop may amount to only a few tenths of a degree (F.) over a period of several minutes, or again the drop may be as much as 4 degrees in 6 minutes or 3 degrees in 4 minutes (Figure 4). At times this fall in temperature may be more or less continuous for 30 minutes. The extent and rapidity of this drop depend in part upon the circumstances of the bird's capture, its activity before

TABLE VII.—*Fall in Body Temperature of Birds when Held in the Hand after Capture*

Species	Sex	Initial Temperature	Temperature after 10 Minutes	Temperature after 20 Minutes
Eastern house wren	Male	108.3° F. (42.4° C.)	105.5° F. (40.8° C.)	104.6° F. (40.3° C.)
"	Male	107.6° F. (42.0° C.)	108.7° F. (42.6° C.)	108.4° F. (42.4° C.)
"	Male	110.0° F. (43.3° C.)	110.5° F. (43.6° C.)	110.3° F. (43.5° C.)
"	Male	110.4° F. (43.6° C.)	109.7° F. (43.2° C.)	109.9° F. (43.3° C.)
"	Male	111.5° F. (44.2° C.)	110.4° F. (43.6° C.)	110.6° F. (43.7° C.)
"	Male	111.2° F. (44.0° C.)	110.3° F. (43.5° C.)	109.1° F. (42.8° C.)
"	Male	110.7° F. (43.7° C.)	108.8° F. (42.7° C.)	106.0° F. (41.1° C.)
"	Female	112.0° F. (44.4° C.)	111.5° F. (44.2° C.)	111.1° F. (44.0° C.)
"	Female	110.5° F. (43.6° C.)	110.2° F. (43.4° C.)	109.3° F. (43.0° C.)
"	Female	110.8° F. (43.8° C.)	110.4° F. (43.6° C.)	110.2° F. (43.4° C.)
"	Female	110.5° F. (43.6° C.)	110.1° F. (43.4° C.)	....
"	Female	111.0° F. (43.9° C.)	109.9° F. (43.3° C.)	....
"	Female	109.9° F. (43.3° C.)	109.8° F. (43.2° C.)	109.7° F. (43.2° C.)
"	Female	111.6° F. (44.3° C.)	111.0° F. (43.9° C.)	110.8° F. (43.8° C.)
"	Female	108.8° F. (42.7° C.)	110.4° F. (43.6° C.)	....
"	Female	111.7° F. (44.3° C.)	111.7° F. (44.3° C.)	....
Average of 16 birds		110.4° F. (43.6° C.)	109.9° F. (43.3° C.)	109.2° F. (42.9° C.)
Eastern robin...	Male	110.2° F. (43.4° C.)	109.3° F. (43.0° C.)	107.6° F. (42.0° C.)
" " ...	Male	111.0° F. (43.9° C.)	110.7° F. (43.7° C.)	....
" " ...	Female	111.6° F. (44.2° C.)	108.5° F. (42.5° C.)	....
Eastern chipping sparrow	Male	111.9° F. (44.4° C.)	110.5° F. (43.5° C.)	110.3° F. (43.5° C.)
"	Female	112.7° F. (44.8° C.)	112.5° F. (44.7° C.)	108.6° F. (42.6° C.)
"	Female	108.2° F. (42.3° C.)	107.7° F. (42.1° C.)	....
Eastern song sparrow	Female	111.8° F. (44.3° C.)	108.3° F. (42.4° C.)	106.4° F. (41.3° C.)
White-breasted nuthatch	Male	109.5° F. (43.1° C.)	108.9° F. (42.7° C.)	....
Eastern crow....	Male	106.7° F. (41.5° C.)	105.7° F. (41.0° C.)	....
Northern downy woodpecker	Male	109.5° F. (43.1° C.)	108.3° F. (42.4° C.)	106.7° F. (41.5° C.)
Eastern hairy woodpecker	Female	109.0° F. (42.8° C.)	107.0° F. (41.7° C.)	....

TABLE VII (Continued).—*Fall in Body Temperature of Birds when Held in the Hand after Capture*

Species	Sex	Temperature After 30 Minutes	Temperature After 60 Minutes
Eastern house wren	Male	104.6° F. (40.3° C.)	103.7° F. (39.8° C.)
" " "	Male	108.1° F. (42.3° C.)	107.9° F. (42.2° C.)
" " "	Male	109.2° F. (42.9° C.)	106.9° F. (41.6° C.)
" " "	Male	....	....
" " "	Male	110.6° F. (43.7° C.)	110.0° F. (43.3° C.)
" " "	Male	107.2° F. (41.8° C.)	....
" " "	Male	105.3° F. (40.7° C.)	....
" " "	Female	110.5° F. (43.6° C.)	....
" " "	Female	108.3° F. (42.4° C.)	....
" " "	Female	109.7° F. (43.2° C.)	109.3° F. (43.0° C.)
" " "	Female	....	....
" " "	Female	....	....
" " "	Female	109.6° F. (43.1° C.)	109.4° F. (43.0° C.)
" " "	Female	....	....
" " "	Female	....	....
" " "	Female	....	....
Average of 16 birds		108.3° F. (42.4° C.)	107.8° F. (42.1° C.)
Eastern robin	Male	106.7° F. (42.0° C.)	....
" "	Male	....	....
" "	Female	....	....
Eastern chipping sparrow	Male	108.9° F. (42.7° C.)	....
" " "	Female	108.7° F. (42.6° C.)	....
" " "	Female	....	....
Eastern song sparrow	Female	105.2° F. (40.8° C.)	....
White-breasted nuthatch	Male	....	....
Eastern crow	Male	....	....
Northern downy woodpecker	Male	105.7° F. (41.0° C.)	104.2° F. (40.1° C.)
Eastern hairy woodpecker	Female	....	....

capture, the food it has taken, its struggling in the hand, and the degree to which it may be quieted. Ordinarily the drop becomes less apparent after a few minutes. After this, the bird's temperature fluctuates to a greater or less degree (Figure 4). This is true in all species studied. Gradually the temperature sinks, however, and the fluctuations keep dropping lower and lower until after some hours the standard temperature is reached. Stoner (1928) took the temperature of house wrens at one minute intervals with a clinical thermometer and also found that it dropped from 110.6° F. (43.7° C.) to 105.8° F. (41.0° C.). Activity then raised the temperature from 105.8° F. (41.0° C.) to 106.5° F. (41.4° C.).

If the bird has been at rest, there is at first obtained a temperature of a medium degree rather than the maximum. Then, as the bird strives to escape, its temperature may rise by reason of the muscular activity brought into play. After the excitement wears off, the temperature again drops (Figure 4).

In all cases the birds eventually become quieted in the hand, and all movement ceases except for occasional slight struggles. Muscular activity is generally recognized as one of the most important factors in the production of heat in the body. Hence when muscular activity ceases, heat production is decreased, and the body temperature drops.

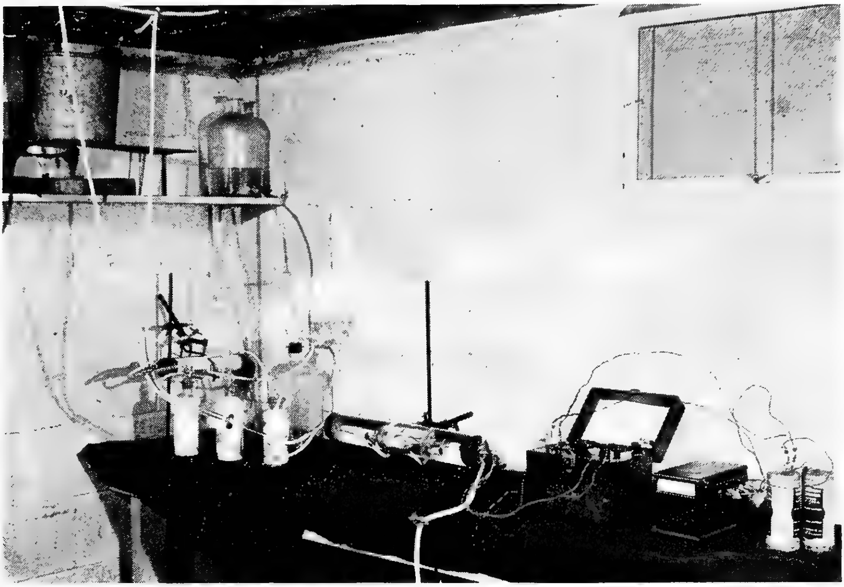
The effect of muscular exercise is even more apparent when the body temperature drops to the standard level. This is well shown in Figure 1. Here even the slightest movements cause a rise of temperature. The stimulating effect which food has is absent in this case, so that the rise in temperature is clearly due to muscular activity alone. This effect of activity in wild birds is in harmony with the rise in temperature of man which has been observed as a result of work (Pembrey, 1898; Benedict and Snell, 1902), and also in the domestic fowl (Féré, 1899).

Effect of food and of starvation.—Ever since the time of Lavoisier and Sequin, 1789 (Benedict and Carpenter, 1918, page 10), it has been known that the ingestion of food causes an increase of metabolism in animals. According to Rubner, proteins, carbohydrates, and fats each have a specific dynamic action, stimulating heat production in the cells of the body. From the experiments of Benedict and Carpenter (1918), it appears that the proteins have more effect than any other nutrient in increasing metabolism in man, and that it makes little difference whether the protein is of animal or plant origin. Carbohydrates of various kinds and fats have striking influences upon the metabolism, but the increases produced are less. Lusk (1921) discussed in detail the role of nutrition in the metabolism of animals. According to Groebbels (1928–a) the specific dynamic action of food has the effect of increasing the oxygen intake 20%–30% in doves. It is of interest in this connection that the food of the eastern house wren is largely insects, and so proteinaceous. Hence the food eaten must be one factor in maintaining the metabolism at the high level that it attains. A higher rate of metabolism implies of necessity a greater heat production. A larger or smaller part of the increased heat production caused through absorption of food may be lost through increased heat dissipation.

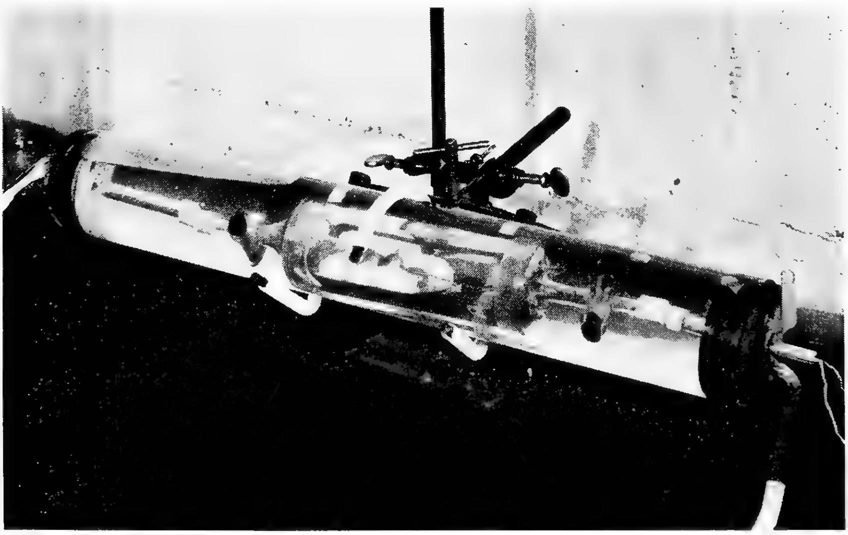
With all the birds used for the determination of standard temperature, time had to be allowed not only for the birds to attain the greatest muscular repose but also to attain a post-absorptive state as regards food. If this were not done, the standard temperature could not be attained, even when the bird was limited in its activity. Benedict and Riddle (1929), in the case of ring doves and common pigeons, noted a progressive decrease in the respiratory quotient during the first 24 hours, this indicating a change from a predominantly carbohydrate metabolism to one of predominantly fats or possibly proteins. The latter condition of standard metabolism is apparently attained in less than 5 hours in the house wren, probably because digestion is completed more rapidly.

In Table VII we have already noted that during the first hour when bird temperatures were taken continuously by means of thermocouples down their throats, their body temperature was gradually falling. This fall in body temperature is a fluctuating one marked by short periods of rising and falling temperature, dependent primarily on the activity of the bird. This tendency for a gradual fall in temperature continues for 4 to 5 hours in the case of the house wren, until standard metabolic or essentially fasting conditions are reached. It is only then that the constant standard temperature may be obtained. This fall in body temperature is apparently due, in addition to cessation from exercise, to the difference in the metabolism of the bird occasioned by this change from an active feeding and absorptive condition to one of fasting. External air temperature is not a factor here, since in our experiments it was fairly uniform, and, as will be shown later, it does not, anyway, appreciably affect the body temperature. The nutritional state of the bird is an important consideration, therefore, in determining the body temperature.

Experiments were performed with individual birds which were confined in a small cage, alternately with food and without food for periods of time, and their temperature then taken. All this work was done with eastern song sparrows and eastern chipping sparrows, since they feed more freely in captivity than do strictly insectivorous species. In determining the effect of a lack of food



A.—Apparatus Used for Studying the Effect of Variations in Air Temperature on the Body Temperature of Adult Birds, Immature Birds, and Eggs.



B.—Water Bath Used in Apparatus for Studying the Effect of Variations in Air Temperature on Birds. Note the inner air chamber containing eggs, the thermocouples inserted into this chamber through the air exit tube, and the water bath that surrounds the air chamber.

on bird temperature, a sufficient time must be allowed for the species to get into a post-absorptive condition. In the case of the sparrows this must be at least 2.5 hours, preferably longer.

A few experiments yielded significant results, as indicated in Figure 5. In these cases, the natural body food reserve was

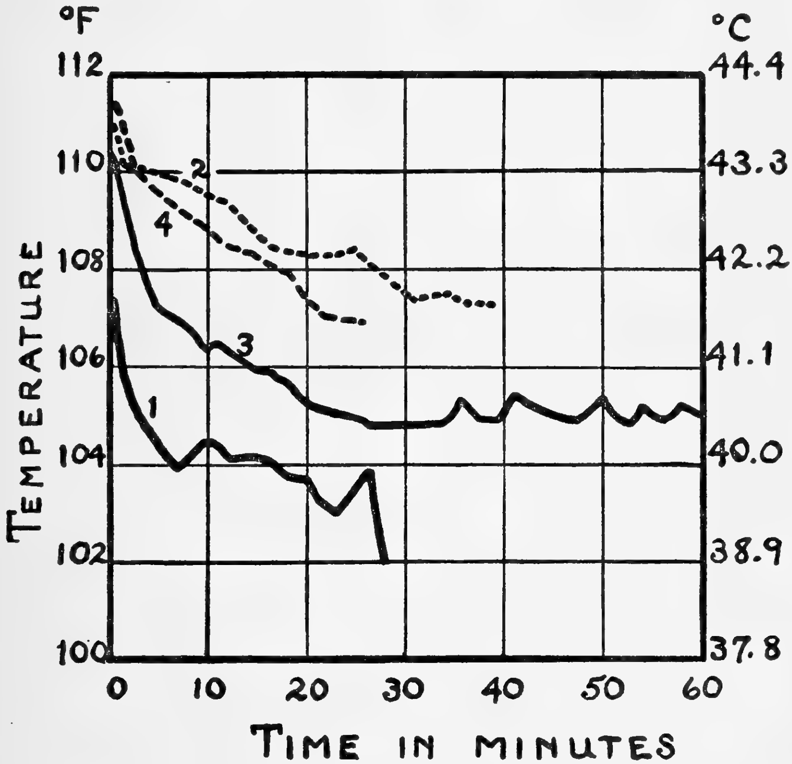


FIGURE 5.—BODY TEMPERATURE OF AN EASTERN CHIPPING SPARROW HELD IN THE HAND. Lines 1 and 3 are after periods when the bird had been deprived of food; 2 and 4 after periods when the bird had freely consumed food for some time. High initial temperature is result of struggle during insertion of the thermocouple.

probably reduced before the experiments began, due to several days' confinement, so that the bird was unusually sensitive to the presence or absence of the stimulating effect of food.

An average of the initial temperatures at each period of observation gives for the intervals when the bird had all the food it desired, 111.1° F. (44.0° C.), and for the intervals when it was deprived of food for about 2.5 hours, 108.9° F. (42.7° C.). These two figures, however, include also the effect of muscular exertion concomitant with the removal from the cage and insertion of a thermocouple down its throat. At the end of 25 minutes, when the bird had become relatively quiet, the average of the two records of the bird with food is 107.7° F. (42.1° C), while without food it is 104.2° F. (40.1° C.). It is thus clear that the ingestion of food into the body is associated with a rise in the bird's temperature, and that, along with muscular activity, it must be considered a factor in maintaining the bird's body temperature.

When a bird is deprived of food for a prolonged time, actual starvation or under-nutrition occurs. This is concomitant with a marked decrease in heat production. With ring doves, Benedict and Riddle (1929) found a decrease from 3934 calories per 150 grams of body weight, which was the rate 24 hours after the birds had been deprived of food, to 3343 calories after 48 hours. With such a marked decrease in heat production, it is reasonable to expect a lowered body temperature in starved birds, and this is what actually occurs.

The most extensive work that we have found in the literature relating to the effect of starvation on the body temperature of birds is that by Chossat in 1843. His work was principally with pigeons and doves which he kept without food till they either died or were at the point of death. The general conclusion that he reached in regard to the effect of starvation on body temperature may be summarized in the following quotation (page 309): "Il résulte là que *l'inanitiation* a pour effet d'accroître progressivement l'oscillation diurne de la chaleur jusqu'à ce que le refroidissement devienne assez grand pour que la réaction diurne ascensionnelle ne s'opère plus, ou presque plus, et que l'animal périsse prochainement de froid." He believed that lack of food caused a break of the temperature control mechanism, and that death was due actually to the low body temperatures reached rather than to any other cause. Our own work confirms the drop in body temperature observed by Chossat, as do also a few experiments by Groebbels (1928–b).

In the case of the eastern house wren, when the air temperature is medium, the most pronounced effect of lack of food begins to be felt at about the seventh hour. The temperature falls beneath the level of standard metabolism, and apparently the whole general metabolism of the bird becomes depressed. This is very apparent in the behavior and appearance of the bird, for it becomes very listless, inactive, and weak, and the breathing becomes marked. The bird tends to maintain one position consistently, eyes closed, and the feathers raised and ruffled all over the body. The head is lowered and the bird becomes unresponsive to outside stimuli. It may be picked up and placed on its side, where it will remain. The body temperature continues to drop, until finally, with a general contraction of the muscles all over the body and a shivering, the bird dies. This final general contracting of the muscles is sufficient to raise the body temperature in eastern chipping sparrows from one-tenth to three-tenths of a degree. Some birds die quietly without showing this slight rise in temperature. Seven birds have died from the effects of lack of food while under observation. The temperatures of two eastern house wrens at that time were 94.0° F. (34.4° C.) and 87.5° F. (30.8° C.); of three eastern chipping sparrows, 98.6° F. (37.0° C.), 96.6° F. (35.9° C.), and 87.4° F. (30.8° C.); and two English sparrows, 89.1° F. (31.2° C.) and 84.8° F. (29.3° C.). Death in the smaller passeriform birds from lack of food and at ordinary air temperatures occurs within a very few hours.

We are not willing to agree, in entirety, with Chossat that death of birds from starvation is due merely to the breaking down of the temperature control mechanism. In experiments to be described later in another connection, the body temperature of adult house wrens has been lowered to even below 75° F. (23.9° C.) before they had a chance to become starved, yet the birds lived when their temperature rose again as a result of artificial heating. Death from starvation in our birds occurred at body temperatures from 84.8° F. (29.3° C.) to 98.6° F. (35.9° C.). The cause of death in birds long deprived of food seems to be, therefore, some defect caused by under-nourishment and not directly the low body temperature reached, although if this low body temperature is long maintained, it is undoubtedly important. Lusk (1921) discusses certain theories as to the cause of death by starvation in mammals including man, but leaves the question unsettled.

In summarizing the importance of food to passeriform birds, it is evident that the metabolism of food is important for maintaining the body temperature. When birds are subjected to prolonged starvation, there is a lowering of body temperature below that which is normal, and death eventually occurs. This gives evidence for the belief that under natural wild conditions birds must have continual access to an abundant food supply; and if for any reason this is not forthcoming, death will follow.

Groebbels (1928–a) would classify all birds in two main categories according to their sensitiveness to food supply. His first class would be characterized by a good chemical heat regulation, fewer requirements in the way of food, greater resistance to hunger, greater sluggishness in movement, lower body temperature, and lower metabolism. His second class would be characterized by a higher body temperature which could be maintained only with an abundance of food and great activity, and would be further characterized by a high rate of digestion, less resistance to hunger, and greater rate of metabolism. All the birds considered in this text would fall into his second class, as undoubtedly would most passeriform species.

Effect of fluctuations in air temperature.—The possible effect of high and low air temperatures on the body temperature of animals has been the subject of investigation by scientists for a good many years. Edwards (1839) discusses the subject and sums up the previous literature. He believed that he found a seasonal variation in the temperature of sparrows. Pembrey (1898) summarizes the discussion up to nearly the end of the century. Sutherland (1899) states that birds perish when their temperature reaches 113° F. (45.0° C.). This figure is commonly seen in discussions concerning the upper thermal death point of animals. More recently, Wetmore (1921) finds that moderate fluctuations in air temperature are not constantly correlated with variations in the body temperature of most birds as long as they are able to obtain sufficient food and maintain their vitality. Rowan (1925) kept juncos successfully under artificial conditions out of doors all through a severe winter, by supplying them with plenty of food.

In our study, some attention was paid to the experimental determination of the limits in body temperature that birds can resist.

These variations in body temperature were induced comparatively rapidly by changing the air temperature to which the birds were subjected. Special apparatus had to be arranged for this, the details of which are well enough brought out in the accompanying photographs (Plate III) to render extensive description unnecessary. The bird was placed in an inner glass chamber through which a constant rapid flow of air was forced by water pressure, or, later, by water suction. Around this inner chamber, water was run in a larger glass tubing. By varying the temperature of the water introduced into this outer chamber, either by heating it on an electric hot plate or cooling it with ice, a wide range of temperature in the air of the inner bird chamber could be obtained practically at will, and, with some attention, could be maintained as long as desired; or the change from one temperature to another could be made either rapidly or slowly. The bird's body temperature was obtained by means of a thermocouple down its throat. The temperature of the air just before it reached the bird was determined by means of another thermocouple. The records were read on the indicator potentiometer, and an accuracy of about one-tenth of a degree was obtained. The rate of ventilation of air through the bird chamber averaged more than 100 cc. per minute.

It was not possible, during the short period available for these experiments, to develop a method of controlling and varying the relative humidity of the air to determine what effect this may have on the thermal resistance and regulation in birds. However, the humidities that occurred were measured by means of wet and dry bulb thermometers placed well into the bird chamber. At air temperatures from about 70° F. (21.1° C.) down, the air was nearly saturated, probably varying from 90% to 100% relative humidity. Hence, the lower thermal limits for birds were determined under these conditions. It is to be remembered that during the breeding season of these birds, the minimum air temperature for the day out-of-doors almost always come at night and that at this time the normal humidity is usually over 90%, so the conditions under experimental control actually approximated the natural conditions in this respect to which the birds are normally subjected. When this same air was heated to 115° F. (46.1° C.) the relative humidity would be considerably decreased. Reference to the psychrometric chart prepared by the Carrier Engineering Company indicates that the humidity would be about 30%. Thus the humidity approximated natural conditions out-of-doors during the hottest time of day. There is no evidence to indicate that the wide differences in relative humidity in these experiments had any effect on the body temperature of the birds.

Controls were obtained in each experiment by keeping the bird in the tube under room temperature and the proper ventilation for several minutes before any variations in the air temperature were produced. The bird's temperature was taken during this period and determined as normal before the experiment was begun. In later work, an electric refrigerator was used for obtaining the low air temperatures desired, and the birds placed inside this.

Experiments were performed on more than 55 individuals of 13 species, although only in the eastern house wren were the upper and lower limits of tolerance for body temperature approximately determined. The average length of the experiments was less than 2 hours. All the birds were used as soon as possible after capture, and so any depression of metabolism and body temperature as a result of lack of food was avoided. Muscular activity on the part of the bird was eliminated except for minor twitching and struggling, as the bird was placed in a loose-fitting, large-meshed bag made of mosquito-netting, to which the thermocouple was attached. Typical graphs showing the results obtained are given in Figures 6, 7, 8, and 9.

From these studies, it was evident that small variations in air temperature, when they are within the limits to which the birds are accustomed, have no effect on the body temperature. A variation of 2 or 3 degrees in body temperature, particularly if it is a decrease in temperature from an initial high figure, would normally be expected to occur in the bird's temperature regardless of external air temperature, due to cessation of muscular activities, and so allowance must be made for this. For instance, in Figure 8, a drop of 13 degrees in the air temperature from 73° F. (22.8° C.) to about 60° F. (15.6° C.) corresponds to a drop in the bird's temperature from 109.0° F. (42.8° C.) to 107.0° F. (41.7° C.), but this drop would probably have occurred even were the air temperature maintained constant. However, in another instance (Figure 7), the air temperature was increased from 71° F. (22.8° C.) rapidly at first, then more gradually to 96.5° F. (35.8° C.). This rise of 25.5° F. (14.3° C.) in 37 minutes produced an increase in the bird's temperature over a similar period of 3.0° F. (1.7° C.). These particular cases are typical of others. Thus it seems that moderate fluctuations in the normal air temperature have little or no effect on the bird's temperature, although large fluctuations occurring within a short time may produce some temporary variation.

Upper lethal body temperature.—After showing experimentally that moderate fluctuations in air temperature have practically no effect on the body temperature of the house wren, a study was next made of the upper and lower limits of body temperature that the bird could withstand. Four records are available in regard to the upper lethal body temperature in the house wren. The same apparatus was used as was described in the preceding section. The bird's body temperature was caused to rise by raising the air temperature rather rapidly to a high degree.

On several occasions, the body temperature of different species of birds between 112.0° F. (44.4° C.) and 113.5° F. (45.3° C.)

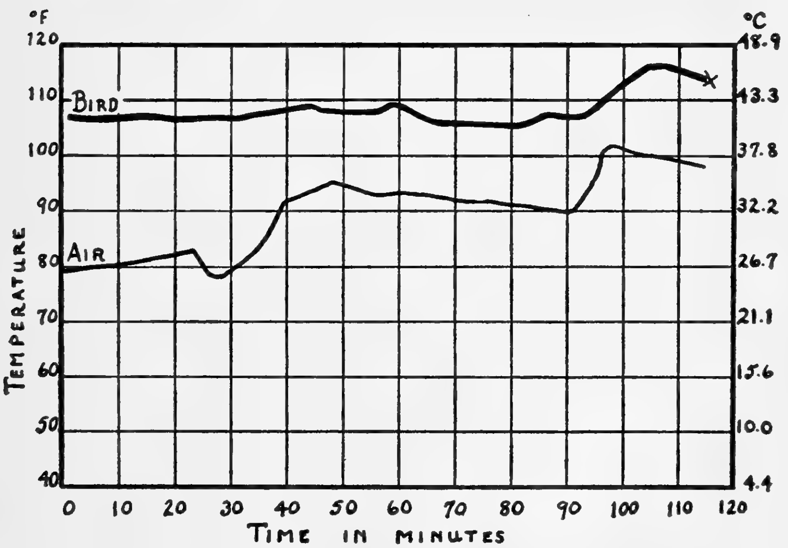


FIGURE 6.—EFFECT OF A HIGH AND RISING AIR TEMPERATURE ON THE BODY TEMPERATURE OF AN ADULT EASTERN HOUSE WREN, IN CONFINEMENT. The cross marks point of bird's death.

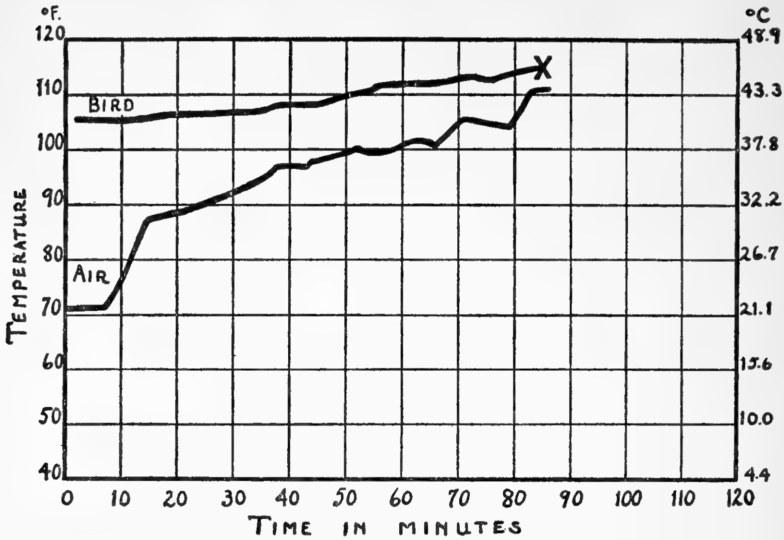


FIGURE 7.—EFFECT OF A HIGH AND RISING AIR TEMPERATURE ON THE BODY TEMPERATURE OF AN ADULT EASTERN HOUSE WREN IN CONFINEMENT. The cross marks point of bird's death.

has been obtained in the laboratory (page 32). These temperatures are not lethal, although they probably represent the maximum body temperature attained under natural conditions. In four experimental cases (Figures 6 and 7) death occurred in eastern house wrens after their body temperature had risen respectively to 116.1° F. (46.7° C.), 115.9° F. (46.6° C.), 115.1° F. (46.2° C.), and 118.2° F. (47.9° C.). The average of the records is 116.3° F. (46.8° C.). In two other instances, body temperatures caused to rise to 113.0° F. (45.0° C.) and 114.0° F. (45.6° C.) respectively, did not produce death. The temperature of 116.3° F. (46.8° C.) may be taken, therefore, as the approximate upper lethal body temperature.

A peculiar feature in this connection is that in 3 out of the 4 cases that resulted in death, the body temperature of the bird dropped from the maximum point before death actually occurred, although, in 2 out of these 3 cases, the air temperature remained nearly constant. The amount of this drop in body temperature was 2.5° F. (1.4° C.) and 8.3° F. (4.6° C.) respectively;

while in the third, in which the bird was removed to a cool room, it amounted to 26.1° F. (14.5° C.). This break and drop in body temperature is correlated with a decrease in the rate of the respiratory movements (page 54). Possibly the beginning of the drop marks the point of the breaking down of the physiological constitution of the organism, beyond which recovery is impossible. Death in cold-blooded organisms as a result of high temperatures is usually attributed to the coagulation and precipitation of proteins in the protoplasm. Probably something of the sort occurs here, but the precise cause of death from high temperatures in warm-blooded animals still needs to be determined. Pütter (1911) discusses some of the theories for the death of animals at high temperatures, and suggests that it may be due to the suffocation of the cells, on account of their inability to get sufficient oxygen at a rate rapid enough for their greatly increased metabolism.

The average temperature of the air at the time the maximum body temperatures of the birds were reached in the four instances was 100.2° F. (37.9° C.). Although birds are quickly affected by high air temperatures, this air temperature of 100.2° F. (37.9° C.) does not necessarily represent the upper limit of tolerance for the bird under natural conditions, because the birds in these experiments were in confinement under artificial unnatural laboratory conditions. In other experiments not here reported, where natural conditions were more closely imitated, birds have withstood higher air temperatures for short periods.

Lower lethal body temperature.—Over 50 birds of 13 species (Table VIII) were used for studying the effect of low body temperatures (Figures 8 and 9). Use was made of the same apparatus discussed in the preceding two sections. The object of the experiments was to lower the air temperature until the temperature control mechanism in the bird was broken, then determine the lowest body temperature that could be endured. The birds were taken directly from the traps and used in the experiments, and so all were probably well supplied with food in their digestive tracts at the beginning of the experiments. Nevertheless the temperature control mechanism of the bird was easily broken because of the unnatural confinement of the bird, in which there was little opportunity for movement or for fluffing out the feathers. In

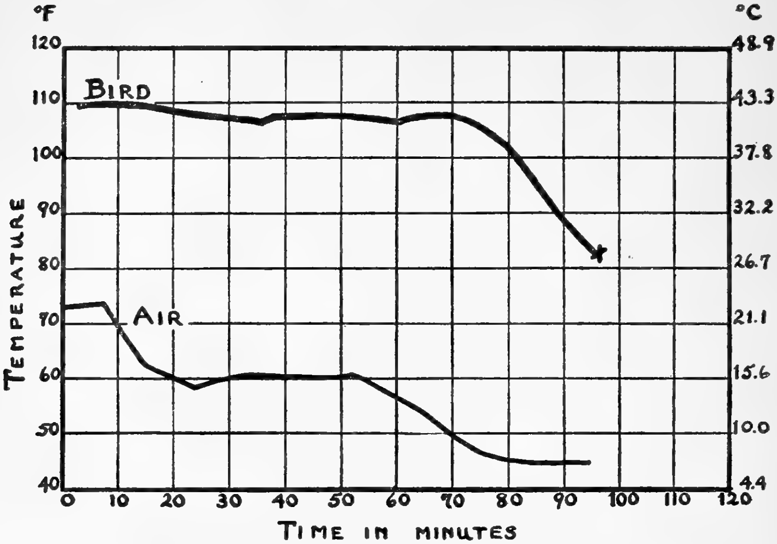


FIGURE 8.—EFFECT OF A LOW AND FALLING AIR TEMPERATURE ON THE BODY TEMPERATURE OF AN ADULT EASTERN HOUSE WREN IN CONFINEMENT. The cross marks point of bird's death.

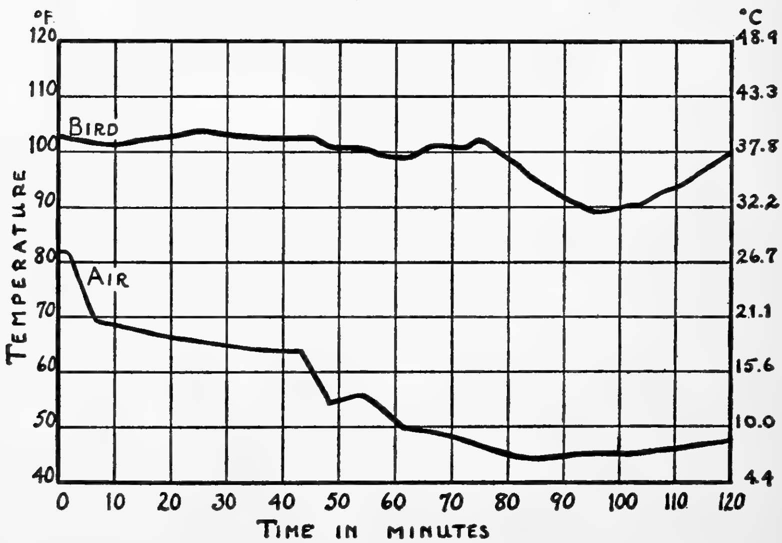


FIGURE 9.—EFFECT OF A LOW AND FALLING AIR TEMPERATURE ON THE BODY TEMPERATURE OF AN ADULT EASTERN HOUSE WREN IN CONFINEMENT. Note how the bird's temperature rises near the end, even though the air temperature remains nearly continuously low.

the case of 16 more carefully controlled experiments with the eastern house wren, the temperature of the air averaged 50° F. (10° C.) at the time that the temperature control mechanisms of the birds were broken and body temperatures began to drop rapidly below normal. This air temperature does not represent, however, the limit of tolerance for the bird under natural conditions.

Birds may recover their control of body temperature even after their temperature has fallen considerably below normal (Table VIII). This is well illustrated in Figure 9. The body temperature of this particular bird returned to its former high level even though previously it had fallen to 89.1° F. (31.7° C.), and this was accomplished entirely on the bird's own resources, without application of outside heat and while the air temperature remained below 48° F. (8.9° C.). Other birds, however, had to be returned to a warm room or even placed in an incubator before they were able to regain their normal body temperatures.

TABLE VIII.—*Number of Cases in Which Adult Birds Have Recovered Their Normal Temperature after Their Body Temperature Had Been Reduced Experimentally to the Indicated Levels*[1]

Species	100–95° F. (37.8°–35.0° C.)	95–90° F. (35.0°–32.2° C.)	90–85° F. (32.2°–29.4° C.)	85–80° F. (29.4°–26.7° C.)	80–75° F. (26.7°–23.9° C.)	75–70° F. (23.9°–21.1° C.)
Eastern house wren	26	19	7	4	2	1
Eastern cardinal	5	1	....	....	....	....
Catbird.........	5	3	....	....	....	....
Eastern bob-white	4	2	....	....	....	....
Eastern chipping sparrow.	4	3	....	....	....	....
Eastern song sparrow	3	....	....	....	....	....
Eastern field sparrow	1	....	....	....	....	....
Red-eyed towhee	1	....	....	....	....	....
Brown thrasher	2	1	....	....	....	....
Eastern cowbird	1	1	....	....	....	....
Northern yellow-throat	1	....	....	....	....	....
Northern downy woodpecker	1	1	1	....	....	....
Eastern mourning dove	1	1	....	....	....	....

[1]No deaths occurred.

Table VIII shows very clearly that the body temperature of several species of birds may be reduced to 90° F. (32.2° C.), at least, without danger that death will occur, although their normal temperatures are above 104° F. (40° C.).

In the case of the eastern house wren, a special study was made to determine actually how low the body temperature could be reduced and still allow recovery. The lowest such record obtained was 74.6° F. (23.7° C.). Although this body temperature was maintained only a few minutes it was necessary to work with the bird placed in an incubator for more than 1.5 hours before the normal body temperature was regained. The bird was liberated in an active condition. The low body temperature attained was very clearly close to the lethal point.

The next objective was to determine the actual degree of body temperature at which death occurs. Two adult house wrens were used. Death in one of these birds occurred when the body temperature had dropped to only 82.2° F. (27.9° C.). This is abnormally high and represents an exceptional condition. The other bird did not die until its body temperature had been reduced to 71.0° F. (21.7° C.). This degree of temperature appears to be more nearly correct, and when taken with the records in Table VIII, indicates that the lower lethal body temperature in the eastern house wren and possibly other passeriform species is approximately 71.0° F. (21.7° C.).

Death of birds from low temperature is not due, therefore, to "freezing," since they died a long time before the freezing temperature was reached. Ansiaux (1890) performed experiments similar to these on dogs, and came to the conclusion that death from low temperature was due to a stopping of the heart-beat, which resulted in a cerebral anemia. Respiratory movements persisted after the circulation of blood had entirely ceased. Britton (1922), working on cats, supposes that death at low temperature is due to a paralysis of the respiratory center.

RATE OF RESPIRATORY MOVEMENTS AT DIFFERENT BODY TEMPERATURES

Numerous studies by various workers have shown that the speed of physiological processes varies directly with the temperature until a certain high point is reached, above which there is usually a decline or a slowing up of the rate. This principle is rather easily demonstrable on cold-blooded organisms. In warm-blooded forms the tendency probably remains fundamentally the same, but here the different physiological processes are more highly organized, and their relation to each other is so much more intricate that the effect of temperature is not always so apparent. Then, too, the presence of a regulating mechanism for the maintenance of a fairly uniform body temperature further complicates the relationship.

In this study, it was possible to determine the rate of the respiratory movements of the same bird at different body temperatures. This was done simply enough by actually counting, with watch in hand, the exhalations and inhalations, and getting the rate per minute. This was done while the birds were subjected to the high and low body temperatures discussed in the above sections. The rates, as determined on several individuals of each sex, are given in Table IX.

As the available records of the eastern house wren are more than of other species and cover a wider range of temperatures, more detailed discussion is possible with that species (Figure 10). At

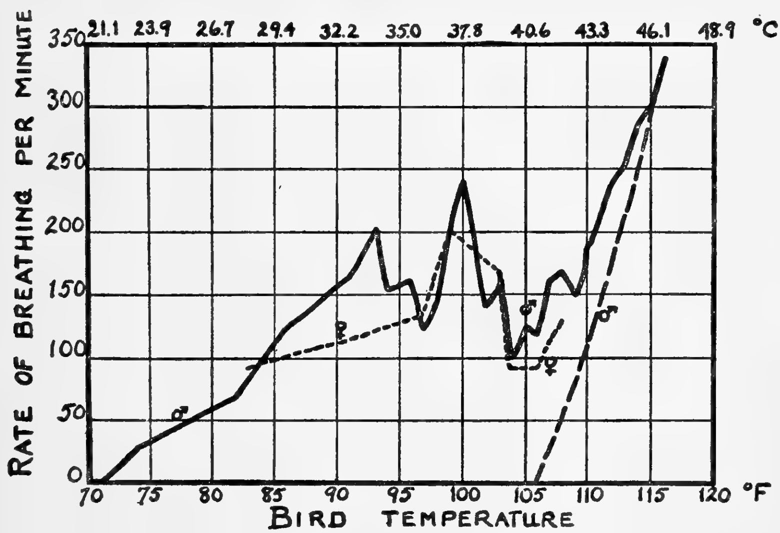


FIGURE 10.—RATE OF BREATHING MOVEMENTS IN THE ADULT EASTERN HOUSE WREN AT DIFFERENT BODY TEMPERATURES. The continuous line is for the male; the short broken line is for the female. The long broken line (for the male) at right shows how rapidly the breathing rate decreases as the body temperature falls, after reaching the upper lethal body temperature.

TABLE IX.—*Rate of Respiratory Movements at Different Body Temperatures*

Body Temperature	Male		Female	
	Number of Records	Average Rate per Minute	Number of Records	Average Rate per Minute
Eastern House Wren (Adults)				
71° F. (21.7° C.)	1	0 (death)	..	..
74° F. (23.3° C.)	1	28	..	..
82° F. (27.8° C.)	1	68	..	..
83° F. (28.3° C.)	..	..	1	92
86° F. (30.0° C.)	2	122	..	..
88° F. (31.1° C.)	..	..	1	106
91° F. (32.8° C.)	1	164	..	..
93° F. (33.9° C.)	1	202	..	..
94° F. (34.4° C.)	1	152	..	..
96° F. (35.6° C.)	1	160	..	..
97° F. (36.1° C.)	1	122	1	136
98° F. (36.7° C.)	2	144	..	..
99° F. (37.2° C.)	3	201	1	200
100° F. (37.8° C.)	1	240	..	..
102° F. (38.9° C.)	4	140	..	..
103° F. (39.4° C.)	5	165	2	166
104° F. (40.0° C.)	19	100	1	91
105° F. (40.6° C.)	17	126	8	92
106° F. (41.1° C.)	10	118	13	93
107° F. (41.7° C.)	4	163	7	113
108° F. (42.2° C.)	3	170	5	130
109° F. (42.8° C.)	2	146	..	..
110° F. (43.3° C.)	2	188	..	..
112° F. (44.4° C.)	1	240	..	..
113° F. (45.0° C.)	1	256	..	..
114° F. (45.6° C.)	1	288	..	..
115° F. (46.1° C.)	1	300	..	..
116° F. (46.7° C.)	1	340	..	..
115° F. (46.1° C.)[1]	1	324	..	..
114° F. (45.6° C.)[1]	1	248	..	..
113° F. (45.0° C.)[1]	1	214	..	..
106° F. (41.1° C.)[1]	1	0	..	..
Eastern Robin				
104° F. (40.0° C.)	..	..	1	48
105° F. (40.6° C.)	3	40	..	..
106° F. (41.1° C.)	8	49	1	40
107° F. (41.7° C.)	2	66	..	..
108° F. (42.2° C.)	2	74	1	79
109° F. (42.8° C.)	1	94	..	..

[1]Body temperature decreasing after upper lethal temperature reached.

Table IX (Continued).—*Rate of Respiratory Movements at Different Body Temperatures*

White-breasted Nuthatch, Male

Body Temperature	Number of Records	Average Rate per Minute
106° F. (41.1° C.)	1	65
107° F. (41.7° C.)	1	108

Eastern Chipping Sparrow

Body Temperature	Male		Female[1]	
	Number of Records	Average Rate per Minute	Number of Records	Average Rate per Minute
98° F. (36.7° C.)	1	108	..	..
104° F. (40.0° C.)	2	81	..	..
105° F. (40.6° C.)	10	75	1	77
106° F. (41.1° C.)	5	91	7	74
107° F. (41.7° C.)	3	97	4	64
108° F. (42.2° C.)	1	104	2	120
109° F. (42.8° C.)	1	157	1	140
111° F. (43.9° C.)	1	147	..	..
112° F. (44.4° C.)	..	..	1	157

[1] In one female not included in the averages, the rate per minute at 105° F. (40.6° C.) was 200, at 108° F. (42.2° C.), 219, due possibly to factors other than temperature.

Northern Downy Woodpecker, Male

Body Temperature	Number of Records	Average Rate per Minute
99° F. (37.2° C.)	1	88
104° F. (40.0° C.)	2	108
109° F. (42.8° C.)	1	131

Eastern Hairy Woodpecker, Female

Body Temperature	Number of Records	Average Rate per Minute
105° F. (40.6° C.)	2	130
107° F. (41.7° C.)	3	129

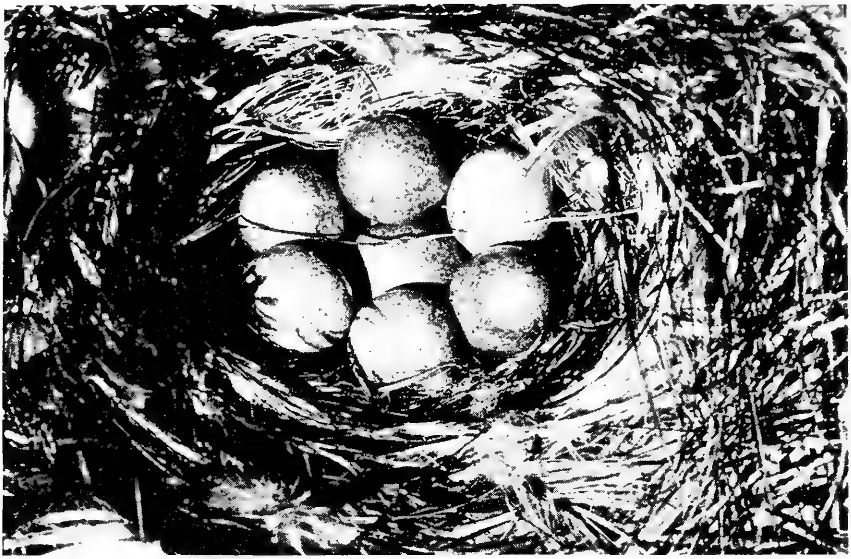
Eastern Yellow Warbler, Female

Body Temperature	Number of Records	Average Rate per Minute
104° F. (40.0° C.)	1	132

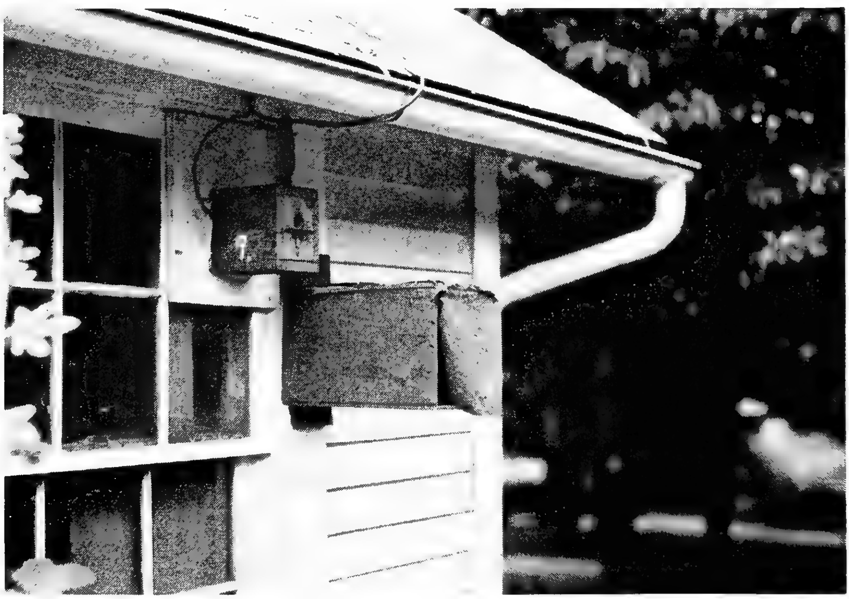
standard temperature (male, 104.4° F. [40.2° C.]; female, 105.0° F. [40.6° C.]), the rate of the respiratory movements is less than at body temperatures either directly below or above this standard temperature. This is to be expected, since the bird when at standard temperature is at complete rest and relaxation. As the body temperature rises the rate of respiration greatly increases until the upper lethal limit is reached; then it decreases. In 2 out of 3 instances this decrease was correlated with a drop also in body temperature. The highest rate recorded for the house wren is 340 times a minute in a male at a body temperature of 116° F. (46.7° C.).

As the body temperature falls below the standard level, the breathing increases in rate until it becomes very rapid at a body temperature of 100° F. (37.8° C.), but then begins a more or less fluctuating decline until death results. The low rate of breathing at standard temperature is due, as suggested, to the complete relaxation of the bird. As the temperature drops or rises from this, the bird awakens, becomes more or less active, and as a result breathing increases. High normal body temperature occurs only after considerable activity or excitement of the bird, which would also cause increase of respiration. At high temperature, also, the increase of breathing is due to an attempt of the regulating mechanism to increase the heat loss from the body. As the temperature control is broken at the upper limit, the breathing rate decreases, probably due to the general disablement of the body.

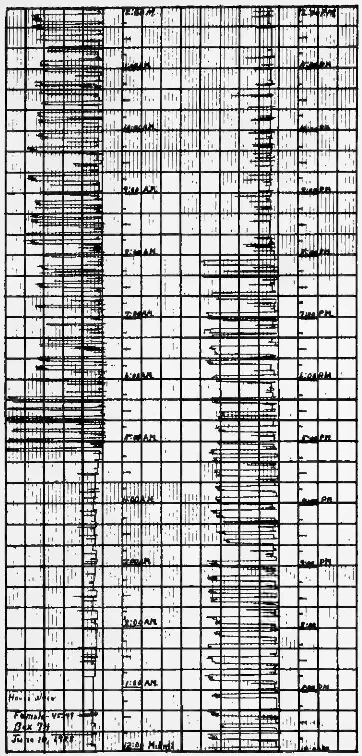
As the body temperature drops below the standard level to 100°, the increase in breathing is due largely to the activity of the bird. It would be interesting to know the part played by the air sacs in the breathing. One would expect that there is a rapid and thorough aeration of the air sacs in the increased breathing at high body temperatures and a complete closure of them at these low temperatures. As the body temperature drops below 100° F. (37.8° C.), the temperature control is broken and the breathing decreases. The rise in the rate at a body temperature of 93° F. (33.9° C.) may be due partly to increased activity, but may, in addition, have some particular significance in the respiratory mechanism, though at present this is not clear. If the normal range of the bird's temperature be considered as from 102.0° F. (38.9° C.) to 113.0° F. (45.0° C.), the rate of 256 times per minute is the maximum rate



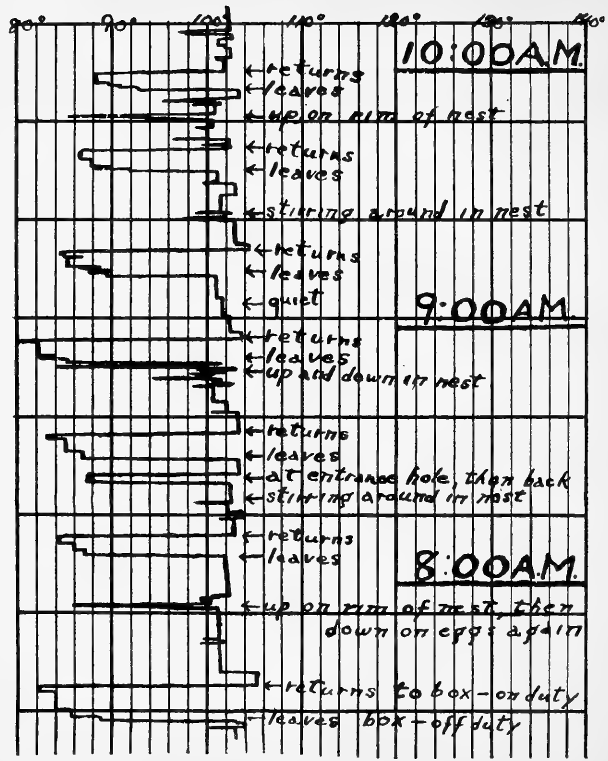
A.—NEST OF AN EASTERN HOUSE WREN IN A BOX SHOWING POSITION OF A THREAD THERMOCOUPLE ABOVE THE EGGS.



B.—NEST BOX OF AN EASTERN HOUSE WREN SHOWING THE THERMOCOUPLE WIRES THAT CONNECT THE NEST WITH THE RECORDING POTENTIOMETER IN THE LABORATORY. The larger box at the right shelters a thermograph which records air temperature.



A.—Type of Daily Record of Bird Temperature, Obtained by a Recording Potentiometer Connected with the Nest of an Eastern House Wren.



B.—Details of a Portion of a Daily Record of the Body Temperature of an Eastern House Wren, Correlated with the Bird's Activity during Attentive and Inattentive Periods.

of respiration in the normal behavior of the bird. In a few instances it has been possible to count at close range the breathing of female house wrens as they incubated their eggs without their being aware of the presence of man. Records obtained varied from 128 to 140 times per minute, but these observations are too limited for the setting of any limits for the rate at different times and circumstances under natural conditions.

The breathing rate is variable both in the individual bird and in different individuals. While watching particular individuals, under constant conditions, periods may be discerned when the breathing is accelerated, while at other times it is diminished. The breathing rate in different individuals may vary considerably even when their body temperatures are approximately the same. Undoubtedly other factors besides temperature are involved in the determination of this rate.

A comparison of the rate of breathing for the different species given in Table IX, particularly at standard temperatures (104°–105° F. [40.0°–40.6 C.]), shows that the eastern robin has the slowest rate. The eastern chipping sparrow breathes faster than the eastern robin but somewhat more slowly than the eastern house wren. The rate for the eastern house wren is comparatively high, although equalled by that of the two woodpeckers. The single record for the eastern yellow warbler is high.

There is also a difference between the sexes in the rate of respiration. This is very marked in the eastern house wren at and about the level of standard temperature (104°–106° F. [40.0°–40.6° C.]), the rate for the male averaging 112 (46 records) and for the female 92 (22 records). This is a difference of 20 in favor of the male. A difference in favor of the male continues as the body temperature increases at least as far as 108° (42.2° C.), after which it probably disappears. Below the standard level, the rate appears to be approximately the same in the two sexes. This difference in breathing rate at the standard temperature is just the reverse of the difference in the standard temperature between the two sexes, and may for this reason have some significance. With more rapid respiration, the body would become cooled faster, and hence the standard temperature in the male would reasonably be lower even if the metabolism were nearly equal.

SKIN TEMPERATURE

Recently Kallir (1930), using copper-constantan thermocouples, has obtained skin temperatures of some 10 species of birds. He found that the skin temperature was highest under the wings, over the furcula, and possibly on the upper rump. The head and the region above the base of the tail have the lowest temperature of the entire body with the exception of the unfeathered legs. The temperature of the last varies considerably with the surrounding air temperature. He also found that the skin temperature of a dove without feathers was lower than in a normal animal. In young sparrows, before the development of a temperature control, he found that the skin temperature varied with that of the surrounding air. This paper brings up several interesting points. Kallir gives data also on the temperature of various internal organs.

In the eastern house wren, it was desirable to determine the relation between the body temperature and skin temperature of different portions of the body, partly to furnish data for aid in a study of the temperature controlling mechanism of the bird; partly to investigate the relation between the body temperature of the bird and the temperature applied to eggs in incubation; and partly to correlate with the body temperature the skin temperature records obtained of the bird as she sits in the nest.

The skin temperature was taken with a loop thermocouple (page 16, Plate I–A). One person held the bird gently and loosely in the left hand, and with the right hand thrust the sensitive junction of this loop under the feathers. He then pressed down the feathers lightly over the outside of the thermocouple so that temperatures as normal as possible of the skin beneath the feathers could be obtained. Another person manipulated the indicator potentiometer, and read and recorded the results. Care was taken to read the body temperature of the bird by another thermocouple thrust down its throat just before and sometimes also just after the skin temperature was taken, so that errors due to normal fluctuations in the body temperature could be eliminated. The two thermocouples used for comparing these temperatures were tested under controlled conditions and found to be reading within a tenth of a degree of each other.

In Table X, all the measurements of the skin temperature of house wrens are compiled for different parts of the body, at different body temperatures, and separately for each sex.

From Table X it is seen that belly temperatures in males and females average the same; that the breast of the female averages 1.7° F. (1.0° C.) warmer than the breast of the male; that the temperature of the side of the body in the female is the same as in the male; and that the back of the female is 1.0° F. (0.6° C.) cooler. This relation will be clearer if we assume 108.5° F. (42.5° C.) as the body temperature of both male and female, then the skin temperatures would be as shown in Table XI.

It is interesting that the breast temperature of the male is so much lower than that of the female. This would seem to indicate that the circulation of blood must be better and richer in this region

TABLE X.—*Skin Temperature of the Eastern House Wren*
Female (15 Birds)

Body Temperature	Number of Records of Belly Temperature	Average Difference between Belly and Internal Body Temperature	Number of Records of Breast Temperature	Average Difference between Breast and Internal Body Temperature
112°–113° F. (44.4°–45.0° C.)	2	—1.8° F. (1.0° C.)	..	....
111°–112° F. (43.9°–44.4° C.)	2	—1.5° F. (0.8° C.)	..	....
110°–111° F. (43.3°–43.9° C.)	6	—1.3° F. (0.7° C.)	6	—2.2° F. (1.2° C.)
109°–110° F. (42.8°–43.3° C.)	15	—1.4° F. (0.8° C.)	17	—1.5° F. (0.8° C.)
108°–109° F. (42.2°–42.8° C.)	15	—1.4° F. (0.8° C.)	38	—1.0° F. (0.6° C.)
107°–108° F. (41.7°–42.2° C.)	15	—1.2° F. (0.7° C.)	34	—1.0° F. (0.6° C.)
106°–107° F. (41.1°–41.7° C.)	13	—1.0° F. (0.6° C.)	20	—1.2° F. (0.7° C.)
105°–106° F. (40.6°–41.1° C.)	8	—1.1° F. (0.6° C.)	12	—1.1° F. (0.6° C.)
104°–105° F. (40.0°–40.6° C.)	6	—0.8° F. (0.4° C.)	3	—1.1° F. (0.6° C.)
	Total 82	Average —1.3° F. (0.7° C.)	Total 130	Average —1.3°.F. (0.7° C.)

Body Temperature	Number of Records on Side of Body	Average Difference between Side of Body and Internal Body Temperature	Number of Records of Back Temperature	Average Difference between Back and Internal Body Temperature
112°–113° F. (44.4°–45.0° C.)	..	....	..	....
111°–112° F. (43.9°–44.4° C.)	..	....	..	....
110°–111° F. (43.3°–43.9° C.)	..	....	..	....
109°–110° F. (42.8°–43.3° C.)	2	—2.0° F. (1.1° C.)	2	—3.9° F. (2.2° C.)
108°–109° F. (42.2°–42.8° C.)	8	—1.8° F. (1.0° C.)	2	—2.8° F. (1.6° C.)
107°–108° F. (41.7°–42.2° C.)	2	—1.8° F. (1.0° C.)	5	—2.2° F. (1.2° C.)
106°–107° F. (41.1°–41.7° C.)	1	—1.8° F. (1.0° C.)	2	—2.4° F. (1.3° C.)
105°–106° F. (40.6°–41.1° C.)	..	....	2	—3.2° F. (1.8° C.)
104°–105° F. (40.0°–40.6° C.)	..	....	..	....
	Total 13	Average —1.8° F. (1.0° C.)	Total 13	Average —2.9° F. (1.6° C.)

TABLE X (Continued).—*Skin Temperature of the Eastern House Wren*
Males (9 Birds)

Body Temperature	Number of Records of Belly Temperature	Average Difference between Belly and Internal Body Temperature	Number of Records of Breast Temperature	Average Difference between Breast and Internal Body Temperature
110°–111° F. (43.3°–43.9° C.)	..	....	4	—3.2° F. (1.8° C.)
109°–110° F. (42.8°–43.3° C.)	2	—1.4° F. (0.8° C.)	6	—3.2° F. (1.8° C.)
108°–109° F. (42.2°–42.8° C.)	4	—1.4° F. (0.8° C.)	12	—2.7° F. (1.5° C.)
107°–108° F. (41.7°–42.2° C.)	5	—1.5° F. (0.8° C.)	6	—2.9° F. (1.6° C.)
106°–107° F. (41.1°–41.7° C.)	6	—1.1° F. (0.6° C.)	..	....
105°–106° F. (40.6°–41.1° C.)	2	—1.0° F. (0.6° C.)	..	....
104°–105° F. (40.0°–40.6° C.)	..	....	..	....
	Total 19	Average —1.3° F. (0.7° C.)	Total 28	Average —3.0° F. (1.7° C.)

Body Temperature	Number of Records on Side of Body	Average Difference between Side of Body and Internal Body Temperature	Number of Records of Back Temperature	Average Difference between Back and Internal Body Temperature
110°–111° F. (43.3°–43.9° C.)	..	....	..	....
109°–110° F. (42.8°–43.3° C.)	..	....	..	....
108°–109° F. (42.2°–42.8° C.)	6	—2.0° F. (1.1° C.)	2	—2.5° F. (1.4° C.)
107°–108° F. (41.7°–42.2° C.)	5	—2.4° F. (1.3° C.)	3	—1.6° F. (0.9° C.)
106°–107° F. (41.1°–41.7° C.)	5	—1.7° F. (1.0° C.)	6	—2.2° F. (1.2° C.)
105°–106° F. (40.6°–41.1° C.)	4	—1.2° F. (0.7° C.)	4	—1.7° F. (1.0° C.)
104°–105° F. (40.0°–40.6° C.)	..	....	2	—1.7° F. (1.0° C.)
	Total 20	Average —1.8° F. (1.0° C.)	Total 17	Average —1.9° F. (1.1° C.)

in the female during the breeding season than in the male. However, the fact that the back of the male is a whole degree higher than in the female may indicate that the difference in the skin temperature between the sexes may be due to some other cause.

In the female the feathers are lost from both the belly and breast during the breeding season and the skin becomes loose and

TABLE XI.—*Average Differences in Skin Temperature between Sexes of the Eastern House Wren*

	Male	Female
(Body)	(108.5° F. [42.5° C.])	(108.5° F. [42.5° C.])
Belly	107.2° F. (41.8° C.)	107.2° F. (41.8° C.)
Breast	105.5° F. (40.8° C.)	107.2° F. (41.8° C.)
Side	106.7° F. (41.5° C.)	106.7° F. (41.5° C.)
Back	106.6° F. (41.4° C.)	105.6° F. (40.9° C.)

wrinkled. This facilitates the close application of heat to the eggs. The loss of feathers is completed during the first egg laying period, and does not occur in the male. That this loss of feathers is important is shown by the following record obtained of a female before she had begun to lose her belly feathers. Her body temperature at that time was 109.2° F. (42.9° C.), the temperature on the outside surface of the feathers was 97.0° F. (36.1° C.), partly under the feathers, 101.2° F. (38.4° C.), and next the skin, 107.8° F. (42.1° C.). The air temperature was about 60° F. (15.6° C.). Thus by shedding its feathers, the bird was enabled to apply a temperature to the eggs 10° F. (5.6° C.) higher than it otherwise would have been able. The looseness and consequent wrinkling of the skin is due to the release of skin from the base of the calami of the feathers when these are lost.

The relation between internal body and skin temperatures does not remain exactly constant at all body temperatures. This is brought out to some extent in the averages shown in Table X, but is even more evident in cases of some individual birds. The tendency is toward a greater difference between body and skin temperatures when the bird's temperature is high than when it is low. When the bird is first caught and its temperature is taken, the difference between skin and body temperatures is large. This seems to indicate that in the bird's excitement and exertion, the internal body temperature rose more rapidly than did the skin temperature. As the bird is held gently in one's hand, it becomes quiet, and its temperature drops. However, the body temperature drops more rapidly than does the skin temperature, so that the difference between the two becomes less than it was at first. This shows that the body temperature is more rapidly variable than the skin temperature. This would be possible only if temperature regulation is carried out mainly through the respiration and not through the skin. The probable manner of temperature regulation will be discussed more fully in a later section (page 94).

In the nude human subject, it has been shown that the temperature of the skin varies with air temperature (Benedict, Miles, and Johnson, 1919). One would expect considerably less correlation in this respect in birds, because their skin is covered with an efficient insulating coat of feathers. Even in the case of incubating females that have lost most of the feathers from the midventral surface of the body, this area is well covered by the overlapping of feathers from the side when the bird is off the nest.

On 5 different female house wrens, several determinations of the skin temperature were made of breast and belly with the feathers drawn back so that the skin and thermocouple were exposed. No consistent difference in readings was obtained from those taken with the skin and thermocouple well covered with feathers. The bird is so small and the circulation of blood is apparently so rapid that when only a small area of the skin is exposed, no appreciable lowering of skin temperature occurs.

A test was next made to determine whether or not the skin temperature is affected when the air temperature is lowered. A series of determinations of skin temperature on 6 female house wrens was first made at ordinary high room temperatures of mid-summer. The bird was then placed in a damp basement room of lower air temperature and left for 1.25 hours before another comparable series of readings was taken at the lower degree. The results are shown in Table XII. All the readings were taken with the skin and thermocouple covered with feathers.

A study of Table XII shows that a lowering of 14° F. (7.8° C.) in air temperature is correlated with a lower belly temperature in

TABLE XII.—*Relation between Skin and Internal Body Temperatures of the Female Eastern House Wren at Different Air Temperatures*

Band Number of Bird	Air Temperature	Number of Records of Belly Temperature	Difference between Belly and Internal Body Temperature	Number of Records of Breast Temperature	Difference between Breast and Internal Body Temperature
F45565	86° F. (30.0° C.)	5	—1.3° F. (0.7° C.)	7	—1.1° F. (0.6° C.)
C94314	87° F. (30.6° C.)	5	—1.2° F. (0.7° C.)	7	—0.9° F. (0.5° C.)
C68978	88° F. (31.1° C.)	4	—0.4° F. (0.2° C.)	8	—1.2° F. (0.7° C.)
F45745	86° F. (30.0° C.)	4	—1.2° F. (0.7° C.)	8	—1.1° F. (0.6° C.)
F45359	88° F. (31.1° C.)	3	—0.8° F. (0.4° C.)	7	—1.2° F. (0.7° C.)
C94401	88° F. (31.1° C.)	4	—1.1° F. (0.6° C.)	8	—1.3° F. (0.7° C.)
Average of 6 birds....	87° F. (30.6° C.)	(25)	—1.0° F. (0.6° C.)	(45)	—1.1° F. (0.6° C.)
F45565	72° F. (22.2° C.)	4	—1.1° F. (0.6° C.)	9	—1.5° F. (0.8° C.)
C94314	72° F. (22.2° C.)	3	—1.0° F. (0.6° C.)	6	—1.0° F. (0.6° C.)
C68978	73° F. (22.8° C.)	4	—1.6° F. (0.9° C.)	11	—1.7° F. (1.0° C.)
F45745	73° F. (22.8° C.)	4	—1.3° F. (0.7° C.)	8	—1.0° F. (0.6° C.)
F45359	74° F. (23.3° C.)	4	—1.4° F. (0.8° C.)	6	—1.2° F. (0.7° C.)
C94401	74° F. (23.3° C.)	3	—0.9° F. (0.5° C.)	7	—1.1° F. (0.6° C.)
Average of 6 birds....	73° F. (22.8° C.)	(22)	—1.2° F. (0.7° C.)	(47)	—1.2° F. (0.7° C.)

3 instances and a higher belly temperature in 3 other instances. The breast temperature is lower in 3 cases, higher in 2, and the same in 1. Apparently the variations noted are largely those that may occur under any circumstances and are not due to differences in air temperature. In the averages for all 6 birds, the one-tenth or two-tenths of a degree difference is too small to have any great significance. The inference from these data is that the peripheral circulation of blood is so rapid and perfect and the skin is so well insulated with feathers, that variations in air temperature to which birds are exposed do not greatly affect the relation between skin and body temperatures.

It would be desirable for the sake of comparison to have available on other species than the house wren a series of skin temperatures like those above. We have only a few on hand. Twelve records on 3 other species of Passeriformes give an average belly temperature of 1.2° F. (0.7° C.) below that of the body. In the early part of these investigations we took a series of skin temperature readings with the mercury thermometer. Ten records on 7 passeriform species gave an average belly temperature of 1.0° F. (0.6° C.) below that of the body. Although these data are too inadequate for comprehensive discussion, they indicate that the skin temperature of some other small passeriform species during the breeding season is similar to that of the house wren.

To summarize: the skin temperature of small passeriform species is always lower than the body temperature; is less variable than body temperature; is not the same on different parts of the body; is not the same in both sexes on all parts of the body; and is unaffected by moderate changes in air temperature.

BODY TEMPERATURE OF BIRDS UNDER NATURAL CONDITIONS

Practically all the discussion concerning the temperature of birds in the preceding pages has been with the bird under more or less controlled and experimental conditions. In the following pages, there is considered the normal temperature of adult birds in their free natural environment. Because of obvious difficulties, this discussion pertains only to the female during the incubation period. One is probably justified, however, in believing that the male reacts to the same conditions as the female and in much the same manner.

So far as we have been able to ascertain, there has been no previous work done on the temperature of free wild birds under natural conditions, hence there is no literature on the subject to review. The eastern house wren is the principal species of our research, although records on several other species have been obtained.

Method.—To obtain readings of temperature of an adult bird as she sat on her eggs in the nest, use was made of a thread thermocouple (Plate I–A). This was stretched across the nest from one side to the other slightly above the eggs, so that the sensitive junction came halfway across the nest (Plate IV–A). The wire was not made so tight or rigid as to annoy the adult bird when she came in to incubate, but was fastened with sufficient firmness that it could not be pulled out of position. As it is sufficiently flexible to permit some adjustment by the adult bird to suit her comfort, it is much like a coarse thread over the eggs. When the bird came in and sat down on her eggs to incubate them, she necessarily had to sit on this thermocouple wire. Her weight was sufficient to press down the wire to the top level of the eggs so that normal incubation was not interfered with, yet the wire was taut enough to keep the sensitive thermojunction continuously pressed against her skin. In this way the skin temperature of the bird while she sat in the nest could be obtained. The thermocouple wires ran back from the nest to some building or shelter near by where temperature records were obtained by the use of indicator and recording potentiometers, without the bird's being in the least aware that they were being taken (Plate IV–B).

One objection to this method that might be raised is that the presence of the wire in the nest would disturb the bird so that she would not behave or react under exactly natural conditions. In a very few instances, this actually occurred. In working with birds as well as with human beings, individuality of the subject is always a factor that must be considered. With a few individual house wrens, normal records were not obtained, and these are not considered in this discussion. In other cases, the bird would be annoyed by the wire for the first day or two, but then become so accustomed to it as to give it no further attention. Occasionally, records could be obtained every day during the 12 or 13 days of incubation so that any slight disturbance during the first day or two was of little consequence. In a few cases, the thermocouple was placed in the nest before the set of eggs was laid or completed, and the bird became accustomed to the wire gradually. Some individual birds paid no attention at all to the wire, even from the first, and these naturally gave us the best records and our most reliable data. Through observation, the behavior of these birds in the nest was checked by birds in other nests where there were no thermocouples.

In order to interpret the records obtained in terms of body temperature, a constant had to be determined for the relation of skin temperature to body temperature in the female house wren and other species. To obtain such a constant was one of the objects in the study of skin temperature discussed above. The thermocouple in the nest obtains the skin temperature of the under side of the bird. The sensitive junction of the thermocouple rests on the lower part of the breast or on the belly. During incubation, the belly and breast of the female house wren are bare of feathers, so that there is no interference in this way. This is true of also other passeriform species. Likewise, when the incubating bird settles on the eggs she fluffs out the feathers on the side of the body, so there is generally a good contact between the skin and eggs, and also between the skin and the thermocouple.

In the study above, a difference between the temperature of the belly and breast and that of the body of 1.3° F. (0.7° C.) was obtained, the body temperature being always the higher. Therefore, adding 1.3° F. (0.7° C.) to the records of skin temperature obtained of the bird in the nest gives the approximate body temperature. This is subject to some final error, although the errors in individual records are sometimes of a plus, sometimes of a minus nature, so are largely eliminated when several hundred records are averaged, as is the case in nearly all of the following tables and figures. The probable error in the records of belly and breast temperatures of female house wrens given in Table X is ± 0.36° F. (0.20° C.). Since the body temperature records, as ordinarily obtained, are more variable than skin temperatures, as indicated in Table X, the actual fluctuations in body temperature were slightly greater than is indicated in the tables and figures that follow, since these are built upon records of skin temperature only. The results obtained from this method of determining the normal temperature of living wild birds under natural conditions have considerable importance and reasonable accuracy. From Table XII, we see that differences in air temperature do not appreciably affect the relation between skin and body temperature, because of the rapid circulation of blood. On the same account, the cool eggs in the nest do not lower the skin temperature more rapidly than they do the body temperature.

Many records of the skin temperature of the bird in the nest were obtained during the incubation period by the use of the thermocouple arranged in the nest as just described and the indicator potentiometer. Some of these records are graphically shown in Figure 11. An addition of 1.3° F. (0.7° C.) was made so that the variations of temperature might be interpreted in terms of the body temperature of the bird.

Average temperature of female birds on the nest during incubation.—For a proper understanding of this discussion of temperature, it is desirable first to say a few words concerning periods of attentiveness and inattentiveness in the bird's nesting behavior. This is an absolutely necessary concept that must be borne continually in mind in any discussion of nesting activities, particularly with such passeriform species as the eastern house wren. In a previous paper (Baldwin and Kendeigh, 1927), we have considered this in some detail. The essential points to bear in mind are that in the case of the species here considered, the female bird, which alone sits on the eggs, does not incubate continuously all day long without interruption, but that she is, instead, almost continuously going to and from the nest (Plate V). She will sit on the eggs for a few minutes, then leave them to get something to eat for herself, return to the eggs for another period of incubation, only to leave again a few minutes later. The periods she spends engaged in the duties of reproduction we call "attentive periods," while the periods during which she is away looking after her own sustenance we call "inattentive periods." These periods alternate regularly throughout the day from the time the bird first leaves the box in the morning after a night's stay until she settles down again at dusk. For the 12 female birds that furnished the data for this investigation, the average number of attentive periods per day was 33.7, and their average duration was 20.2 minutes. The number of inattentive periods per day averaged 34.7, and their length 7.6 minutes (Table XIII). The temperature of the bird can be obtained only during the period of attentiveness, but it can be estimated for the remaining time.

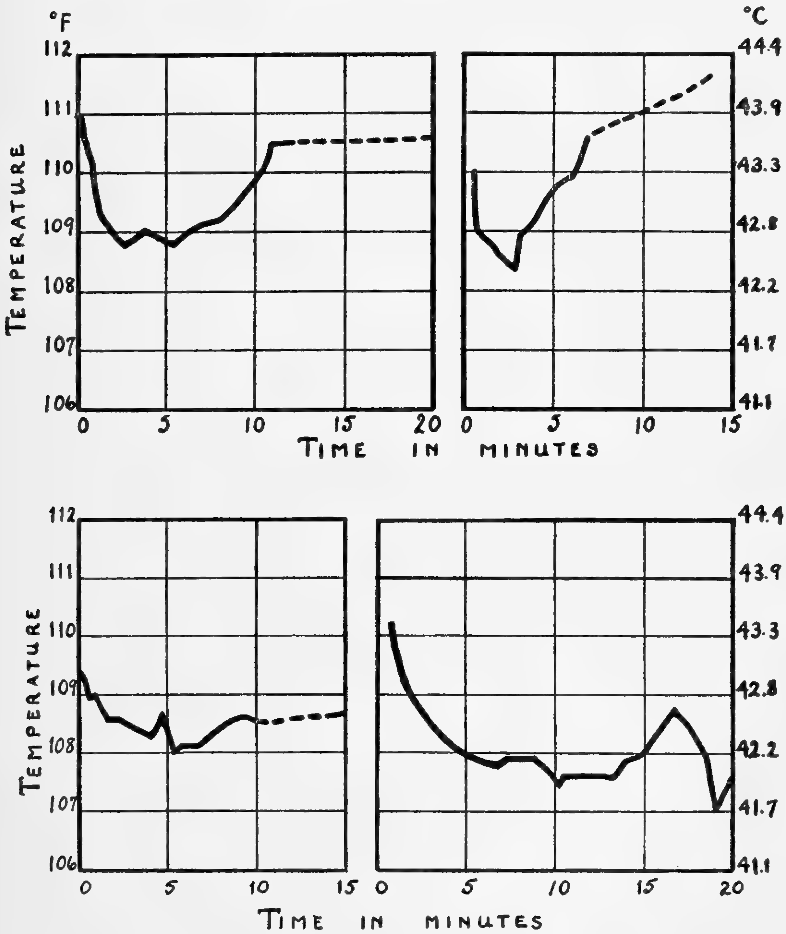


FIGURE 11.—TYPICAL VARIATIONS IN BODY TEMPERATURE OF THE ADULT FEMALE EASTERN HOUSE WREN. Shown while incubating eggs, both during periods of attentiveness (continuous line) and inattentiveness (broken line).

As may be seen from the graphs (Figure 11) the body temperature of the bird is high as it first comes to the nest after a period of absence. During the preceding inattentive period the bird has been exerting itself in flying around and hunting food, it has been taking new food into its alimentary tract, and perhaps it has been

TABLE XIII.—*Periods of Attentiveness and Inattentiveness in Various Species of Birds (Females) Whose Body Temperatures Are Given in Table XIV*

Species	Date of Records Obtained during Incubation Period	Number of Days' Record	Average Number of Attentive Periods per Day	Average Duration of Attentive Periods	Average Number of Inattentive Periods	Average Duration of Inattentive Periods per Day
				minutes		*minutes*
Eastern house wren						
(No. 1).........	July 23–30, 1929	8	45.8	8.5	46.8	10.0
(No. 2).........	July 4–18, 1930	13	45.7	12.5	46.7	7.0
(No. 3).........	May 27–June 6, 1931 ..	9	39.3	15.8	40.3	6.9
Eastern robin						
(No. 1).........	June 24–25, 1931	2	41.0	15.1	42.0	7.7
(No. 2).........	July 16–25, 1931	10	46.7	14.4	47.7	6.4
Wood thrush......	June 12–14, 1931	3	24.5	25.9	25.5	11.4
Cedar waxwing....	July 29–August 4, 1931	7	21.7	37.4	22.7	3.8
Catbird (No. 1)...	June 21–24, 1931	4	29.2	24.4	30.2	7.0
" (No. 2)...	July 8–12, 1931	5	22.2	33.0	23.2	7.8
Eastern song sparrow	June 18–21, 1931	2	23.0	28.2	24.0	7.6
Eastern chipping sparrow	July 20–22, 1931	3	36.0	17.8	37.0	6.8
Eastern wood pewee	August 5–15, 1929	9	29.1	19.7	30.1	9.2
Grand average: 8 species, 12 females, 75 days			33.7	20.2	34.7	7.6

scolding intruders or been emotionally excited in other ways. All of these factors, as our experimental work has shown, tend to raise the bird's body temperature. The fact that the bird's temperature is high when it first comes to the nest is, therefore, easily explained.

As the bird settles down on the eggs and becomes quiet, its body temperature drops. This is the same phenomenon that occurs, as shown previously, when the bird is held in the hand. It is due almost entirely to a decrease in heat production with the inactivity of the muscles. The bird is more at ease emotionally, and instances are known, in other species, of birds' practically going to sleep during the daytime while incubating their eggs. Undoubtedly also, the eggs with their lower temperature, coming into contact with the bare skin of the breast and belly, help to augment the rate of this decrease of body temperature.

After continuing to drop for 2, 3, 5 minutes, or even longer, the body temperature may then become constant, may fluctuate more or less considerably, or begin to rise again. As long as the bird remains quiet, the temperature is fairly uniform. Ordinarily, however, the house wren stirs around intermittently, perhaps to take a new position on the eggs or to shift the position of her legs, to inspect the nest's contents, or to survey some disturbance outside. Such activity, even though slight, is almost always accompanied by a temporary rise in body temperature. Sometimes, temperatures obtained at such times may be higher than the initial temperature of the bird when it first came to the nest.

Near the end of the period of attentiveness, the temperature of the bird usually, but not always, rises. The last temperature for the attentive period is almost always higher than at some intermediate time during the period, and in some instances may approach the initial temperature. Occasionally, the last temperature may be even higher than the initial one, but this is not the rule, as usually it is somewhat lower. Sometimes, this rise in temperature at the end of the attentive period may be explained by the stirring around of the bird in the nest. In other cases, however, it appears to be due to the warming up of the eggs and nest until they demand less heat from the brooding adult, thus conserving the body heat of the adult.

During the period of inattentiveness the body temperature generally rises. The temperature at the beginning of this period may be considered the last record obtained before the bird leaves the nest, while the temperature at the end of this period is the temperature of the bird when she first returns to the nest. As has been stated before, this latter temperature is usually the higher of the two, indicating that the activity of the bird while away from the nest gathering food is sufficient to raise its temperature. In Table XIV the averages of a large number of records of these different temperatures are shown.

From this analysis of the temperature of the bird during its periods of attentiveness and inattentiveness in incubation, we may pass to more general considerations.

The data for the body temperature graphs in Figure 11 were obtained by means of the indicator potentiometer. This instrument, however, must be manipulated by hand and constantly attended to if a continuous record of the bird's temperature is desired. To obtain automatically a continuous record of the bird's temperature at all hours of day and night throughout the breeding season, use was made of recording potentiometers (page 16). These give a continuous automatic record of the bird's temperature (Plate V) and require only a minimum amount of attention. Two of these instruments have been used constantly throughout the season.

More than 13,000 records of body temperature of birds have been compiled in Table XIV. These were obtained by continuous and automatic recording for a total of 75 days and nights. By *initial temperature* is meant the body temperature of the bird as she first returns to the nest after a period of absence, that is, it is the first temperature of the bird during a period of attentiveness. As this temperature is not always the highest for the period of attentiveness, a separate column is therefore provided for the *highest temperature* during the attentive period, and one, also, for the *lowest temperature*. The *last temperature* is the temperature of the bird at the end of the attentive period just before she leaves for a period of absence. Averages are obtained for these four temperatures for all the periods during each day, and then the various days are averaged together to give the temperatures for each individual as shown in the table.

The *median temperature of the attentive periods* is the median between the average highest and the average lowest temperature during the attentive periods, given in preceding columns of Table XIV. The body temperature fluctuates considerably during the attentive periods, but it is believed that the median comes as close to the true average of all these fluctuations as can be conveniently computed. The *median temperature of the inattentive periods* is, similarly, a median between two temperatures: the average last temperature of the attentive periods, which is at the same time the initial temperature of the inattentive periods, and the average initial temperature of the attentive periods, which is the last temperature of the inattentive periods. The temperature of the bird during the active daylight hours is obtained by averaging the median temperature of the bird during the periods of attentiveness and inattentiveness in proportion to the time duration of these two periods in minutes (Table XIII). It is, therefore, the *average median temperature during the active day.* Although at night the bird sits on the eggs constantly, median temperatures for each 15 minutes are, for the purpose of analysis, read off, and these then averaged to provide the *average median temperature during the night.* The temperatures of the bird during the day and the night are averaged in proportion to the length of these two periods in hours to give the *average median daily temperature.* Table XIV presents averages of these bird temperatures over several consecutive days during the incubation period.

The temperature of a passeriform bird, such as the species listed in Table XIV, averages 107.6° F. (42.0° C.) when it comes on the eggs for an attentive period of incubation. Due to agitation and stirring around while on the nest, the bird's temperature may mount to an average of 108.1° F. (42.3° C.), but falls to an average of 106.5° F. (41.4° C.) when she becomes quiet. Before she leaves the eggs at the end of an attentive period her temperature rises again to an average of 107.2° F. (41.8° C.). Thus, there is a fluctuation of 1.6° F. (0.9° C.) in the bird's temperature during the few minutes when she is on the eggs.

The average temperature of the bird at night is low, 104.6° F. (40.3° C.). This is largely due to the bird's being much less active on the eggs at night than she is during the day, and also because she is without food during this long period. As a consequence, the bird's temperature at night approximates its standard temperature (Table III). Actually it may and it usually does go below what was determined as standard temperature during the day (see graphs of daily rhythm in body temperature, Figures 13-25). This is in harmony with the results obtained by Benedict and Riddle (1929), who found that in pigeons and doves the standard metabolism is nearly 15% lower at night than it is during the day.

The lowest average body temperature given in Table XIV, 105.4° F. (40.8° C.), is for an eastern house wren (No. 3) and the highest, 107.2° F. (41.8° C.), is for an eastern robin (No. 1). This difference amounts to 1.8° F. (1.0° C.), but the difference between the lowest and highest average body temperature of individual house wrens is 1.3° F. (0.7° C.), which is almost as much. The difference between the 2 robin records is 1.2° F. (0.7° C.),

TABLE XIV.—*Body Temperature of Various Passeriform Birds (Females) on the Nest during the Period of Incubation*[1]

Species	Average Initial Temperature of Attentive Periods	Average Highest Temperature of Attentive Periods	Average Lowest Temperature of Attentive Periods	Average Last Temperature of Attentive Periods	Median Temperature of Attentive Periods[2]
Eastern house wren					
(No. 1)....	108.0° F. (42.2° C.)	108.3° F. (42.4° C.)	106.9° F. (41.6° C.)	107.4° F. (41.9° C.)	107.6° F. (42.0° C.)
(No. 2)....	108.0° F. (42.2° C.)	108.7° F. (42.6° C.)	106.8° F. (41.6° C.)	107.8° F. (42.1° C.)	107.8° F. (42.1° C.)
(No. 3)....	107.0° F. (41.7° C.)	107.2° F. (41.8° C.)	105.9° F. (41.1° C.)	106.5° F. (41.4° C.)	106.6° F. (41.4° C.)
Eastern robin					
(No. 1)....	108.4° F. (42.4° C.)	108.8° F. (42.7° C.)	107.2° F. (41.8° C.)	107.8° F. (42.1° C.)	108.0° F. (42.2° C.)
(No. 2)....	107.0° F. (41.7° C.)	107.4° F. (41.9° C.)	106.5° F. (41.4° C.)	107.0° F. (41.7° C.)	107.0° F. (41.7° C.)
Wood thrush	107.1° F. (41.7° C.)	107.2° F. (41.8° C.)	105.5° F. (40.8° C.)	106.1° F. (41.2° C.)	106.5° F. (41.4° C.)
Cedar waxwing...	107.3° F. (41.8° C.)	107.9° F. (42.2° C.)	105.9° F. (41.1° C.)	106.8° F. (41.6° C.)	106.9° F. (41.6° C.)
Catbird					
(No. 1)....	107.8° F. (42.1° C.)	108.0° F. (42.2° C.)	106.4° F. (41.3° C.)	107.0° F. (41.7° C.)	107.2° F. (41.8° C.)
(No. 2)....	106.8° F. (41.6° C.)	107.4° F. (41.9° C.)	105.6° F. (40.9° C.)	106.4° F. (41.3° C.)	106.5° F. (41.4° C.)
Eastern song sparrow	107.6° F. (42.0° C.)	108.2° F. (42.3° C.)	106.8° F. (41.6° C.)	107.4° F. (41.9° C.)	107.5° F. (42.0° C.)
Eastern chipping sparrow	108.5° F. (42.5° C.)	108.8° F. (42.7° C.)	107.7° F. (42.1° C.)	108.3° F. (42.4° C.)	108.3° F. (42.4° C.)
Eastern wood pewee	108.3° F. (42.4° C.)	109.0° F. (42.8° C.)	106.4° F. (41.3° C.)	107.4° F. (41.9° C.)	107.7° F. (42.1° C.)
Grand average...	107.6° F. (42.0° C.)	108.1° F. (42.3° C.)	106.5° F. (41.4° C.)	107.2° F. (41.8° C.)	107.3° F (41.8° C.)

[1]For the dates on which these records were obtained and the number and duration of the periods of attentiveness and inattentiveness, see Table XIII.

[2]The median temperature of the attentive periods is the median of the average highest and the average lowest temperatures of the attentive periods, given in preceding columns.

TABLE XIV (Continued).—*Body Temperature of Various Passeriform Birds (Females) on the Nest during the Period of Incubation*

Species	Median Temperature of Inattentive Periods[3]	Average Median Temperature during Day[4]	Average Median Temperature during Night[5]	Average Median Daily Temperature[6]
Eastern house wren (No. 1)	107.7° F. (42.1° C.)	107.7° F. (42.1° C.)	103.6° F. (39.8° C.)	106.0° F. (41.1° C.)
" " " (No. 2)	107.9° F. (42.2° C.)	107.8° F. (42.1° C.)	105.1° F. (40.6° C.)	106.7° F. (41.5° C.)
" " " (No. 3)	106.8° F. (41.6° C.)	106.7° F. (41.5° C.)	103.7° F. (39.8° C.)	105.4° F. (40.8° C.)
Eastern robin (No. 1)	108.2° F. (42.3° C.)	108.1° F. (42.3° C.)	105.4° F. (40.8° C.)	107.2° F. (41.8° C.)
" " (No. 2)	107.0° F. (41.7° C.)	107.0° F. (41.7° C.)	104.3° F. (40.2° C.)	106.0° F. (41.1° C.)
Wood thrush	106.6° F. (41.4° C.)	106.5° F. (41.4° C.)	103.9° F. (39.9° C.)	105.6° F. (40.9° C.)
Cedar waxwing	107.1° F. (41.7° C.)	106.9° F. (41.6° C.)	104.6° F. (40.3° C.)	105.9° F. (41.1° C.)
Catbird (No. 1)	107.4° F. (41.9° C.)	107.2° F. (41.8° C.)	105.2° F. (40.7° C.)	106.5° F. (41.4° C.)
" (No. 2)	106.6° F. (41.4° C.)	106.5° F. (41.4° C.)	104.8° F. (40.4° C.)	105.9° F. (41.1° C.)
Eastern song sparrow	107.5° F. (42.0° C.)	107.5° F. (42.0° C.)	104.2° F. (40.1° C.)	106.0° F. (41.1° C.)
Eastern chipping sparrow	108.4° F. (42.4° C.)	108.3° F. (42.4° C.)	105.1° F. (40.6° C.)	107.0° F. (41.7° C.)
Eastern wood pewee	107.8° F. (42.1° C.)	107.8° F. (42.1° C.)	105.1° F. (40.6° C.)	106.9° F. (41.6° C.)
Grand average	107.4° F. (41.9° C.)	107.3° F. (41.8° C.)	104.6° F. (40.3° C.)	106.3° F. (41.3° C.)

[3]The median temperature of the inattentive periods is the median of the average last and the average initial temperatures of the attentive periods given in preceding columns, since these are respectively the initial and last temperatures of the inattentive periods.

[4]The average median temperature during the active day is the weighted average of the median temperatures of the attentive and inattentive periods given in preceding columns, combined and averaged in proportion to the length of these periods in minutes. (See Table XIII.)

[5]The average median temperature during the night is the average of median temperatures obtained at fifteen minute intervals.

[6]The average median daily temperature is the weighted average of the bird's temperature during the day and during the night given in preceding columns, combined and averaged in proportion to the length of these periods in hours.

and between the 2 catbird records is 0.6° F. (0.3° C.). From these data the conclusion seems warranted that there is no important difference in body temperature between these species of passeriform birds.

In Table XIV there is given also an average body temperature for 12 individuals of 8 species of passeriform birds. Although the number of birds is small, this figure has, nevertheless, considerable significance. The average temperature during the breeding season maintained within the body of several passeriform species may be stated to be approximately 106.3° F. (41.3° C.). However, passeriform birds must not be thought of as possessing a constant temperature of 106.3° F. (41.3° C.). In fact, the body temperature of a bird is characterized more by its fluctuations than by its constancy. It is proper to say that the temperature of a passeriform bird is a variable, ranging from an average of 104.6° F. (40.3° C.) at night to 107.3° F. (41.8° C.) during the day, with temporary fluctuations both above and below these limits.

Fluctuation in body temperature from day to day.—The question arises as to the amount of fluctuation in the average body temperature of birds from one day to the next, and the possible correlation of these fluctuations with variations in air temperature and activity. The average body temperature over consecutive days of several species of birds was obtained as described on pages 68–69.

Air temperatures were obtained simultaneously with the bird temperatures, not by means of thermocouples, but by use of a Tycos thermograph placed in a small box shelter usually a little below and to the side of the nest box (Plate IV–B). In this position, where it was subjected to nearly identical conditions of sun and wind as was the nest box, it furnished a record approximating closely the exact conditions obtained in the nest, to which the birds were subjected during most of the incubation period. This thermograph records continuously on a chart and needs attention only once a week. Temperature records were taken from this chart once every hour and averaged for all hours of the day and night to give the average daily air temperature.

There is seldom more variation than a few tenths of a degree in the average body temperature of a wild bird from one day to the next (Figure 12). These small variations have significance, how-

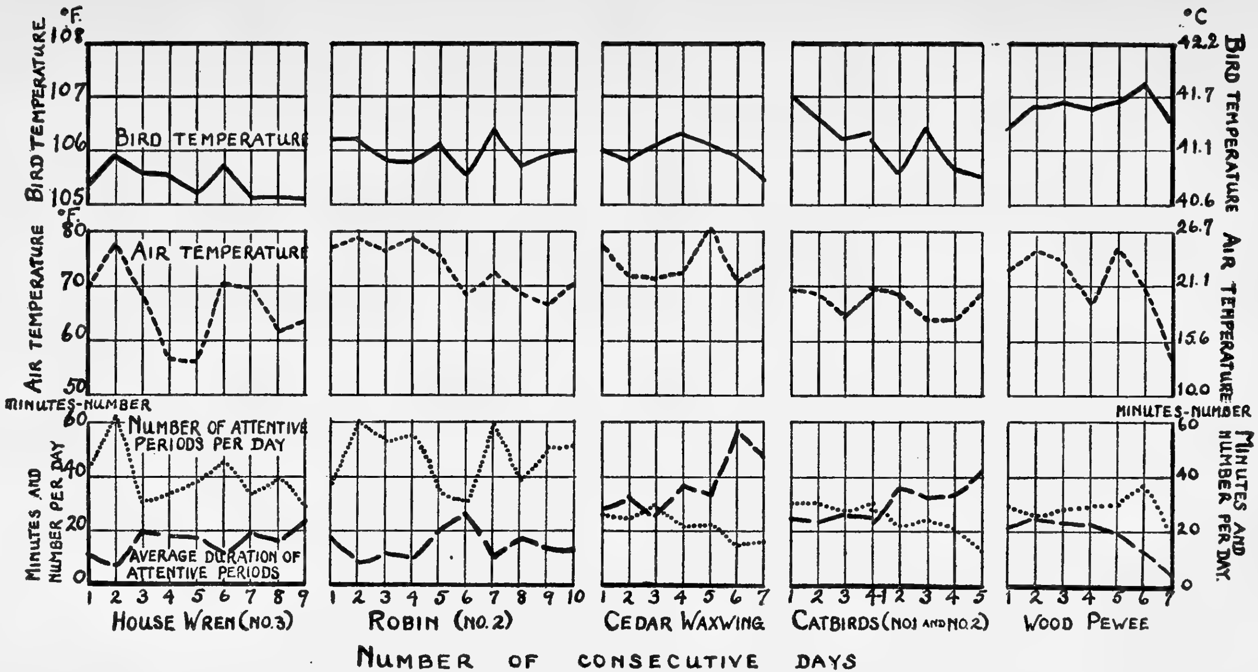


FIGURE 12.—DAILY VARIATION IN BODY TEMPERATURE OF SEVERAL INDIVIDUAL BIRDS OF DIFFERENT SPECIES. These are correlated with variations of air temperature over the same period. The lower set of graphs, indicating number and average duration of attentive periods, is a criterion of the birds' activity.

ever, since they may show some correlation with daily variation in other factors. Records from only those birds where conditions were best controlled are used in this comparison. Although variations as small as these between single temperature records of the potentiometer would fall within the possible error of the instrumental recording and be without significance, these are averages of many records each day and thus not so easily considered errors of recording.

There seems to be some positive correlation (Figure 12) between variations in bird and air temperature in the case of the house wren (No. 3). However, the variation in air temperature amounts to several degrees, while that in the temperature of the bird is only a few tenths of one degree. In the records for the other birds given in Figure 12, slight correlations frequently occur, but they are less evident and not entirely consistent. In part of the catbird record (No. 2), the correlation is inverse. The relation between variations in the average temperature of birds and moderate variations in air temperature from day to day seems to be only very slight.

Any positive correlation that may exist between daily variations in bird and air temperatures must be of either a direct or indirect character. In the experimental work previously discussed (pages 42–45) it was found that slight fluctuations in the air temperature have little or no effect on the bird's temperature, although large fluctuations, occurring within a short time, may produce some temporary variation. Approximately the same amount of direct correlation appears to hold under natural conditions, i. e., the average body temperature of the bird is not greatly affected by variations in air temperature, unless these are extreme.

On the other hand there may be some correlation between bird and air temperature through the effect of variations in air temperature on the bird's activity. The amount of activity of a bird was shown in the experimental work (pages 34–37) to be one of the chief causes for variation in its body temperature. As a measure of the bird's activity, also the number of attentive periods per day and their average duration are plotted in Figure 12.

The number of attentive periods indicates the number of times that the bird goes to and from the nest each day, while the length of the attentive period shows how long she stayed at the nest each time. The daily variation in the length of the inattentive period is too small to be considered. The more visits that the bird makes to the nest each day, the shorter the time that she stays there on each of the visits. This would be expected, since the length of a bird's day is rather uniform and is controlled more by light and darkness than by temperature. A bird is less active while sitting on the nest than she is while off hunting for food and flying. Therefore, the shorter these attentive periods are and the more numerous, the more active is the bird. A study of Figure 12 indicates that the bird is generally more active on warm days than on cool days. On cool days the bird must be more attentive to incubating the eggs.

The days of greater activity correspond loosely with the days when the bird's temperature is higher, and vice versa. It seems, therefore, that daily variations in the amount of a bird's activities are more important in affecting its body temperature than are variations in air temperature.

The record for the eastern wood pewee in Figure 12 has one point of interest which needs special comment. On the seventh day of recording, the air temperature dropped very low, and considerable rain fell during most of the day. This is correlated with a decided drop in the temperature of the bird and also with a greatly decreased activity and less time on the nest. This species of bird feeds almost entirely on insects caught in the air. It is probable that the cold, damp weather drove these insects out of the air, so that the bird suffered from lack of food and as a consequence was unable to maintain its previous activity and body temperature. It came to the nest to incubate only 17 times on this day instead of the normal 30 times. After the middle of the afternoon, however, the weather improved, the bird came to the nest more frequently, and its body temperature rose to a high level again.

The question is frequently asked, is there not an increase in the body temperature of the sitting female during the period of incubation? There are no data in our records to indicate such a rise in temperature (Figure 12). Simpson (1911) found no increase in the temperature of a domestic hen during incubation, although he did find that its temperature rose at the time of the hatching of the eggs. The hatching of eggs of passeriform species is a more gradual process with fewer eggs involved than in the case of the domestic fowl, and in the species that we have studied, no such rise has been noted in the bird's temperature on the days on which the eggs hatched.

No study has been made of seasonal variations in the body temperature of native birds under natural conditions. Sutherland Simpson (1912) carried out an interesting investigation in this connection on the seasonal changes of temperature in the domestic fowl. He took rectal temperatures with mercury thermometers on the same individuals of 6 breeds of chickens every month throughout the year at about the same date and same hour. He found that the bird's body temperature was lowest in December, January, and February, and highest in June, July, and August. He explains the higher temperatures of his birds during the summer as a result of the higher air temperatures, but it seems probable to us that they were due primarily to the greater activity of the birds in the summer, while the higher air temperatures played only a secondary role.

It is probable that the average daily temperature of wild birds, when determined by averaging their body temperatures for all hours of the day and night, is higher in the summer than in the winter. This is not to be explained on the basis of higher summer air temperatures. Rather, it is correlated with a greater amount of activity on the part of the birds during the summer, occasioned by the longer duration of the daily periods of light. As stated above (page 69), the average body temperature of a bird is determined by combining and averaging the temperature of the bird at night, when it is low, and the temperature of the bird during the day, when it is high, in proportion to the length of nighttime and daytime in hours. In northern Ohio, for instance, the daily number of hours of light in the middle of the summer may be over 15, with the number of hours of darkness only 9; while in the middle of winter, the duration of daylight may be only a little more than 9 hours long, while the duration of the night may be nearly 15. This variation in relative length of day and night at different seasons of the year should cause marked seasonal variations in average daily body temperatures of permanently resident birds.

Daily rhythm in body temperature.—Chossat (1843) appears to have been the first to make a serious study of the daily temperature rhythm in birds. His work has already been cited above (page 40). It was limited to pigeons and doves in confinement. Corin and van Beneden (1887) were the next to work on this problem, their subjects being also pigeons. Their curve shows that the minimum daily temperature comes at 4:00 A. M. and the maximum at 4:00 P. M. The next work done was that of Simpson and Galbraith in 1905. Their study was more extensive and they obtained curves and data on some 12 species of birds. They found that the mean temperature of all species with which they worked was about the same, 105.8°–107.6° F. (41.0°–42.0° C.), but that the mean daily temperature range varied considerably in different species, being greater in smaller birds than in larger, amounting in some cases to over 7° F. (3.9° C.). They conclude that "the temperature curve of diurnal birds is essentially similar to that of man and other homoiothermal mammals, except that the maxima occur earlier in the afternoon and the minima earlier in the morning. In nocturnal birds (owls), on the other hand, the curve is inverted, the maximum occurring about midnight or in the early morning and the minimum about noon or shortly after. As in diurnal birds, the temperature is highest during the natural period of activity (night) and lowest during the period of rest (day)." Riddle, in 1908, obtained a curve showing the daily rhythm of body temperature of 6 ducks, 5 ring doves, and 5 chicks. He found an average variation of 1.3° F. (0.7° C.) between different times of day. The lowest temperatures came between 1:00 and 5:00 o'clock A. M. and the highest about noon. There was a rise in temperature throughout the morning, and a fall throughout the afternoon and evening. Hildén and Stenbäck (1916) secured a generalized composite temperature curve from 6 species of birds obtained principally from zoological gardens, and from which temperature readings were taken every 3 hours by means of a thermometer thrust up the cloaca. The time of minimum temperature in this curve is 9:00 o'clock P. M., and the maximum at noon, with the temperature rising during the morning and falling during the afternoon. In some of their curves for individual birds, there is evident a rapid and pronounced increase of temperature at the beginning of the daylight periods and a similar decrease of temperature at the end. Wetmore (1921) offers a few observations on the daily variations in wild birds, but his work on this subject is not extensive. Groebbels (1928–b, 1931) in Europe is now working on the daily temperature rhythm of migrating birds.

As discussed above, in the present investigation we have been obtaining nearly continuous records of the body temperature of birds by means of thermocouples placed in the nests and by recording potentiometers. These furnish records both day and night for weeks at a time all through the incubating periods. One particular advantage of this method and of the data obtained is that they are of wild birds under entirely undisturbed and perfectly natural conditions. Records are available for 12 different birds of 8 species over a period of 75 days and nights, including first and second nestings.

To obtain the curves given below (Figures 13–25) for the various hours of the day, 4 temperatures are first transcribed from the potentiometer record for each attentive period. These are the initial, highest, lowest, and last temperatures, which have been discussed in some detail above. The last temperature of one attentive period and the first of the next are averaged to give the median temperature of the bird while away from the nest, and the highest and lowest temperatures of each attentive period are averaged to give the median temperature of the bird while at the nest. The figures thus obtained are then averaged together equally to give the average median body temperature of the bird for each half hour. The time is indicated at each hour and each half hour of the day, but this includes in either case a period from 15 minutes before to 15 minutes after the time stated. At night, median temperatures are recorded directly from the potentiometer chart every 15 minutes. The hourly variations of temperature for each bird were determined for several days and nights. These were then averaged together to get a composite record for each individual. To obtain an average curve for more general application to passeriform species, the records of these 12 birds are averaged together equally (Figure 13). This, of course, is for only the female sex, and can be considered to hold only during the breeding season. The air temperature at the nest was obtained by taking readings from the air thermograph chart every hour and averaging these over the same period of days on which the bird's temperature was recorded.

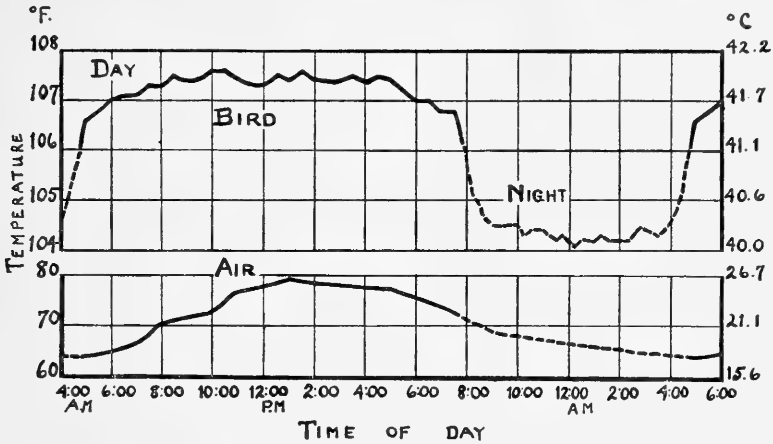


FIGURE 13.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF PASSERIFORM BIRDS. These records comprise 8 species, 12 individuals, and 75 days, correlated with air temperature, and show the effect of activity during the day (continuous line), against the quiet of night (broken line).

It will be easier to understand the normal daily variations in body temperature of birds and the effect of different modifying factors, if there is considered first the curve for the 8 species based on the averages obtained as just described (Figure 13). This composite curve together with a curve showing the daily rhythm in air temperature over the same period are given for comparative purposes in the same figure. It will be recalled that the hours used in this discussion relate to the longitude of Cleveland, Ohio, and are given in Eastern Standard time.

The birds leave the nest in the early morning and commence the daily activities of feeding and incubating at about 4:45 o'clock, as is indicated on the graph. The body temperature then averages about 106° F. (41.1° C.). During the next 5 hours the average increases to 107.6° F. (42.0° C.), which is the maximum average temperature reached by the bird during the day. After that it fluctuates up and down throughout most of the afternoon. From 5:00 o'clock in the afternoon until the end of the day's activity at 7:45 o'clock, there is a pronounced drop of 1.1° F. (0.6° C.).

During the incubating period, the female spends every night on the nest, otherwise the eggs would become greatly cooled. Her usual time of retirement is shortly after the sun goes down, or about 7:45 P. M. The most rapid drop in body temperature for the whole 24 hour period occurs during the next hour and a quarter. This amounts to 1.8° F. (1.0° C.). From our experimental and observational studies above, we have repeatedly shown that whenever the bird becomes quiet and relaxed physically its body temperature drops.

The bird's temperature does not remain uniform during the night. On the contrary there is considerable variation. The bird does not sleep continuously for long at a time, in fact seldom more than a few minutes. Then it stirs around in the nest, stretches its legs, takes a new position on the eggs, or may entirely leave the nest. On one occasion in our records, we noted that a female house wren left the nest around 8:50 o'clock P. M. after it had retired normally more than an hour before, and did not return until 1:04 A. M. early the next morning. In other instances, the bird has left the nest at night for shorter periods. These cases, however, are exceptional. It is sufficient to note here that the bird is more or less active at night. These activities temporarily raise its temperature and are the cause of some of the fluctuations to be noted.

In previous studies on the temperature rhythm in man and other animals, most authors are accustomed to point out times of rather definite maximum and minimum temperatures. This curve (Figure 13) shows a fluctuating maximum from 10:00 A. M. until 5:00 P. M. The daily maximum air temperature comes at 1:00 P. M. at this time of the year at Cleveland, Ohio.

The night body temperatures reach the lowest point of 104.1° F. (40.1° C.) at 12:15 A. M., but are almost as low continuously until 2:15 A. M. From this time until 3:30 A. M. there is a slight increase of temperature which reaches 104.5° F. (40.3° C.) and then falls back to 104.3° F. (40.2° C.), but this is probably not significant. It is at this time that the bird rests more quietly and for longer periods of time without stirring than at any other time of the day. This can be determined from the potentiometer records, for, of course, as soon as the bird rises off the thermocouple, a drop in the temperature reading is obtained. Also at this time, the bird has been the longest without food, so one would expect for this reason that the temperature would be low. The air temperature reaches a minimum at about 5:00 A. M. at this time of the year at Cleveland, Ohio.

After 3:30 A. M. until the bird leaves the nest to begin its day's activities at 4:45 A. M., the rise in body temperature is very rapid (1.7° F., [0.9° C.]) and reaches 106.0° F. (41.1° C.). This rapid rise during the hour or so before the bird leaves the box may be the result partly of the bird's becoming more and more uneasy on the nest as the amount of light outside the box is increasing, and partly the result of the bird's becoming more alert mentally and perhaps even more or less excited. The male bird is about and active before the female and frequently comes around the nest, singing lustily, which would arouse the female and tend to increase her body temperature.

In addition to the composite curve for several species above explained, it is worth while to study also the daily temperature rhythm in each individual bird separately. These are shown in Figures 14–25. Each curve is the average of several days' records for the same individual. In general, the individual curves agree with the composite one already considered.

The minimum bird temperature is always reached some little time before the minimum air temperature, usually several hours before. There is a correspondence, however, between the time

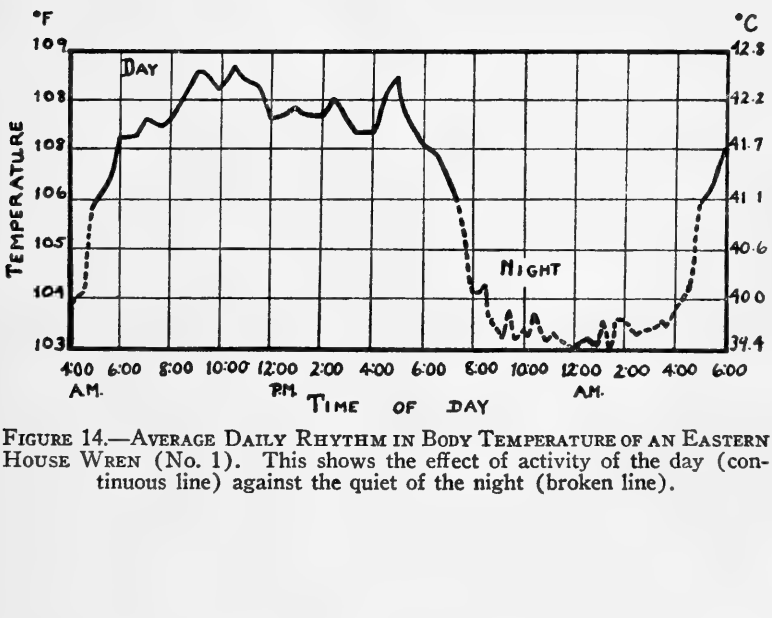


Figure 14.—Average Daily Rhythm in Body Temperature of an Eastern House Wren (No. 1). This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

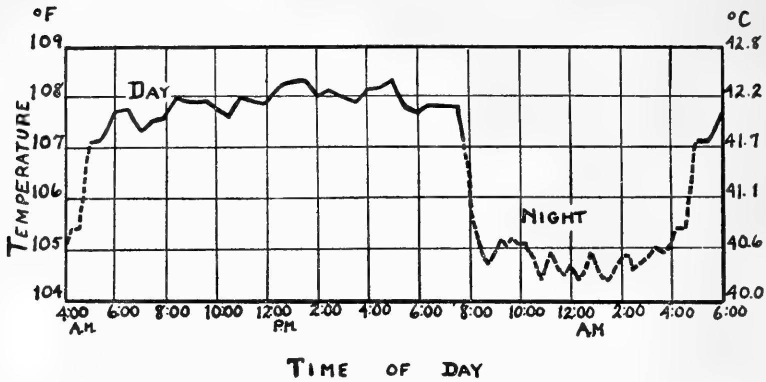


FIGURE 15.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF AN EASTERN HOUSE WREN (No. 2). This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

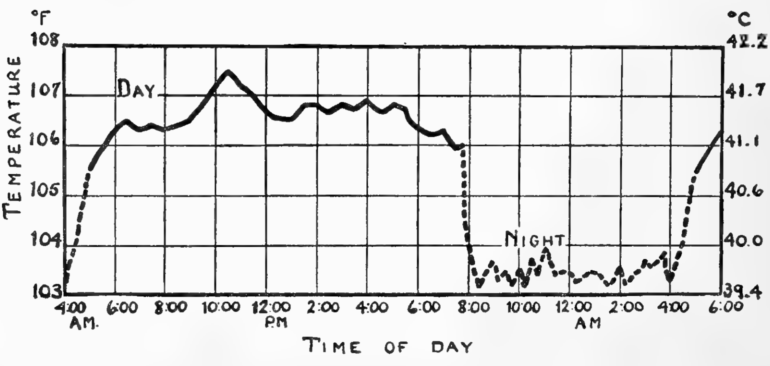


FIGURE 16.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF AN EASTERN HOUSE WREN (No. 3). This shows the effect of activity of the day (continuous line) and quiet of the night (broken line).

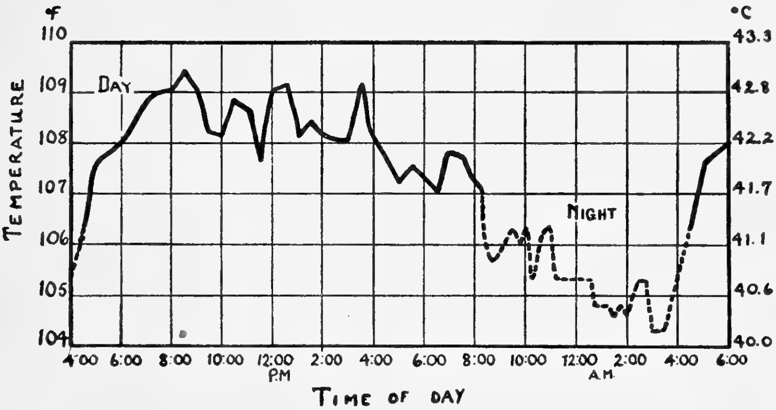


FIGURE 17.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF AN EASTERN ROBIN (No. 1). This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

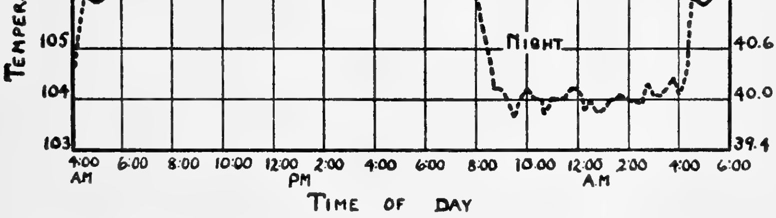


FIGURE 18.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF AN EASTERN ROBIN (No. 2). This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

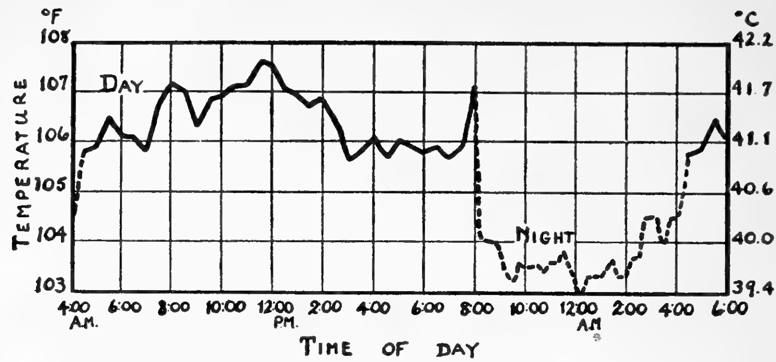


FIGURE 19.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF A WOOD THRUSH. This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

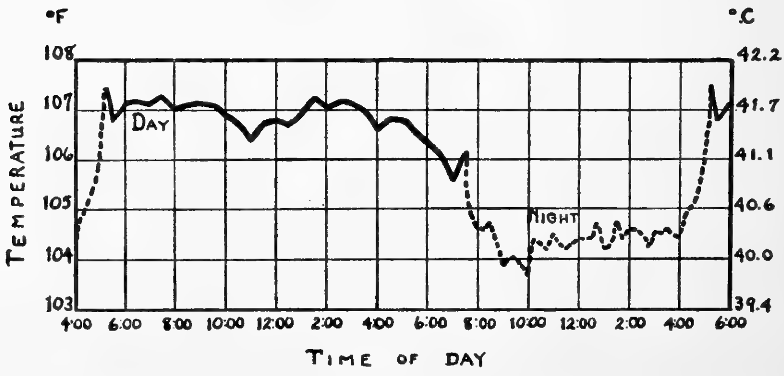


FIGURE 20.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF A CEDAR WAXWING. This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

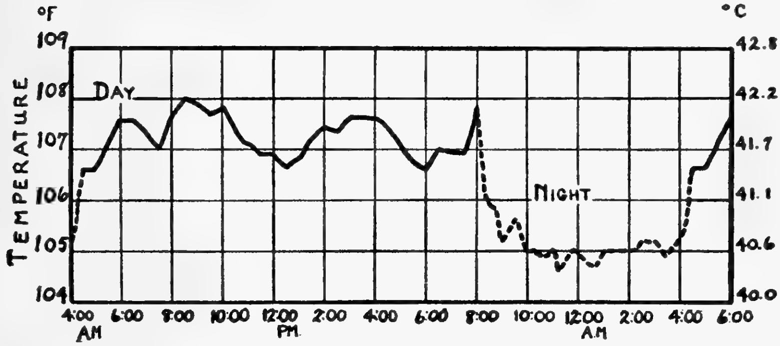


FIGURE 21.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF A CATBIRD (No. 1). This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

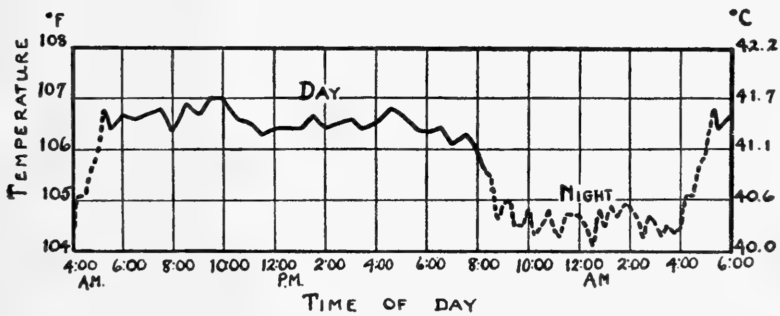


FIGURE 22.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF A CATBIRD (No. 2). This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

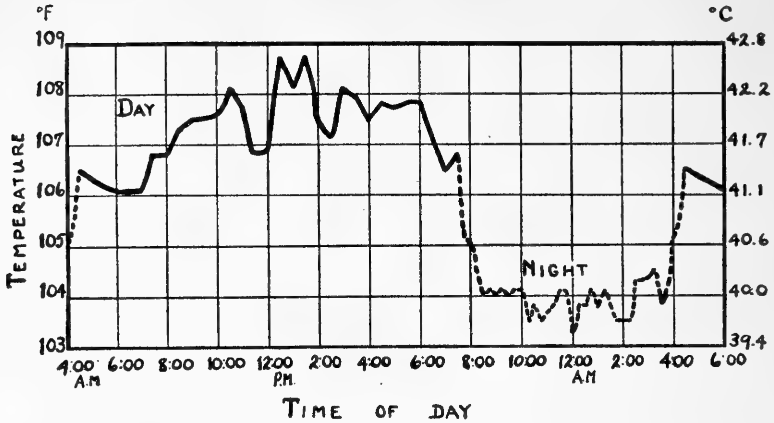


FIGURE 23.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF AN EASTERN SONG SPARROW. This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

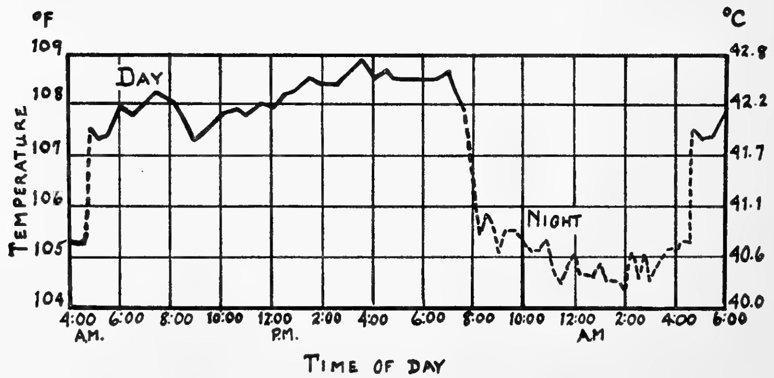


FIGURE 24.—AVERAGE DAILY RHYTHM IN TEMPERATURE OF AN EASTERN CHIPPING SPARROW. This shows the effect of activity during the day (continuous line) and effect of quiet during the night (broken line).

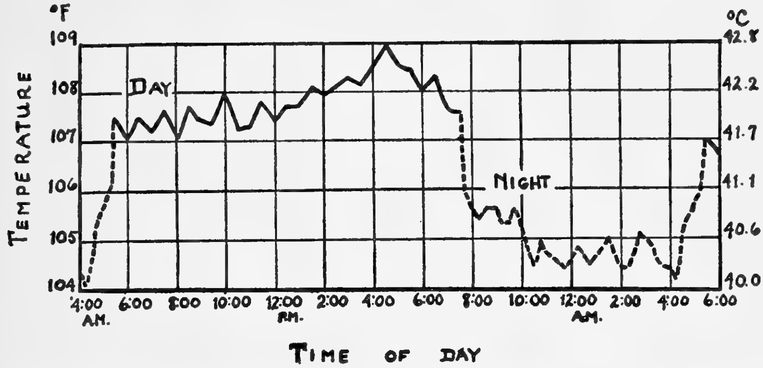


FIGURE 25.—AVERAGE DAILY RHYTHM IN BODY TEMPERATURE OF AN EASTERN WOOD PEWEE. This shows the effect of activity of the day (continuous line) against the quiet of the night (broken line).

that the maximum points in bird and air temperatures are reached, which is usually in the early or middle afternoon. Figure 16 for an eastern house wren and Figure 18 for an eastern robin are of special interest in this respect. The nests of both of these birds were situated on the eastern side of white buildings where they had the full morning sun but were shaded in the afternoon. The result was that the rise in air temperature was very rapid in the morning and quickly reached the maximum for the day. The bird's temperature was very visibly affected, as shown by the sharp peak in the curve at a little after 10:00 A. M. in each case. It was not infrequent for the temperature in the nest to be over 100° F. (37.8° C.) when the adult was absent. Aside from this more or less artificial maximum in the morning, the highest body temperatures for the day were reached in the middle of the afternoon.

The times of day at which the maximum and minimum body temperatures were reached in the different birds are summarized in Table XV.

Both the maximum and minimum temperatures may be reached not just once but several times, or may be approached to within so very few tenths of a degree as to present no significant difference, and these are all noted in Table XV. It is seen that the maximum body temperature may be reached at nearly any time of the day, but not later than 5:30 P. M., and not ordinarily before 8:30 A. M.

TABLE XV.—*Time of Daily Maximum and Minimum Bird Temperatures*

Species	Time of Day Maximum Body Temperature Reached	Time of Day Minimum Body Temperature Reached
Eastern house wren (No. 1)...	9:00–10:30 A. M.; 5:00 P. M.	12:00–1:30 A. M.
" " " (No. 2)...	1:00–1:30 P. M.; 5:00 P. M.	10:45 P. M.; 12:15 A. M.; 1:15–1:30 A. M.
" " " (No. 3)...	10:30 A. M.; 1:30–5:00 P. M.	8:30–10:15 P. M.; 12:15 A. M.; 1:30 A. M.; 2:15 A. M.
Eastern robin (No. 1)........	8:30 A. M.; 12:30 P. M.; 3:30 P. M.	3:00–3:30 A. M.
" " (No. 2)........	10:30 A. M.; 4:30–5:30 P. M.	9:30 P. M.; 10:45 P. M.; 12:15–1:00 A. M.
Wood thrush................	11:30 A. M.–12:00 Noon	12:15 A. M.
Cedar waxwing.............	5:15 A. M.; 7:30 A. M.; 1:30 P. M..................	9:00–10:00 P. M.
Catbird (No. 1).............	8:30–10:00 A. M.	11:15 P. M.; 12:45 A. M.
" (No. 2).............	9:30–10:00 A. M.	12:30 A. M.
Eastern song sparrow........	12:30–1:30 P. M.	10:15 P. M.; 10:45 P. M.; 12:00 P. M.; 1:45 A. M.; 2:15 A. M.
Eastern chipping sparrow.....	3:30 P. M..................	2:00 A. M.
Eastern wood pewee.........	4:30 P. M..................	4:15 A. M.

Early afternoon seems to be the most characteristic of any single time.

Likewise, the daily minimum body temperature may come at nearly any time between 8:30 P. M. and 4:15 A. M., although it comes most frequently around midnight. The chief value of this table is that it indicates to some degree the flexibility and variability of the bird's body temperature.

The question arises next as to the extent of this daily fluctuation in bird temperature. Table XVI was prepared from the highest mean body temperature during any half hour of the day and the lowest mean body temperature from any 15 minute period during the night regardless of the time at which such temperatures occurred. These maximum and minimum temperatures of each day were averaged then for each individual for the whole period of observation.

From Table XVI, it is seen that the average daily range in the bird's temperature amounts to 5.3° F. (3.0° C.). This is very close to the true range, while 108.7° F. (42.6° C.) and 103.4° F. (39.7° C.) are very nearly the true extremes that the body temperature reaches daily. These temperatures do not, however, represent the greatest temporary extremes to which the body temperature may go. The daily maximum temperatures given are for half-hour periods determined in the manner above explained

TABLE XVI.—*Daily Extremes and Range in Temperature of Female Birds on the Nest during Incubation Period*

Species	Number of Days' Record	Average Daily Maximum Temperature	Average Daily Minimum Temperature	Average Daily Range in Bird Temperature	Average Daily Range in Air Temperature at Nest
Eastern house wren (No. 1)	8	109.4° F. (43.0° C.)	102.5° F. (39.2° C.)	6.9° F. (3.9° C.)	29.6° F. (16.6° C.)
" " " (No. 2)	13	109.5° F. (43.1° C.)	104.0° F. (40.0° C.)	5.5° F. (3.1° C.)	19.7° F. (11.0° C.)
" " " (No. 3)	9	108.0° F. (42.2° C.)	102.5° F. (39.2° C.)	5.5° F. (3.1° C.)	25.3° F. (14.2° C.)
Eastern robin (No. 1)......	2	109.6° F. (43.1° C.)	104.3° F. (40.2° C.)	5.3° F. (3.0° C.)	22.0° F. (12.3° C.)
" " (No. 2)......	10	108.6° F. (42.6° C.)	102.8° F. (39.3° C.)	5.8° F. (3.2° C.)	17.3° F. (9.7° C.)
Wood thrush..............	3	107.8° F. (42.1° C.)	102.5° F. (39.2° C.)	5.3° F. (3.0° C.)	13.3° F. (7.4° C.)
Cedar waxwing............	7	107.8° F. (42.1° C.)	103.2° F. (39.6° C.)	4.6° F. (2.6° C.)	17.0° F. (9.5° C.)
Catbird (No. 1)............	4	108.5° F. (42.5° C.)	104.2° F. (40.1° C.)	4.3° F. (2.4° C.)	17.2° F. (9.6° C.)
" (No. 2)............	5	107.7° F. (42.1° C.)	103.8° F. (39.9° C.)	3.9° F. (2.2° C.)	14.8° F. (8.3° C.)
Eastern song sparrow......	2	109.3° F. (43.0° C.)	104.3° F. (40.2° C.)	5.0° F. (2.8° C.)	16.5° F. (9.2° C.)
Eastern chipping sparrow...	3	109.2° F. (42.9° C.)	103.6° F. (39.8° C.)	5.6° F. (3.1° C.)	15.0° F. (8.4° C.)
Eastern wood pewee.......	9	109.3° F. (43.0° C.)	103.2° F. (39.6° C.)	6.1° F. (3.4° C.)	15.9° F. (8.9° C.)
Grand average..........	(75 days)	108.7° F. (42.6° C.)	103.4° F. (39.7° C.)	5.3° F. (3.0° C.)	18.6° F. (10.4° C.)

(page 78). During this half-hour period of highest *average* temperature during the day, the bird's temperature may go considerably higher for short periods from excitement or unusually great exertion (pages 34–37). Temperatures as high as 112.3° F. (44.6° C.) have been recorded of an eastern robin on the nest, and similar high temperatures are not uncommon for other species. The minimum temperature of 103.4° F. (39.7° C.) is about the lowest ordinarily reached, although, in a few instances, a minimum temperature of 102.0° F. (38.9° C.) has been obtained. An extreme variation in body temperature for different hours of the day amounting to over 10° F. (5.6° C.) may be expected under certain conditions. The fluctuations in bird temperature are dependent largely upon activity, as explained above (pages 34–37), and not primarily on the range in air temperature. However, in Table XVI the greatest range in a bird's temperature is correlated indirectly with the greatest range in air temperature (eastern house wren No. 1), while the least range in a bird's temperature is correlated with the next to the least range in air temperature (catbird No. 2).

The cause for a daily rhythm in body temperature is complex. It is shown by experimental work that activity raises a bird's temperature and that inactivity lowers it. That this is of primary importance in the natural daily rhythm of temperature cannot be questioned. This is particularly evident from the very rapid increase in body temperature that takes place with the beginning of activities early in the morning, and the correspondingly rapid decrease in the evening when this activity ceases for the day. We know also that the digestion of food stimulates metabolism and heat production in the body tissues and affects the bird's temperature. This stimulating influence would be felt more during the daytime than at night. The standard metabolism is probably lower at night than during the day (Benedict and Riddle, 1929). The fluctuation in air temperature may be important indirectly by modifying activity. When air temperature becomes extreme it may have a direct importance. The maximum bird's temperature comes at about the time of the maximum air temperature. The minimum bird's temperature, however, comes several hours before the minimum temperature of the air. Mental activity and excitement during the day increase the functional and muscular activities of the body, which in turn may raise the body temperature. At night, the bird is at rest, quiet, and more or less asleep, so that these functional and muscular activities are at the minimum. All these factors are of importance, then, in producing this daily rhythm of body temperature. In addition, other internal physiological processes in the body may vary rhythmically and be involved, but these have not been measured.

Experimental control and reversal of daily temperature rhythm.—If activity is one of the chief factors in influencing bird temperatures, and light the chief controlling factor in regulating bird activities in nature, then by reversing and controlling the light period of the day, the bird's temperature should vary accordingly.

Simpson and Galbraith (1905) showed that in owls which are normally active at night and inactive during the day, the temperature rhythm is just the reverse of that in diurnal birds. The most extensive experimental work on reversal of the normal temperature rhythm in birds has been done by Hildén and Stenbäck (1916), already quoted above. After they obtained a set of curves showing the normal daily temperature variation, they reversed the periods of activity. During the day, from 6:00 A. M. to 6:00 P. M., they kept the birds in the dark. From 6:00 to 9:00 P. M. and from 3:00 to 6:00 A. M., the birds were kept in weak light to simulate dusk and dawn, while from 9:00 P. M. to 3:00 A. M. the birds were in bright light. They found that there was a complete reversal in the daily rhythm, so that the maximum body temperature now came during the night (light period) and the minimum temperature during the day (dark period). When the birds were replaced in normal conditions of lightness and darkness, the temperature rhythm returned in a very few days to the normal mode of variation. This was irrespective of variations in air temperature.

Our own experiments in reversal of the daily temperature rhythm in birds have been rather limited, but have produced something in the way of results which indicate that the temperature rhythm of birds captured in the wild state may be artificially reversed in much the same manner as in the caged birds worked with by Hildén and Stenbäck. Eastern chipping sparrows, English sparrows, and eastern song sparrows were used in this work. Several attempts were made to change the activities of many individuals, by subjecting them to light from electric bulbs at night and to darkness during the day. For some reason, the birds in most cases died, although some, at least, had been kept under caged conditions in good health for several days previous to the experiment. The reason for their dying may possibly have been a too precipitous reversal of the normal periods of activity. However, in at least four experiments, significant results were obtained, of which one is shown in Figure 26. During the experiment a female eastern chipping sparrow was confined in a small cage and kept supplied with food, which was freely eaten, and with water. The first control record obtained (Figure 21 [1]) by means of the indicator potentiometer and a thermocouple down the throat, between 10:16 and 10:56 in the morning, shows the normal tem-

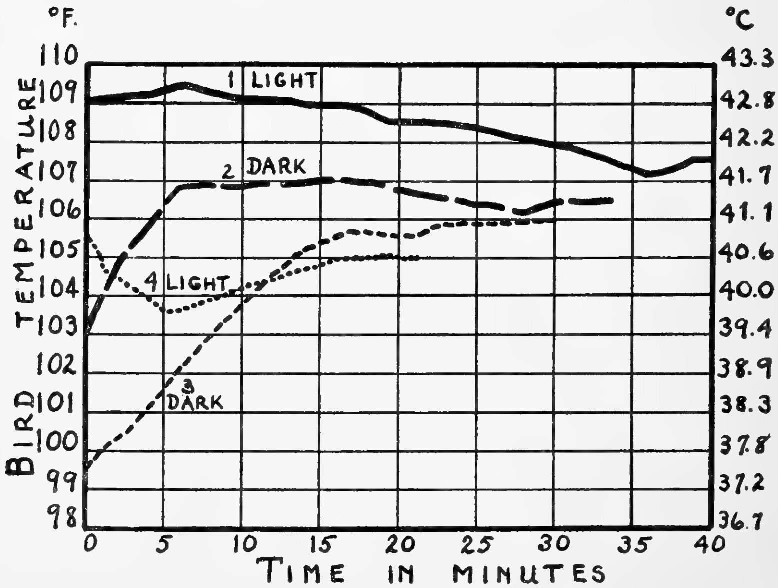


FIGURE 26.—REVERSAL OF DAILY RHYTHM IN BODY TEMPERATURE OF AN EASTERN CHIPPING SPARROW, BY CONTROLLING THE PERIODS OF LIGHT AND DARKNESS. 1—Control; Temperature of bird during normal day period, 10:16–10:56 A. M. 2—Control: Temperature of bird during normal night period, 11:27–12:00 P. M. 3—Reversal: Temperature of bird confined in dark during the day, 11:06–11:36 A. M. 4—Reversal: Temperature of bird kept in light during the night, 10:18–10:39 P. M.

perature of the bird during the day. The second record obtained, between 11:27 and 12:00 P. M., gives the corresponding control at night (Figure 26 [2]). Then during the next 4 days, conditions were gradually changed until the bird was in the light at night, commencing at about 6:15 P. M., and in the dark during the day, beginning at 7:45 A. M. The normal daily rhythm in air temperature was not interfered with and so does not explain the results obtained. A record of the bird's temperature was then taken from 11:06 to 11:36 A. M. when it had been in the dark (Figure 26 [3]). The first temperature of the bird obtained at this time was 99.3° F. (37.4° C.), which is very low and shows the effect of inactivity. However, the body temperature of the bird rose to nearly 106° F. (41.1° C.) during the next half hour, a result produced by excitement and exertion when its temperature was being taken. At 10:18 that evening, the bird's temperature was again taken after it had been active in artificially produced light. The first temperature of the bird obtained at this time was 105.3° F. (40.7° C.) (Figure 26 [4]). The first records of the temperature of the bird obtained are, in the case of these experiments, the most significant, as they show the immediate effect of the light and dark periods on the activity of the bird. Although the experimental results are much lower than the control records, the temperature of the bird after being in the dark was in each instance (Figure 26 [2 and 3]) lower than it was after being in the light (Figure 26 [1 and 4]), although in the second case (Figure 26 [3]) the dark period came at midday, rather than at midnight as in the control (Figure 26 [2]). The three other successful experiments support these results. Thus, these experiments substantiate the results obtained by Hildén and Stenbäck, in that by controlling and reversing the periods of activity, the rhythm of body temperature may be controlled and reversed.

Various anaesthetics will exert a profoundly quieting effect on the activities of birds, and render them more or less motionless for long periods of time. James Stevenson, in this laboratory, has studied the effect of urethane upon the body temperatures of starlings—and one of his figures is reproduced here (Figure 27). The urethane was dissolved in distilled water and introduced into the stomach. One hundred and fifty milligrams were first given to the bird to put it into anaesthesia, and 50 milligrams were

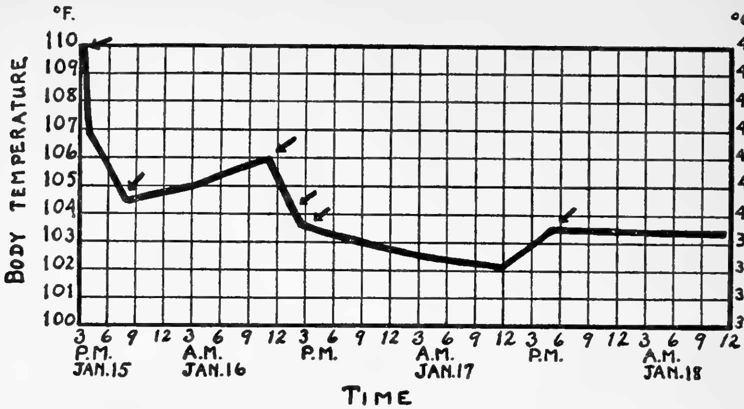


FIGURE 27.—FLUCTUATION IN BODY TEMPERATURE OF A STARLING IN ANAESTHESIA. Arrows indicate times at which the anaesthetic was given.

given at repeated intervals thereafter. Temperatures were taken intermittently by means of a thermocouple put down the throat. The room temperature fluctuated slightly around 72° F. (22.2° C.).

Figure 27 shows that the body temperature falls rapidly at first, but that after a time it becomes more or less constant. The normal daily temperature rhythm is destroyed (compare with Figure 13), the body temperature becomes profoundly lowered although the air temperature is constant, and such minor fluctuations in body temperature as do occur are due to the bird's temporarily coming partway out of anaesthesia. This again substantiates the idea that it is muscular activity which is mainly responsible for causing the regular daily rhythm in body temperature.

MECHANISM OF TEMPERATURE CONTROL

Much has been written concerning the mechanism of temperature control in warm-blooded animals, particularly in mammals, and every text-book of physiology devotes several pages to the discussion of this important subject. (For particularly good accounts see Edwards, 1839; Gavarret, 1855; Pembrey, 1898; Hill, 1906; Pütter, 1911; Lusk, 1921; Barbour, 1921; Starling, 1926; and Bazett, 1927.) Less is known concerning temperature regulation in birds than in mammals, and, in fact, the exact mechanism is still uncertain. It is desirable here to bring together the latest information on the subject and to offer some suggestions based on the results of our own investigations.

Two factors are involved in determining the temperature of any animal—heat production and heat loss. In many homoiothermal animals, particularly mammals, the balance between the two is maintained approximately constant, so that the "Eigenwärme" is nearly the same under all conditions of the environment. Variations in the body temperature may be caused by changes in either the heat production or the heat loss. The proper maintenance of a balance between the two is the function partly of the nervous system, and partly, as we shall show later, of the endocrine or ductless glands. The body temperature of birds is unique because it is so variable, much more so than in many mammals, notably man.

Most of the general metabolic processes in the body tissues are exothermic in that some of the energy is lost or liberated in the form of heat. Metabolism in muscular tissues is probably the most important single factor in the production of heat. Heat is liberated in great amounts when the muscle contracts, both during the contraction and recovery phases. Muscular activities of various sorts are therefore responsible for a considerable amount of heat production. Unless there is a corresponding increase in heat loss there is a rise in the body temperature. Even when at rest, striated muscle is more or less contracted and so is continually liberating heat. When the body temperature of mammals becomes reduced, shivering may occur. This is more or less involuntary, and must be considered as a factor in temperature regulation since it increases heat production. Shivering occurs also in birds. The beating of the heart is a continual source of some heat to the body. Heat is, likewise, produced by the muscular movements involved in respiration.

It has been shown by Rubner and others that food stimulates metabolism. The heat value of one gram of protein is 4.1 large calories, of one gram of carbohydrate 4.1 large calories, and of one gram of fat 9.3 large calories. The carbohydrates are particularly important in heat production because they are readily available and easily oxidized. The activities of the different glands of the body are probably also sources of heat production because of the chemical changes occurring in them.

Benedict and Riddle (1929) have shown that starvation lowers the metabolism in birds very markedly. This agrees with our finding that the body temperature decreases when the birds are deprived of food. The body temperature of the bird is dependent on the heat produced during general metabolism, therefore a marked reduction in the heat produced brings about a lowering of body temperature.

The effect of air temperature in stimulating or depressing metabolism and heat production in the bodies of animals has been known many years. Voit in 1904 (Lusk, 1921) found that the heat production of a pigeon is doubled after removing its feathers. Low air temperatures stimulate heat production, which is usually entirely compensated for by regulation of the rate of heat loss, so that the balance between heat produced and heat lost is maintained. High air temperatures that are not extreme act in the opposite manner by depressing the metabolism, while heat loss must be correspondingly changed if the body temperature is to remain constant. That air temperatures do affect heat production in birds to a remarkable degree is shown in recent experiments by Riddle, Christman, and Benedict (1930) on ring doves. Here it was found that there was a reduction in the metabolism of male birds at 86° F. (30.0° C.) of 28.1 per cent of what it was at 68° F. (20.0° C.), while in females, the reduction was 20.3 per cent. Groebbels (1920) has also done extensive work on the metabolism of birds in relation to air temperatures and with similar results.

The influence of the nervous system in the regulation of heat production has been generally realized, and there have been attempts to locate in mammals a temperature regulating center in the corpus striatum of the brain. This may be effective through a regulation of the increase or decrease of physical activities in cold or hot weather, through regulating the amount and kinds of food consumed, or by modifying the tone and metabolism in muscle and body tissues. This is usually considered "chemical regulation."

That the endocrine glands may play a role in chemical regulation of body temperature has become generally appreciated only during the last few years. Various investigators have, however, pretty well established the fact that at least certain of the endocrine organs, particularly the thyroids and adrenals, are important in regulating the metabolism of the body and thereby regulating the body temperature (Cramer and McCall, 1916; Cramer, 1916, 1918; Cannon, Querido, Britton, and Bright, 1927). The thyroid gland undergoes marked fluctuations in activity, and this is correlated inversely with air temperature (Cramer, 1916; Mills, 1918; Cramer and Ludford, 1926; Riddle and Fisher, 1925). In the work of Riddle and Fisher (1925), "three kinds or species of pigeons were kept on the same diet throughout the year and killed during all months of a three-year period. The weights of the thyroids from these three species indicate a nearly simultaneous enlargement in autumn and winter months and a progressive decrease in size during the months of spring and summer. These size changes promptly follow the onset of a colder autumn and warmer vernal temperatures. Promptness of change, rather than evident delay, is indicated by practically all the data obtained. This seasonal enlargement of the thyroid is probably associated with seasonal increase of the thyroid function and increased heat production." Bergtold (1926) calls attention to the fact that the same relation and seasonal variation have been found in the crow.

Cassidy, Dworkin, and Finney (1926) describe a relation between insulin, blood sugar, and body temperature, which may be of importance in normal regulation of body heat.

With regard to the regulation of heat loss from the body, the feathers with which birds are covered form an excellent insulating wrap. Loss of heat by radiation and conduction is, therefore, greatly handicapped in birds as compared with man and some other mammals. Birds do not possess sweat glands, hence this means of cooling the body cannot be considered. Insensible perspiration in animals without sweat glands is sometimes considerable (Bazett, 1927). The feathers and the dead air space which they include are better adapted to conserve heat than to dissipate it, so there can be only a small percentage of loss from the general surface of the body. In man, much heat is lost from the skin in warm weather when the arterioles enlarge and bring more blood into this region. In cold weather these arterioles contract, so heat is saved. From the data on skin temperatures of birds presented herein, there is some evidence that the temperature of the skin is lower, relative to the temperature of the body, when the body temperature is high than when it is low. This would argue that the blood vessels do not become expanded when the body temperature rises, and that there is very little loss of heat through the feathers.

Experiments of taking the temperature of birds before and after the removal of the feathers have been performed. Edwards (1839) was the first to do this. He minimizes the importance of feathers in temperature regulation. "An adult sparrow which has had all its feathers clipped off does not at first suffer loss of temperature to the extent of more than a degree, and by-and-by recovers even this; . . ." Our own work does not entirely confirm this statement. Temperatures were taken of a juvenal English sparrow in a basement room when the air temperature averaged 70° F. (21.1° C.). The bird maintained a temperature around 106.7° F. (41.5° C.) for some time. The feathers were then clipped off and the bird's temperature again taken. This time the bird had a temperature of 104.0° F. (40.0° C.) and this it maintained for nearly half an hour—probably through increased heat production. Then, however, its body temperature dropped to 88.8° F. (31.6° C.), when the experiment terminated.

Another experiment performed with 3 juvenal English sparrows consisted in determining the length of time during which they could resist air temperatures with and without feathers. Two of the birds were placed at a constant temperature of 40° F. (4.4° C.) in a refrigerator, one with feathers in normal condition to act as a control, the other with all feathers cut off with shears. The third bird, also without feathers, was placed in a small incubator at 99° F. (37.2° C.). The control bird at 40° F. (4.4° C.) and the defeathered bird at 99° F. (37.2° C.) each lived about 12 hours, but the bird placed at 40° F. (4.4° C.) without feathers died within 4.5 hours. Clipping off the feathers reduced the survival time, therefore, to little more than a third of normal, due probably to the more rapid heat loss and wasting of reserves through increased metabolism. The clipped bird at 99° F. (37.2° C.) survived longer because the high air temperature compensated for the lack of feather covering. All of these birds were without food.

The fluffing out of the body feathers to increase the thickness of the insulating coat and the amount of non-conductive air contained therein is another device for cutting down the rate and amount of heat lost from the body. Birds are frequently seen in nature with feathers fluffed out in this manner, particularly during cold weather (Allen, 1925, page 36), and this is a rather common habit of roosting birds on cool nights.

In the course of the experimental work reported in the first part of this paper (pages 47–50), it was found that the temperature of the eastern house wren confined closely in a small sack made of mosquito netting fell more or less rapidly below normal when the bird was subjected to low air temperature. This fall or break in the bird's temperature regulation began, on the average, when the air temperature fell to 50° F. (10.0° C.). This does not mean that this species of bird is unable to withstand such air temperatures in nature, because we have proved elsewhere in work to be reported in a future paper (Kendeigh) that the eastern house wren will withstand even lower temperatures for several hours, provided it is not confined too closely but is allowed some little freedom, particularly enough to allow it to fluff out its feathers. Observations on this species indicate that the feathers are not fluffed out until some low degree of temperature is reached. It seems, therefore, that the break in the bird's temperature regulation at 50° F. (10.0° C.) was due, in part, to the bird's being prevented from fluffing out its feathers, which would naturally have taken place when the air temperature reached this degree. Since the probable error of this mean temperature for the 16 birds experimented on is only ±2.9° F. (1.6° C.), this temperature must represent a definite time or degree at which the act of fluffing out the bird's feathers takes place, and signifies that this act is an important one in the general mechanism of temperature regulation.

Feathers undoubtedly have an important place in regulation of temperature. Their function is primarily to conserve rather than to dissipate body heat. Therefore, they are of considerable importance to the bird in the winter. In summer they probably protect the bird considerably from the direct heat radiation of the sun, which would otherwise produce an overheating of the body and consequent death (page 121). The molting season in many species occurs during late July and August, the hottest part of the year, and all the feathers are renewed before the cold season begins.

The pigmentation of the feathers may have an importance in temperature regulation which has not been appreciated. The absorption, transmission, or reflection of the sun's rays by different pigments may be of vital concern to the bird aside from the color effects produced. Cartwright and Harrold (1925) and Hadwen (1926) have discussed this subject, but much experimental work needs yet to be done before definite judgment can be pronounced.

In individuals and species of different size among the mammals, body size is considered important. The proportionate amount of the body surface decreases as the body bulk increases. Therefore, there must be a higher heat production per unit of weight in small animals than in larger to compensate for the greater heat loss. There is some evidence that size is an important factor among different species of birds, since Regnault and Reiset (Lusk, 1921, page 120) found that the heat production in sparrows per unit weight was ten times greater than in fowls.

The warming of ingested food to body temperature and the loss of heat in the excreta is an important source of heat loss, considering the rapid rate at which food passes through the alimentary tract in birds.

When, in the course of evolution, the body became covered with feathers, the bird lost the most important area for the dissipation of the heat metabolism. This had to be compensated for in some way, and it appears to have been accomplished through the expansion of the respiratory system into all parts of the body in the form of air-sacs. True air-sacs occur only in birds, although, according to Heilmann (1926), they have their prototype in the reptilian lung.

The air-sacs in the pigeon have been described in detail by Müller (1908). There are 5 main groups, as follows: *sacci abdominales* in the abdominal region; *sacci intermedii posteriores* and *sacci intermedii anteriores* in the thoracic cavity; *saccus interclavicularis,* proximal to the syrinx in the thorax; and *sacci cervicales* in the region of the nape of the neck. All of these are pairs except the interclavicular, and this is really the result of a fusion in the course of development. These air-sacs are connected directly with the bronchi, and are really enlargements of the bronchi that have emerged from the surface of the lung and penetrated between the organs of the body. They have thus direct communication with the outside air through the bronchi, syrinx, trachea, larynx, and buccal-pharyngeal cavity. The size of the air-sacs as hollow vesicles varies with the respiration and the inspiration and expiration of air. Smaller diverticula diverge from these larger sacs and ramify to various parts of the body and into the hollow cavities of the bones. The walls of the air-sacs are thin but elastic and contain very few blood vessels, except within the bones where they are plentifully supplied. The ostia, or the openings from the bronchi of the lungs into the air-sacs, are large and conspicuous. The presence of both radial and oblique muscle fibers forming a sphincter around these ostia was formerly suspected, but could not be verified by Müller. These air-sacs thus form a hollow air system penetrating to nearly all parts of the bird's body in a manner comparable to the tracheal system in insects.

Locy and Larsell (1916) have studied in some detail the development of air-sacs in the chicken. They find that between the seventh and ninth days of incubation the air-sacs emerge and on the ninth day project beyond the lung. From the account of these authors, the air-sacs are apparently fully developed by the end of the first day after hatching, although they very probably increase in size with the growth of the chick. The lung of the chick becomes functional as an organ of respiration shortly before hatching, and there is every reason to believe that the air-sacs may begin to function at about the same time.

Locy and Larsell (1916) have made an important advance in the understanding of the function of the air-sacs by their study of "recurrent bronchi." In the course of embryonic development, the air-sacs are formed as terminal expansions of secondary or tertiary branches of the bronchial tree. The air-sacs then form outgrowths which reenter the lungs as recurrent bronchi and connect with other branches of the main bronchial tree. The recurrent bronchi have their openings from the air-sacs very close to the point where the incurrent bronchi enter. By their anastomosing with other branches they are brought into communication with all parts of the lung. The air-sacs then are not dead air spaces, but a circulation of air is possible from the main bronchi into the air-sacs and back into the lung and main bronchi through the recurrent bronchi.

Much has been written concerning the air-sacs in birds, and many theories have been formulated concerning their possible physiological function, yet very little is actually known about them in different species of birds. The most important theories regarding their use to the bird are that they aid respiration, that they lighten the bird and so facilitate flying, and that they serve for temperature regulation of the body. It is possible and indeed probable that the air-sacs serve all three purposes, so that there need be no conflict between the advocates of each idea. It is our purpose here to discuss only the role of the air-sacs in temperature regulation.

Wetmore (1921) discusses in a general way the manner in which the air-sacs may function in regulating temperature, although he was not the first to propound the theory. The manner in which the system of air tubes penetrates between the heat-forming organs all over the body, the way they approximately parallel the main blood channels, and enter into the middle of some of the thickest groups of muscles by means of bones, makes them appear very well adapted indeed to care for the heat generated by these tissues. The presence of recurrent bronchi also makes possible a circulation of air in air-sacs with each respiratory movement, which may take care of a considerable amount of heat. It has been assumed that at low air temperature the movement of air in and out of the air-sacs may be less than when the air temperature is high. In this way the body may be kept warm at low air temperatures and cooled at higher air temperatures.

Just how this ventilation of the air-sacs may be regulated is not known. However, if recurrent bronchi are of general occurrence in the class of birds, and if the circulation is complete as indicated, then there is an apparatus at hand in the recurrent bronchi themselves to regulate this passage of air through the sacs. In mammals, the bronchioles of the lung are surrounded by plain muscle which is maintained in a state of tone by a branch of the vagus nerve. The nerve contains both bronchioconstrictor and bronchiodilator fibers. A secretion of the adrenal glands also affects the contraction of the bronchioles. In birds, the same arrangement and innervation may be assumed, and it would not be impossible that the walls of the recurrent bronchi or the bronchioles may be capable of considerable contraction or dilation. In this way the passage of air through the sacs could be controlled—reflexly over the nervous system—with the stimulus being temperatures either above or below normal.

Not only would the internal parts of the body be cooled through the radiation of heat into the air-sacs from the surrounding muscles, glands, and blood vessels, but the evaporation here of water could be also an important item. Hári (1917), experimenting with geese, found that of the total heat lost by birds at 81° F. (27.2° C.), 50.5% was lost by evaporation of water; but at 61° F. (16.1° C.) only 20% was lost in this way. This shows, as one would expect, greater evaporation of water from the body at higher temperatures, probably through the air-sacs.

Much work needs to be done on this problem of bird respiration, and some interesting findings very probably await the investigator who has the patience and technique for undertaking this research. In this connection, the experiments of Victorow (1909) need to be mentioned. Working with doves, he first made an anatomical study of their air-sacs, and then attempted to determine their role in cooling the body. He etherized his birds and mechanically destroyed the functioning of the air-sacs. He then tetanized the flight muscles by means of an electric induction current. This produced a rise of temperature within a short time of respectively 4.7° F. (2.6° C.) and 5.8° F. (3.2° C.) in 2 cases. In 2 control birds, where the air-sacs were left intact but the operation details were similar, when the flight muscles were tetanized, a rise in body temperature of only 1.3° F. (0.7° C.) and 1.6° F. (0.9° C.) occurred. This would indicate that excess heat is eliminated through this air-sac system.

A little evidence was presented in a former paper (Kendeigh and Baldwin, 1928) from the development of temperature control in young birds, which would indicate that in the eastern house wren the air-sacs begin to function at about the time that the bird acquires a temperature control—that is, between the fourth and ninth days after hatching. In chickens, the air-sacs are fully developed soon after hatching, and temperature control is established at the same time.

As a further study of the development of air-sacs in birds, a preliminary attempt was made to determine the progressive decrease in specific gravity of young house wrens during the first 12 days after hatching. By a simple device involving the displacement of water in a small calibrated tube, it was possible to determine the volume of the birds in cubic millimeters. Since a cubic millimeter of water weighs approximately 1 milligram, the specific gravity of the bird could be determined by dividing the volume of the bird in millimeters by the weight of the bird in milligrams. What few data were obtained indicate a high specific gravity of the birds at hatching but a considerable decrease during the period in the nest. This might be taken as an argument that the air-sacs are forming and penetrating into the body and bones of the bird at the same time that the temperature regulation is becoming established, and that the development of the two may be interrelated.

Thus it would seem that the temperature control mechanism in birds is a complex apparatus. It is difficult to evaluate the importance of each of the different factors involved. Undoubtedly, the body temperature of the bird is dependent upon a proper balance between all the factors.

BODY TEMPERATURE OF NESTLING BIRDS

POIKILOTHERMIC (COLD-BLOODED) STAGE IN DEVELOPMENT OF WARM-BLOODED ANIMALS

In the case of the human species, newly-born babies do not have body temperatures as high as adults nor is their temperature control as well perfected (Raudnitz, 1888; Babák, 1902; Benedict and Talbot, 1915). Both their body metabolism and temperature are variable and subject to differences in environmental temperature. This fact is well known to physicians and nurses, and care is always taken to keep the baby warm by artificial means. According to Kimber and Gray (1923), "the human fetus is cold-blooded," and the heat regulating mechanism is not "in working order" during the first few weeks after birth.

In certain other species of mammals, a similar lack of temperature control has been shown to be true (Sumner, 1913). In mice, the power of heat regulation for moderate air temperatures (68°–77° F. [20.0°–25.0° C.]), is pretty well established at about the age of 10 days. For lower temperatures, however, the power of regulation is not developed until much later, apparently not until the age of 20 days. In a more recent work (Stier and Pincus, 1928), it was shown that when 2-day old mice were exposed to a temperature of 61° F. (16.1° C.) they assumed a body temperature only about 0.2° F. (0.1° C.) higher; although when the air temperature was 93° F. (33.9° C.) their body temperatures were 3°–5° F. (1.7°–2.8° C.) higher. In his classic review of 1839, Edwards tells that when young puppies were exposed to low temperatures their body temperature dropped to within 1.0° F. (0.6° C.) of the environment. He further states, "They may be said to be, to all intents and purposes, cold-blooded animals, with reference to temperature, during the earliest period of life; they are only truly warm-blooded animals in a later stage of their existence."

Other young animals, however, as illustrated by the guinea-pig and goat, have, apparently, a fairly well developed regulating mechanism at birth. This may be correlated with the better development of also the nervous and circulatory systems at birth.

With regard to the production of heat, Edwards divides the young of birds into two groups. "The one comprises those that are hatched with the skin naked, and which cool in a temperate air in the same manner as cold-blooded animals; the other embraces those that are produced with a downy covering, and maintain their temperature at a considerable elevation in the ordinary heat of spring and summer." He tells of a young sparrow's losing 22° F. (12.2° C.) of its body temperature in 1 hour and 7 minutes when subjected to an air temperature of 72° F. (22.2° C.). Pembrey, Gordon, and Warren (1894), working on the respiration of the domestic fowl, found that "the developing chick during the greater part of the period of incubation responds to changes of external temperature in a similar manner to that of a cold-blooded animal; that towards the end of incubation, about the 20th and 21st day, there is an intermediate stage in which no marked response is observed, and this apparently neutral condition is succeeded, when the chick is hatched, by a stage in which the chick reacts as a warm-blooded animal." From some preliminary work of our own on the temperature of chicks soon after hatching, a comparatively stabilized control of body temperature was demonstrated, although this control was less perfect than in other chicks 3 days old. The domestic fowl would fall into Edwards's second group.

Leichtentritt (1919) subjected newly hatched chickens, sparrows, and blackbirds to low and high air temperatures, and found that they had an undeveloped temperature control. Wetmore (1921) gives a few data indicative that young birds have lower and more variable temperatures than adults. The most extensive discussion of the development of temperature control in an altricial species is one by the authors (Kendeigh and Baldwin, 1928). Here it was shown that the ability for maintaining a fairly constant temperature was not attained in the eastern house wren until the ninth day after hatching. Before the ninth day the birds are essentially cold-blooded.

Recently, Gardner (1930) has reported an interesting study on the temperature of nestling birds of 24 species, using mercury thermometers, and he finds their temperatures to be variable. The effect of various factors on body temperature was ascertained. Age in these birds was important, since their temperature rose gradually as the time after hatching lengthened. He states that the temperature of the nestlings, at the time of leaving the nest, is, in most cases, considerably below the average temperature normal to the species. This statement is doubtful, because his information as to the "mean temperature normal to the species" is uncertain. He is right, however, in considering air temperature important in its relation to nestling bird temperatures. Exertion or muscular activity, he finds, raises the temperature of nestling birds. This is certainly the case with adult birds; but we have found, in the case of nestling house wrens, that before they have fully developed a temperature control, exertion or struggling frequently lowers the body temperature, due to the cooling effect of increased respiration that takes place at the same time and which sometimes is more than enough to compensate for the increased heat produced by the activity (Kendeigh and Baldwin, 1928). Gardner was working with larger birds in this connection, i.e., turkey vulture, red-tailed hawk, and great horned owl, and it is quite possible that they behave differently. He is quite right in saying that handling of birds may cause a drop in body temperature, and that fatigue, hunger, illness, and absence of the incubating parents have the same effect. His evidence regarding the effect of ingesting cold masses of food on body temperature is not altogether convincing, although his conclusion that a transitory lowering of temperature is produced is not illogical.

The evidence presented in the preceding paragraphs indicates that, so far as temperature reactions are concerned, all warm-blooded animals—birds and mammals, including man—pass through a poikilothermal or cold-blooded state in the course of their development. In some of these animals, such as the chicken, guinea-pig, and man, this stage is, for the most part, passed through before birth, but in other species this does not occur till several days afterwards. That this is of interest from the phylogenetic standpoint is at once apparent, and constitutes another link in the evidence that mammals and birds arose in times past from cold-blooded ancestors, and that in the course of their ontogenetic development this phylogenetic stage is still represented.

DEVELOPMENT OF TEMPERATURE CONTROL IN YOUNG BIRDS

In our former paper (Kendeigh and Baldwin, 1928), the development of temperature control in nestling house wrens was traced in some detail. More work has been done on the subject since that paper was published so that a new curve of development (Figure 28) has been made. This is in general very similar to the one first published but it is altered somewhat for the last few days.

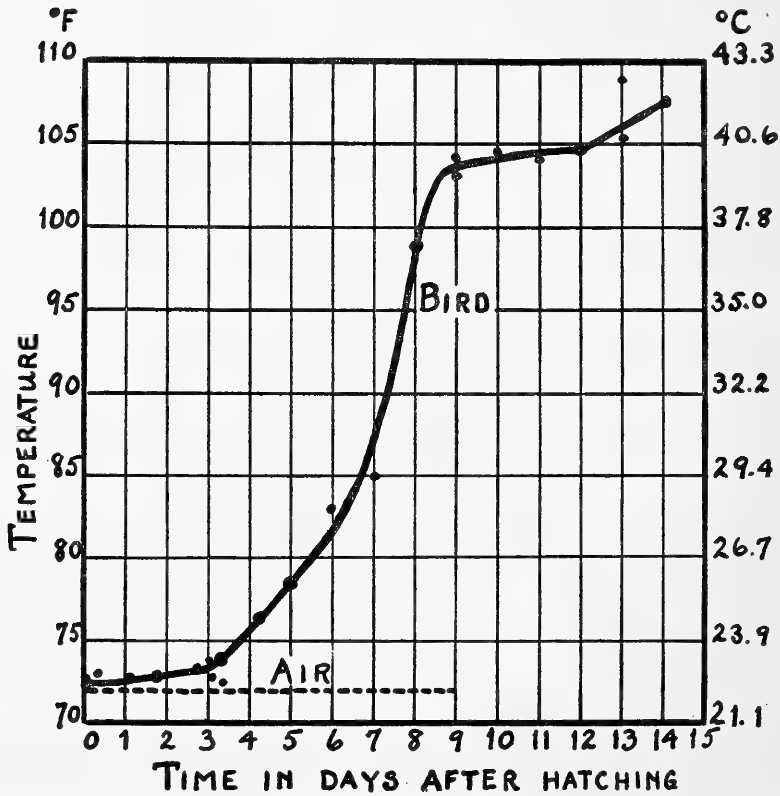


FIGURE 28.—DEVELOPMENT OF TEMPERATURE CONTROL IN NESTLING EASTERN HOUSE WRENS. Note the rapid and progressive gain from the fourth to the ninth day. The temperature control mechanism is established after the ninth day. Before that time, the bird's temperature varies more or less with that of the air. The number of degrees that the body temperature can attain above the air on the bird's own resources is shown for the first nine days above a uniform air temperature of 72°F. (22.2°C.).

The points on this curve represent the highest body temperature that the young birds could attain when removed from the nest and placed alone in semi-darkness at a room temperature of approximately 72.0° F. (22.2° C.).

The sigmoid (S-shaped) nature of the curve is evident up to 12 days. The factors involved in the development of temperature control, are, as given in our earlier paper, first, that the mass or size of the body increases proportionally faster than the surface. This would cause an increase in the amount of heat production with more protoplasmic material involved, yet the surface

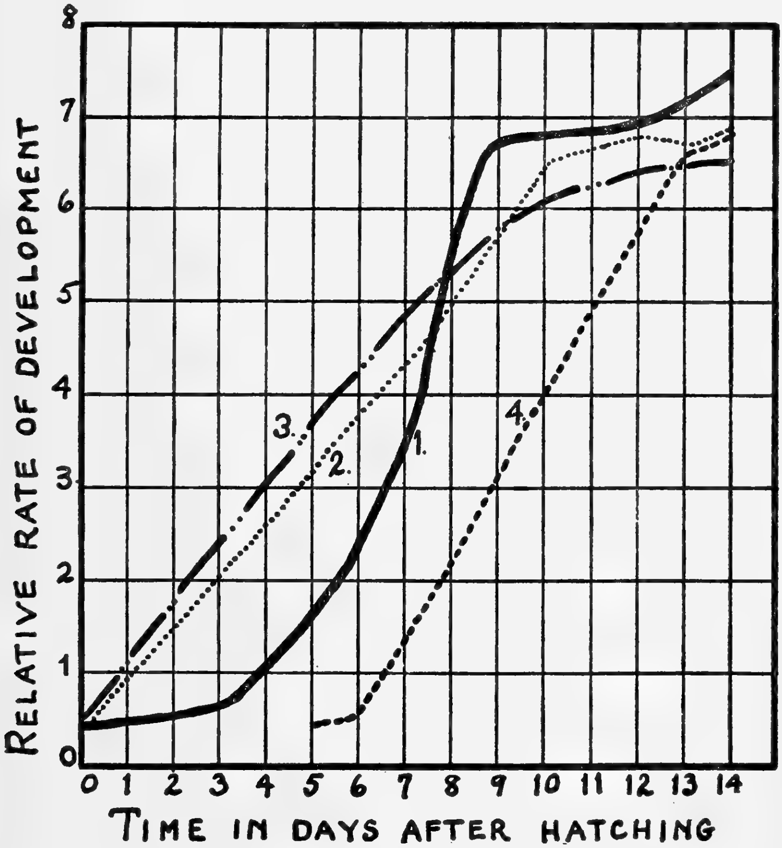


FIGURE 29.—CORRELATION OF (1) DEVELOPMENT OF TEMPERATURE CONTROL IN THE EASTERN HOUSE WREN WITH (2) DEVELOPMENT OF BODY WEIGHT, (3) BODY SIZE, AND (4) FEATHERS.

for heat dissipation would not increase sufficiently to keep up with the heat produced, so that the body temperature would be raised. This effect continues for about 10 days, after which the body does not increase much in weight or size (Figure 29). However, the influence of this factor is most apparent during the first 3 or 4 days, because its proportionate influence then is greater and other factors do not obscure it so much. In our investigations, size was measured by the length from the anterior end of the sternum to the anus.

Another factor involved in the development of temperature control is the growth of feathers. The curve showing feather growth (Figure 29) is an average for feathers on all feather tracts of the body, and is taken from data obtained by Boulton (1926) at this laboratory. External feather development begins soon after the first rapid ascent in the general curve of temperature control, and rapid feather development occurs throughout the period of most rapid temperature development. After 9 days the curve for temperature control flattens out, while that of feather development continues at nearly the same rate as before. This would indicate either that the development of feathers is not the only factor or the most important factor involved, or that the elongation of feathers beyond a certain point is not important.

A factor that we believe of considerable importance in the temperature regulation mechanism is the development of air-sacs and the use of respiration for the proper interchange of heated and cooled air in the body. There is some evidence to indicate that the development of these is sufficient between the fourth and ninth days definitely to establish a temperature control at the end of this time (Kendeigh and Baldwin, 1928). Gross anatomical examination of newly hatched nestling wrens does not reveal the presence of air-sacs, although late in the nestling period they occur. Two diseased birds respectively 9 and 10 days old possessed bloated abdominal air-sacs as though the normal mechanism were not functioning properly at this time. Further evidence in this connection is presented in the section dealing with the rate of respiratory movements in young birds. Coupled with the functioning of these organs and other factors involved is, of course, the development of a nervous system sufficient to control their activities.

The closing of the fenestra in the interauricular septum of the heart and the atrophy of the ductus Botalli with the development of a complete double circulation of blood are probably also involved (Locy and Larsell, 1916), and may account, in part, for the gradual increase in body temperature during the developmental period.

The metabolism of the body tissues in the production of heat is, of course, a factor of prime importance. Air-sacs and respiration could not alone give a control of body temperature, since they are involved only in regulating the loss of heat, not in its production. There is undoubtedly an increase in total heat production in the young bird as it becomes older, but this has not yet been measured. The amount of heat production is probably tied up with also the development of nervous and endocrine regulation, so that the whole development is very complex.

The most rapid development of temperature control (Figure 28), begins when the nestling is 4 days old and continues until it is 9 days old. After that the curve flattens out for 3 days, but from 12 to 14 days it rises again. Possibly this latter increase in temperature is due to some effect of the control mechanism, but it may be due to an actual increase in heat production by the young birds.

Some direct studies of standard metabolism of young domestic chickens at various ages have been made for comparison with the adults. Mitchell, Card, and Haines (1927) found that "the metabolism per unit of surface is distinctly below the adult level at hatching, rises rapidly to a maximum, and then decreases again to the adult level that is maintained for a considerable fraction of the life span. For the chicken, the peak in the curve appears to be reached at 30 to 40 days of age, and the adult level at about 70 to 80 days." For altricial species, these time intervals would be different, coming probably earlier. Groebbels (1928–a) states and gives evidence that the oxygen intake of altricial nestlings is higher than that of adults. In a recent study of metabolism during growth in the common pigeon, Riddle, Nussmann, and Benedict (1932) found that 3 days after hatching the metabolism of the bird was 20% higher than the standard metabolism of the young adult; at 11 days after hatching, it was about 100% higher; while at 23 and 25 days after hatching, the rate of metabolism was in rapid decline that continued until the adult level was reached.

In order to obtain some data for comparison between adult and young house wrens with regard to their basic temperature regulation, standard temperatures (page 22) of nestling birds from the age of 11 to 36 days were obtained in the same way as for adults; i.e., after the birds remained 2 hours without food and were at as near complete rest as was possible to attain. The air temperature averaged 74.1° F. (23.4° C.).

TABLE XVII.—*Standard Temperature of Immature Eastern House Wrens after Establishment of Temperature Control*

Age	Date	Standard Temperature
11 days	July 25, 1928	104.0° F. (40.0° C.)
12 "	July 26, 1928	104.0° F. (40.0° C.)
13 "	August 10, 1927	104.5° F. (40.3° C.)
14 "	August 7, 1928	104.5° F. (40.3° C.)
14 "	August 14, 1928	104.9° F. (40.5° C.)
14 "	August 7, 1927	105.1° F. (40.6° C.)
14 "	August 9, 1928	105.4° F. (40.8° C.)
15 "	August 10, 1928	105.5° F. (40.8° C.)
36 "	August 20, 1928	104.2° F. (40.1° C.)
Average (9 records)		104.7° F. (40.4° C.)

In these records no distinction was made between sexes (Table XVII). The average result of 104.7° F. (40.4° C.) is of interest, since it is exactly half way between the values obtained for the standard temperatures of the two sexes of adult birds, which was 104.4° F. (40.2° C.) for the male and 105.0° F. (40.6° C.) for the female. There is evident a gradual rise in the standard temperature of these young birds from 11 days to 15 days of age. This may be directly correlated with the rise also in the curve for temperature control, particularly during the last 2 days. The temperature record for the 36-day-old bird is again low, simulating the standard temperature found in adult males. If the standard temperature is any measure at all of standard metabolism, then the statement made by Mitchell, Card, and Haines quoted above would hold for the house wren also, although the point of maximum metabolism would be attained at an earlier age.

The temperature control mechanism is more or less functional when the bird becomes 9 days old. The bird is then able to withstand moderate air temperatures on its own resources. A perfect control against low air temperature is not, however, developed for some time after leaving the nest. During damp, cold weather the young birds are likely to suffer greatly. Rainy days in particular are likely to be hard on young birds, as illustrated by 2 cases which have come to our attention; one was a bird 15 days out of the nest which had a gullet temperature of only 102.6° F. (39.2° C.); another 21 days out, had a temperature of 100.7° F. (38.2° C.). Many birds, in this juvenal period, undoubtedly perish each year during unfavorable weather conditions.

Although there is thus developed a complex control mechanism in young birds for resistance to low air temperatures, practically no resistance to high temperatures is developed. In fact, young birds before developing feathers are able to withstand high air temperatures better than adults, when placed under similar conditions in the laboratory. Referring again to our former paper (Kendeigh and Baldwin, 1928), we presented data showing that, when young birds of different ages were placed at an air temperature of 102° F. (38.9° C.) the body temperature of the older birds with feathers rose several degrees higher than did that of the young birds. This rise in temperature is probably due to the inability of the older birds to dissipate excess heat fast enough. The feathers then become a liability, since they prevent radiation from the general surface of the body. Practically the only ready means of losing heat is respiration; and the bird, therefore, responds by accelerating its rate of breathing, sometimes more than 300 per cent, so that doubtless there is a considerably increased circulation of air through the air-sacs and lungs. The efficiency of this control is, however, very limited, and within a short time, if the high air temperature persists, the bird dies of hyperpyrexia. Feathers, however, serve as an important protection of birds against sun temperatures, as will be discussed later (page 121).

RATE OF RESPIRATORY MOVEMENTS IN YOUNG BIRDS

Many determinations of the rate of respiratory movements at different body temperatures in young house wrens of different ages were made, and these produced some interesting results. The breathing rate of nestling house wrens recently hatched is comparable to that in young mice before they also have attained an adequate temperature control (Pincus, 1931). In the eastern house wren the number of respirations per minute was measured by actual count with watch in hand. The rate varies directly with body temperature in the younger birds but becomes modified at certain temperatures in older individuals. For instance, in birds only recently hatched, respiration was 24 times a minute when the body temperature was 83° F. (28.3° C.); 10 times at 78° F. (25.6° C.); 6 times at 72° F. (22.2° C.); 2 times at 62° F. (16.7° C.); 1 per minute between 59° F. (15.0° C.) and 57° F. (13.9° C.); about 2 in 3 minutes from 57° F. (13.9° C.) down; while at 49° F. (9.4° C.) the bird ceased breathing altogether. Several times with birds only a few hours old, all visible breathing movements of the body had ceased, and the birds, believed dead, were removed from the apparatus; but to determine certainly whether or not they really had succumbed, they were placed in an incubator and found after a few minutes to be as much alive and active as ever. Visible breathing movements cease, therefore, particularly in very young birds, at a temperature still too high actually to produce the death of the organism. In this state, the bird is comparable to a hibernating mammal or a dormant poikilotherm, although the bird cannot exist as long. In one instance, in a bird 5 days old a peculiar type of respiration was observed when the body temperature had dropped to 54° F. (12.2° C.); that is, the bird breathed 3 times close together, then waited a while and again breathed 3 times together. In other individual birds, when the actual body movements involved in normal respiration had ceased, there were discernible on closer examination slight movements of the mandibles, indicating that there may still have been some slight movement of air in and out of the body. This general behavior of the respiratory system in respect to temperature is another proof of the poikilothermic nature of the young house wren.

As the young bird becomes older it breathes more and more rapidly when compared at normal body temperatures. The highest rate that we have observed in young birds is 380 times per minute in a bird 10 days old at a body temperature of 114° F. (45.6° C.). At a body temperature of 104° F. (40.0° C.), the rate is 102-106 times a minute for birds of an age of 5 days or more. This is slightly higher than the rate of adults at the same body temperature.

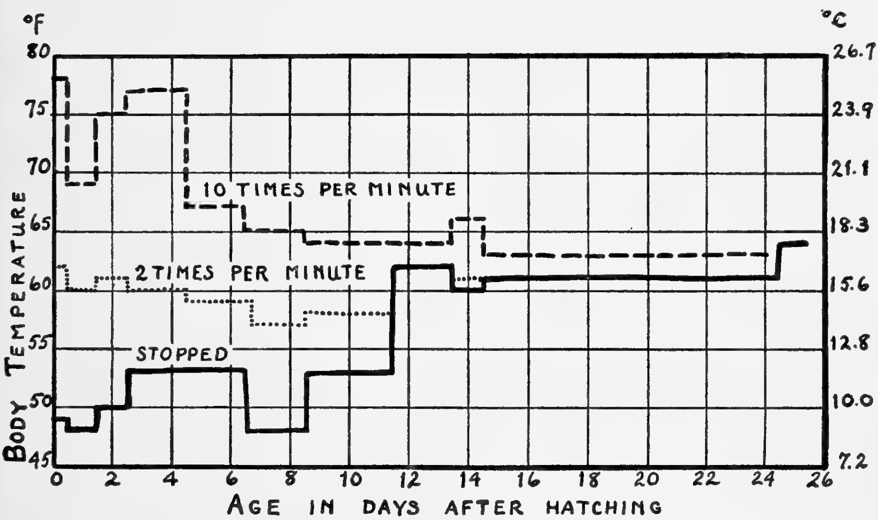


FIGURE 30.—VARIATION IN THE EXTENT TO WHICH THE BODY TEMPERATURE OF IMMATURE EASTERN HOUSE WRENS OF DIFFERENT AGES MUST BE LOWERED TO REDUCE THE RATE OF BREATHING TO TEN TIMES PER MINUTE, TO TWO TIMES PER MINUTE, AND TO STOP IT ALTOGETHER.

The body temperature at which young birds cease breathing is higher as they become older (Figure 30). This is probably due to the fact that the respiratory mechanism is becoming more and more attuned to functioning in a homoiothermic condition. The body temperature at which breathing becomes reduced to 2 times per minute runs about the same throughout the first 25 days. However, the body temperature required to reduce the number of respirations to 10 per minute is lower, the older the bird. This indicates again that the younger birds are less able than the older ones to maintain a constant and high rate of breathing, and are more subject to the temperature influence of the environment.

In the curve of respiration for the adult bird presented above (Figure 10), the breathing is less at a body temperature of 104°–105° F. (40.0°–40.6° C.) than either immediately above or below. When is this sort of a curve first found in young birds?

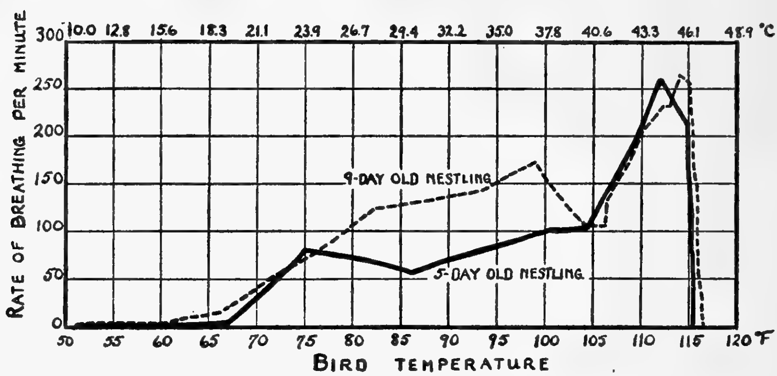


FIGURE 31.—RATE OF BREATHING MOVEMENTS IN NESTLING EASTERN HOUSE WRENS OF TWO DIFFERENT AGES AT DIFFERENT BODY TEMPERATURES.

In Figure 31, similar curves are plotted for the rate of respiration at different body temperatures of house wrens respectively 5 days and 9 days old. No curve is given for birds younger than 5 days, but all the evidence indicates that the rate of the respiratory movements varies more or less directly with body temperature. With the bird 5 days old this is nearly true, but there is a flattening of the curve between 75° F. (23.9° C.) and 104° F. (40.0° C.). Two individuals are made use of here to complete the entire range of temperatures. With the birds 9 days old, 2 individuals are again made use of in order to have the entire scale of temperatures represented. The composite curve for the bird 9 days old is very similar in many respects to that of the adult birds. There is a minimum rate at 104°–106° F. (40.0°–41.1° C.), an increase as the body temperature both rises and falls, and then as the temperature control is broken by a drop in temperature, a direct variation with temperature. The attaining of this curve at this age seems to us to be of considerable significance, because it is between the fourth and ninth days that temperature control is obtained, and it is supposedly during this time that the air-sacs begin to function in respiration. This, then, would be another argument in favor of the air-sacs and respiration as a vital factor in the temperature regulating mechanism.

As the body temperature rises, the rate of respiration increases to a maximum and then rapidly decreases in birds of both 5 and 9 days of age. This is the same thing that occurs in adult birds, although in young birds the fall in rate of respiration, after the maximum is reached, occurs before the body temperature has attained its maximum.

RESISTANCE OF YOUNG BIRDS TO HIGH TEMPERATURE

The temperature responses of young house wrens to high and low air temperatures were determined in a similar manner as were those of the adults (pages 42–50). Use was made of the air chamber in which the bird was placed, and the temperature was varied by means of a water bath running around this (Plate III). The humidity approximated that of normal air temperature outside and was the same as in the experiments with adult birds. The rate of ventilation averaged about 60 cubic centimeters per minute, and this was amply sufficient, as was shown by the behavior of the controls run before the experiments were started.

A few figures (Figures 32-34) are here given to show the manner in which a young bird's temperature increases as the air temperature is raised. In Table XVIII, the lethal points in both

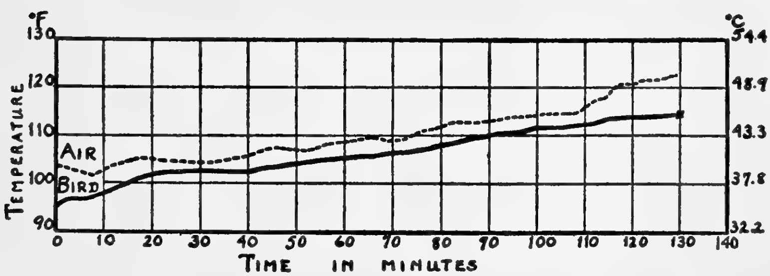


Figure 32.—Effect of a High and Rising Air Temperature on the Body Temperature of a Nestling Eastern House Wren One Hour Old. The cross marks point of the bird's death.

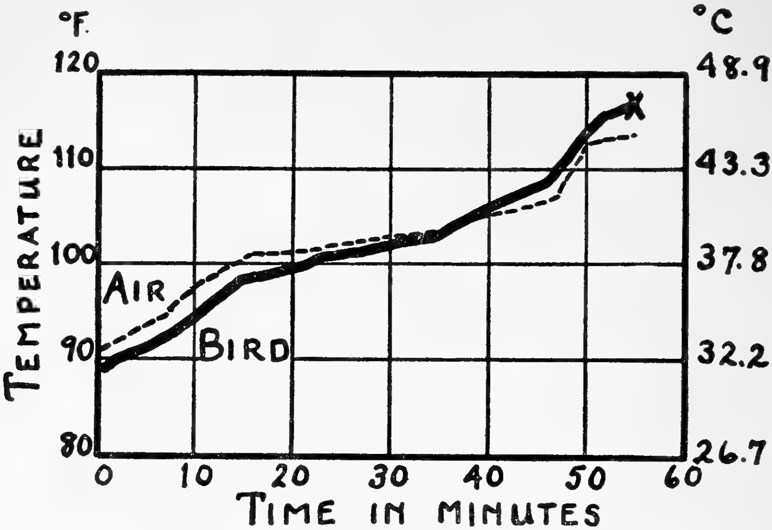


FIGURE 33.—EFFECT OF A HIGH AND RISING AIR TEMPERATURE ON THE BODY TEMPERATURE OF A NESTLING EASTERN HOUSE WREN THREE DAYS OLD. The cross marks point of bird's death.

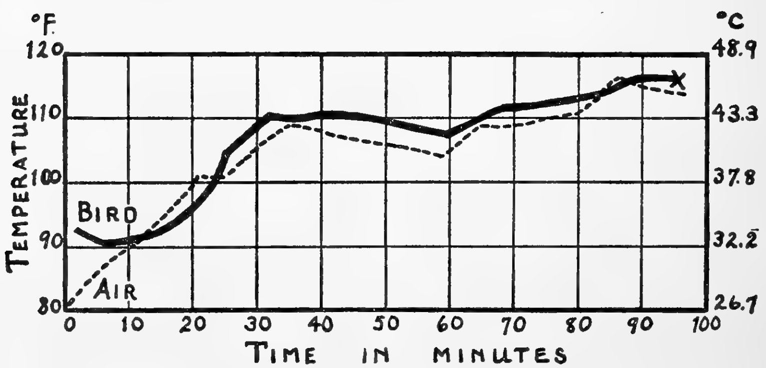


FIGURE 34.—EFFECT OF A HIGH AND RISING AIR TEMPERATURE ON THE BODY TEMPERATURE OF A NESTLING EASTERN HOUSE WREN SEVEN DAYS OLD. The cross marks point of bird's death.

bird and air temperatures are shown. When these danger points were reached in less than an hour or in an hour and a half, the rate of temperature change is indicated in that table respectively as (46.6° C.). The rate at which the air and bird temperatures are raised or lowered more slowly, the rate of change is designated "moderate."

The upper lethal body temperature, in the 10 instances determined for various ages of immature birds, averages 115.9° F. (46.6° C.). The rate at which the air and bird temperatures are raised, is, however, important. In the 6 cases, where this was

TABLE XVIII.—*Effect of High and Low Air Temperatures on the Body Temperature of the Immature Eastern House Wren*

Air Temperature Raised				
Age of Bird	Highest Body Temperature Attained	Air Temperature at Same Time	Rapidity of Temperature Change in Air and Bird	Survival of Bird
1 hour	114.1° F. (45.6° C.)	116.1°–117.7° F. (46.7°–47.6° C.)	Moderate	No
1.5–2 days	116.1° F. (46.7° C.)	107.2°–119.2° F. (41.8°–48.4° C.)	Very fast	No
2.5–3 "	117.0° F. (47.2° C.)	113.0° F. (45.0° C.)	Fast	No
3 "	113.5° F. (45.3° C.)	105.5°–119.5° F. (40.8°–48.6° C.)	Fluctuating	Yes
5 "	115.5° F. (46.4° C.)	117.0° F. (47.2° C.)	Moderate	No
7 "	116.0° F. (46.7° C.)	114.9° F. (46.1° C.)	Moderate	No
9 "	116.6° F. (47.0° C.)	115.0° F. (46.1° C.)	Moderate	No
10 "	117.1° F. (47.3° C.)	107.8° F. (42.1° C.)	Fast	No
10 "	116.9° F. (47.2° C.)	111.4° F. (44.1° C.)	Fast	Yes
11 "	118.5° F. (48.1° C.)	120.0° F. (48.9° C.)	Very fast	No
13 "	116.1° F. (46.7° C.)	107.4°–111.0° F. (41.9°–43.9° C.)	Moderate	No
16 "	111.6° F. (44.2° C.)	107.1°–105.2° F. (41.7°–40.7° C.)	Moderate	No
Air Temperature Lowered				
Age of Bird	Lowest Body Temperature	Air Temperature at Same Time	Rapidity of Temperature Change in Air and Bird	Survival of Bird
Just hatched	49.0° F. (9.4° C.)	45.3° F. (7.4° C.)	Moderate	Yes
6 hours	52.4° F. (11.3° C.)	50.0° F. (10.0° C.)	Fast	Yes
1 day	47.4° F. (8.6° C.)	47.0° F. (8.3° C.)	Moderate	No
2 days	49.4° F. (9.7° C.)	47.4° F. (8.6° C.)	Moderate	Yes
3 "	50.7° F. (10.4° C.)	47.2°–50.1° F. (8.4°–10.1° C.)	Fast	Yes
5 "	56.0°–47.0° F. (13.3°–8.3° C.)	50.0°–46.0° F. (10.0°–7.8° C.)	Moderate	No
5 "	44.2° F. (6.8° C.)	43.5° F. (6.4° C.)	Fast	No
7 "	46.5° F. (8.1° C.)	44.5° F. (7.0° C.)	Moderate	No
9 "	47.6° F. (8.7° C.)	47.0° F. (8.3° C.)	Moderate	Yes
12 "	50.5° F. (10.3° C.)	48.5° F. (9.2° C.)	Moderate	No
14 "	60.0° F. (15.6° C.)	53.8° F. (12.1° C.)	Fast	No
15 "	61.5° F. (16.4° C.)	50.9° F. (10.5° C.)	Moderate	Yes
25 "	63.2° F. (17.3° C.)	59.0° F. (15.0° C.)	Moderate	No
5 weeks	72.6° F. (22.6° C.)	62.6° F. (17.0° C.)	Fast	Yes

moderate, the average is 115.0° F. (46.1° C.); and in the 4 cases where it was rapid, it is 117.2° F. (47.3° C.), a difference of 2.2° F. (1.2° C.). The age of the young birds has apparently no effect upon the point at which the lethal body temperature is reached. In fact, except for the rate at which the temperature was reached, the amount of variation is very small, and the lethal body temperature is nearly the same as that determined for the adult birds, which is 116.3° F. (46.8° C.). Apparently after the temperature control is broken, the body tissue reacts similarly regardless of age. The dying of the 16-day-old bird when its body temperature rose only to 111.6 F. (44.2° C.) is exceptional.

The exact temperature of the air that is effective in producing death is difficult to determine with entire satisfaction in every case. The bird reacts positively to all variations in the air temperature, either up or down, provided, of course, that these are of sufficient degree. The attempt was made, however, to ascertain the lowest point at which a high temperature would cause the bird's death, and this was more or less successfully done. The average air temperature for all 11 birds when death occurred was 113.3° F. (45.2° C.). Age is an important factor here. If we average together the air temperatures causing the death of birds that have just hatched to those 3 days of age inclusive, we get 113.9° F. (45.5° C.). A similar average for birds from the ages of 5 to 10 days is 113.2° F. (45.1° C.), and from 11 to 16 days 107.7° F. (42.1° C.). The record of 120° F. (48.9° C.) in air temperature for an 11-day-old bird is not included in this average, since the temperature was increased so very fast in that experiment that the results are not typical. However, even if included, the average for the older birds would be nearly a degree and a half less than that of the second group. For adult birds, a similar average would be approximately 100° F. (37.8° C.) air temperature. There is thus, with increasing age, a progressive decrease in tolerance to the high air temperature that birds can resist. This is probably due to the greater difficulty that the birds have of dissipating excess heat when they become larger and covered with feathers. Here again, the warning is given that these critical air temperatures were obtained with birds in confinement and are probably not applicable in all detail for birds under natural conditions.

In order to see how long young house wrens would survive the full effect of the heat of the sun, 3 birds were placed in open boxes exposed directly to the sun at 2:02 P. M. on one bright, clear day. One of the birds had hatched on that morning, another was 4 days old, while the third was 14 days old. At 2:11 o'clock, all birds were alive, but breathing rapidly and panting. At 2:17, the 2 younger birds were dead. The oldest bird lived throughout the experiment, which was continued until 3:30 P. M. The general air temperature in the shade at 2:30 P. M., taken at our regular weather station, was 85.5° F. (29.7° C.). However, a thermometer, the bulb of which was wrapped several times around with black mosquito netting and placed exposed to the sun near the birds, gave a reading of 109°–110° F. (42.8°–43.3° C.). The 2 naked younger birds did not live 15 minutes, the older feathered one was not killed. This appears at first contradictory to our experimental results. Further analysis, however, suggests that the feathers of the oldest bird, the only one to survive, served a very useful function of protecting the bird from the direct insolation of the sun, so that the body of the bird was actually subjected to a much lower air temperature than were the 2 naked young. Feathers may furnish birds as much protection in the summer by shielding them from direct solar radiation as they do in the winter by insulating them against intense cold.

The fatal effect of high body temperatures is almost instantaneous. Sometimes only a few seconds or at most only a very few minutes are all that are required. However, by lowering the body temperature after the upper lethal temperature is reached, this short period before death may be prolonged for a few minutes.

RESISTANCE OF YOUNG BIRDS TO LOW TEMPERATURE

That the body temperature of young birds is very responsive to low air temperature when they are exposed directly to it was shown in some detail in our former paper (Kendeigh and Baldwin, 1928). They are dependent on outside sources of heat for the maintaining of their own temperature, and if this fails them their body temperature drops at once. In Figure 35, which is illustrative of many others that might be given, the correspondence in the

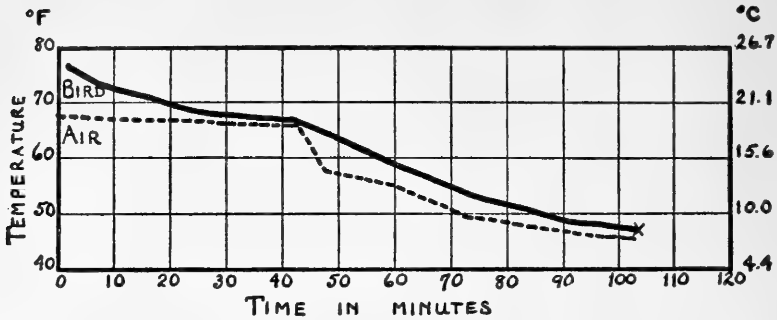


FIGURE 35.—EFFECT OF A FALL IN AIR TEMPERATURE ON THE BODY TEMPERATURE OF A NESTLING EASTERN HOUSE WREN FIVE DAYS OLD. The cross marks the point of bird's death.

curves for the body and air temperatures is well marked. In young house wrens just hatched, the evaporation of water from the skin sometimes lowers the body temperature to or below the air temperature. The temperature of the living bird does not ordinarily decrease quite to air temperature, however. Ordinarily the normal metabolism or heat production of the bird is sufficient to keep the body temperature above that of the air, even with birds less than a day old, and this difference may persist for several hours. In the case of 1 young bird, 3 days old, an average of 1.5° F. (0.8° C.) above that of the air, which was 65°–66° F. (18.3°–18.9° C.), was maintained with very little fluctuation for nearly 14 hours. When the air temperature is fluctuating or rising too rapidly, the bird's temperature may then drop below that of the air, due to a lag in the warming up of the bird, but this would naturally be expected.

After realizing that the body temperature of young birds is dependent on that of the environment, and that a drop in the environmental temperature causes a rapid and corresponding drop in the temperature of the bird, the question arises as to how low the temperature of the young bird can be caused to drop before death ensues, and what temperature of the air is required to do this. To determine this, use was made of the temperature bath as above described (Plate III), but with ice water instead of water which had been heated. Air temperatures down to 44° F. (6.7° C.) could be obtained in this way, which was sufficiently low for most of the experimentation.

It is more difficult to kill a bird by low temperature than by high. This is because heat is a more potent destructive agent to protoplasm than is chill, and because the normal body temperature maintained by birds is nearer the upper lethal limit than the lower. Adult house wrens do not survive a lowering of their body temperature to 71.0° F. (21.7° C.). The temperature of young birds may drop much below this without death's resulting. Age is, in this connection, a very important factor (Table XVIII), so the data on young birds are here presented in the reverse order of the age of the birds.

A juvenal house wren, 5 weeks old, survived a lowering of its body temperature to 72.6° F. (22.6° C.). Another, 25 days old, was killed when its body temperature dropped to 63.2° F. (17.3° C.). A house wren 15 days old survived a body temperature of 61.5° F. (16.4° C.); but a bird 14 days old was killed at 60.0° F. (15.6° C.), and a 12-day bird died at about 50.5° F. (10.3° C.). The effect of these low body temperatures seems to be an absolute one, i.e., the effect is immediate if it is to occur at all. The length of exposure was not here an important factor, since the bird's temperature dropped continuously until it reached a certain degree that proved fatal. The case of the bird 3 days old, above mentioned, shows that low temperatures which are not fatal can be endured for several hours. Death results in such cases only when starvation has greatly weakened the bird's resistance. This will be considered in more detail later. In the last 3 cases above, the air temperature ranged from about 48.5°–53.8° F. (9.3°–12.1° C.).

In a previous section (pages 108–113), we showed that nestling house wrens develop a temperature control mechanism which enables them after an age of 9 days to maintain their body temperature constant at a moderate air temperature (72° F. [22.2° C.]). This does not permit them to withstand the unusually low air temperatures produced in this series of experiments, particularly when the air temperatures are purposely lowered at a very rapid rate.

Of house wrens from 5 to 9 days old, 1 bird, 9 days old, survived a body temperature of 47.6° F. (8.7° C.). A house wren, 7 days old, was killed at 46.5° F. (8.1° C.), and one 5 days old at 44.2° F. (6.8° C.). Another bird, 5 days old, died somewhere between 56° F. (13.3° C.) and 47° F. (8.3° C). The range in air temperature was from 43.5° F. (6.4° C.) to about 48.0° F. (8.9° C.). These figures must be considered as only approximate, for it is not always easy to determine the exact moment when death occurs, since in very young birds life may linger on for some time even after visible breathing has ceased. The stopping of the respiratory movements is a danger signal, however, and one that could be ascertained rather readily in these experiments. In any case of doubt as to whether the bird had actually died or not, the bird was removed and placed in an incubator for several minutes at a temperature of approximately 100° F. (37.8° C.).

For house wrens less than 5 days old there are 5 records. Four of these survived body temperatures from 49.0° F. to 52.4° F. (9.4° C. to 11.3° C.) and air temperatures from 45.3° to 50.0° F. (7.4° to 10.0° C.). One bird about 1 day old died at a body temperature of 47.4° F. (8.6° C.) with the air temperature at 47.0° F. (8.3° C.).

From the data given above it would seem, therefore, that 47.0° F. (8.3° C.) is approximately the low lethal body temperature for those young birds that have not yet developed a temperature control; and that this corresponds to an effective air temperature from a few tenths of a degree to 2° or 3° F. (1.1° or 1.7° C.) below this, depending on the age and size of the birds. Reduction of body temperature to any degree above this limit is not fatal. The young birds may be again warmed, returned to the nest, and develop normally. Gross (1930) states that young prairie chickens when cooled to a nearly lifeless condition will also recover rapidly when again brooded.

SURVIVAL TIME OF YOUNG BIRDS AT HIGH AND LOW TEMPERATURES

Our next series of experiments was for the purpose of determining the survival time of young birds without food at normal temperatures of the nest, and also when exposed to low air temperatures. Young birds of different ages were taken from the nest, brought to the laboratory, and placed either in a well-ventilated incubator at 99° F. (37.2° C.) or in open boxes at a room temperature of 66° F. (18.9° C.). The humidity at the higher temperature averaged about 65%, while that at the lower was at least 82%. Of course, the food factor is an important one in such a case, as the birds were not fed at any time during the experiment —this would have been useless, as any food forcibly ingested would not have been digested by young birds at greatly reduced temperatures. The problem really amounts, then, to the determination of how long young birds can live without food at one temperature as compared with another.

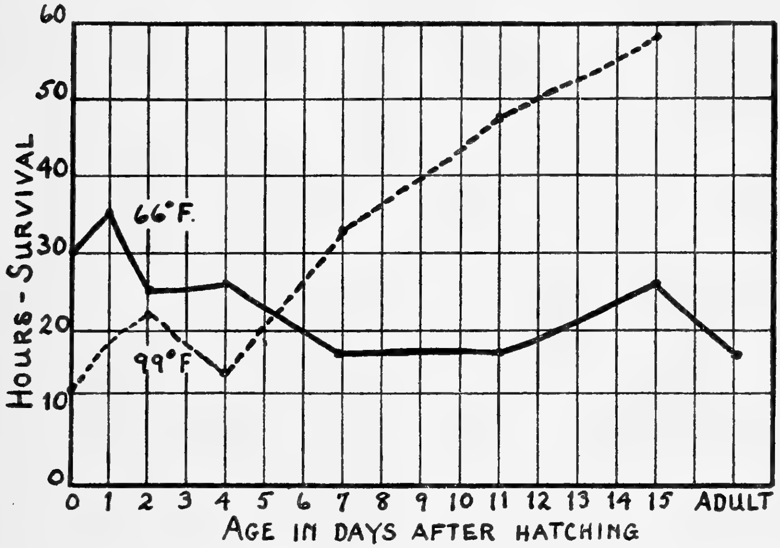


FIGURE 36.—SURVIVAL TIME OF NESTLING EASTERN HOUSE WRENS OF DIFFERENT AGES AT DIFFERENT AIR TEMPERATURES AND WITHOUT FOOD. The air temperatures used were 66°F. (18.9°C.) and 99°F. (37.2°C.).

The results are shown in Figure 36. The survival time is plotted in hours against the age of the birds in days. The accuracy of the survival time as determined is about 2 hours, plus or minus. The figure shows that young birds less than 5 days old live longer at the lower temperature than at the higher, while above the age of 6 days the reverse is true. This is interesting when we remember that it is between the fourth and ninth days that the birds develop a temperature regulation, and that previously to this they react as cold-blooded animals.

That cold-blooded animals would live longer at low temperatures than at high is natural and a fact well known. Some physiological processes have been found to obey van't Hoff's law for chemical reactions. This law states that for every rise of 18° F. (10.0° C.) there is a twofold or threefold increase in the rate of reaction. Metabolism of these young birds would be kept normal and high at the incubator temperature, but greatly reduced in rate at room temperature. Therefore, the reserve resources of the bird would be more quickly exhausted at the high temperature than the lower, and, as a result, death would come sooner.

After the development of temperature control in young birds, other factors are more certainly of importance. At a temperature of 99° F. (37.2° C.), the body temperature would be maintained fully as well out of as in the nest. Death then would come only when the reserve sources of energy for the maintenance of the necessary physiological activities were exhausted. This is twice as long or more after 10 days of age as before 5. Possibly this may mean that the reserve supplies in the body are at least twice as ample in these older birds. At the low air temperature of 66° F. (18.9° C.), however, these older birds cannot for long maintain their normal high body temperatures. It is probably some effect of continuous low body temperature in addition to starvation that brings about death of the birds at this greater age. The physiological processes and functions are then becoming more highly developed and attuned to the stable homoiothermic condition so that they are more quickly and seriously effected when disturbed by a drop in body temperature than earlier in life before they had become so adapted.

Table XIX.—*Survival Time and Loss in Weight of Nestling Eastern House Wrens when Confined without Food at Different Air Temperatures*

Age at Beginning of Experiments	Temperature to Which Exposed	Survival Time	Initial Weight	Loss	Decrease of Weight
		hours	*mg.*	*mg.*	*per cent*
2 hours	98°–100° F. (36.7°–37.8° C.)	12	998	147	14.7
2 days	98°– 99° F. (36.7°–37.2° C.)	22	3424	483	14.1
11 days	98°–101° F. (36.7°–38.3° C.)	47.5	10444	4515	43.2
....	....	......	......	......	......
2 days	62°– 64° F. (16.7°–17.8° C.)	25	1654	23	1.4
4 days	63°– 66° F. (17.2°–18.9° C.)	26	4622	34	0.7

In 5 instances (Table XIX), weights of the house wrens were taken at the beginning and at the end of the experiments. There was a loss of weight in all cases.

The number of records are few but the results are interesting. The percentage loss in weight of those birds subjected to high temperature is considerably greater than of those subjected to low temperature. This could be explained by considering that death at the high temperature was actually due to complete starvation, while death at low temperature, even though it did not come so soon, was not due to starvation alone in the usual sense of the term, but also to the disturbance of proper physiological functioning by prolonged exposure to the low temperature. The loss in weight of the 2 birds at low temperature is really negligible. At the higher air temperatures the considerably greater percentage loss in weight of the 11-day-old bird over the 2 others is interesting. We do not have available the proportionate weights of the different organs of the body at various ages, but it is certainly obvious from mere observation that in very young birds most of the body is made up of vital organs such as the liver, heart, and particularly the digestive tract. There is very little "flesh," or muscle. This is not true in the case of birds 11 days old, for at this time the muscular tissue is much better developed, while the proportionate size of the vital organs has diminished. According to Kumagawa's work (Howell, 1928), where the percentages in weight of the different organs to the body as a whole in normal and starved conditions were determined in the dog for a 24-day fast, the greatest actual loss in weight occurs in muscle tissue and the next greatest in the fat. This is true in spite of the fact that the greatest percentage loss in weight occurs in the glandular organs. The reason for the greater decrease of weight in the bird 11 days old as compared with the younger ones is therefore clear.

NORMAL TEMPERATURE OF YOUNG BIRDS IN THE NEST

In order to determine how much the temperature of a newly hatched house wren fluctuates in the nest as a result of the intermittent brooding and absence of the adult bird, use was made of a thermocouple thermometer, similar to those used in other experiments described above. This was run through the side of the nest box and nest and down the throat of the young house wren which had hatched only a few hours previously. Other thermocouples of the thread type were run across the nest, one just above the young bird, to determine the temperature to which the bird was subjected when the adult was brooding, and when she was away, and the other just beneath the young bird to determine the temperature at the bottom of the nest. The leads on these thermocouples were then run back into a blind where the temperatures were taken by means of the indicator potentiometer.

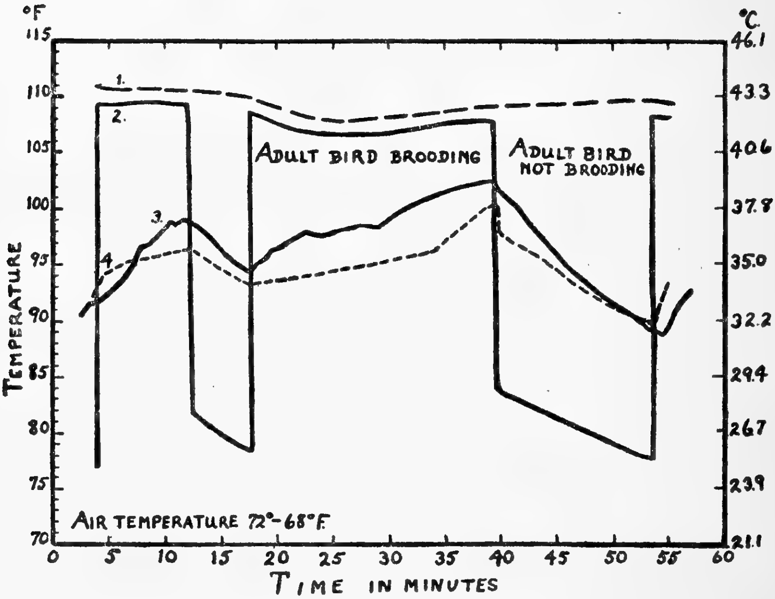


FIGURE 37.—NATURAL FLUCTUATIONS IN BODY TEMPERATURE OF A NEWLY HATCHED EASTERN HOUSE WREN UNDER NORMAL CONDITIONS IN THE NEST. 1—Body temperature of adult bird; 2—temperature at top of nest just above young bird; 3—body temperature of nestling bird; 4—temperature in bottom of nest underneath young bird.

The results of this experiment are shown by the graph in Figure 37, reproduced from our former paper (Kendeigh and Baldwin, 1928). While the adult female brooded, the temperature of the young bird rose; when she was away, the young bird's temperature dropped. The greatest variation during this period was a drop from about 102° F. (38.9° C.) to 88° F. (31.1° C.) in a period of approximately 16 minutes.

In order to obtain some idea of the normal temperature of young house wrens in the nest at all ages before flight, use was made of mercury thermometers. Temperatures of the young in two nest boxes were taken each day at the end of several periods when the adult bird had been away (inattentive periods), and again at the end of several brooding or feeding periods (attentive periods). These 2 sets of temperatures were averaged and compared for each day. The data for one of these nests are shown in the graph (Figure 38). The greatest difference between

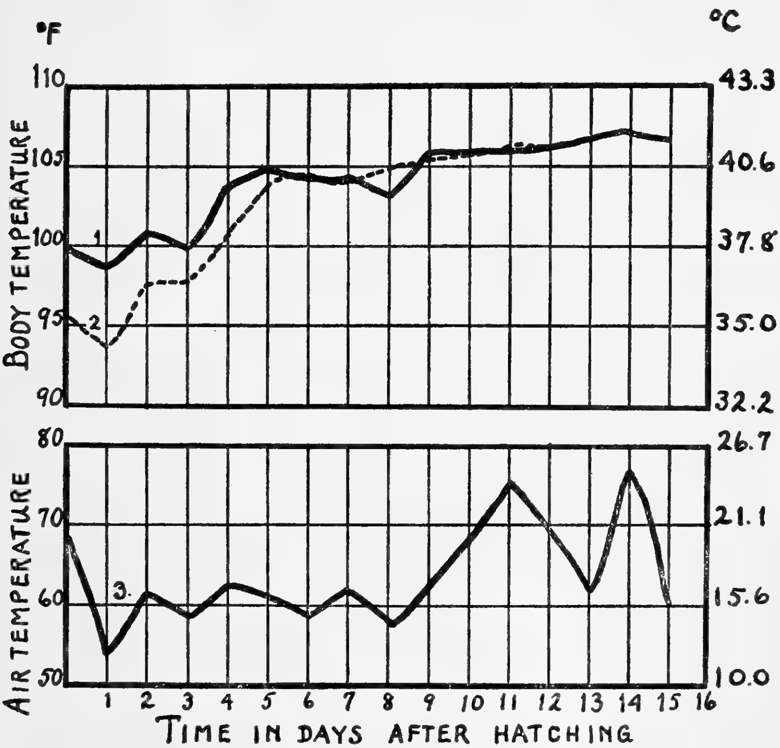


FIGURE 38.—DEVELOPMENT OF BODY TEMPERATURE OF IMMATURE EASTERN HOUSE WRENS IN THE NEST AND CORRELATION WITH AIR TEMPERATURES. 1—Temperature of the birds at end of attentive periods; 2—temperature of the birds at end of inattentive periods; 3—air temperature.

these 2 sets of temperatures, i.e., before and after brooding, occurred during the first 5 days. This is to be expected, for it is at this time that the young birds are most dependent on outside sources of heat for maintaining their body temperature. The average difference for the birds at one nest (Figure 38) for each of the first 5 days was 4.4° F. (2.4° C.), 4.9° F. (2.7° C.), 3.2° F. (1.8° C.), 2.3° F. (1.3° C.), and 3.1° F. (1.7° C.), the higher temperatures coming at the end of periods of attentiveness. For the birds at another nest the average differences for the first 5 days were 5.5° F. (3.1° C.), 7.7° F. (4.3° C.), 4.9° F. (2.7° C.), 2.0° F. (1.1° C.), and 1.4° F. (0.8° C.).

The temperature of the young birds during this early period shows a positive correlation with variations in the temperature of the air. This correlation persisted until the ninth day for the birds at one box (Figure 38). After the fifth day, there is little difference between the temperature of the young at the end of the attentive and inattentive periods. On some days it is higher in one, but on the next it may be higher in the other. This less variation in the temperature of young birds during the latter period of nest life is to be expected, since the young birds then develop a temperature control. Active brooding by the adult bird for the most part ceases when the young birds acquire this control over the body temperature.

In some cases, during the latter half of the nest period, the nestling bird's temperature is higher at the end of an inattentive period than normally at the end of an attentive one. This may be explained by a tendency of the young bird to conserve its heat, as it is quiet when the female is away, while the greater exposure of body to heat radiation when reaching for food, the greater respiration, and the ingestion of the cold mass which the female brings would tend to lower its temperature when the female is present. That the average normal variation in the young bird's temperature in the nest during the day under average environmental conditions is so small, attests to the faithfulness of the parents in caring for the young and the efficiency of their type of nest and nesting behavior.

There is a gradual increase in the body temperature of the young birds during the period in the nest. In the case of the young birds at the first nest (Figure 38), this increase was from 98.0° F.

(36.7° C.), as an average for the first day, to 106.7° F. (41.5° C.) for the last. This increase is rather uniform and persistent, and amounts to 8.7° F. (4.8° C.). This makes an average increase per day of 0.58° F. (0.32° C.). In the young at the other nest there was an increase in temperature from 96.2° F. (35.9° C.) to 106.6° F. (41.4° C.), or 10.4° F. (5.7° C.). This makes a daily increase of 0.65° F. (0.36° C.). The average daily increment in temperature for these 2 broods of young house wrens averages 0.62° F. (0.34° C.). The average temperature of these 2 sets of nestlings, 106.6° F. (41.4° C.) and 106.7° F. (41.5° C.), on the last day in the box is below the average day temperature of adult females during the summer, which we found to be 107.3° F. (41.8° C.). Stoner (1928) found a similar gradual and regular increase in the temperature of nestling house wrens until flight ability was attained, the rate of this increase averaging 0.5° F. (0.3° C.) daily.

By the use of recording potentiometers with the thermocouples placed in the bottom of the nest, continuous records of the skin temperature of young house wrens were obtained throughout the day. This has a value for comparison, since the relation between skin and body temperatures is sufficiently constant to enable us to interpret in terms of body temperature the records obtained. Even after the body becomes partly covered with feathers, the general trend in the body temperature of young birds may be followed throughout the day as long as they remain in the nest, even though the exact skin temperature is not obtained. This enables us to state the following as taken from our former paper, and this agrees in general with the findings of Kelso (1931) on desert horned larks and of Stoner (1928) on house wrens. The difference in the amount of temperature variation in the young during the daytime as compared with night is rather marked. At night, when the adult female is constantly brooding, the temperature of the young is uniform. Occasionally, there is discernible a slight lowering in the temperature from the first part of the night until early morning, but this amounts to not more than 1° or 2° F. (0.6° or 1.1° C.). During the day, on the other hand, the variation in the temperature of young birds is great, particularly during the first few days out of the shell. During the first 2 or 3 hours in the morning, after the adults begin their morning activities, the temperature of the young is at its lowest point, since the adults are brooding during only a part of the time, and the air temperature is itself at or near its daily minimum. As the air temperature becomes warmer during the day, the temperature of the young also rises, so that during the early afternoon it reaches the maximum. There is then usually a decline until night. Occasionally, just before dark, before the adult has gone into the nest box to brood for the night, the temperature of the young may drop, but the drop is usually not so great as during early morning. The temperature of the young at night is lower than while they are being brooded during the day, but is generally higher than when the adult is not brooding during the day. The temperature of the young is distinctly correlated with atmospheric temperature variations, since the two closely follow each other, although that of the young birds is necessarily more fluctuating. When there is a distinct daily rhythm in the air temperature, there is also one in the temperature of the young birds; but when there is none or very little in the air temperature, the temperature of the young is more uniform. The maximum points in the air and bird rhythms come at approximately the same time.

TEMPERATURE OF EGGS AND NEST

Very little work has ever been done to determine the actual temperature of eggs during incubation, and even fewer data are available on nest temperatures. Temperature is undoubtedly one of the most important factors concerned in the incubation of eggs. This is amply realized by many authors, but it was Bergtold (1917) who particularly emphasized its importance in the study of incubation periods of different species under natural conditions.

Murray (1826) appears to have been about the first to record in print the temperature of eggs. He thrust the bulb of a small thermometer through holes drilled in the shell of hens' eggs and determined the temperature in different positions and at various depths. He concludes that the egg maintains a temperature superior to that of the external medium.

Baerensprung (1851) determined the temperature of eggs in a somewhat similar fashion, by thrusting the bulb of a thermometer through the shell of hens' eggs into the center of the yolk. He found that the temperature of eggs under incubation is not constant and is dependent on the temperature of the surroundings. No constant differences between egg and air temperatures were determined, although he did find that living eggs under incubation maintained a temperature of a few tenths of a degree above that of dead or infertile eggs. He concludes, "Zu dem Zweck dieser Untersuchung genügt der Nachweis des Factums, dass der im Ei eingeschlossene Foetus eine Eigenwärme überhaupt erzeugt."

Eycleshymer (1907) has the next contribution to the subject. He determined first the approximate temperature applied to hens' eggs by fitting a self-registering thermometer into the upper surface of a block of wood shaped to simulate an egg and placing this in the nest. He found that temperatures obtained in this way increased from 102.2° F. (39.0° C.) on the first day of incubation to 104.6° F. (40.3° C.) on the last. Actual egg temperatures were taken by fitting the egg into a tight rubber bag, immersing it in water at 98° F. (36.7° C.), and then thrusting a thermometer through the shell into the center of the yolk. The hen's temperature was taken by placing a thermometer in the groin for about 5 minutes. He found that the egg temperature averaged lower than that of the hen, and was approximately 101° F. (38.3° C.) for the first week, 102° F. (38.9° C.) for the second, and 103° F. (39.4° C.) for the third. In order to obtain these temperatures in artificial incubation, the incubator had to be run at 102°–103° F. (38.9°–39.4° C.) for the first half, and 103°–104° F. (39.4°–40.0° C.) for the latter half.

FLUCTUATION IN EGG TEMPERATURE UNDER EXPERIMENTAL CONDITIONS

In order to study the possible variations in the temperature of the eastern house wren's eggs, the rapidity of response to variations of external temperature, the degree of approximation to external temperature, and similar problems, a study was first made of the temperatures of eggs under controlled conditions. Temperatures were taken with the indicator potentiometer and thermocouple. Moran (1925) in his studies used thermocouples to obtain the temperature of hens' eggs.

The thermocouple thermometer used in our work was made as small and delicate as possible, well insulated so that it was certain that only the temperature at the tip was recorded, and thrust into the egg. A small opening in the shell was made by a delicate egg drill, and the thermocouple thrust just within the membrane that lines the base of the air space at the large end of the egg. This air space was not punctured, but the thermocouple was approximated to it so that the egg contents would, thereby, be less disturbed. The thermocouple was not in the air space or in the yolk mass but rather at one side of the latter. In some instances, the tip was close to the inside of the shell on the other side of the egg from which it entered, at other times at various depths within the egg, and still in other instances less than half way through. In all instances, however, the thermocouple lay close to the embryo although not actually penetrating it. Thus the egg temperature was determined rather than that of the embryo, but, undoubtedly, this means very little discrepancy and may be disregarded.

In this experimental work no difference was noted in the response of the egg as determined from the different positions of the thermocouple. The opening left around the sides of the thermocouple was closed by means of collodion which quickly dried and hardened after being applied. The egg with its thermocouple was fastened firmly on cotton batting in a small open box so that it could be shifted about without danger of the thermocouple's harming the egg. To get the air temperature, another thermocouple was fastened in the box close to the egg. The two thermocouples when later compared at the same air temperature gave identical readings.

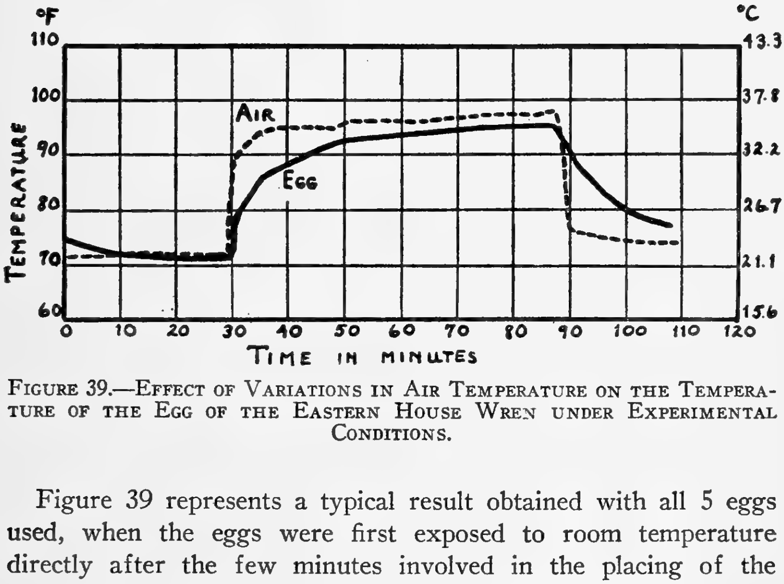


FIGURE 39.—EFFECT OF VARIATIONS IN AIR TEMPERATURE ON THE TEMPERATURE OF THE EGG OF THE EASTERN HOUSE WREN UNDER EXPERIMENTAL CONDITIONS.

Figure 39 represents a typical result obtained with all 5 eggs used, when the eggs were first exposed to room temperature directly after the few minutes involved in the placing of the thermocouple, and then placed in an incubator, after which they were again exposed to room temperature. Readings of temperature were taken every few minutes. At the termination of each experiment, the thermocouple was withdrawn from the egg, and, on examination, the embryo was found still to be alive.

The temperature of the egg responds very quickly to variations in the temperature of the air, both rising and falling, although there is in all cases a very perceptible lag. If given time, however, the egg approximates the air temperature and frequently drops below this. This is true both at room temperatures and incubator temperatures.

In order to study more accurately the exact relation between egg and air temperatures, use was made of another instrument (Plate II–B). This is described in the first section of this paper (page 21). The difference in potential between 2 thermocouples is measured by means of a sensitive galvanometer, and this is calibrated into degrees Fahrenheit. One thermocouple was placed approximately half way through the egg, while the other was held about an inch away to get air temperature. The whole was then placed in a covered dark box to avoid possible error from air currents and also from the warming of the air by the observer's presence within a few feet. Accuracy of recording by this means is greater the smaller the difference in thermoelectric potential between the 2 thermocouples; the accuracy here attained was within a few hundredths of a degree, since the difference between air and egg temperatures amounted in no instance to more than 1.0° F. (0.6° C.). The results obtained are not voluminous but are presented in Table XX for preliminary discussion.

Two determinations of temperature were made with each egg, one at a low, the other at a high temperature. In all instances, the eggs were held under the same conditions for 2 or 3 hours or even longer, until it was certain that the relation between egg and air temperatures had become stabilized. As before, at the end of each experiment the egg was opened and the embryo ascertained to be alive. The differences between egg and air temperatures determined at the lower degrees are more satisfactory than those at the higher. This is because, at the higher incubator temperatures, there was some continual fluctuation in air temperature amounting to a few tenths of a degree. At the lower temperatures, there were no fluctuations in air temperature discernible.

In the case of eggs of less than 10 days' incubation, temperatures were below those of the surrounding air. The explanation of this difference lies probably in the cooling effect of water which is being continuously evaporated from the surface of the egg. The average loss in weight of house wrens' eggs in the nest from the first day of steady incubation until the last has been determined by daily weighings. For 22 eggs distributed in 4 sets through the summer, this amounts to 13.3% of the original weight. This

TABLE XX.—*Relation between Temperature of Eggs and That of the Surrounding Air*

Species	Number of Days' Incubation of Egg	Air Temperature	Relative Air Humidity *per cent*	Difference between Egg and Air Temperature	Air Temperature	Relative Air Humidity *per cent*	Difference between Egg and Air Temperature
Eastern house wren	0	69° F. (20.6° C.)	88	—0.2° F. (—0.1° C.)	93° F. (33.9° C.)	45	—0.2° F. (—0.1° C.)
"	2	63° F. (17.2° C.)	90	—0.3° F. (—0.2° C.)	98° F. (36.7° C.)	38	—0.2° F. (—0.1° C.)
"	3	68° F. (20.0° C.)	86	0.0° F. (0.0° C.)	96° F. (35.6° C.)	47	—0.4° F. (—0.2° C.)
"	5	67° F. (19.4° C.)	81	—0.6° F. (—0.3° C.)	98° F. (36.7° C.)	67	—0.6° F. (—0.3° C.)
"	7	70° F. (21.1° C.)	77	—0.1° F. (—0.1° C.)	....	......	....
"	10	69° F. (20.6° C.)	69	—0.1° F. (—0.1° C.)	97° F. (36.1° C.)	67	+0.4° F. (+0.2° C.)
"	10	67° F. (19.4° C.)	74	+0.1° F. (+0.1° C.)	99° F. (37.2° C.)	64	0.0° F. (0.0° C.)
"	12	70° F. (21.1° C.)	89	+0.2° F. (+0.1° C.)	98° F. (36.7° C.)	58	+0.8° F. (+0.4° C.)
Eastern robin	7	64° F. (17.8° C.)	77	—0.2° F. (—0.1° C.)	99° F. (37.2° C.)	67	—0.6° F. (—0.3° C.)
" "	12	65° F. (18.3° C.)	66	+0.2° F. (+0.1° C.)	99° F. (37.2° C.)	47	+1.0° F. (+0.6° C.)
Eastern song sparrow	3	65° F. (18.3° C.)	81	—0.2° F. (—0.1° C.)	98° F. (36.7° C.)	31	—1.0° F. (—0.6° C.)
"	9	71° F. (21.7° C.)	89	—0.1° F. (—0.1° C.)	96° F. (35.6° C.)	53	—0.2° F. (—0.1° C.)

means that, on the average, 16.3 milligrams were lost per day per egg. The greatest proportion of this loss in weight is due to water evaporated. The metabolism of the embryo in the egg causes some small amount of heat production, but with the relatively large surface for heat loss in proportion to the volume of the egg, this excess heat is rapidly dissipated. The temperature of the egg in relation to the temperature of the air is determined by the balance between the amount of heat received, the amount produced, and the amount dissipated.

As the embryo becomes formed in the egg and the yolk is absorbed and transformed into active protoplasm, the amount of material exhibiting metabolism and heat production increases. This causes a disturbance in the balance originally set between heat production and heat loss, with the consequence that the egg assumes a higher relative temperature. This is shown in the table, although it amounts to only a few tenths of a degree (F.). In the case of a house wren's egg of 12 days incubation, the temperature was maintained at 0.2° F. (0.1° C.) above that of the air. Young house wrens recently hatched (approximately 13 days after the beginning of steady incubation) are able, as we have shown, to maintain a body temperature only 0.4° F. (0.2° C.) above the corresponding air temperature. There is consequently an inherent tendency for the embryo (and nestling) to increase the body temperature, at first very slightly, from the first days of incubation entirely through the developmental period until it is ready to leave the nest.

All the work on the temperature of hen's eggs, particularly that of Eycleshymer (1907), indicates a temperature above that of the surrounding air (or water) for the entire period of incubation. Some preliminary work of our own on hens' eggs in an incubator confirms this. In house wrens' eggs, a temperature of the egg below that of the air was obtained for the early days of incubation. It is probable here that a difference in the size of the eggs, together with a difference in the thickness of the shell, are important. The egg of the eastern house wren or eastern robin is much smaller than that of the domestic fowl, hence the amount of surface exposed for heat dissipation is much greater in proportion to the volume of the egg concerned with heat production. Eycleshymer also found an increase in the temperature of the hen's egg (2.0° F.

[1.1° C.]) during incubation, which was considerably more than in the case of either the eastern house wren, eastern song sparrow, or eastern robin. This may be correlated with the degree of development which the chick attains before hatching, which is greater than in an altricial species.

RESISTANCE OF EMBRYOS TO HIGH TEMPERATURE

Poultry raisers are usually advised not to allow the incubator temperature to rise above 105° F. (40.6° C.), as this would greatly decrease the number of eggs that would hatch. A temperature of 103° F. (39.4° C.) is usually the highest average running temperature advised. With higher temperatures, abnormal chicks bearing monstrosities of various sorts are likely to be produced. Lippincott (1921) states that when the incubator is run at temperatures between 103° F. (39.4° C.) and 108° F. (42.2° C.), 90% of the embryos have abnormalities in their nervous systems by the 72nd hour. Likewise when the incubator is run at a temperature too low, as between 94° F. (34.4° C.) and 101° F. (38.3° C.), 67% of the embryos have abnormal nervous systems by the 72nd hour. Lamson and Kirkpatrick (1918) place 110° F. (43.3° C.) as the upper thermal limit at which eggs will hatch, but say that at 112° F. (44.4° C.), eggs may be kept for 15 hours at certain stages and still the strongest embryos will hatch. This is, however, approaching the very highest limit at which development will occur, and is, therefore, much too high for practical work in artificial incubation.

In our work we have run a series of experiments with house wrens' eggs at different temperatures to determine the effect on later development (Table XXI). Eggs were taken from the nests when they had been incubated normally for 5 or 7 days and placed in the same temperature apparatus in which we studied the resistance of older birds to high and low body temperatures (Plate III), but it was possible to keep only 2 eggs at each temperature. After an hour they were replaced in the nests and left to the normal care of the adult birds. Two sets of controls were used, 4 eggs left in the nests without disturbance in order to get a check on the normal time of hatching, and 4 eggs kept in the temperature apparatus similarly to those experimented with, but at air temperatures of 99° F. (37.2° C.) and 101° F. (38.3° C.), which approximate normal temperatures in the nest. All of these air temperatures were maintained fairly constant. The actual egg temperature undoubtedly approximated very closely the air temperature. The time of hatching of the eggs in the nests was then noted.

TABLE XXI.—*Effect of Exposure to High Air Temperatures on the Hatching of the Eastern House Wren's Eggs*

Number of Eggs Used	Air Temperature to Which Egg Exposed for One Hour	Number to Hatch	Number Failing to Hatch
4	In Nest (Control)	3	1 (Infertile?)
2	99° F. (37.2° C.)	2	0
2	101° F. (38.3° C.)	2[1]	0
2	106° F. (41.1° C.)	1	1
2	111° F. (43.9° C.)	1	1
2	114° F. (45.6° C.)	0	2
2	116° F. (46.7° C.)	0	2

[1]One pipped, then died.

All of the control eggs, except 1 which was probably infertile, hatched at the normal time, both those left undisturbed in the nest and those that had been placed in the temperature apparatus. This indicates that the disturbance and the handling of the eggs in themselves could be eliminated from the consideration of the results obtained, and any effect could be attributed directly to the high temperature. Of the 2 eggs subjected to 106° F. (41.1° C.), 1 hatched on normal time, the other did not hatch at all. On examination, the embryo was found to have been killed at the time of the experiment. Of the 2 eggs subjected to 111° F. (43.9° C.), 1 hatched at the normal time, the other was found to have been killed at the time of the experiment. Both of the embryos subjected to 114° F. (45.6° C.) and 116° F. (46.7° C.) were found to have been killed at the time of the experiment. The conclusion to be drawn from this is that there is a 50% likelihood that egg embryos partly incubated will survive an hour's subjection to air temperatures of 106° F. (41.1° C.) or 111° F. (43.9° C.), but that they will all be killed at 114° F. (45.6° C.) or 116° F. (46.7° C.). The eggs that hatched did so at the time expected of undisturbed eggs, so that no delay was caused as was the case with eggs subjected to low temperatures, which will be discussed later.

It is interesting that in the case of eggs, young birds, and adults of the house wren, body temperatures between 114° F. (45.6° C.) and 116° F. (46.7° C.) were absolutely fatal. Age seems not to be a factor, but this latter temperature appears to be the upper lethal point for the bird at all stages of development. The amount of variation in this limit is relatively small. Lower temperatures can be endured, but as soon as the body temperature reaches this high point, death is almost certain and usually immediate. That this holds true for the youngest as well as the oldest stages would indicate that some fundamental reactions are disturbed and that these probably lie in the physical or chemical nature of the protoplasm of the cells itself—rather than a possible disturbance in the functioning of some organ, although this may also occur.

RESISTANCE OF EMBRYOS TO LOW TEMPERATURE

Just how low a temperature of the air and egg the embryo in the egg is able to resist was not determined by our laboratory experiments, except that temperatures down to 63° F. (17.2° C.) were readily resisted, although the exposure time was brief. Edwards (1902) found that in eggs of the domestic fowl there may be slight development of the embryo at air temperatures even as low as 68° F. (20.0° C.). The temperature of the egg, as we have shown, closely approximates that of the air. One house wren's nest containing 7 eggs deserted by the adults dropped in air temperature to 52° F. (11.1° C.) on the following night. The eggs, which had 2 days' incubation, were not removed until the following afternoon, when they were placed in an incubator. When opened a few hours later, 5 out of the 7 were still alive. In some embryological work, house wrens' embryos have been removed and kept in saline solution at temperatures below 75° F. (23.9° C.) for more than 7 hours before death resulted. Lamson and Kirkpatrick (1918) state that hens' eggs from strong stock will stand 4 to 5 hours exposure at 50° F. (10.0° C.) after the first 24 hours of incubation. The length of this exposure may be increased without harmful results up to 15 hours on the tenth to twelfth days. After the 17th day, continued exposure at this air temperature for more than 6 hours kills the embryo. Moran (1925) studied the microscopic nature of the contents of fresh hens' eggs as affected by various low temperatures. He measured the actual temperature of the eggs by means of thermocouples. He states in the summary that below 32° F. (0° C.) the eggs quickly lose their fertility and that at approximately 21.2° to 19.4° F. (—6.2° to —7.4° C.) the embryo of the egg immediately dies. He states also that there is an optimum temperature for fresh fertile eggs in the region of 46.4° to 50° F. (8.0° to 10.0° C.), at which temperature they maintain their fertility for the longest space of time. Advisers in poultry production commonly say that fresh eggs to maintain their vitality the longest should be kept at air temperatures around 50° F. (10.0° C.) (Atwood, 1917; Lamson and Kirkpatrick, 1918). Lipschutz and Illanes (1929) found that normal chicks developed after eggs had been exposed to 21.2° to 24.8° F. (—6° to —4° C.), but not to 14.0° F. (—10.5° C.). Dougherty (1926) in extensive experiments with hens' eggs found that exposure of fresh eggs to 28° to 32° F. (—2.2° to 0° C.) for 3 successive nightly periods of 14 hours each plus a continuous period of 38 hours did not result in any significant reduction in the percentage of chicks hatched. However, an exposure to these same temperatures for 4 successive nights plus a continuous period of 38 hours did result in a reduction in the percentage of chicks hatched. All of this evidence tends to show that egg embryos can withstand body temperatures even lower than can nestling birds or adults.

This greater resistance of embryos to low temperature is of significance. If we compare our above given data on the lower lethal body temperatures of adult birds and young birds (about 71° F. [21.7° C.] for adults to 47° F. [8.3° C.] for young nestlings) with this evidence for eggs, we find with increasing age a gradual decrease in resistance. The younger the organism is, the lower the body temperature that can be tolerated without causing death. Likewise the younger an animal is, the more exactly does it react like a cold-blooded animal. Many cold-blooded animals are not killed by low temperature except when their body fluids become frozen, and as these are naturally rich in salts, this point may not be reached for several degrees below the freezing point of water. Living protoplasm that has had most of its water removed can withstand an extremely low temperature. Apparently with the development of a temperature control mechanism for the maintenance of a constant uniform high body temperature, this ability of the protoplasm to resist low temperature has been sacrificed—or, it may be that in the course of evolution the warm-blooded condition developed because the protoplasm lost the ability to withstand low temperature. At any rate, the greater resistance of eggs and young birds to low body temperature is another proof of the fact that, in their ontogenetic development, birds pass from a low cold-blooded to a high warm-blooded state.

A series of experiments was undertaken to ascertain what effect the exposing of house wrens' eggs to low air temperature at different stages of incubation and for different lengths of time would have on their hatching under normal conditions. Eggs at the desired stages were removed from the nest and placed in a room temperature of 60° to 70° F. (15.6° to 21.1° C.) and a humidity between 80% and 90%. Here they were left for the desired interval and then returned to the nest. Note was kept as to whether or not they hatched, and, if so, how long after the control eggs, which had not been removed. The data so far accumulated are not extensive but permit compilation and analyzing in the manner indicated in Table XXII.

In Table XXII the expression "failure to hatch" means that the exposure was a fatal one, and that later examination of the embryo in the egg showed conclusively that no life remained.

TABLE XXII.—*Effect on Hatching of the Exposure of the Eastern House Wren's Eggs for Various Lengths of Time to Air Temperatures of 60° to 70° F. (15.6° to 21.1° C.) and Relative Humidities of 80% to 90%*

Hours Exposure	1 to 8 Days Incubated				11 to 13 Days Incubated			
	Number of Eggs Used	Number That Failed to Hatch	Number That Hatched	Hours Delay in Hatching	Number of Eggs Used	Number That Failed to Hatch	Number That Hatched	Hours Delay in Hatching
3–16	11	1	10	6.9	5	0	5	0
20–48	11	10	1	6.0	5	4	1	36

This examination of the embryos brought out the interesting fact that some embryos that did not hatch were not killed at the time of exposure to the low air temperature but died at some later period. The exposure, therefore, tended to lower the vitality and general resistance of the embryo even when death did not actually take place at the time. This is further brought out by the evident delay of hatching in many instances of embryos which did live. The normal time of hatching is indicated by the control eggs. The number of hours delay in hatching is the number of hours left after the length of exposure has been subtracted from the number of hours intervening between the hatching of the control eggs and those on which the experiment was made. Apparently the subjection of the embryo to a low air temperature even for a relatively brief portion of the incubation period has the effect of greatly slowing the rate of complete development.

Even though the general tendency is that the younger the bird, the lower the temperature it can withstand, eggs in earlier stages of incubation were, on the contrary, more delayed by this exposure than were the later stages. On the eleventh to thirteenth days of incubation, exposure for 16 hours or less to an air temperature of 60° to 70° F. (15.6° to 21.1° C.) did not delay the normal time of hatching after allowing for the time that the eggs were out of the nest. However, it must be remembered that we are not here dealing with resistance to the lethal action of extremely low temperature, as we were above, but with retardation of developmental processes. Exposures of 20 hours or more were fatal at all stages, with 2 exceptions. One egg, kept out of the nest for 24 hours on the eleventh day of incubation, hatched, but not until after a delay of 36 hours. Another egg, kept out for 30 hours on the sixth day of incubation, hatched, and this only 6 hours late. This is the longest time that we have succeeded in exposing any partly incubated egg to low temperature and have it hatch.

This evidence, together with that from the literature, shows that fresh eggs may withstand a lowering of their temperature nearly to freezing for a short period of time; and that partly incubated eggs can withstand lowering of their temperature to a medium degree for as long as 16 hours, but that this may cause a delay, except during very late stages of incubation, in the time of their hatching.

FLUCTUATION OF EGG TEMPERATURE IN THE NEST

After studying the possibilities for the variation of the temperature of the egg without the consequent death of the enclosed embryo, it is important to inquire concerning the normal fluctuations in the temperature of eggs in the nest under natural conditions. By the use of thermocouples this was possible without disturbing the natural behavior of the adult bird. It is well to bear in mind throughout all discussion of work done with the eastern house wren under natural conditions, that we are here dealing with an unusual species of bird—unusual in the sense that it permits maximum disturbance with minimum alteration of normal and natural behavior. We may approach its nests, remove eggs or young, alter the location of nesting boxes, or even shift the nest from one type of box to another, or make drastic changes in other ways, all with the assurance that when we have finished, the adult birds will be back again, at least within 10 minutes, frequently within 2 minutes, and behaving as if nothing had happened. This has been checked over and over again after all sorts of disturbance. However, in studying natural conditions, the nest was disturbed as little as possible. We feel then, that when we say that our results and information are for normal natural conditions, they should be accepted at this value.

In order to obtain the temperature of eggs in the nest, a delicate thermocouple thermometer was thrust into the egg as before, so that in practically all cases the functional tip of the thermocouple lay next to the embryo on the upper side of the egg, without puncturing or injuring the embryo. At the end of the experiment this was always checked by examination for signs of life. The egg so treated was returned and placed in the middle of the set at the bottom of the cavity so as to be in an average position. The thermocouple wires were run from the egg through a small hole made in the bottom of the nest and nest box. This hole was then plugged so that no circulation of air through it was possible. The wires were thence run into a small movable blind immediately back of the box, where the temperature readings were taken. One thread thermocouple was also run across the nest just above the eggs so as to obtain the temperature applied by the sitting bird,

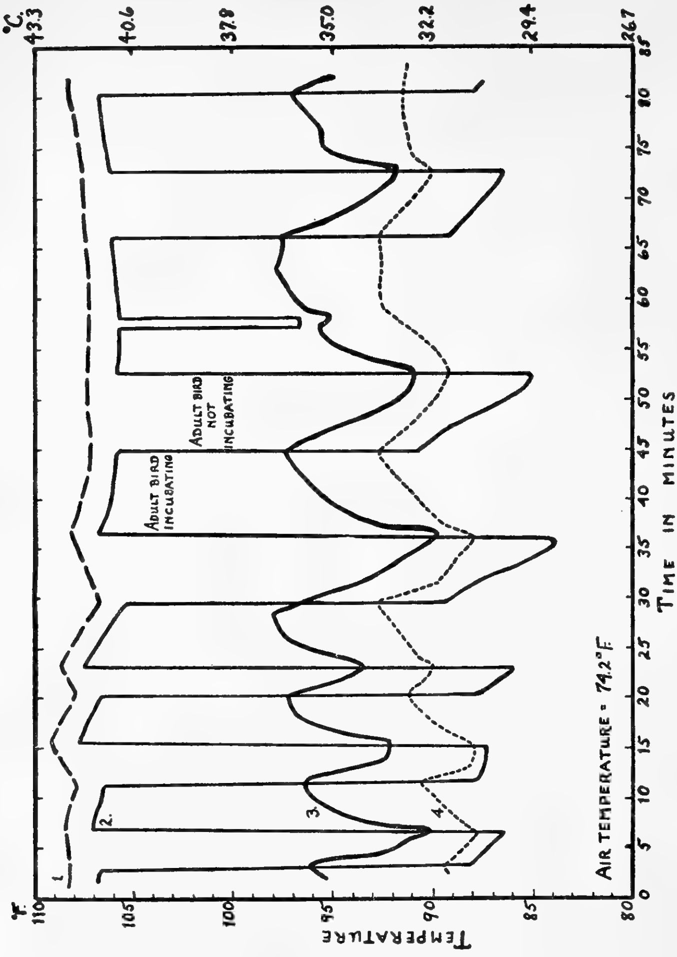


FIGURE 40.—NATURAL FLUCTUATIONS IN TEMPERATURE OF THE EASTERN HOUSE WREN'S EGG UNDER NORMAL CONDITIONS IN THE NEST. 1—Body temperature of adult bird; 2—temperature at top of nest just above egg; 3—egg temperature; 4—temperature in bottom of nest beneath egg.

and another was stretched across the bottom of the nest just under the eggs.

Figure 40 gives very typical results and illustrates well the normal fluctuation in the temperature of eggs in the nest. Here the body temperature of the adult bird is, for comparison, interpolated. During the periods of attentiveness, when the bird is on the nest incubating, her body temperature gradually decreases. The temperature applied to the top surface of the eggs, which is actually the skin temperature of the under surface of the body, decreases at a corresponding rate. However, the temperature applied to the eggs is so much higher than the temperature of the egg itself that this slight reduction does not in the least prevent a gradual rise in the temperature of the egg. If the attentive period is short, that is, less than about 5 to 10 minutes, the egg temperature may rise continuously as long as the bird remains on the nest. When the attentive periods are longer, the egg temperature at length comes to an equilibrium and may then remain more or less constant, which is, for instance, the condition at night. The average maximum egg temperature during the daylight hours, as determined from studies over 26 attentive periods during the day, is 98.5° F. (37.0° C.). The highest single record obtained was 101.5° F. (38.6° C.). When the bird is on the nest for periods shorter than usual, the egg does not warm up as much as when the bird remains longer, but an unusually long incubating period does not necessarily mean an unusually high egg temperature, as already stated. The body temperature of the bird at night and hence the temperature applied to the eggs, is less than during the day, but as the bird then sits more steadily the equilibrium of egg temperature is about the same as during the day. There is enough lag in the response of the egg temperature to variations in applied air temperature so that slight movements or turnings of the bird on the nest do not materially affect the egg's temperature, but when the bird is more uneasy or actually leaves the nest for brief intervals, the temperature of the egg decreases.

During periods of inattentiveness, when the adult bird is entirely away from the nest, the temperature of the egg falls continuously. This fall does not terminate at some equilibrium point as during the periods of attentiveness, but will continue to fall until the general air temperature is reached. This seldom occurs naturally, however, because the return of the bird after a few minutes starts the warming process all over again. The average minimum temperature that the eggs reached during 26 inattentive periods was 93.1° F. (34.0° C.), and the lowest natural record we have is 89.0° F. (31.7° C.), The normal fluctuation of egg temperatures in the nest is, therefore, 5.4° F. (3.0° C.).

The temperature of the air is important also. During cold weather, the egg temperature drops more rapidly than during warm weather. But there is some compensation for this, since attentive periods tend to average longer during cool weather while inattentive periods average shorter. Thus the egg is maintained in about the same range of temperature under all conditions.

TEMPERATURE OF INCUBATION

It is desirable to know the optimum temperature of incubation for comparative purposes among different species of birds in order that correlations with ontogenetic and phylogenetic development, lengths of the incubation period, structure of the nest, habitat of nest, and general nesting behavior of the birds may be made. In the present literature one can find reliable data on this point for only the domestic fowl, other domesticated or semi-domesticated birds, and a few game species. The general opinion is that temperatures ranging from 100° to 103° F. (37.8° to 39.4° C.) are best for these species, particularly the domestic fowl. These temperatures generally refer to those taken by means of a thermometer hung in an artificial incubator with the bulb close to the eggs but not touching them.

Eycleshymer (1907) found with domestic fowls higher egg temperatures in the latter part of the incubation period than in the first part, and attempts to explain this on the basis of a higher body temperature of the incubating hen. According to the careful work of Simpson (1911), no such increase in the body temperature of the incubating hen occurs during the period of incubation. If it be found that the temperature applied to eggs in natural nests increases with the advance of incubation, this will probably be due to the disappearing of feathers on the ventral side of the body, these either being plucked out by the bird or lost in some other manner. With the house wren, these belly and breast feathers are lost during the first egg laying period of the season. Female birds of this species caught before any eggs are laid have the ventral side of the body covered with feathers; other birds caught midway of the egg laying period have already lost many of these feathers; but the skin of the belly does not become entirely bare until about the time that the last egg is laid. As a result, the records that we have obtained show that during the first egg laying period there is a very marked and noticeable increase in temperature applied, but that by the time the last egg is laid there is no further increase. The temperature applied to house wrens' eggs in the nest does not increase during the course of the incubation period (pages 75–76).

One of the principal themes in Bergtold's discussion of the incubation periods in birds (1917) is not correct, since he states that the optimum incubation temperature for any species is the temperature of the incubating parent. The average body temperature of the incubating adult female house wren is 106.3° F. (41.3° C.), but this temperature becomes greatly lowered as the heat is transferred from inside the body to the skin, to the nest, and finally into the egg itself. The embryo itself is not subjected to 106.3° F. (41.3° C.), hence this cannot be its optimum temperature for incubation. The temperature of incubation must be the temperature of the egg itself.

In order to study this problem of the correct incubation temperature, we have, during the last 5 years, been attempting to incubate the eggs of species of wild birds artificially. This we are doing in a small electric incubator with thermostatic control, good ventilation, and with other conditions favorable.

The eggs of certain species, such as those of the domestic pigeon, have been carried through from a fresh condition until the hatching of perfectly normal young birds. This was at a temperature of 102° F. (38.9° C.), as measured by a mercury thermometer suspended from the top, so that the bulb was at the level of the eggs, fairly close, but not touching them.

In addition to the domestic pigeon, we have tried eggs of the eastern house wren, catbird, eastern robin, eastern phoebe, northern crested flycatcher, cedar waxwing, and killdeer, but most of the experimentation has been done with eggs of the eastern house wren. We desired first to ascertain optimum conditions for the incubation of the house wren's eggs, and then to vary different factors in turn, to determine the effect produced on the development of the embryo—all to correlate with the conditions found in the natural nests of the species. Turning of eggs, cooling of eggs daily, ventilation, and humidity are factors involved, in addition to the temperature, so the problem is no small one.

Temperatures of 103° F. (39.4° C.) and 104° F. (40.0° C.) were tried first with no success at all. At a temperature of 102° F.

(38.9° C.), embryos could be started to develop, or if the eggs were put into the incubator after a week or so of natural incubation in the nest, they could be carried through to hatching; but no fresh eggs could be hatched at this temperature, as the embryo invariably died sooner or later. At a temperature of 101° F. (38.3° C.), 1 house wren's egg, placed in the incubator when fresh, hatched 14 days later. Other embryos placed in the incubator at the same time died, although in some instances not until the eggshell was already pipped. When constant temperatures were used at 99.5° F. (37.5° C.), 98.0° F. (36.7° C), and 97.5° F. (36.4° C.), only 1 out of 18 eggs hatched, although several others were brought up to the last day. The best success that we have thus far attained has been by starting the development of embryos with the incubator temperature at 95° F. (35.0° C.), then after a day raising it to 97° F. (36.1° C.), and finally to 100° F. (37.8° C.) for most of the period. The humidity was held at about 64%, the eggs were turned once a day until the last 3 or 4 days, and were cooled about a half hour during each of the first 4 days. Under these conditions approximately half the eggs hatched. A more detailed report on this study of artificial incubation will be presented when the study is completed. All that it is desired to show here is the indication that the house wren's eggs are best developed at a temperature of 100° F. (37.8° C.) or below, rather than above, and that a lower temperature is required during the early part of the incubation in order to begin the development, than is desirable to continue the development through the later stages. In natural nests of the house wren, the first eggs laid receive only a little incubation during the early days, but as succeeding eggs are laid, more and more heat is applied to them daily until the last egg is laid, when normal incubation begins in earnest. The first eggs laid receive a gradual increase in heat daily to initiate their development, but the last egg apparently starts its development at the highest degree.

In the data on egg temperatures given in the preceding pages, the actual internal temperature of the house wren's eggs in the nest was found to fluctuate under natural conditions between the limits of 98.5° F. (37.0° C.) and 93.1° F. (34.0° C.). This temperature is even lower than that at which the eggs were maintained artificially in the incubator. Because of the temperature fluctuation of the house wren's egg in the nest, the difficulty of stating any one degree of temperature as the optimum is obvious. It is quite possible that the house wren's embryo develops best in a fluctuating temperature; and that for normal development such fluctuating temperatures rather than constant ones are required. It is very desirable that more research on this point be conducted.

FLUCTUATION IN TEMPERATURE OF THE NEST

The temperature at the top of a house wren's nest, which for our purpose may be considered the level of the top surface of the eggs, undergoes greater fluctuations than that of any other part (Figure 40). This is, of course, to be expected, since it receives the skin temperature of the female while she is incubating and is the most exposed portion of the nest when she is away. When the female leaves, the temperature at the top of the nest drops precipitously at first. Then, as the temperature of the nest falls, because of a circulation of cold air that comes into the nest box from the outside, the temperature of the top of the nest continues to drop more slowly, the rapidity and extent of the drop being dependent on the difference between the temperature of the nest and the general temperature of the atmosphere. It is, therefore, greatest when the atmospheric temperature is lowest. The decrease in nest temperature gradually slows down as the atmospheric temperature is approached more and more closely, but the return of the adult bird to brood long before it reaches this point checks its downward progress.

The bottom and the back of the nest are the most thermostatic portions. They fluctuate in temperature as the adult bird is on or off, but the fluctuations are much smaller than those of the other portions of the nest. When the bird is sitting on the eggs, the bottom of the nest beneath the eggs receives less heat, of course, than does the top, and so warms up more slowly. However, when the sitting bird leaves, it is the portion of the nest least exposed and so cools off less rapidly than any other part. Also the cluster of eggs not only radiates heat in all directions but forms pockets between the individual eggs where the ready circulation of cold air is greatly hampered. The house wren's nest, in addition, is usually well lined with cast-off chickens' feathers, so that very much of the heat is conserved. The temperature of the bottom, together with the back of the nest, is, therefore, higher than that of any other portions during the time that the adult bird is absent. The egg temperature is usually above the bottom temperature at first, but approaches it more and more closely the longer the incubating bird remains away, and may eventually become lower. If the nest is deserted for a sufficiently long time, all parts of the nest including the eggs settle down to about the same temperature, which is that of the outside air.

The temperature at the side of the nest is obtained by placing thread thermocouples about midway between the level of the top and the lower surfaces of the eggs. The sides of the nest we distinguish from the front and back with reference to the entrance of the nest box. The sides of the nest are rather variable in their fluctuations of temperature, due largely to the different positions assumed by the adult bird as she sits on the eggs; but the bird usually sits facing the front. The temperature of the sides ordinarily averages several degrees below the bottom temperature, but may occasionally fluctuate above the latter. The temperature of the sides rises when the bird is on and falls when she is off, but the extent of the fluctuation is usually not great.

The temperature at the front of the nest is also variable, occasionally being higher than the bottom but usually averaging lower, both when the bird is on and when she is off the nest.

As illustrated in Figure 41 (Table XXIII), after the adult bird has been incubating, the temperature gradients all begin at the top level of the eggs from the skin of the bird and project downward and outward in all directions, and from the bottom to the sides. After the bird is gone, all the gradients begin at the bottom and back of the nest and project upward and around and probably diverge as they get above the nest cavity. This general scheme varies slightly, dependent on the structure and shape of the nest, on the length of time that the adult has been present or away, and also on the position of the bird in the nest, but should hold for average circumstances. The fact that the eggs maintain a higher temperature, at least for a time, than any part of the nest when the adult bird is away means that some heat is continuously being radiated from their surfaces in all directions. This complicates the gradient relations to some extent, particularly the one between

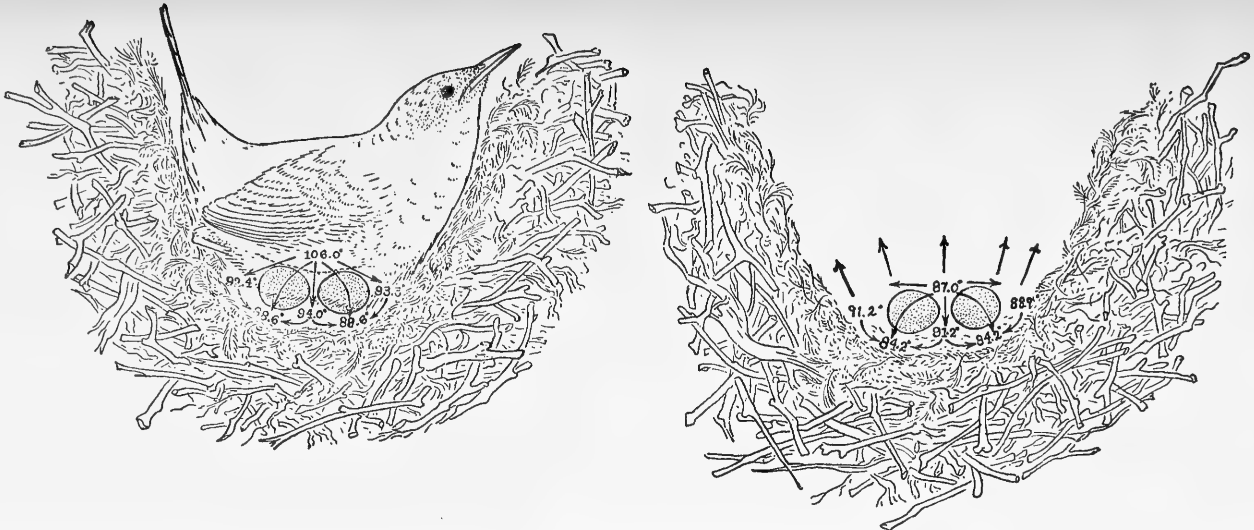


Figure 41.—Temperature Gradients in the Nest of an Eastern House Wren during the Period of Attentiveness when She is on (Left), and during the Period of Inattentiveness when She is off (Right). (*Drawn by Dr. James Manson Valentine.*)

Table XXIII.—*The Temperature of Different Parts of the Nest of the Eastern House Wren, both when the Bird Is Incubating and when It Is off the Nest*

	Top of Nest	Bottom of Nest	Side of Nest	Front of Nest	Back of Nest
Bird on..........	106.0° F. (41.1° C.)	94.0° F. (34.4° C.)	88.6° F. (31.4° C.)	93.3° F. (34.1° C.)	92.4° F. (33.6° C.)
Bird off..........	87.0° F. (30.6° C.)	91.2° F. (32.9° C.)	84.2° F. (29.0° C.)	88.9° F. (31.6° C.)	91.2° F. (32.9° C.)

the bottom of the nest and the top of the eggs. The gradient is probably very slight until the upper level of the eggs is reached and then falls rapidly. These data and averages are for several hours' records at 4 different nests.

The interrelations of nest, air, eggs, skin of bird, and body of bird are thus seen to be complex. Marked variations in any one of them or in the relations of any two of them very probably affect the temperature to which the embryo in the egg is subjected. Since the bird embryos cannot regulate their own temperature, the reason for fluctuations is evident. The embryo to survive and develop must endure these fluctuations. It is probable that during the course of evolution the embryo has not only become adjusted to these conditions but has become so adapted that such conditions are its optimum. The behavior of the adult bird is adjusted to maintain these conditions and to keep them as constant as possible. In different species of birds in this same region (northern Ohio) and in other regions, nest conditions and nesting behavior are different. It is important that these species be studied, not only for comparative purposes of physiology, but also to correlate them with the ecological conditions of their environment.

SUMMARY AND CONCLUSIONS

1. The purpose of these researches was to learn the physiology of bird temperature and the relation and dependency of bird temperature on environmental conditions. Experimental studies under controlled conditions were undertaken to analyze the factors affecting avian temperature, and careful studies were then made of the manner in which these same factors affect the bird under natural conditions. This study is, in part, a contribution to our knowledge of the physiological ecology of birds. (Pages 7–9.)

2. Several passeriform species were studied, but most of the work was performed on the eastern house wren, *Troglodytes aedon aedon,* which is ecologically a typical member of preclimax communities in the Acer-Fagus and Quercus-Castanea Associations of the eastern United States and Canada. (Pages 8–10.)

3. Mercury thermometers were at first employed, but soon found inadequate for the type of investigation in view. Use was then made of copper-constantan thermocouples prepared in different ways for various purposes. Temperatures were determined by both indicator and recording potentiometer pyrometers. (Pages 12–21.)

4. To afford a basis for comparing the influence of other factors, the standard temperature was determined, i.e., the body temperature of birds at standard metabolism. For the eastern house wren, this is 104.4° F. (40.2° C.) in the male and 105.0° F. (40.6° C.) in the female. Standard temperatures determined for 4 other species are approximately similar. (Pages 22–31.)

5. Aside from the standard temperature, which is fairly constant during the daytime, the body temperature normal to the eastern house wren and other passeriform species is characterized by great variableness. (Page 31.)

6. Emotional excitement, through its effect on activity and other functions, tends indirectly to increase the body temperature. The most important single factor causing variations in temperature is muscular activity. An increase in activity is followed im-

mediately by a rise in body temperature, while a decrease in activity is followed by a fall. The maintenance of high temperature is dependent on a constant and adequate supply of food. Starvation causes a drop in body temperature below standard level. (Pages 31–42.)

7. Under experimental conditions, the body temperature of adult birds is normally unaffected by fluctuations in air temperature so long as these fluctuations are not extreme and do not occur too rapidly. Birds are more quickly and seriously affected by a rise in body temperature than by a lowering. The lower and upper lethal limits of body temperature for the adult eastern house wren are 71.0° F. (21.9° C.) and 116.3° F. (46.8° C.), respectively. (Pages 42–50.)

8. Variations in the rate of the respiratory movements of adult birds is probably of significance in temperature regulation. The breathing rate is low at standard temperature. In the male eastern house wren, this average is 112 times a minute, and in the female 92. At lower body temperatures, this rate of breathing increases to 240 times a minute at 100° F. (37.8° C.), then decreases as the body temperature falls. At high body temperatures, the rate also increases, in one instance up to 340 times a minute at 116° F. (46.7° C.). After the upper lethal body temperature is reached, the rate of breathing steadily decreases. (Pages 50–55.)

9. The skin temperature of passeriform birds, as illustrated by the eastern house wren, is lower than that of the body, varies in different parts of the body, and is not in all cases the same in the 2 sexes. The skin temperature of the breast and belly averages 1.3° F. (0.7° C.) lower than that inside the body, and is not affected by differences in air temperature. (Pages 56–61.)

10. During the periods of attentiveness, when the adult female is incubating the eggs, her body temperature is high as she first comes on the nest. It then drops as she settles down and becomes quiet, but rises again before she leaves a few minutes later. During the period of inattentiveness, when the female is away procuring food for herself, her temperature, in general, rises. The average initial body temperature, during a period of attentiveness on the nest, in the case of 12 individuals of 8 passeriform species, was ascertained to be 107.6° F. (42.0° C.); the average highest temperature while on the nest is 108.1° F. (42.3° C.); the lowest

is 106.5° F. (41.4° C.); and the last temperature of the bird before she leaves is 107.2° F. (41.8° C.). The temperature of the female while actually incubating the eggs during the day (attentive periods) averages 107.3° F. (41.8° C.), while her temperature during the short periods of absence (inattentive periods) averages 107.4° F. (41.9° C.). (Pages 64–72.)

11. Considering the daylight period as a whole, the body temperature of female birds of 8 passeriform species averages 107.3° F. (41.8° C.) during the incubation period. At night there is a marked drop in average body temperature to 104.6° F. (40.3° C.). Averaging together day and night records for the entire 24-hour day in proper proportions gives 106.3° F. (41.3° C.) as the average body temperature of female birds during the breeding season. No significant difference in body temperature has been noted between the different passeriform species. (Pages 68–72.)

12. There is occasionally a slight positive correlation discernible between fluctuations of bird temperature and of air temperature from day to day, but such correlations are not always present, and may be indirect through the effect of air temperature on activity. (Pages 72–76.)

13. No rise was noted in the temperature of the sitting female during the period of incubation. (Pages 75–76.)

14. There is a decided and rather abrupt daily rhythm of body temperature in passeriform birds. The average body temperature rises gradually during the morning from the beginning of the day's activities (about 4:45 A. M.) until the maximum is reached during the middle of the day. It decreases again during the late afternoon. When the bird settles on the nest for the night (about 7:45 P. M.), the temperature for a short time thereafter (1.25 hours) falls very rapidly (1.8° F. [1.0° C.]). It then decreases gradually until the minimum is reached about midnight. After that, the body temperature fluctuates more or less until 3:30 A. M. There is then a rapid rise (1.7° F. [0.9° C.]) in the body temperature of the female during the short period (1.25 hours) just before leaving the nest for the first time in the morning. There is considerable variation in the time at which both the maximum and minimum body temperatures are reached. This daily rhythm is explained on the basis of the experimental work reported in the

first part of this paper. Variation in muscular activity at different times of the day is the most important single factor involved. Other related influencing factors are air temperature, the digestion and absorption of food, and mental activity and rest. (Pages 76–91.)

15. There is in 8 species of passeriform female birds on the nest during incubation a daily variation between average extremes of body temperature amounting to 5.3° F. (103.4° to 108.7° F.) or 2.9° C. (39.7° C. to 42.6° C.). The lowest apparently normal body temperature that has been obtained in any of these passeriform birds is 102.0° F. (38.9° C.), while the highest is 112.3° F. (44.6° C.). The greatest possible normal fluctuation in passeriform bird temperature, then, is over 10° F. (5.6° C.). (Pages 88–90.)

16. The daily rhythm in body temperature was experimentally controlled and reversed by appropriately regulating the period of the bird's activity. An anaesthetic used on a bird destroyed the daily rhythm entirely, and body temperatures were maintained constant. This again indicates the importance of muscular exertions in the variability of a bird's temperature. (Pages 91–94.)

17. In birds, as in other animals, two factors are concerned in temperature regulation: the mechanism regulating heat production, and the mechanism regulating heat loss. Muscular activity greatly affects heat production and is very important in causing variations in body temperature. High air temperatures depress, while low temperatures stimulate heat production. Starvation decreases, but food stimulates the amount of heat produced, and so these factors are concerned in regulating body temperature. Aside from a probable nervous control over heat production, a hormonal regulation may also be very important. Because of the covering of feathers, only a little heat is lost through the general body surface. Feathers are of great aid, therefore, in protecting the bird in cold weather. The mechanism whereby heat is dissipated is largely centered in the lungs and air-sacs, and is regulated with the respiration. (Pages 94–104.)

18. Young eastern house wrens are distinctly poikilothermic (cold-blooded) in their temperature reactions. The development of temperature control was determined experimentally to follow the sigmoid growth curve. It is relatively complete when the bird becomes 9 days old. Factors involved in the devel-

opment of this temperature control are increase in total heat production, decrease in proportion of body surface to bulk, development of feathers, development of functioning air-sacs, and development of nervous and hormonal control. (Pages 105–113.)

19. Before the development of a temperature control in the young eastern house wren, the rate of respiratory movements varies directly with the temperature. As soon as temperature control is attained, the rate of respiration varies as in the adult. (Pages 114–117.)

20. Lethal results follow quickly when the body temperature of the young eastern house wren is raised to 115.9° F. (46.6° C.) or above. The degree of body temperature that is lethal is approximately the same for all ages. Excessive heat kills young birds more quickly than does cold. (Pages 117–121.)

21. For the nestling eastern house wren, 10 days or older, a drop in body temperature below 60° F. (15.6° C.) proves fatal. For the house wren before the development of temperature control (up to 9 days of age), the low lethal body temperature is approximately 47.0° F. (8.3° C.). This is produced by an air temperature slightly lower. There is thus with age a decrease in the extent to which body temperature can be lowered without harm. (Pages 121–124.)

22. Before the development of a temperature control, the survival time without food of the nestling eastern house wren is longer at low air temperature than at high air temperature. After the attainment of a temperature control, however, survival time at low air temperature is not so long as at high. (Pages 124–127.)

23. The temperature of young birds in the nest before development of a temperature control varies directly with that of the nest, and fluctuates up and down between the times of brooding and inattentiveness by the adult bird. During the period in the nest there is a gradual rise of body temperature independent of environmental conditions and dependent upon the development of the temperature regulating mechanism. This rise amounts to 0.6° F. (0.3° C.) per day. (Pages 127–132.)

24. Egg temperature under experimental control varies directly and rapidly with air temperature. The temperature of the egg in relation to air temperature increases during the incubation period, due probably to heat generated by the developing embryo. Some

evidence is presented that the eastern house wren's embryos can withstand extreme temperatures from freezing up to 114° F. (45.6° C.). When subjected to low temperatures (60°–70° F. [15.6°–21.1° C.]), embryos at all stages will survive an exposure of as much as 16 hours (in one case 24 hours, in another 30 hours). During the first 8 days of incubation, a delay in hatching of about 6.9 hours was produced by exposure to low air temperatures; but during the latter days of incubation, no delay was produced. (Pages 134–144.)

25. Comparing the resistance of eggs, young birds, and adults to high body temperature, only slight, probably insignificant, differences were found to occur. However, a progressive decrease in endurance to low body temperature occurs with increase of age. (Pages 141, 142.)

26. The temperature of the eastern house wren's egg in the nest was found to fluctuate between the average limits of 98.5° F. (37.0° C.) and 93.1° F. (34.0° C.), the higher temperature occurring when the adult is incubating. The optimum incubation temperature for the eastern house wren is 100° F. (37.8° C.) or below, rather than above. The suggestion is made that probably fluctuating temperature is more favorable for incubation in this species than is constant temperature. (Pages 145–151.)

27. Fluctuations of temperature in the nest were determined to be greatest at the level of the upper surface of the eggs and least at the bottom and back. Gradients extend downward and around the eggs when the adult is incubating and in reverse direction when the adult is absent. (Pages 151–154.)

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INDEX TO VOLUME III

Owing to the nature of the matter in this volume, some of the wording in this index is paraphrased from the actual wording in the text. Page references to authors on the pages of the bibliography are preceded by the abbreviation (bibliog.).

CONTRIBUTIONS FROM
THE BALDWIN BIRD RESEARCH LABORATORY

For convenience in reference and library use there are listed below the published papers from the Baldwin Bird Research Laboratory produced by S. Prentiss Baldwin, his assistants, and collaborators.

Contribution No. 1.—Baldwin, S. Prentiss. **Bird Banding by Means of Systematic Trapping.** Abstract of the Proceedings of the Linnaean Society of New York, No. 31, [for] 1918–1919 [December 23, 1919], pp. 23–56, pls. I–VII. This paper describes the methods and results of the systematic trapping and banding of birds at Cleveland, Ohio, and Thomasville, Georgia. (Reprinted in No. 19.)

Contribution No. 2.—Baldwin, S. Prentiss. **Recent Returns from Trapping and Banding Birds.** The Auk, Vol. XXXVIII, No. 2, April, 1921, pp. 228–237. A report of bird banding at Thomasville, Georgia, and Cleveland, Ohio, during 1919 and 1920.

Contribution No. 3.—Baldwin, S. Prentiss. **The Marriage Relations of the House Wren.** The Auk, Vol. XXXVIII, No. 2, April, 1921, pp. 237–244. Mating habits and genealogy, as learned from banded birds, are here discussed. (Reprinted in No. 19.)

Contribution No. 4.—Baldwin, S. Prentiss. **Adventures in Bird Banding in 1921.** The Auk, Vol. XXXIX, No. 2, April, 1922, pp. 210–224, pls. VIII–IX. Bird banding results in 1921 at Thomasville, Georgia, and Cleveland, Ohio, are here given.

Contribution No. 5.—Talbot, Lester R. **Bird Banding at Thomasville, Georgia, in 1922.** The Auk, Vol. XXXIX, No. 3, July, 1922, pp. 334–350, pls. XV–XVII. Report of Mr. Talbot, who operated the Thomasville bird banding station for Mr. Baldwin in February and March, 1922.

Contribution No. 6.—Musselman, Thomas E. **Bird Banding at Thomasville, Georgia, 1923.** The Auk, Vol. XL, No. 3, July, 1923, pp. 442–452, pls. XXV–XXVII. Report of Mr. Musselman, who operated the Thomasville bird banding station with Mr. Baldwin in February and March, 1923.

Contribution No. 7.—May, John B. **Bird Banding at Thomasville, Georgia, 1924.** The Auk, Vol. XLI, No. 3, July 1924, pp. 451–462, pls. XXVII–XXVIII. Report of Doctor May, who operated the Thomasville bird banding station with Mr. Baldwin from January to April, 1924.

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Contribution No. 9.—Baldwin, S. Prentiss. **History of the Quail Investigation.** The Wilson Bulletin, Vol. XXXVII, No. 2, June, 1925, pp. 98–100.

Contribution No. 10.—Baldwin, S. Prentiss; and Kendeigh, S. Charles. **Attentiveness and Inattentiveness in the Nesting Behavior of the House Wren.** The Auk, Vol. XLIV, No. 2, April, 1927, pp. 206–216, pls. X–XIII. Explains the use of potentiometer and thermocouple in keeping record of nest temperature and movements of female house wren during incubation.

Contribution No. 11.—Boulton, Rudyerd. **Ptilosis of the House Wren.** The Auk, Vol. XLIV, No. 3, July, 1927, 387–414, figs. 1–12. Prepared while Mr. Boulton was acting as assistant at the Baldwin Bird Research Laboratory during the summer of 1926.

Contribution No. 12.—Musselman, Thomas E. **Foot Disease of Chipping Sparrow (Spizella passerina).** The Auk, Vol. XLV, No. 2, April, 1928, pp. 137–147, pl. VII. A study of bird pox, especially as it appears at Thomasville, Georgia.

Contribution No. 13.—Baldwin, S. Prentiss; and Bowen, W. Wedgwood. **Nesting and Local Distribution of the House Wren.** The Auk, Vol. XLV, No. 2, April, 1928, pp. 186–199, figs. 1–5. This paper describes the plan and purposes of the "outfield" work on the house wren at the Baldwin Bird Research Laboratory in 1927.

Contribution No. 14.—Kendeigh, S. Charles; and Baldwin, S. Prentiss. **Development of Temperature Control in Nestling House Wrens.** American Naturalist, Vol. LXII, No. 680, May–June, 1928, pp. 249–278. A study of body temperature and methods of taking body temperature of birds.

Contribution No. 15.—Lincoln, Frederick C. **Bibliography of Bird Banding in America.** The Auk, Vol. XLV, No. 4, Supplement, October, 1928, pp. 1–73. Although this paper was not prepared by a member of the staff of the Baldwin Bird Research Laboratory, it was written at the request of Mr. Baldwin, by Mr. Lincoln, of the United States Biological Survey, by permission of the Biological Survey.

Contribution No. 16.—Baldwin, S. Prentiss. **A Bird Research Laboratory.** Bulletin of the Northeastern Bird Banding Association, Vol. IV, No. 4, October, 1928, pp. 115–120. A description of the organization and purposes of the Baldwin Bird Research Laboratory.

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Contribution No. 20.—Baldwin, S. Prentiss. **"Bird Sanctuary" Suggestions.** Ohio Journal of Science, Vol. XXXI, No. 3, May, 1931, pp. 172–176. Suggestions for the establishment and maintenance of sanctuaries for birds, in parks, estates, cemeteries, and golf grounds.

CONTRIBUTION No. 21.—BALDWIN, S. PRENTISS; AND KENDEIGH, S. CHARLES. **Physiology of the Temperature of Birds.** Scientific Publications of the Cleveland Museum of Natural History, Vol. III, October 15, 1932, pp. 1–196; pls. Frontispiece, I–V; figs. 1–41. A study of the temperature of passeriform birds, adults, nestlings, and eggs.

CONTRIBUTION No. 22.—PATTEN, BRADLEY MERRILL; AND KRAMER, THEODORE C. **A Moving-picture Apparatus for Microscopic Work.** Anatomical Records, Vol. LII, No. 2, March 25, 1932, pp. 169–189. Description of an apparatus for taking motion pictures of microscopic living objects.

CONTRIBUTION No. 23.—KENDEIGH, S. CHARLES. **A Study of Merriam's Temperature Laws.** Wilson Bulletin, Vol. XLIV, No. 3, September 21, 1932, pp. 129–143. A critical examination of the conclusions reached by Dr. C. Hart Merriam in his studies of the laws governing temperature control of the distribution of animals and plants.

CONTRIBUTION No. 24.—BALDWIN, S. PRENTISS; KENDEIGH, S. CHARLES; AND FRANKS, ROSCOE W. **Protect Hawks and Owls in Ohio.** The Ohio Journal of Science, Vol. XXXII, No. 5, September, 1932. Arguments for the protection of all species of hawks and owls.

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