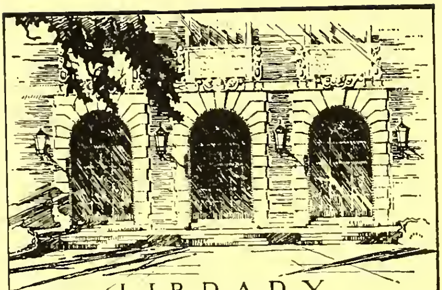

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CONTENTS

Parental Care and Its Evolution in Birds

S. CHARLES KENDEIGH

ILLINOIS BIOLOGICAL MONOGRAPHS: *Volume* XXII, *Nos. 1-3*

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Contents

I. Introduction

The study of bird behavior is of intense interest to a great many people. A few fortunate individuals are able to pursue this study vocationally, but to most it can be no more than a hobby. Bird behavior is complex, varied, and challenging at all seasons of the year. Each season induces some different activity, such as migration, mating, nesting, molting, or flocking. One must go into the out-of-doors to study these activities, but he need not go farther than his backyard to find much of interest and importance. Certain psychological analyses of how and why birds behave as they do and the testing of sense organs, reflexes, and conditioned responses may be done in the laboratory, but it is necessary to study the bird in the field under free, natural conditions to get normal behavior in its full complexity and significance.

Early ornithological studies were concerned principally with making collections of specimens, and with morphology, classification nomenclature, distribution, and economic values. Buffon, of the eighteenth century in Europe, and Audubon, of the early nineteenth century in North America, were unique in opposing this emphasis and in compiling information on the life histories of birds and on natural history in general.

Toward the end of the nineteenth century and into the twentieth century an increasing number of ornithologists gained prominence, in part or in entirety, because of their attention to out-of-door studies of bird behavior. In North America the following names come to mind: William Brewster, Charles Bendire, Frank L. Burns, Frank M. Chapman, Francis H. Herrick, Henry Mousley, Arthur C. Bent, Arthur A. Allen, to mention a few. Bendire (1892) made an outstanding compilation in his *Life histories of North American Birds with special reference to their breeding habits and eggs.* This was the authoritative reference for a long period. In 1919, an ambitious new series was begun under the authorship of A. C. Bent which sought to include information on all phases of the life histories of all species and subspecies of North American birds. During the next thirty years, seventeen volumes appeared and the series is not yet complete. Needless to say, Bent's *Life Histories* have exerted a tremendous influence and stimulus in ornithology.

Jourdain (1930) has traced the early development of interest in attentive behavior in England and Europe. Three outstanding recent compilations of life history information have been *Die Vögel Mitteleuropas*, prepared by Oskar and Magdalena Heinroth between 1924 and 1933; Niethammer's *Handbuch der deutschen Vogelkunde* 1937-38; and *The*

Handbook of British Birds by H. F. Witherby, F. C. R. Jourdain, Norman F. Ticehurst, and Bernard W. Tucker. The five volumes of this last work were issued between 1938 and 1941.

These lengthy compilations are extremely useful in bringing together in one place a vast amount of information on the life histories of every species, in exposing the great vacancies in our knowledge of even the most common species, and serving as a point of departure for the more detailed, specialized approach of modern research.

The modern period of life history studies began about 1920 and is characterized by the emphasis placed on such special concepts as "territory" (H. E. Howard 1920, Nice 1941), "despotism" (Schjelderup-Ebbe 1922), and "releasers" (K. Lorenz 1935, N. Tinbergen 1948); and on the use of such techniques as bird-banding (Baldwin 1919, 1921) and nest activity recording-mechanisms (Bussman 1924, Baldwin and Kendeigh 1927, Kendeigh and Baldwin 1930, Kluijver 1933). In addition, there is an increasing effort being made to uncover the physiological basis or conditioning influence on behavior (Rowan 1931, Kendeigh 1934).

Before the modern period, bird observers had frequently noticed how incubating birds left the nest to get food for themselves and the frequency with which they fed the young in the nest. It required mechanical recording, however, to demonstrate the regularity and length of the periods on and off the nest during the incubation period and to give emphasis to this phase of nesting behavior. Baldwin and Kendeigh (1927) called these intervals spent on and off the nest, periods of attentiveness and inattentiveness respectively, and emphasized the importance of this underlying rhythm throughout the reproductive period. The periods of attentiveness are defined as those intervals of time when a bird of either sex is actually engaged in nesting activities, whether these activities be singing, nest building, incubating, brooding, feeding the young, or scolding at enemies. Periods of inattentiveness alternate with periods of attentiveness and are the time intervals devoted to feeding, bathing, preening, or resting.

Essentially there are two basic drives involved, that of self-maintenance or existence and that of reproduction. Attentive behavior is that phase of life history wherein the interplay between these two drives becomes expressed. Attentive behavior is nearly synonymous with parental care except that it is concerned more with the time relations of nesting activities, while parental care also includes other behavior mechanisms and relationships between adults and young. It is primarily with the timing aspect of parental care that this discussion is concerned.

The house wren, *Troglodytes aedon,* is the species that will receive the most detailed treatment in this study. The field data were collected primarily at the Baldwin Bird Research Laboratory, formerly located at Gates Mills, near Cleveland, Ohio, during the years 1925 to 1939 inclusive. This species had long been the object of concentrated attention at this laboratory; it was numerous, its nests placed in boxes were easily accessible, and considerable information of other kinds had been worked out about it. The study of attentive behavior was part of the program that involved a detailed comprehensive study of the life history of the species.

Many other species were also available on the fifteen acres surrounding the laboratory, so as time was available for observations and as instruments were free for registering nesting activities, attention was paid to the attentive behavior of seventeen other species. Two additional species were studied at the Edmund Niles Huyck Preserve near Rensselaerville, New York.

Altogether, some 127 separate automatic recordings were made of nesting activities of the house wren and some 39 recordings made of other species. Usable data were obtained from some 1,075 daily 24-hour records of the house wren and some 428 daily records of other species. Probably the usable daily records constituted between one-half and two-thirds of all those actually obtained, several of which were imperfect in one way or another.

The analysis of this large amount of data was no small task. The first thing necessary was to convert the graphical record made by the automatic recorders into time intervals that could be compiled, classified in various ways, and from which averages could be made. The writer had the help of several assistants over the years for the handling of the records. Miss Mae McNab was especially helpful in devoting much time to inscribing the hourly intervals on the original records. Student assistants employed under the National Youth Administration during the 1930's were largely responsible for converting the graphical record into numerical tables and computing averages. Most of the computations were made on an automatic calculating instrument and rechecked at least once. The supervision of this statistical work and the final interpretation of the data were, of course, the author's responsibility.

The review of literature bearing on this subject, especially in the summary of attentive behavior in the various families of the birds of the world, was begun shortly after the study was initiated and kept more or less up to date as new publications appeared. Several hundred reference cards accumulated, and all of these references had to be consulted and pertinent data compiled. Student research assistants were helpful in this connection, although when the time came to the actual writing of the summaries, the original literature often had to be consulted a second time. The review of literature was essentially completed by January, 1950, and it is believed that all important publications bearing on attentive behavior up to that date have been consulted and listed in the last section of this paper.

Finally, I wish to acknowledge the indispensable role of Dr. S. Prentiss Baldwin in this study. Without him the study would probably never have been undertaken. Dr. Baldwin organized and financed the Baldwin Bird Research Laboratory, where I was employed as a research associate for the summer periods of fifteen years. He had an unusually open mind for new techniques and ideas in ornithological research, and, what is just as important, was willing to devote time and money for developing them. He had many stimulating new ideas of his own, and his constant day-by-day contact with all phases of the work going on in his laboratory was a continuous source of inspiration and encouragement. Dr. Baldwin died on December 31, 1938. Had he lived, he would certainly have been a joint author of this paper. As it is, this book is contribution No. 44 from his laboratory, the Baldwin Bird Research Laboratory, Gates Mills, Ohio.

I wish also to express my indebtedness to Mrs. Margaret M. Nice, who read the entire manuscript and offered many valuable suggestions and criticisms. Chapter V was read by David Lack, of England, R. E. Moreau, formerly of Tanganyika, South Africa, Alexander F. Skutch, of Central America, and L. E. Richdale, of New Zealand. Each of these men is an authority on the birds in his area and the world-wide coverage attempted in the review of the literature on parental care has benefited from their suggestions, from their citations to literature which I had overlooked, and from unpublished data that they gave me. I hereby acknowledge my obligation to them.

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II. Methods of Study

The extensive development of this study of attentive behavior was made possible by the invention and adaptation of automatic instruments to record all the visits of the parent birds to the nest. These instruments permitted 24-hour daily registration of all trips and the amount of time spent at and away from the nest. Observation alone could not have amassed such a voluminous record without a prodigious expenditure of time and expense.

Mechanical Methods

The automatic recording of animal activity, including that of birds, over long continuous periods has been practiced in the laboratory (Szymanski 1914). Devising equipment for use out-of-doors presents special difficulties, as it is highly desirable that the bird or animal be interfered with as little as possible and that it lead an entirely normal and natural existence. However, a number of methods have now been devised or adapted for the automatic recording of trips made by birds to and from their nests. These may be conveniently classified under three different main types of equipment. The thermocouple and potentiometer, and the itograph constituted the equipment used in the accumulation of the original data of this report.

Thermocouple and potentiometer. Baldwin and Kendeigh described in 1927 the adaptation of the thermocouple and recording potentiometer to registering nesting activities. Details need not be repeated except briefly to explain that the thermocouple is an electric circuit made of two different metals, in this case copper and constantan, with a recording potentiometer included in the circuit. The apparatus records temperature. When heat is applied to one junction of the thermocouple and the other junction is held constant, there is a difference in electrical potential established with the resulting flow of a minute amount of electric current. The potentiometer contains a sensitive galvanometer, a slide wire, and a system of levers, cams, writing device, etc., to measure the flow of electric current and record automatically in degrees of temperature the amount of heat applied at the warm junction. The apparatus used was purchased from The Leeds and Northrup Company, Philadelphia, Pennsylvania.

The warm junction of the circuit may be carried as far as 200 feet from the potentiometer and placed so as to record the nest temperature. The end of the warm junction is made in the form of a thin, flexible wire which is threaded through the nest from one side to the other in such a way that the junction itself lies just above or on the eggs. The visits of the adult are recorded when the incubating bird settles on the eggs and applies heat to them. The departure is instantaneously recorded by a drop in temperature.

The thermocouple will register a visit only when the bird applies heat to the eggs. It will not record a visit to the rim of the nest only, nor the time spent at the nest when not actually incubating. Obviously this method is useful only during the incubation and brooding periods. The thermocouple can be placed in almost any kind of a nest with little difficulty. Recording potentiometers require electric current, however, and this is a limiting factor. Indicator potentiometers, operated manually, are available that do not require electric current, but there is little advantage in their use over observation.

Perch contacts and electromagnet. The *itograph* was first described in 1930 (Kendeigh and Baldwin). It is based on quite a different principle from the thermocouple and does not register temperature (Fig. 1). The necessary parts are a double set of perch contacts at the entrance of the nest, a set of dry-cell batteries, an electromagnet with a pen attachment, and some means of unwinding a roll of paper at a uniform rate. Two types of itographs were used in this study: a multiple type, which had seven electromagnets and pens recording simultaneously on a wide strip of paper that was unrolled by an electric motor in the laboratory; and a portable type, which had a single electromagnet that registered on a narrow strip of paper, unwound by a 48-hour clock, and did not require connection to an electric current. It is possible to make an efficient portable itograph using a doorbell for the electromagnet and an alarm clock to unwind the paper (Hann 1937). The portable itograph is light in weight and may be used almost anywhere in the field. The itograph records all trips to the nest; it will therefore record nest building and feeding the young as well as incubation. The total time at the nest is registered, not just the time on the eggs.

The portion of the setup requiring special ingenuity in adapting to the nest location is the double-perch arrangement. Two perches instead of one are used so that the record will show whether the bird is entering or leaving the nest. The two perches are balanced on a central pivot with springs so that the electric circuit to the electromagnet is closed only when the perch is pressed down. On entering the nest, the bird will press the outer perch down first, then the inner perch. This will swing the pen attached to the electromagnet first to the right, then to the left. On leaving the nest, the perches are pressed down in the reverse order, and the pen will swing first to the left and then to the right.

Three sets of perches have so far been devised, as shown in figure 1.

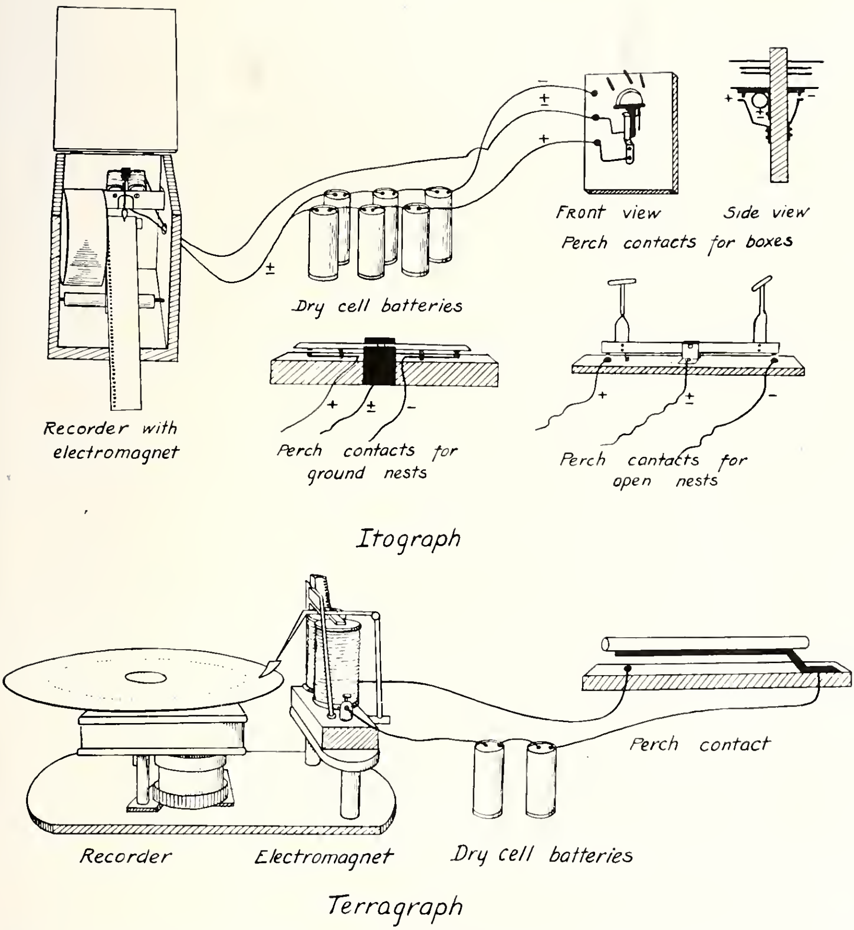

FIG. 1. Apparatus for the automatic recording of trips made by adult birds to their nest. Both the itograph and terragraph use an electromagnet with a pen attachment which writes on paper moved at a constant rate by a clock. The itograph uses a double-perch arrangement that may be adapted to different nest sites and which distinguishes between the arrival and departure of the bird at the nest by the direction in which the pen is moved on the paper. The terragraph uses only a single contact at the nest.

For such birds as house wrens that nest in boxes, the adaptation is fairly simple with one perch just outside and the other just inside the small hole through which the birds must enter and leave the nesting cavity. With open nests, it is necessary to enclose all approaches to the nest except one, and then build a short tunnel on that one side in which to place the double perch. The enclosure is made of wire-mesh hardware cloth. The perches may be varied in size to fit the bird. The third type of perch has each of the two sections separately hinged in the middle and is made low and flat so that it can be partly buried in the bottom of a kingfisher's nesting tunnel. For a comparison of data obtained during the incubation period from the itograph and the temperature-recorder, see pp. 26-27.

The *terragraph* is also an electromagnetic instrument and was invented by a German, Count von Hegendorf, for studying the habits of foxes and badgers. It was first applied to bird activities by Bussman (1924, 1933).

The apparatus consists of a clock with a horizontal disk attachment 19 cm. in diameter which makes one revolution with the clock in each twenty-four hours. On this disk is placed a paper dial-plate marked with hours and half-hours with a carbon paper on top, both being held in place by a tin disk 15 cm. in diameter, which is tightened by means of a central nut.

A telegraph magnet with a pencil attachment is stationed near the disk. When the circuit is made, the pencil presses on the carbon paper, making a short line 4 mm. in length on the paper disk beneath.

The contact at the nest consists of two small pieces of wood fastened together at one end by a flat steel spring (Fig. 1). This contact is placed in circuit by means of insulated copper wire with two pocket batteries and the telegraph magnet, so that when a bird alights on the contact the magnet records on the paper disk.

This instrument is adapted primarily for recording the rate of feeding the young in the nest, and several sets of data for different species are given. A single mark is made in the record for each feeding trip as the bird stands on the perch during the feeding process. The instrument is less useful for recording attentive behavior during incubation, as there is no distinction made in the marks to indicate whether the bird is coming to or leaving the nest or whether the bird alights on the perch and then immediately leaves. The most important difference between the itograph and the terragraph is that the itograph does record the direction of movement with its two marks.

Kluijver (1933) used a mechanical recording apparatus which he called the *aphisigraph,* in his intensive study of the starling and later of the great tit (1950). The perch contact appears very similar to that used with Bussman's terragraph. It was placed directly beneath the entrance to the nest cavity and recorded only the entrance of the bird to its nest. There was a second hole on the side of the box through which the bird left. Trap arrangements prevented the bird's going in or out in the wrong direction. Ruiter (1941) also used an aphisigraph for measuring the rate of feeding of young European redstarts.

Schantz (1939) used an electrical apparatus to announce or record the arrival of robins at their nest. He does not describe the details of his setup but states that it was impossible for the adults to come to the nest without ringing an electric bell or making a recording on paper tape.

The mechanical registration of visits by the willow warbler to its nest made by Kuusisto (1941) utilized an electromagnet and a pen writing on paper unrolled at a uniform rate by a clock and a system of weights. He had two types of contacts at the nest. A thermo-contact was a glass tube containing mercury with one end expanded like a thermometer. Two platinum points were inserted in the tube so that, when the bird applied heat on the nest, the expansion of mercury closed the circuit. This contact was usable only when the bird was incubating or brooding. It had certain disadvantages in that an egg would occasionally get against the contact and insulate it against the heat of the incubating parent, and in that one minute was required to warm the mercury sufficiently to close the circuit. Kuusisto's pressure contact was in the form of a cradle or seesaw that closed a circuit momentarily when the bird settled in the nest and again on leaving but did not distinguish between entrance and exit. Koskimies (1950) used a modification of this apparatus in his study of the swift, *Apus* (*Micropus*) *apus*.

Marples and Gurr (1943) also used a mercury contact at the perch, but the closure of the circuit did not depend on a change in temperature. The perch was similar to that used by Bussman, but the contact on the lower half of the perch was a small cup of mercury into which a small wire projecting from the upper half would dip when the perch was pressed down by the weight of the bird. The two halves of the perch were hinged at one end, and the upper half was supported on the lower half at the other end by a spring adapted to the weight of the bird. The recording mechanism differed in the use of a sharp-pointed lever which was activated by an electromagnet to scratch a mark on the smoked drum of a kymograph.

Nohring (1943) does not describe the self-recording device that he used at one nest of the pied flycatcher, but apparently it included a nest box constructed with a double floor, the upper one supported by a spring which carried the weight of the nest and made a contact when the bird entered.

Pullen (1946) installed an electric recorder at the nest box of a blue tit which was operated by a very sensitive switch fitted in the entrance, so arranged that passage of a bird, either in or out, was recorded as a spot on a moving strip of paper. Gibb (1950) used a trigger at the entrance to a nest of the great tit and an automatic counter of some sort which is not described.

Photoelectric cell. An entirely different principle was used by Yates (1942) in his recording of the visits of a house wren to its nest. ". . . a photoelectric cell with a suitable six-volt lamp was installed and concealed in such a manner that the wren had to cut the beam on each trip she made for food. This interruption operated a relay connected with an electrically-actuated counter." This equipment would seem to have great possibilities, especially if it were connected with a recorder rather than a counter, but it has not been used extensively.

Observational Methods

Although there are many advantages in using mechanical recording of nesting activities, direct observations should never be dispensed with. Much can be learned through observations that cannot be recorded automatically. The part played by each sex must be determined by observation, and also the number of young fed per visit to the nest. Other behaviorisms associated with attentiveness need description, such as the ceremony of nest relief, turning of eggs, sanitation, kind and amount of food brought to young on each visit, feeding of incubating bird by its mate, associated songs and call-notes, and similar items. Furthermore, direct observations should always be made to check the accuracy of automatically recording devices. Instrumental technique requires constant attention, adjustment, and checking; and the more the results obtained from it can be verified by observation, the more reliable and satisfactory they become. Birds often make unexpected movements or have exceptional activities and, unless these can be checked through observation, the interpretation of the record obtained from the apparatus will be faulty.

Instrumental techniques have not yet been designed which are suitable for all species of birds, although the fabrication of such equipment is a challenge to research workers interested in the quantitative side of ornithology. This means that observational methods must be used entirely if information on some species is to be secured. Further, it is not always convenient or practicable to take apparatus into distant or less accessible locations.

Blinds are often useful to enable the observer to be closer to the nest and observe activities in greater detail. Herrick (1901) long ago described the use of blinds, and various types of blinds have been employed since, both for close observations of nest life and for photography. Very often, however, one does not need to use blinds but may obtain all the information he requires by sitting quietly at a distance and taking his observations through a high-powered field glass.

All-day observations are very desirable, even if they can be carried out only at intervals. As will be repeatedly shown later (Figs. 9-14), the rate of activities at the nest varies greatly from hour to hour during the day. Comparison of rates of attentiveness at different nests or by different observations on different species is not trustworthy if the information is obtained at different times of day. All-day observations take in all these hourly variations, give a more complete record of the species' behavior, and make comparisons more reliable. Usually, all-day observations require the cooperation of two or more observers relieving each other at intervals. R. E. Moreau was able to employ natives in Tanganyika, Africa, to obtain observations over long continuous periods of time. The long hours of observation by Otto Steinfatt at the nests of many species are also noteworthy. In selecting the particular days for making all-day observations, one should keep in mind that the rate of nest building activity may decline greatly after the first day; that the amount of attentiveness usually increases day by day during the egg-laying period; that the rate of attentiveness is fairly constant throughout the incubation period except for the first and last days and as modified by pronounced changes in temperature; that the amount of brooding after the young hatch progressively declines after the first two or three days; and that the rate of feeding increases as the young birds get older.

Often, it is not possible or convenient to take all-day observations. Perhaps only a few hours are available. In choosing the time of day for taking these observations, the usual daily rhythm of bird activities should be kept in mind. Often the activity of the bird is unusually great or unusually low or modified in some way during the first hour or two in early morning. It is well to avoid these hours if more nearly average rates are desired. Normally, however, maximum activity occurs at some early hour and then declines steadily to late morning or midday. During the afternoon, activity is usually minimum but rises again in late afternoon or evening. Probably the best time for observations of a few hours only and for getting nearly average rates is between 0600 and 1200 hours. The midday recession in the rate of the bird's activity is less pronounced or may actually be eliminated on cool days, so that similar data may be obtained at almost any hour. On the other hand, activity may become reduced on hot days. All of these variables need to be considered in evaluating data and making comparisons. The description of the conditions and circumstances under which the observations are made should be as complete as possible in the presentation of the data.

Presentation and Evaluation of Data

Pitelka (1941) and Moreau and Pitelka (1943) have discussed the proper presentation of attentive data. One important point emphasized is that the data should be presented in table form. Details and important information are often lost or obscure if given in the text of a publication. Graphs may supplement the tables but should never replace them, as it is very difficult for the reader to compile statistics from a graph. Furthermore, a certain amount of condensing and averaging of the data by the author is desirable. The reader quickly becomes confused and discouraged when he is required to work through the raw data as it comes from the record or directly from observations.

Desirable information that should be presented includes the stage of the nesting cycle, number and age of young, which sex of adult is active or whether both are, length of record, time of day, and weather (especially temperature). Data should be given for each sex on the average length of the attentive and inattentive periods. It is not sufficient merely to state the percentage of time the adult birds are attentive, as the length of the attentive and inattentive periods cannot be computed from this information. However, if the length of the attentive and inattentive periods are known, the percentage of time that the bird is attentive can be easily calculated, as can also the number of periods per hour. When both sexes incubate, the attentive and inattentive periods are often of equal length as one bird is on while the other is off. When neither sex is on the eggs between exchanges, these average intervals should be added to the inattentive period. If there is a ceremony at nest relief, this should be described; also call-notes or other behaviorisms associated with attentive behavior.

In respect to feeding the young, it is always desirable to know the average number of trips to the nest by each sex per hour. It is not sufficient to know only the average interval between visits. One cannot compute the number of visits per hour from the average interval unless he also knows the average duration of the visits. This knowledge is desirable, but very often it is not given in the published reports of observers. Sometimes the feeding rate is stated on the basis of an entire day, especially when comparative data are available for the whole growth period. In these cases, the number of hours of feeding per day should also be given so that the hourly rate can be calculated. The assumption is usually made that young are fed on every visit, but this is not always the case. It is desirable to know the average number of young fed on each visit, and this may vary with the age of the young. Additional points worth recording are amount of food given per feeding, amount of brooding, and nest sanitation.

Periods of attentiveness and inattentiveness can be determined as long as the young are regularly brooded. However, with feeding only, they are usually difficult to distinguish, especially if the feeding rate is fast, although close study indicates that they still exist. Probably the analysis of these periods should be based principally on the incubation period.

Attentive behavior is usually quite variable. It is worth while to have some idea of the extent of this variability. This would be best shown by the standard deviation and coefficient of variation, but these calculations are long and tedious and may not always be practicable. They will not be employed in this study. As an alternative a statement of extreme values has some usefulness.

Any reliable information, however scant, on the attentive behavior of rare species is worth while. On common species a study of attentive behavior should be based on more extensive data. Moreau and Pitelka (1943) seem to agree that, with exceptions, the minimum period of continuous observation within any one day should be five hours. Actually no such general statement is justifiable. In many orders below the Passeriformes, a single attentive period during incubation or a single inattentive period between consecutive feedings of the young may be much longer than this. With such species, one needs to keep continuous records at nests, either by observation or mechanical instruments, for days at a time. But with species that have a fast attentive rhythm, even two or three hours of observations are of value. Such observations should be repeated, however, at the same time of day throughout the nesting cycle to show changes with the stage of incubation or growth of young, and should be repeated at various times on certain days to show changes in the daily rhythm.

The daily rhythm in attentive behavior is conveniently shown during the incubation period by the number of minutes each hour spent at the nest, or it may be shown by the percentage of time spent in attentiveness. During the feeding of the young, the number of trips to the nest per hour is the most obvious method of presentation. We prefer to consider the hour as extending from one-half hour mark to the next rather than from the beginning of the hour to its end. This permits tabulating and graphing the data on the even hour rather than on the half-hour.

An important aspect of attentive behavior is the activity of the birds at night, especially in regard to which sex incubates or broods, how soon the adult starts spending the night on the eggs as they are being laid, how late during the growth of the young she continues to brood, and whether or not the adult leaves the nest at night or shows other restlessness. In this connection it is desirable to know for each sex the exact time in relation to sunset and sunrise that the night period begins and ends.

III. Attentive Behavior of the House Wren

Since more information is available on the attentive behavior of the house wren, *Troglodytes aedon,* than on any other species, the concept will be treated extensively in this species before comparisons are made with other forms.

Territorial Activities of the Male at the Nest Site

Since wrens nest in natural cavities or prefer boxes when they are available, recording of their activities at the nest site is obtainable with the itograph. A part of the procedure in establishing territories, along with singing and fighting, is the finding and holding of anywhere between one and seven nest sites. The location of these nest sites helps to outline the territory, and their possession is indicated by the insertion of sticks, spider nests, and other materials that make up the nest foundation. The male may visit all of his boxes each day. Neglecting to do so permits the intrusion of other males and the loss of this portion of his territory. The intruder may be challenged, but sometimes he is not. Usually, the male is more active at some one preferred box than at others, but the female, when she comes, may choose some other box for her nesting than the one preferred by the male.

The need for regular attendance at all boxes in a male's territory is shown in the accounts of territories 153 and 154. The complete history of these territories, as well as others listed by number in this paper, may be found in Kendeigh (1941c). Male, L24956 was forced to care for the young alone when the female deserted on June 15. This he did successfully, and the young left on June 25 and wandered outside the territorial boundaries with the male attending them. This exposed his territory to invasion by male 34-86085 from the adjacent territory. The itograph shows that a bird, probably this invading male, made 49 visits to the box on June 26. On June 27, the owner returned and attempted to defend his possessions, but he was distracted by the need to feed his young, and he lost in the competition. Altogether, 238 trips to the box were made on this day by the two males. There was no disturbance of the nest structure nor were there additions made to it; the males simply went in and out at frequent intervals.

In repossessing a nest box that has already been used, the male removes the nest lining that the previous female inserted and completely cleans out the nest cavity. Then, when he obtains a new mate or the same mate a second time, she inserts fresh nest lining. The male ordinarily tears out the old nest lining with considerable energy and gusto, singing vigorously. Usually two days are used for this task, but it may extend over four days. The average of eight records on different males gives an average of 113 trips to the nest each day.

Ordinary activity at a box to insure its continued possession is not in-

TABLE 1A. Activity of male house wrens alone at the nest box.

Band number	New (N) or return (R)	Year	Territory	Box	First date	*Ordinary activity* Number of days record	Average number of trips per day	Extremes
A38398	R	1930	98	51	June 23	7	22	4–67
A38398	R	1930	98	51	July 12	6	25	12–42
A94242	N	1927	63	6	...	...	...	...
A94249	R	1928	75	11	June 1	6	42	9–87
B97018	N	1929	90	9	June 16	13	24	3–45
B97018	N	1929	90	9	July 7	6	5	3–13
B97018	N	1929	90	49	July 2	17	12	2–35
C68252	R	1931	111	74	July 11	7	52	1–148
C68252	R	1932	122	53	July 12	3	19	6–26
Unknown	N	1932	123	10	July 8	6	59	14–133
C68800	N	1930	99	10	June 22	8	50	31–127
C68800	N	1930	99	10	July 11	4	10	6–13
Unknown	N	1930	103	68	June 22	6	43	19–70
C68801	R	1931	106	10	June 12	11	64	5–178
C68801	R	1931	106	30	June 19	5	57	12–154
C68801	R	1931	106	25	June 25	7	34	4–184
C68910	R	1931	105	3A	July 11	6	44	3–81
C68910	R	1931	105	10	July 25	2	7	1–13
C68910	R	1933	129	49	June 28	11	29	0–218
C68911	N	1930	96	25	July 20	6	2	1–9
F45763	N	1932	121	49	June 30	3	30	23–36
F45946	N	1932	117	10	June 18	3	36	6–91
F45946	N	1932	117	25	July 10	4	8	5–15
H18580	N	1933	126	10	July 2	8	28	9–76
H18582	N	1933	128	25	June 24	8	22	3–98
H18600	R	1934	141	25	July 12	18	12	1–25
L24956	N	1934	139	10	June 9	5	30	12–63
L24993	N	1934	140	10	June 17	4	60	33–106
35-13634	N	1936	164	53	June 6	8	14	0–77
35-13634	N	1936	164	53	July 3	14	10	0–39
35-13634	N	1936	164	49	July 4	13	8	0–22

Table 1B. Activity of male house wrens alone at the nest box.

Band number	First date	Number of days record	Average number of trips per day	*Removing nest lining* Extremes	Attentive periods recorded	Attentive periods (min.)	Inattentive periods (min.)
A38398	July 9	1	167	. . .	43	5.4	6.5
A94242	June 19	1	86	. . .			
A94249	May 30	2	112	95–129	10	9.0	10.6
B97018	July 13	4	75	36–107	23	9.0	14.6
C68252	July 14	1	65	. . .	18	3.7	43.8
F45763	June 28	2	81	79–83	33	4.8	14.7
H18580	June 30	2	196	146–245			
H18582	June 30	2	121	75–167	21	4.8	34.3

tense. An average of 30 records on 18 different males gives 29 visits per day (Table 1), but the number is variable. This average may be somewhat high, as itograph connections were not often made to a box where there was evidently little or no activity. When the male is busy carrying in sticks or is excited by competition and singing, the number of trips to the box may exceed 100. At other times, days may be skipped with no visits or only a very few. Sticks may or may not be taken to the nests on these infrequent visits, and it is not practicable to divide the activity of the male during this period on the basis of whether or not additions of nest material are made.

There is a tendency for return males that nested the preceding year to be more active than new birds nesting for the first time. The number of trips to the box per day, however, is only 34 and 25, respectively, and, with the variability noticeable, this difference is probably not very significant.

Itograph records were simultaneously obtained in three instances at two boxes in the territory of a single male. With B97018 in territory 90, the male averaged 5 visits per day at one box and 12 at another. Male C68801, in territory 106, averaged 64 visits at one box and nearly the same, 57, at another. Likewise, with 35-13634 in territory 164, the average numbers of trips to each of two boxes were 10 and 8. In territory 117, male F45946, had a female with a nest in box 26 and averaged only 8 trips per day to his former nest site at box 25.

The males may possibly be more active in May in establishing possession of new nest sites upon their arrival from the south than they are in preparation for second nestings in late June and July. Unfortunately, no quantitative data are available for May. However, during the first two weeks of June there is no significant variation from the general average for June and July.

The arrival of a new female to inspect a box and for mating purposes is a stimulant to the male for increased activity. For instance, male H18600 in territory 141 averaged 12 visits to his box in over 18 days, but on June 20 a female was observed in his territory in the early morning and there is a record of 44 trips for the day. Perhaps the female was responsible for the recording of a half dozen of these trips, but the male's excitement was evidenced by increased activity at the box during the rest of the day, after the female had gone elsewhere.

A similar record is that of the male in territory 90. From June 16 to 29, when the male was alone, he averaged 24 visits per day to this box, but with a new female nearby the trips recorded to this box for the insertion of more sticks averaged 125 on June 30 and July 1. The female may have accounted for some of these recordings, although she did not insert nest lining until July 2 and 3. She deserted without laying any eggs, after which the male averaged only 5 trips to the box per day.

In territory 111, male C68252 was very actively singing on July 12 and made 148 trips to the box. The next day a female inspected the box but did not stay. There is a registration of only 56 trips this day, and two days later the number dwindled to six. On July 18 a female came and accepted him and his box, and 129 trips were made by the two birds to the box.

The activity of bachelor males follows the general pattern of periods of attentiveness alternating with periods of inattentiveness, although it is not often practicable to analyze the length of these periods from the itograph record. The males do not regularly enter the box at the beginning and end of each period, and much of their activity during an attentive period is away from the box. When the male is removing nest lining, however, he often devotes his full attention, sometimes even to cessation of singing, so that some idea of the length of his periods may be obtained. The length of these attentive periods varies considerably, but the average for six males when most active at this task is approximately 6 minutes (Table 1B) with intervening inattentive periods of 20 minutes. One extreme in activity is the male in territory 98 having attentive periods averaging 5.4 minutes spaced only 6.5 minutes apart. This male entered the box 167 times during the day, or about 4 times each attentive period. But in certain attentive periods, males may go in and out of the box many times as often. The other extreme is shown by the male in territory 122 whose attentive periods at the box averaged only 3.7 minutes and were nearly three-quarters of an hour apart. He doubtless had other attentive periods devoted to singing or other activities, during which he did not visit the box at all. Observations of three unmated males around their nest gave an average of 7 minutes for 12 attentive periods devoted entirely to singing, with inattentive periods averaging 6 minutes. A few observations indicate that during an attentive period the intensity of singing starts at a low level, rises to a maximum near the middle, then decreases toward the end. Even when the male is disturbed, he scolds only for intervals, between which he drops to the ground to eat.

Nest Building by the Female

When the female accepts a male and a nest site, she takes primary responsibility for completing the nest. If the nest foundation of sticks is not satisfactory, she will carry in more sticks, and the male will aid her. Herschler (1919) observed a pair carrying in sticks and straw at the rate of five to six times a minute. This joint action is rarely necessary, as the female ordinarily begins insertion of the nest lining immediately, regardless of the size of the nest foundation, and in this the male does not aid. Although the male may accompany the female on her trips back and forth and may occasionally alight on the outer perch of the box, he seldom enters the box after the female arrives, until the young hatch. The record of the itograph during this period is primarily that of the female. The record for box 6 in territory 63 is somewhat unusual in showing 86 visits per day into the box, presumably by the female alone, and 59 contacts per day on the outer perch only, perhaps principally by the male. The data presented in Table 2 is therefore mainly the record of the female's activities.

The average of 13 records over a total of 29 days is 118 trips into the box per day by the female. Observation indicates that the female usually inserts material into the nest lining on each trip, although this is not invariable. Two or three days are normally involved in this task, but sometimes nest lining continues to be added during egg-laying. The average rate of trips per day, from the insertion of the first lining to the laying of the first egg, does not give the true picture of the female's behavior as there is a progressive change in rate from day to day. The record for the female in territory 112 is more representative. The number of trips per day varied over four days as follows: 165, 133, 33, 47. The nest lining was virtually completed during the first two days after mating was consummated, after which there was a period of comparative rest until the first egg was laid. The figures given for the maximum number of visits per day (average maximum: 170) more nearly indicates the rate during actual nest building, and this at times may exceed 300 trips per day. The data on minimum number of visits per day (average minimum: 68) are usually for the interval between the near completion of the nest lining and the laying of the first egg.

Periods of attentiveness and inattentiveness are sometimes evident in the records, but the female may not spend her entire attentive periods at nest building and doubtless may often not visit the box at all during periods of time between active feeding, so the data in this regard are not satisfactory. In two records where an attempt was made to measure the attentive periods they averaged 6.9 and 9.4 minutes, with long inter-

Table 2. Nest building by the female.

Band number	New (N) or return (R)	Year	Territory	Box	First date	Number of days	*Number of trips per day into box* Average	Maximum	Minimum
A94248	N	1927	63	6	June 20	2	86	98	75
B5640	R	1931	112	80A	July 4	4	94	165	33
B45348	N	1928	78	51	June 27	1	104	...	...
B45348	R	1929	90	9	July 3	1	184	...	...
C68253	N	1930	96	25	June 13	2	76	107	44
Unknown	...	1930	98	51	July 11	1	132	...	...
Unknown	...	1931	111	74	July 18	3	80	129	17
C94219	R	1932	120	53	June 5	2	75	97	52
Unknown	...	1931	123	10	July 19	3	72	80	65
L24101	R	1934	146	49	June 23	3	197	294	126
L24987	N	1934	140	10	June 22	2	207	276	138
34-4445	N	1935	154	25	July 4	3	73	116	49
35-13635	N	1936	164	49	May 27	2	159	336	83

vals between. When the bird is very active, however, as the female in territory 164 on May 27, her attentive periods averaged 7 minutes and her inattentive periods only 10 minutes. The next day, with most of the lining in, her attentive periods averaged 15.2 minutes and the intervening periods 44.5 minutes. Probably the record obtained for this female on May 27 represents approximately the true proportions of these periods during the active nest building phase.

The Egg-Laying Period

During the period of forming the set with the laying of one egg each day, the true incubation behavior becomes established. The development of this behavior is a gradual one with progressive changes from day to day, so that averages and comparison of data from different females can be made only for the corresponding days. The egg is usually laid during the first or second attentive period after leaving the box in the morning — not just before leaving the nest in the morning as is the case in the great tit, *Parus major* (Kluijver 1950).

House wrens lay sets varying in size from three to nine eggs, but five- or six-egg sets are the most numerous. Elsewhere (Kendeigh 1941b) we found that high air temperatures inhibit the laying of large sets while low temperatures stimulate it. Air temperatures for the period 48 to 24 hours before the egg is to be laid appeared critical as to whether or not the egg appeared—this being the presumed period of rapid increase in size of the egg cell, just preceding passage from the ovary into the oviduct. To determine if there were any behavior factors associated with these environmental-physiological relations affecting the size of the egg set, separate analyses were made of activity associated with five-egg, six-egg, and seven-egg sets.

After the formation of a nest cavity and the laying of eggs, the thermocouple and potentiometer may be used. Several such records were obtained which have the special advantage of showing the exact time that the female spent on the eggs, which is, of course, of importance to their incubation. At three nests, the temperature-recorder and itograph were run simultaneously: A94248, C68253, C94219. A comparison of these records shows that the female made several trips into the box each day without sitting on the eggs. These trips were of brief duration, so the average duration of the attentive periods as registered by the itograph was shorter than that registered by the temperature-recorder. Likewise, with more trips recorded, the inattentive periods were also of shorter length.

Table 3 was compiled with the above considerations in mind. An average of fragmentary data on seven nests with five-egg sets obtained with the itograph shows, except for the single record for the first day, a progressive increase in number of attentive periods per day, an increase in their length, and a progressive decrease in the length of the intervals away from the box. The attentive periods are similar in length as during the nest-building period until the time the fourth egg is laid, and then they become somewhat longer, averaging 11.9 minutes for the last day. It is quite possible that the periods spent away from the box are broken up by short nonfeeding periods corresponding to periods of attentiveness, so they do not represent inattentive periods in the true sense. The data show clearly that the amount of time spent away from the box decreases as the set nears completion.

The more extensive data obtained with the temperature-recorder permit more detailed analysis, although the measured periods of attentiveness are only for the time spent on the eggs. This, however, is of special interest in relation to the amount of heat applied to the eggs. A comparison of the data for the five-egg and six-egg sets is made in figure 2.

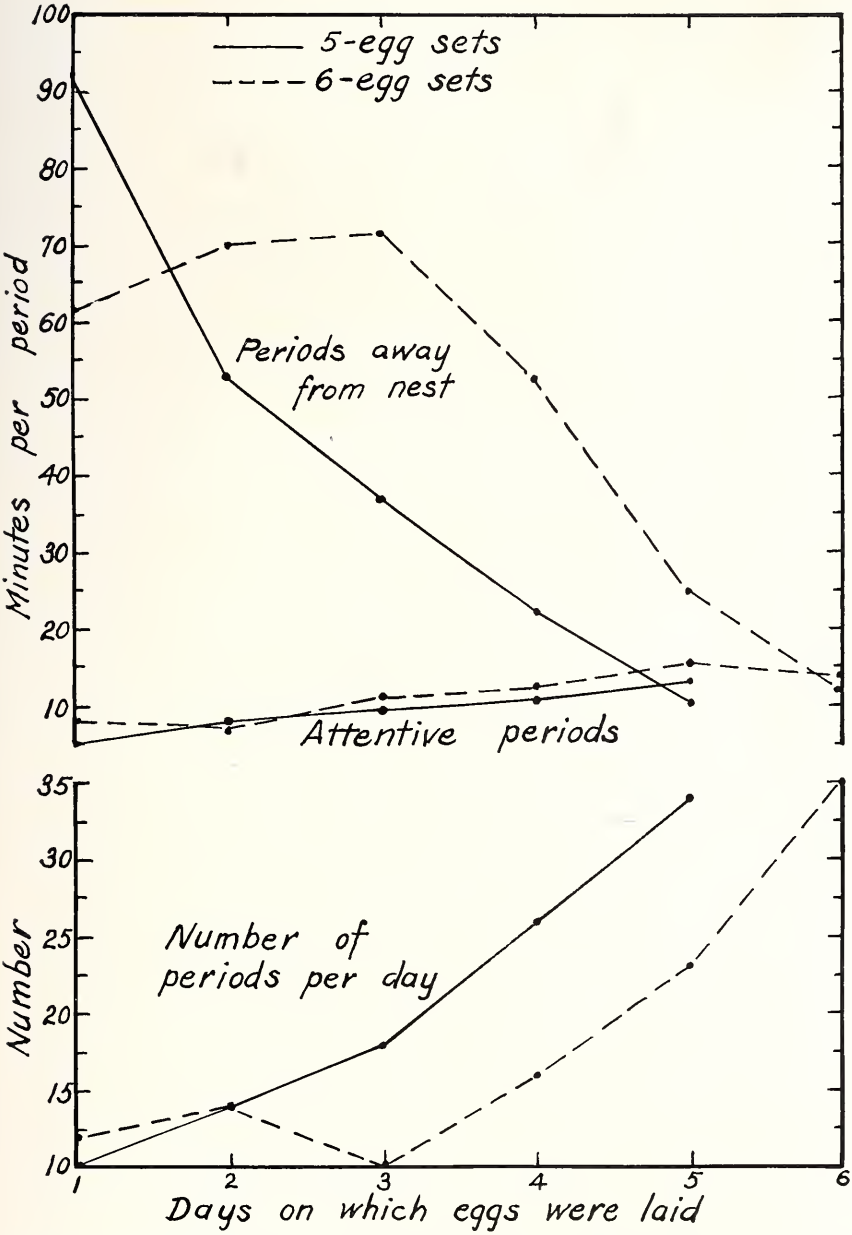

Fig. 2. Comparison of attentive behavior during egg-laying between females laying five-egg and six-egg sets.

For the five-egg sets, the development of the incubating behavior is regular and progressive as shown by increase in number and length of attentive periods, and decrease in periods away from the nest. The same phenomena occur with the six-egg sets, but not until after the third egg is laid. From figure 2, it appears that beginning with the day on which the fourth egg is laid the increase in the number of periods per day in six-egg sets lags about a day behind the increase in five-egg sets. The increase in the average length of the attentive period goes along at the same rate in both set sizes, although averaging longer in duration in the six-egg sets. In both cases the maximum length for the attentive period, 12.7 and 15.7 minutes, respectively, is attained on the day that the fifth egg is laid. The decrease in average length of periods away from the nest lags in the six-egg set about two days behind the five-egg set during the first four days, after which the lag is equivalent to one day. Variations in average time away from the nest is a function of the number and duration of trips or attentive periods made to the nest, and it appears that the chief difference in behavior of the female when laying sets of five or six eggs lies in the number of attentive periods per day.

The total daylight activity of the female during egg-laying averages nearly 16 hours. The total percentage of this time spent on the eggs increases regularly from day to day when sets of five eggs are laid: 5.0, 12.3, 19.9, 32.2, 53.3. When sets of six eggs are laid, there is again evident a lag of a day in developing the same percentage of attentiveness: 11.0, 9.4, 12.4, 18.1, 37.8, 52.6.

It is interesting that these differences in attentive behavior begin to show on the day that the second egg is laid but become particularly definite on the day that the third egg is laid. This is the third 24-hour period before the laying of the sixth egg. As mentioned above, a previous analysis showed that environmental temperature during the second 24-hour period preceding the time of laying exerts a critical influence on whether or not the egg is laid. The present data indicates that this critical period also includes one day earlier, although the relative importance of the third compared with the second 24-hour period preceding laying is not known.

This suggests that differences in behavior are associated with differences in environmental temperatures during this critical period when the size of the set is determined. If air temperatures are favorable, a sixth egg completes its development and this is correlated with a lag in the appearance of incubating behavior. On the other hand, if conditions are not favorable for the maturing of a sixth egg, the incubating behavior develops much faster.

The cessation of egg-laying and onset of broodiness is believed to be under hormonal control. This hormone may be prolactin, described by

TABLE 3. Egg-laying period of the female.

Band number	New (N) or return (R)	Year	Territory	Box	Date laid	First Egg: Number of periods	First Egg: Attentive periods (min.)	First Egg: Periods away from nest (min.)	Second Egg: Number of periods	Second Egg: Attentive periods (min.)	Second Egg: Periods away from nest (min.)	Third Egg: Number of periods	Third Egg: Attentive periods (min.)	Third Egg: Periods away from nest (min.)	Fourth Egg: Number of periods	Fourth Egg: Attentive periods (min.)	Fourth Egg: Periods away from nest (min.)	Fifth Egg: Number of periods	Fifth Egg: Attentive periods (min.)	Fifth Egg: Periods away from nest (min.)	Sixth Egg: Number of periods	Sixth Egg: Attentive periods (min.)	Sixth Egg: Periods away from nest (min.)
5-egg sets—data from itograph																							
A94248	N	1927	68	30	July 30	..	..	...	12	9.2	53.2	21	7.5	29.8	37	8.7	12.8	44	12.4	7.2			
B5640	R	1931	112	80A	July 8	30	2.9	26.5	16	6.4	49.6	17	9.2	39.1	27	13.7	19.1	41	11.5	10.3			
B45348	N	1928	78	51	June 28	..	..	...	13	7.5	49.3	26	8.0	19.7	45	7.5	11.3	50	9.1	8.8			
B45348	R	1929	90	51	July 6	..	..	...	..	...	...	..	...	...	..	...	...	43	11.5	9.2			
B45350	N	1928	75	11	July 10	..	..	...	..	...	...	..	...	..	..	...	...	33	12.7	14.9			
Unknown	?	1930	94	47	June 30	..	..	...	..	...	...	20	10.4	33.3	13	14.1	52.0	36	11.8	13.0			
C68253	N	1930	96	25	June 15	..	..	...	11	12.0	68.5	19	7.0	40.7	15	9.9	50.3	34	14.0	12.4			
Average						30	2.9	26.5	13	8.8	55.2	21	8.4	32.5	27	10.8	29.1	40	11.9	10.8			
5-egg sets—data from temperature-recorder																							
71653	N	1926	59	9	July 19	..	..	...	..	...	...	20	5.4	41.5	32	8.0	13.2	46	12.8	6.6			
664751	N	1928	75	10	July 22	..	..	...	..	...	...	..	...	...	..	...	...	26	14.7	15.1			
A94247	N	1927	65	9	July 1	14	6.3	48.3	21	6.2	28.4	20	13.0	33.7	27	17.0	15.7	34	7.6	6.5			
A94248	N	1927	68	30	July 30	5	4.6	137.2	8	11.6	87.9	13	11.2	50.3	25	14.0	17.8	40	12.6	8.9			
B45321	N	1928	73	70	July 5	..	..	...	16	5.6	46.1	..	...	...	39	5.6	20.6	48	9.8	9.7			
B45536	N	1928	71	80	July 10	..	..	...	13	8.8	49.6	23	11.4	24.6	..	...	...	24	18.0	14.2			
C68253	N	1930	96	25	June 15	..	..	...	..	...	...	14	7.4	35.6	14	10.0	43.4	29	13.1	14.9			
Average						10	5.4	92.8	14	8.0	53.0	18	9.7	37.1	27	10.9	22.1	35	12.7	10.8			
6-egg sets—data from temperature-recorder																							
A38446	N	1926	58	11	July 1	..	..	...	19	5.7	48.1	19	5.9	42.4	29	12.0	22.6	34	12.5	17.9	39	12.9	11.5
B45349	N	1928	73	74	May 24	..	..	...	..	...	...	..	...	...	18	11.5	41.4	21	11.3	28.6	26	10.9	21.6
B96433	N	1929	85	30	July 2	12	8.2	61.2	17	8.4	41.0	..	...	...	17	11.4	34.3	30	13.0	15.9	25	17.8	12.4
C68257	N	1930	97	49	June 11	..	..	...	..	...	...	8	12.6	82.8	12	14.0	58.6	17	26.9	26.9	..	...	...
C68705	N	1930	93	43	June 29	..	..	...	..	...	...	10	12.5	78.0	15	7.5	50.9	24	15.3	19.9	39	15.6	7.0
C94219	R	1932	120	53	June 7	..	..	...	6	9.3	121.0	5	13.6	83.6	6	17.5	107.2	14	15.1	39.7	44	11.9	8.2
Average						12	8.2	61.2	14	7.8	70.0	10	11.2	71.7	16	12.3	52.5	23	15.7	24.8	35	13.8	12.1

Riddle (1938), which is secreted by the anterior pituitary gland; or there may be two hormones involved, one concerned with nest building and incubation, and the other with brooding and care of the young (Nalbandov and Card 1945). The rate at which secretion of hormone occurs during the egg-laying period would determine how soon egg-laying would cease and how soon the incubating behavior would become established. There has been no demonstration as yet that the secretion of these hormones may be directly affected by environmental conditions.

The incubating behavior may be considered fully developed when the attentive periods average longer than the inattentive periods. In the five-egg sets, this condition was reached, in five of the seven records made, on the day that the last egg was laid. In six-egg sets, the inattentive periods did not become shorter than the attentive periods until the sixth and last day of egg-laying. In one of the five records this did not occur until the following day. Likewise, with one record of a seven-egg set, the inattentive periods did not become shorter than the attentive periods until the last day, which in this case was the seventh day. The data for the last three days in this record are as follows:

Day fifth egg laid: 23 periods; attentive period, 13.1 minutes; period away from nest, 25.9 minutes.

Day sixth egg laid: 20 periods; attentive period, 19.5 minutes; period away from nest, 22.0 minutes.

Day seventh egg laid: 23 periods; attentive period, 19.3 minutes; period away from nest, 18.9 minutes.

Thus, although the incubating behavior in its full expression is not established until the last egg is laid, it is in the process of development during most of the egg-laying period.

Figure 3 gives the progress of an unusual record, apparently made by the same female throughout, as all eggs laid were similar in detailed markings and other characteristics. The record was exceptional even during the first four days, in having an unusually large number of short attentive periods. At around 1900 hours on the fourth day, all four eggs were removed from the box, possibly by one of the two male wrens who were then engaged in territorial conflict. In spite of this, the female spent the night in the box and laid egg number five the next morning. However, the number and length of her attentive periods and the percentage of total daylight time that she was attentive dropped considerably. The following day she laid egg number six and her attentiveness began to recover. During the following three days she reverted to carrying in nest lining as well as sitting on the eggs. After this interval she laid eggs seven, eight, and nine on successive days. With the laying of these last three eggs her attentive behavior, which was already considerable, increased still further and became fully characteristic of an incubating bird. It would appear that the normal increase in secretion of the hormone concerned with increasing attentiveness and initiating incubation was temporarily interrupted on the fifth day. This may have been due to the excitement of competition between the two males for territory and for her attentions, and to the removal of her first four eggs. The formation of the fifth and sixth eggs was apparently too far advanced not to be completed. Possibly the interruption in hormone secretion on the fifth day, along with revived mating excitement, started a new ovulation cycle, which culminated five days later in the laying of the seventh,

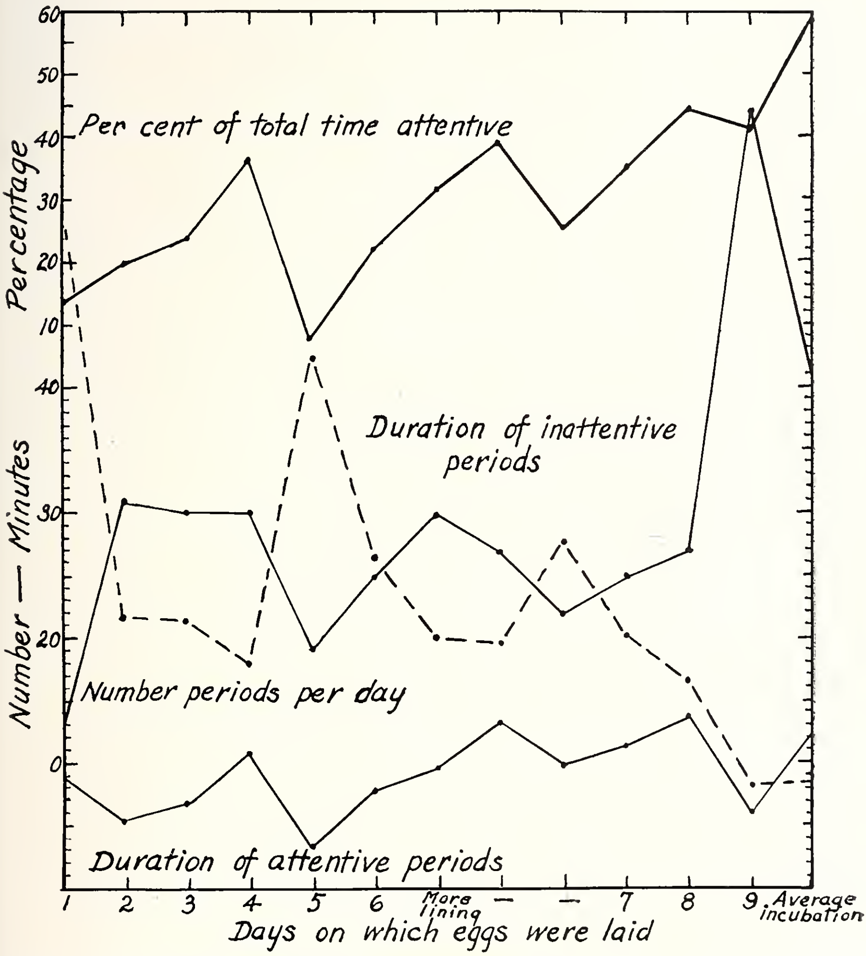

FIG. 3. Unusual egg-laying record of female L24101, at box 49 in territory 160, June 21 to July 2, 1935, recorded on the itograph. In evening of day on which fourth egg was laid, all four eggs disappeared from the nest.

eighth, and ninth eggs. Evidence has accumulated elsewhere (Kendeigh 1941b) that a psychological stimulus, presumably the male's attention and copulation, is necessary to initiate ovulation and egg-laying in at least some passerine species. It may also be necessary that a lack of such intense excitement is required for increased hormone secretion to bring about the cessation of egg-laying and the onset of full incubating behavior. The sequel to this history is that eggs five and six each hatched 15 days after it was laid, eggs seven and eight each 14 days later, and egg nine 13 days later. Since hatching days were respectively 8, 9, 12, 13, and 13 days after the ninth egg was laid, it is obvious that the first ones laid received considerable heat before the last one was laid. The last young hatched, which was smaller than the others, disappeared when only three days old, but the other four young birds left the box together late in the afternoon, 18, 17, 14, and 13 days, respectively, after hatching. The usual period of nest life is 15 days.

Incubation Period

During incubation of the eggs, periods of attentiveness and inattentiveness were recorded both with the temperature-recorder and with the itograph. Data from these two sources are presented in Tables 4 and 5 and are given separately for each day. The first day of steady incubation is the day the last egg is laid, and the data given for this day are the same as in Table 3. The last day of incubation is considered to be the day preceding the one on which the eggs begin to hatch. The number of inattentive periods per day is always one more than the number of attentive periods, since the female spends the night on the eggs and there is an inattentive period preceding the first attentive period in the morning and after the last one in the evening. Table 6 gives a description of the nesting record of each female. Where two or more records are given for the same female they may be separately identified by noting whether they were obtained with the temperature-recorder (TR) Table 4, or the itograph (I) Table 5, and the order in which they are given.

Comparison of potentiometer and itograph records. The data obtained from the temperature-recorder and from the itograph are comparable during incubation, as normally the female enters and leaves the box without delay on each visit and spends all her attentive period on the eggs. This similarity is shown in the averages obtained for the behavior of three females on which both recording devices were employed throughout the period of incubation (94248, C68253, C94219, Table 6). The two sets of data are not, however, identical. There is a tendency for the itograph records to show more periods per day, for the inattentive periods to be shorter, and for a greater total daily period of activity. Part of this discrepancy may be due to faulty interpretation of the record. Occasionally the female may not register on one of the two perches of the box, so that her visit is not completely recorded. Sometimes the male comes onto the outer perch and may even enter the box, although normally the male does not visit the nest during the incubation period. Such trips would be registered in the itograph record but not in the temperature record. Probably the data obtained with the temperature-recorder are more accurate than those from the itograph when the length of individual periods or the averages and totals for single days are concerned. In the averages over the entire incubation period for the above three birds, the discrepancy between the number of periods per day is about 4 per cent, between the length of the attentive periods, about 3 per cent, between the length of the inattentive periods, about 5 per cent, and between the total daily period of activity, about 3 per cent. If the record obtained from the temperature-recorder is accepted as correct, then the accuracy of averages obtained from the itograph may be relied upon within the limits of plus or minus 4 per cent.

Changes with progress of incubation. To demonstrate possible changes in behavior with progress of incubation, data were averaged day by day for those females whose records extended throughout (71653, A94247, A94248, B96433, C68253, C68705, C94219, B45350, B45348). These averages are shown in figure 4, separately for the temperature-recorder and itograph. Data for the three females referred to in the above section are included in both sets of curves.

There is evident in both sets of data a tendency for the number of periods per day to increase for at least the first eight or nine days. The length of the attentive period fluctuates from day to day but shows no consistent tendency for any progressive change. On the other hand, the inattentive periods decrease in length as their number per day increases, and there is an inverse relation between the two. When total time at and away from the nest each day is computed, there is some suggestion that attentive time increases and inattentive time decreases during the first three days, after which they fluctuate around a median during the rest of incubation. For the most part, however, attentive behavior appears essentially uniform throughout incubation.

Average air temperatures were computed for the days on which the records were obtained. The air temperature is the average for the 24-hour day as measured at the Cleveland weather station, some 12 miles away. Although the behavior records are only for the daylight period, it is quite possible that any effect of temperature on the bird at night might be carried over into the behavior on the following day. The variations in mean daily temperature are small, however, and they appear unrelated to variations in attentive behavior.

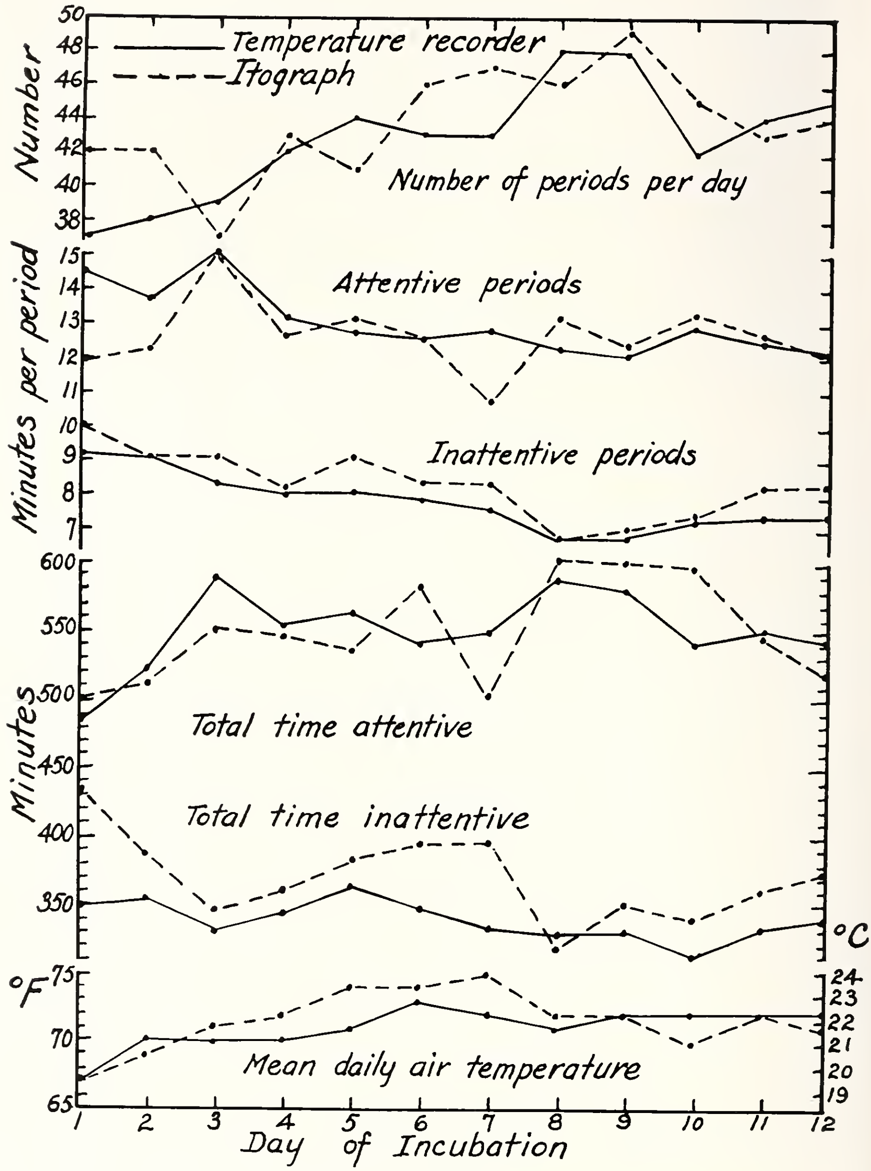

FIG. 4. Changes in attentive behavior with progress of incubation.

TABLE 4. Incubation period: records from temperature-recorder.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
		1st Day				*2nd Day*		
71653	70°F.	46	12.8	6.6	68°F.	46	13.5	5.7
664751	75	26	14.7	15.1	...	...	...	...
A38446	76	39	12.9	11.5	71	37	15.9	9.0
A93420	52	23	19.3	18.9	54	28	20.4	11.5
A94247	64	34	17.6	6.5	72	38	14.0	8.7
A94248	60	40	12.6	8.9	66	41	13.4	7.4
B45321	79	48	9.8	9.7	77	46	9.3	9.4
B45536	66	24	18.0	14.2	69	46	14.0	7.7
B56490	...	...	...	...	...	...	...	...
B96433	76	25	17.8	12.4	74	38	13.5	9.7
B96900	...	...	...	...	...	...	...	...
B97003	...	...	...	...	...	...	...	...
C68253	...	...	...	...	...	...	...	...
C68253	66	29	13.1	14.9	68	36	12.1	12.0
C68253	...	...	...	...	...	...	...	...
C68705	63	39	15.6	7.0	75	33	15.5	10.2
C94219	68	44	11.9	8.2	64	37	14.2	9.7
		3rd Day				*4th Day*		
71653	68	48	12.3	6.3	70	45	11.8	7.4
664751	...	...	...	...	63	26	19.9	10.7
A38446	76	38	12.2	10.5	82	41	10.4	10.1
A93420	63	25	23.5	10.0	66	22	26.1	10.1
A94247	70	36	17.5	6.8	64	50	11.3	6.1
A94248	64	45	12.8	6.3	68	45	11.6	6.8
B45321	75	58	8.3	7.0	69	40	15.1	6.7
B45536	74	38	12.7	11.2	76	43	10.2	9.5
B56490	...	...	...	...	...	...	...	...
B96433	76	41	13.3	8.7	70	37	14.6	8.6
B96900	...	...	...	...	...	...	...	...
B97003	...	...	...	...	74	22	14.5	25.7
C68253	56	18	21.3	18.1	49	20	27.1	15.8
C68253	72	31	18.1	10.9	74	36	14.2	10.4
C68253	...	...	...	...	...	...	...	...
C68705	73	35	15.9	8.6	71	49	12.1	5.5
C94219	66	34	15.5	10.5	70	32	16.6	11.5

TABLE 4 *(cont.)*. Incubation period: records from temperature-recorder.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
		5th Day				*6th Day*		
71653	68°F.	44	14.0	6.8	67°F.	46	12.7	5.7
664751	64	34	13.7	10.9	71	33	14.4	11.1
A38446	71	30	20.3	8.0	66	34	18.2	7.0
A93420	...	...	...	...	...	...	...	...
A94247	70	56	9.3	5.8	73	52	9.8	6.3
A94248	77	45	10.9	8.1	70	42	13.0	7.4
B45321	65	37	16.8	7.2	66	46	13.1	6.3
B45536	80	54	6.9	9.1	76	41	8.8	10.9
B56490	74	42	8.2	12.5	...	...	...	...
B96433	69	36	15.5	8.6	76	42	12.0	8.5
B96900	...	...	...	...	78	46	6.6	11.8
B97003	72	28	15.6	16.4	72	32	15.3	13.1
C68253	49	26	21.2	11.1	52	27	20.5	9.9
C68253	77	31	14.8	13.0	77	31	15.0	11.5
C68253	64	43	11.2	8.6	75	62	6.7	7.2
C68705	70	64	9.3	4.6	76	49	11.3	7.1
C94219	68	34	16.0	9.8	70	39	14.4	8.5
		7th Day				*8th Day*		
71653	68	43	14.0	5.8	69	50	11.3	5.5
664751	72	28	18.4	12.0	80	23	14.0	12.3
A38446	68	34	19.0	7.0	60	43	15.8	5.0
A93420	...	...	...	...	...	...	...	...
A94247	72	62	8.1	5.4	81	73	7.7	4.2
A94248	62	44	13.5	6.5	62	55	10.6	5.7
B45321	...	...	...	...	74	45	9.1	9.6
B45536	79	50	7.2	9.6	74	49	8.4	8.0
B56490	69	50	9.7	7.9	69	47	12.4	7.7
B96433	77	38	13.4	7.9	70	38	14.2	7.4
B96900	76	39	11.5	9.5	74	42	10.7	9.7
B97003	74	40	12.2	9.3	72	39	12.6	10.7
C68253	50	25	21.1	10.3	48	27	19.7	11.5
C68253	77	38	12.0	10.8	71	36	16.9	7.9
C68253	...	...	...	...	64	30	20.4	8.9
C68705	71	44	13.9	6.0	72	44	13.4	6.6
C94219	76	34	14.7	11.0	74	41	12.1	9.7

TABLE 4 *(cont.)*. Incubation period: records from temperature-recorder.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
		9th Day				*10th Day*		
71653	71°F.	50	9.3	5.6	78°F.	42	13.5	5.7
664751	...	...	...	...	...	...	...	...
A38446	60	40	17.5	5.8	...	...	...	...
A93420	...	...	...	...	...	...	...	...
A94247	82	74	5.9	6.0	76	61	8.5	5.6
A94248	64	53	10.3	6.1	67	44	12.4	7.1
B45321	76	54	6.8	9.2	Eggs removed			
B45536	76	53	8.1	7.2	72	60	7.5	6.4
B56490	66	56	8.6	7.3	73	63	7.4	6.9
B96433	70	38	15.2	7.2	68	36	15.1	7.9
B96900	77	43	9.1	10.7	79	41	8.1	13.8
B97003	68	41	15.6	9.0	67	40	13.4	8.7
C68253	48	30	17.3	10.5	56	34	15.7	8.7
C68253	68	32	19.8	7.4	62	43	13.4	7.3
C68253	55	34	18.3	9.0	55	38	16.9	6.5
C68705	71	43	13.2	7.2	76	37	13.9	8.3
C94219	76	46	11.2	8.0	74	34	13.2	9.1
		11th Day				*12th Day*		
71653	78	42	14.1	5.6	76	45	14.0	5.3
664751	...	...	...	...	...	...	...	...
A38446	...	...	...	...	...	...	...	...
A93420	...	...	...	...	...	...	...	...
A94247	74	41	15.6	5.5	77	65	7.3	5.5
A94248	74	45	11.1	7.6	71	37	13.7	8.2
B45321								
B45536	72	68	8.1	6.0	Eggs removed			
B56490	73	60	6.2	8.3	78	57	5.8	7.6
B96433	73	37	13.7	8.5	72	42	12.4	7.1
B96900	83	46	7.7	13.1				
B97003	68	46	10.3	9.5	68	41	14.0	8.0
C68253	62	31	18.2	10.2	73	41	13.0	9.0
C68253	72	50	9.2	8.7	80	37	10.4	11.8
C68253	60	35	16.2	9.1	68	45	11.1	7.8
C68705	60	58	9.7	5.4	61	51	11.6	5.4
C94219	74	36	14.3	10.2	65	37	15.5	8.5

TABLE 4 *(cont.)*. Incubation period: records from temperature-recorder.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
		13th Day				*14th Day*		
71653								
664751	...	...	...	...				
A38446	...	...	...	...				
A93420	...	...	...	...	...	...	...	...
A94247	74°F.	44	13.2	6.1				
A94248	62	44	13.1	6.1	62°F.	36	13.5	9.1
B45321								
B45536								
B56490	75	74	4.0	7.9	74	77	5.8	6.4
B96433								
B96900								
B97003								
C68253	Deserted							
C68253	70	41	12.4	8.7	62	45	12.9	6.7
C68253	70	33	18.9	7.3	62	39	16.1	6.7
				(*15th Day:*	66	29	19.6	8.8)
C68705	70	46	11.5	6.7	76	55	8.8	6.6
C94219	64	38	13.0	8.0				

TABLE 5. Incubation period: records from itograph.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
			1st Day				*2nd Day*	
664751	...	...	...	...	...	...	...	...
A93513	...	...	...	...	...	...	...	...
A93526	...	...	...	...	...	...	...	...
A94248	...	...	...	...	...	...	...	...
A94248	60°F.	44	12.4	7.2	66°F.	43	12.7	7.1
B5640	...	...	...	...	...	...	...	...
B5640	...	...	...	...	...	...	...	...
B5640	70	41	11.5	10.3	77	33	9.4	12.4
B45348	76	50	9.1	8.8	79	48	10.8	8.1
B45348	70	43	11.5	9.2	...	...	...	...
B45348	...	...	...	...	...	...	...	...
B45349	...	...	...	...	...	...	...	...
B45350	66	33	12.7	14.9	69	36	13.6	9.2
Unknown	...	...	...	...	69	51	11.7	5.7
Unknown	70	47	12.0	6.7	69	51	10.5	6.7
C68253	66	34	14.0	12.4	68	36	12.7	11.4
C68257	...	...	...	...	...	...	...	...
C94219	68	48	11.4	7.4	64	48	11.2	9.1
F58248	...	...	...	...	...	...	...	...
H18583	...	...	...	...	...	...	...	...
L24101	70	62	6.1	8.4	79	56	8.1	6.9
L24101	...	...	...	...	...	...	...	...
L24987	...	...	...	...	...	...	...	...
34-86072	...	...	...	...	...	...	...	...
35-13635	...	...	...	...	...	...	...	...
			3rd Day				*4th Day*	
664751	...	...	...	...	...	...	...	...
A93513	...	...	...	...	...	...	...	...
A93526	55	54	9.3	7.3	53	52	9.9	6.8
A94248	...	...	...	...	82	46	7.2	12.7
A94248	64	45	13.3	5.9	68	44	12.4	7.1
B5640	70	36	16.8	8.1	68	41	15.5	5.9
B5640	...	...	...	...	...	...	...	...
B5640	...	...	...	...	...	...	...	...
B45348	79	43	11.6	9.3	70	45	13.1	6.5
B45348	...	...	...	...	...	...	...	...
B45348	...	...	...	...	...	...	...	...

TABLE 5 *(cont.)*. Incubation period: records from itograph.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
	3rd Day Continued				*4th Day Continued*			
B45349	76°F.	37	15.4	8.3	72°F.	42	11.8	8.9
B45350	74	29	18.5	10.1	76	49	10.1	7.9
Unknown	74	67	8.7	4.8	76	50	10.0	7.2
Unknown	76	49	10.8	7.1	...	...	...	...
C68253	72	31	18.0	11.1	74	37	13.8	10.1
C68257	...	...	...	...	...	...	...	...
C94219	66	39	13.8	9.1	70	38	14.3	9.3
F58248	...	...	...	...	64	53	10.3	5.9
H18583	...	...	...	...	...	...	...	...
L24101	77	36	12.2	7.5	80	32	17.9	9.1
L24101	...	...	...	...	...	...	...	...
L24987	...	...	...	...	...	...	...	...
34-86072	...	...	...	...	...	...	...	...
35-13635	...	...	...	...	72	38	12.7	11.0
	5th Day				*6th Day*			
664751	...	...	...	...	66	43	12.5	9.0
A93513	77	57	9.5	6.1	74	52	11.3	5.6
A93526	56	55	10.0	6.1	58	54	9.6	7.2
A94248	80	51	6.0	11.8	74	48	7.8	10.8
A94248	77	45	11.5	7.6	70	43	14.9	6.6
B5640	73	33	19.1	7.7	72	39	13.7	7.6
B5640	...	...	...	...	...	...	...	...
B5640	...	...	...	...	...	...	...	...
B54348	68	49	10.8	7.3	75	66	5.9	7.5
B54348	...	...	...	...	70	91	4.6	3.3
B54348	...	...	...	...	49	57	9.6	5.7
B45349	...	...	...	...	74	52	6.5	9.3
B45350	80	41	12.2	9.3	76	42	9.7	8.8
Unknown	80	38	13.3	9.0	...	...	...	...
Unknown	...	...	...	...	...	...	...	...
C68253	77	29	17.3	12.8	77	32	20.8	11.8
C68257	...	...	...	...	...	...	...	...
C94219	68	40	13.8	8.3	70	46	12.2	7.1
F58248	71	54	8.5	6.9	73	55	8.3	7.0
H18583	...	...	...	...	...	...	...	...
L24101	80	29	18.2	10.3	76	32	12.5	1.17
L24101	...	...	...	...	76	26	21.4	9.4

Table 5 *(cont.)*. Incubation period: records from itograph.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
	5th Day Continued				*6th Day Continued*			
L24987	...	...	...	...	...	...	...	...
34-86072	...	...	...	...	...	...	...	...
35-13635	70°F.	38	15.2	8.3	...	...	...	...
	7th Day				*8th Day*			
664751	68	31	17.1	11.3	68°F.	40	12.8	9.4
A93513	...	...	...	...	67	58	9.6	5.4
A93526	64	54	9.6	6.7	58	59	9.9	5.4
A94248	62	47	10.9	8.6	...	...	...	...
A94248	62	45	13.3	6.0	62	58	9.9	4.8
B5640	62	40	14.0	5.4	63	40	15.6	5.6
B5640	62	38	16.3	6.6	66	34	16.4	7.8
B5640	...	...	...	...	...	...	...	...
B54348	81	64	6.2	7.5	79	50	11.2	6.5
B54348	68	86	4.5	5.1	73	76	4.8	6.4
B54348	49	46	8.3	10.0	52	51	8.2	8.6
B45349	75	48	10.1	8.3	Further record uncertain			
B45350	79	53	6.9	6.9	74	46	11.4	6.7
Unknown	...	...	...	...	...	...	...	...
Unknown	...	...	...	...	...	...	...	...
C68253	77	41	11.1	10.4	71	34	18.7	8.2
C68257	...	...	...	...	...	...	...	...
C94219	76	32	16.1	10.5	74	40	14.4	7.7
F58248	74	53	9.3	7.0	72	58	9.2	6.2
H18583	...	...	...	...	82	62	8.0	6.7
L24101	68	32	17.0	9.2	72	43	11.0	7.0
L24101	69	25	21.8	12.0	64	26	25.0	9.0
L24987	...	...	...	...	...	...	...	...
34-86072	...	...	...	...	...	...	...	...
35-13635	67	41	11.0	10.6	72	37	13.5	10.0
	9th Day				*10th Day*			
664751	...	...	...	...	72	47	9.3	9.9
A93513	67	73	8.0	4.4	73	74	6.8	5.1
A93526	52	63	8.7	5.3	53	55	9.8	6.3
A94248	...	...	...	...	...	...	...	...
A94248	64	57	9.7	5.6	67	53	10.4	5.7
B5640	70	45	13.1	5.7	70	38	16.4	6.7

TABLE 5 *(cont.)*. Incubation period: records from itograph.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
		9th Day Continued				*10th Day Continued*		
B5640	59°F.	40	16.4	6.1	54°F.	46	12.9	6.4
B5640	...	...	...	...	...	...	...	...
B45348	77	74	5.9	6.0	75	62	7.9	6.6
B45348	72	56	8.3	5.0	...	...	...	...
B45348	50	31	11.7	15.4	...	...	...	...
B45349	...	...	...	...	...	...	...	...
B45350	76	44	11.9	7.6	72	38	14.6	7.7
Unknown	...	...	...	...	72	42	13.5	7.0
Unknown	...	...	...	...	...	...	...	...
C68253	68	33	18.8	8.0	62	44	13.4	6.7
C68257	...	...	...	...	...	...	...	...
C94219	76	39	15.4	7.6	74	26	20.3	10.2
F58248	74	51	8.0	8.7	82	64	6.8	6.9
H18583	88	64	9.7	4.7	78	70	6.4	6.3
L24101	...	...	...	...	...	...	...	...
L24101	67	25	23.4	10.4	60	28	20.0	10.1
L24987	...	...	...	...	68	44	12.6	6.9
34-86072	...	...	...	...	...	...	...	...
35-13635	56	40	15.1	6.4	62	48	12.2	5.8
		11th Day				*12th Day*		
664751	76	52	8.1	9.1	79	41	11.5	10.4
A93513	...	...	...	...	66	58	10.8	4.4
A93526	...	...	...	...	58	63	8.8	4.7
A94248	...	...	...	...	...	...	...	...
A94248	74	46	10.6	7.6	71	39	13.4	7.8
B5640	78	39	15.2	6.5	76	46	12.5	6.7
B5640	57	41	14.8	6.3	64	42	15.1	6.6
B5640	...	...	...	...	...	...	...	...
B45348	69	52	10.9	6.2	65	50	12.3	4.9
B45348	...	...	...	...	...	...	...	...
B45348	...	...	...	...	...	...	...	...
B45349	...	...	...	...	...	...	...	...
B45350	72	36	16.1	7.9	74	51	9.6	7.1
Unknown	72	44	12.5	6.8	74	45	12.4	6.5
Unknown	...	...	...	...	...	...	...	...
C68253	72	38	14.5	9.3	80	41	10.2	11.6

TABLE 5 *(cont.)*. Incubation period: records from itograph.

Band number	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
		11th Day Continued				*12th Day Continued*		
C68257	71°F.	35	9.5	15.7	68°F.	43	7.4	13.4.
C94219	74	41	11.4	10.0	65	38	14.4	10.3
F58248	88	50	6.0	12.4	78	58	7.5	8.1
H18583	78	68	8.2	4.8	83	68	9.0	4.0
L24101	...	...	...	...	...	...	...	...
L24101	49	28	21.7	7.8	52	34	17.4	7.0
L24987	68	45	11.9	7.5	72	45	8.8	12.8
34-86072	...	...	...	...	...	...	...	...
35-13635	64	49	10.0	8.0	68	46	9.0	9.8
		13th Day				*14th Day*		
664751	...	...	...	...	...	...	...	...
A93513	...	...	...	...	...	...	...	...
A93526	60	77	7.2	4.4	62	64	9.3	4.5
A94248	...	...	...	...	...	...	...	...
A94248	62	42	13.7	6.2	62	41	14.0	7.2
B5640	74	55	12.2	5.2	...	...	...	...
B5640	66	45	11.6	9.1	...	...	...	...
B5640	...	...	...	...	...	...	...	...
B45348	...	...	...	...	...	...	...	...
B45348	...	...	...	...	...	...	...	...
B45348	62	56	4.8	9.5	...	...	...	...
B45349	...	...	...	...	...	...	...	...
B45350	75	45	11.5	7.4	...	...	...	...
Unknown	75	38	14.7	7.6	Eggs did not hatch			
Unknown	...	...	...	...	...	...	...	...
C68253	70	41	12.6	8.7	62	45	11.9	7.1
C68257	62	57	7.1	8.6	...	...	...	...
C94219	64	52	10.3	7.9	...	...	...	...
F58248	...	...	...	...	...	...	...	...
H18583	68	61	5.0	9.5	...	...	...	...
L24101	...	...	...	...	...	...	...	...
L24101	54	30	19.6	8.0	...	...	...	...
L24987	...	...	...	...	...	...	...	...
34-86072	78	44	14.0	6.8	69	43	12.6	7.9
35-13635	64	45	10.4	9.3	...	...	...	...

TABLE 6. Behavior of individual females during incubation period.[a]

Band number	New (N) or return (R)	Year	Terri-tory	Box	Number of eggs in set	Date of last egg	Length of incubation before hatching begins	Number of days record	Air temperature °F.	Air temperature °C.	Temperature-recorder (TR) or itograph (I)	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)
71653	N	1926	59	9	4	July 23	12	12	71	21.7	TR	46	12.8	6.0
664751	N	1928	75	6	6	June 22	12	6	72	22.2	I	42	11.9	9.8
664751	N	1928	75	10	5	July 26	13	6	71	21.7	TR	28	15.8	12.0
A38446	N	1926	58	11	6	July 6	13	9	70	21.1	TR	37	15.8	8.2
A93420	N	1927	63	11	6	June 1	14	4	59	15.0	TR	24	22.3	12.6
A93513	N	1927	65	51	5	July 12	12	6	71	21.7	I	62	9.3	5.2
A93526	R	1928	76	25	6	May 26	14	11	57	13.9	I	59	9.3	5.9
Unknown	?	1928	76	30	5	July 14	...	8	74	23.3	I	47	12.1	6.8
A94247	N	1927	65	9	5	July 5	13	13	73	22.8	TR	53	11.2	6.0
A94248	N	1927	63	6	6	June 27	14	4	74	23.3	I	48	8.0	11.0
A94248	N	1927	68	30	5	Aug. 3	14	14	66	18.9	I	46	12.3	6.6
A94248	N	1927	68	30	5	Aug. 3	14	14	66	18.9	TR	44	12.3	7.2
B5640	R	1929	92	70	5	July 13	13	11	71	21.7	I	41	14.9	6.5
B5640	R	1931	109	74	5	May 30	13	7	61	16.1	I	41	14.8	7.0
B5640	R	1931	112	80A	3	July 12	13	2	74	23.3	I	37	10.4	11.4
B45321	N	1928	73	70	4	July 9	...	8	73	22.8	TR	47	11.0	8.1
B45348	N	1928	78	51	5	July 2	12	12	74	23.3	I	54	9.6	7.1
B45348	R	1929	90	51	5	July 10	12	5	71	21.7	I	70	6.7	5.8
B45348	R	1930	98	51	8	May 20	13	5	52	11.1	I	48	8.5	9.8
B45349	N	1928	73	74	6	May 29	...	13	58	14.4	TR	61	8.9	6.6
B45349	N	1928	79	47	5	July 20	...	4	74	23.3	I	45	11.0	8.7
B45350	N	1928	75	11	5	July 14	13	13	74	23.3	I	42	12.2	8.6
B45536	N	1928	71	80	5	July 14	...	11	74	23.3	TR	48	10.0	9.1
B56490	N	1929	86	25	6	June 7	14	9	72	22.2	TR	58	7.6	8.1
B96433	N	1929	85	30	6	July 7	12	12	73	22.8	TR	37	14.2	8.5

B96900	N	1929	83	75	4	July 18	11	6	78	25.6	TR	43	9.0	11.4
B97003	N	1929	84	47	6	June 17	12	9	71	21.7	TR	36	13.5	12.3
Unknown	?	1929	91	59	6	July 10	12	3	72	22.2	1	49	11.1	6.8
C68253	N	1930	96	26A	6	May 22	...	10	54	12.2	TR	28	19.5	11.5
C68253	N	1930	96	25	5	June 19	14	14	71	21.7	TR	37	13.9	10.1
C68253	N	1930	96	25	5	June 19	14	14	71	21.7	I	37	14.8	10.0
C68253	R	1931	106	25	6	May 23	...	10	64	17.8	TR	39	15.5	8.0
C68257	N	1930	97	49	5	June 16	13	3	67	19.4	I	45	8.0	12.6
C68705	N	1930	93	43	6	July 4	14	14	70	21.1	TR	46	12.6	6.8
C94219	R	1932	120	53	6	June 12	13	13	70	21.1	TR	37	14.0	9.4
C94219	R	1932	120	53	6	June 12	13	13	70	21.1	I	41	13.8	8.8
F58248	R	1933	129	49	6	May 29	12	9	75	23.9	I	55	8.2	7.7
H18583	N	1933	126	10	6	May 31	13	6	80	26.7	I	66	7.7	6.0
L24101	R	1935	160	49	5	July 2	...	8	75	23.9	I	40	12.9	8.8
L24101	R	1936	166	21A	6	May 17 or 18	13	8	61	16.1	1	28	21.3	9.2
L24987	N	1934	140	10	4	June 29	12	3	69	20.6	I	45	11.1	9.1
34-86072	N	1935	154	21A	5	July 2	14	2	74	23.3	1	44	13.3	7.4
35-13635	N	1936	164	49	6	June 3	13	9	66	18.9	1	42	12.1	8.8
Average								8	69	20.6		45	12.1	8:5

[a] The nesting history of each bird in its territory may be found in Kendeigh (1941c).

One itograph record was obtained on an unidentified female who continued to incubate eggs that failed to hatch for six days beyond the normal period. An average of nine of the first 13 regular days of incubation gives 51 attentive periods per day, 7.7 minutes in length. Inattentive periods average 10.1 minutes. An average of data for three of the following six days shows a reduction in number of attentive periods per day to 40 and their length to 5.7 minutes, while the inattentive periods increased to 16.5 minutes. However, these differences are probably not attributable to the prolonged incubation but more likely to the high air temperatures, which averaged 83° F. (28.3° C.) and had a maximum of 98° F. (36.7° C.). The nest box was exposed to the sun, and doubtless the excessive heat interfered with normal attention to the eggs.

Averages for individuals and the species. The detailed daily data given in Tables 4 and 5 are averaged in Table 6 for each record of each female. There are 40 nesting records involved, obtained on 30 females over a total of 332 days. The average of all these records indicates that 45 attentive periods per day are typical for the species, with these averaging 12.1 minutes in duration and taking up 58.2 per cent of the daytime activity. This compares with 46 inattentive periods averaging 8.5 minutes in length. Considerable variation between records for individual females occurs, however, and these variations need to be explained.

Changes with age, mates, and season. Apparently the age of the female and her nesting experience of previous years do not explain the variations, as the records for three females (B5640, B45348, C68253) obtained over two and three years show no consistent changes.

Female B45348 had the same mate at box 51 in 1928 and 1930, and female C68253 had the same mate at box 26A and box 25 in 1930; otherwise these three females had a different mate for each nesting. It does not appear that a change of mates affected the female's behavior very greatly.

In Table 7, the records are averaged for each of the four months during the nesting season. There is no clear-cut correlation apparent with the progress of the nesting season.

Influence of air temperature. When the records are analyzed in respect to the average air temperature over the entire period during which they were obtained (Table 8), there is some tendency shown for a rise in air temperature to be accompanied by an increase in number of periods per day and a decrease in the average length of the attentive but probably not the inattentive periods. However, the trends are irregular and not altogether convincing.

Further analysis of the influence of temperature is made in figure 5. To obtain the curves shown in this figure, the number and duration

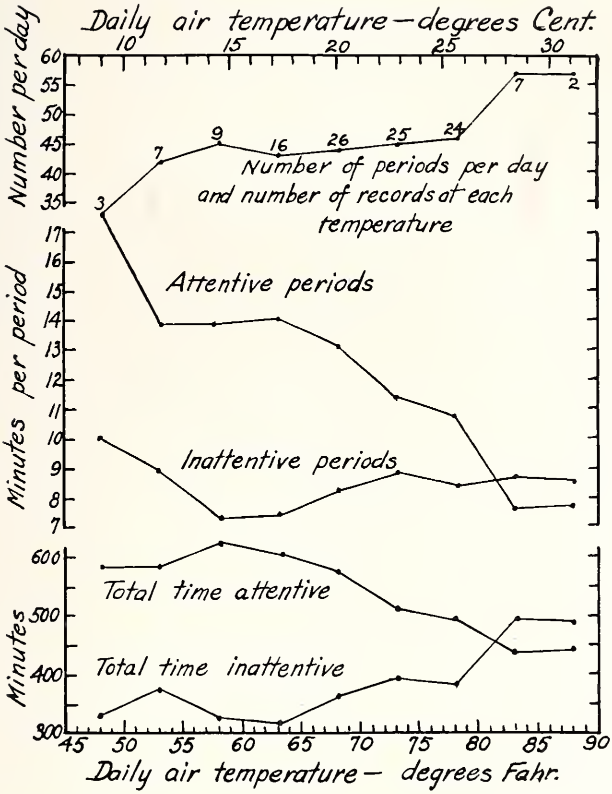

FIG. 5. Changes in attentive behavior correlated with mean daily air temperature.

of the periods each day, as given in Tables 4 and 5, were sorted out and averaged for each female for each five-degree interval of daily air temperature. Averages were then made of the records of all the females in each range of temperature and plotted against the median temperature of this interval. When both an itograph and a temperature record were available for the same nesting, only the latter was used. Averages were made of all data for each temperature regardless of the fact that the record of no single female extended over the complete range of temperature.

Some persistent trends are to be discerned in these curves. There is a tendency for the number of periods per day to increase as the air temperature rises, but this is pronounced only at the extreme temperatures. From 48° to 53° F. (8.9° to 11.7° C.), all three females showed an increase in number of periods per day. In the range from 53° to 78° F. (11.7° to 25.6° C.), only 45 per cent of comparisons of records on individual females from one temperature interval to another showed an increase, so the slight upward trend in the curve for these medium temperatures is probably not statistically reliable. Although the curve rises abruptly to 83° and 88° F. (28.3° and 31.1° C.), only 56 per cent of the records shows such a trend, so there is considerable individual variation between females.

TABLE 7. Variations in attentive behavior with progress of the nesting season.

Month	Number of nestings recorded	Air temperature °F.	Air temperature °C.	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Percentage of total time attentive
May	9	62	16.7	47	12.6	8.0	60.7
June	10	69	20.6	42	12.3	10.3	53.8
July	20	73	22.8	46	11.8	8.0	59.1
August	1	66	18.9	45	12.3	6.9	63.6

TABLE 8. Variations in attentive behavior with differences in air temperature.

Average air temperature °F.	Average air temperature °C.	Number of nestings recorded	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Percentage of total time attentive
53	11.7	2	38	14.0	10.6	56.3
58	14.4	3	48	13.5	8.4	61.2
62	16.7	3	36	17.2	8.1	67.4
68	20.0	7	43	12.3	8.8	57.7
73	22.8	23	46	11.4	8.3	57.3
79	26.1	2	54	8.4	8.7	48.7

With the rise in air temperature, there is a decrease in the average length of the attentive periods. Here again the decrease in length of the periods is most pronounced at extreme temperatures. Considering variations in records of individual females from one temperature interval to the next: 100 per cent show a decrease from 48° to 53° F. (8.9° to 11.7° C.); for the range of medium temperatures of 53° to 78° F. (11.7° to 25.6° C.), only 58 per cent are decreasing; but from 78° to 88° F. (25.6° to 31.1° C.), the percentage goes up to 78.

The curve showing duration of the inattentive periods does not vary in harmony with the other two curves. Sixty-seven per cent of the records on individual females at the lower air temperatures of 48° to 63° F. (8.9° to 17.2° C.) agree in showing a decrease in the length of the period. From 63° to 88° F. (17.2° to 31.1° C.) the reverse is almost exactly true, with 64 per cent of the individual records indicating that the inattentive periods are increasing in length.

The total attentive time at the nest decreases and the inattentive time away from the nest increases progressively from 58° or 63° to 83° F. (14.4° or 17.2° to 28.3° C.). The most pronounced change comes between 78° and 83° F. (25.6° and 28.3° C.). There are no significant changes below 58° F. (14.4° C.) or above 83° F. (28.3° C.). There is likewise no consistent variation with temperature in the combined time of attentiveness and inattentiveness during the day. This varies between 883 and 958 minutes and averages 927 minutes, or 15.4 hours. The percentage of total time that the bird is attentive during the day varies from 61.0 and 65.6 at 48° to 63° F. (8.9° to 17.2° C.), to 47.0 and 47.6 at 83° and 88° F. (28.3° and 31.1° C.).

The range of medium air temperatures, 53° to 78° F., within which there is less pronounced variation in the various phases of attentive behavior correlated with temperature, is approximately the range of air temperatures where this species has its greatest physiological vigor in initiating breeding (Kendeigh and Baldwin 1937), producing the largest sets of eggs and also individual eggs of largest size (Kendeigh 1941b), and with greatest percentage of egg-hatch (Kendeigh 1942). At the lower air temperatures, longer attentive periods are required to maintain the eggs at the normal incubation temperature. This transference of heat from the bird to the egg drains more energy from the incubating female, which requires her in turn to spend longer inattentive periods for feeding in order to replenish that energy. Furthermore, at low air temperatures, insects become more sluggish and difficult to find. The effect of low air temperatures is enhanced when combined with rain. On the other hand, at high air temperatures the eggs do not cool so rapidly, and, should the nest box be exposed to the sun, nest temperatures may become too high for the comfort of the bird herself, with the result that the time at the nest is reduced and the time away is increased. The female may spend part of these prolonged periods off the eggs in no particular activity aside from sitting on a perch near the nest box.

Correlation with length of incubation. An average of 97 records gives an interval of over 26 hours between the hatching of the first and last egg. The eggs tend to hatch in the order laid. If the true length of the incubation period is considered the time from the last egg laid until it hatches (Swanberg 1950), then one day must be added to the data on length of incubation before hatching given in Table 9. The normal incubation period varied for different females from 12 to 15 days. One record of 16 days is probably to be explained by the fact that two thermocouples in the nest, instead of one, disturbed the female so that the incubation temperature was lowered. In Table 9, there is some correla-

TABLE 9. Relation of attentive behavior to length of incubation.

Length of incubation	Number of records	Average temperature °F.	Average temperature °C.	Number of periods per day Average	Number of periods per day Extremes	*Attentive periods* Average (min.)	*Attentive periods* Extremes (min.)	*Inattentive periods* Average (min.)	*Inattentive periods* Extremes (min.)	Percentage of total time attentive
12 days	1	78	25.6	43	. . .	9.0	. . .	11.4	. . .	43.6
13 days	10	72	22.2	50	36-62	10.8	6.7-14.2	7.8	5.2-12.3	57.6
14 days	13	68	20.0	42	28-66	12.8	7.7-21.3	8.9	6.0-12.6	58.4
15 days	9	67	19.4	47	24-61	12.0	7.6-22.3	8.4	5.9-12.6	58.3

tion between the length of attentive periods and the time required for incubation. The attentive periods average longer when incubation extends over 14 and 15 days than when it lasts only 12 or 13 days. Probably there is no direct causal relation between these two factors, as both are influenced by the lower temperature. The effect of temperature on attentive behavior is discussed above. This is not the place to analyze in detail the influence of air temperature on time required for incubation (Kendeigh 1940), but there is significance that in the one record with 12 days of incubation, the nest box was attached to the south side of a building where it received the full glare of the sun throughout the day. Readings taken inside the box showed that the temperature sometimes reached 100°F. in the middle of the day. The adult responded by shortening her attentive periods or staying away entirely for long intervals at a time. With the eggs maintained at an unusually high temperature during the inattentive periods, development of the embryo must have been considerably speeded, with a consequently shorter time required for their hatching.

Influence of male on the female's behavior. Since the great amount of variation in number and length of attentive and inattentive periods is not to be explained by age, by previous nesting experience, or by environmental factors such as temperature except when it becomes extreme, and since there is no direct correlation with length of time required for incubation, then it must be due to differences in inherent characteristics of the individual birds themselves or in the interrelations between the male and female constituting the pair. The innate physiological and psychological peculiarities of individuals cannot be analyzed further at this time, but the influence of the male over the female's behavior is considerable and may be the cause of some of the variation.

The male's influence is easily observed, but differences between males in the amount of this influence have not been put on a quantitative basis.

The male continues to have attentive and inattentive periods throughout the nesting cycle, although these periods are seldom as sharply defined as with the incubating female. Toward the end of her attentive period on the eggs, the male often approaches the box singing, and when the female hears him she often leaves at once. If the male should come too early, the female may persist on the eggs or may leave with what appears to be great reluctance. If she remains on the eggs, the male may leave and return a few minutes later. The occasional reluctance of the female to leave is shown in the following observations:

0932 hours—Female is on eggs. Male approaches box and sings for first time. Female gives a whining note but does not stir. The male sings a second time; the female repeats the whining note. The male sings a third time; the female raises her head and looks out. The male sings a fourth time; the female goes out onto the perch. The male sings a fifth time; the female leaves box.

0939 hours—The female returns as the male is still singing nearby, but he now stops singing and leaves.

When the female does not immediately appear in response to the male's invitation, he may alight on the perch and look into the box. If he sees her he quivers his wings excitedly. This behavior of the male is strong inducement for the female to leave and plays an important part in regulating the length of her attentive periods.

While the female is inattentive, the behavior of the male is variable. Commonly he stays near the nest box as if guarding it. He may sing more or less continuously, although often in a listless manner. Occasionally he may drop to the ground nearby and hunt for food. Once in a while, or regularly in the case of some males, he accompanies the female in her search for food. In such instances, he may or may not accompany her back to the box. If he has remained near the box, he sings more energetically when he sees her approaching and may fly out to meet her. If the female delays too long in her return, the male may start singing vigorously anyway and may even revert to his territory song to induce her to return. After she has entered the box, the male usually becomes quiet and flies off for an inattentive food-searching period of his own.

After a relatively short inattentive period the male again starts to sing, although usually not near the box. One set of observations on a single male gave six minutes for his attentive period and three minutes for his inattentive period. He may visit remote parts of his territory, inspect his other boxes, and may give his territory song. He has time to be occupied before returning to the incubating female, and this is a factor in his occasionally interesting a second female to start nesting at another box within his territory. Frequently, he gets concerned in these other activities and neglects to return to his female when she is due to leave on an inattentive period.

Although the attentive behavior of the male and female is thus synchronized, the timing is not perfect, and the female may leave before the male appears. In cases where the male deserts, the female maintains her usual periods without change. Therefore the presence of the male is not obligatory for the development of attentive behavior in the female. For the most part the male is obliged to fit his behavior to his mate's schedule, rather than the reverse.

Attentiveness is well established in the behavior of the female and must be grounded on fundamental, inherent characteristics. When frightened out of the box soon after an attentive period has begun, she will ordinarily return promptly when the source of the disturbance disappears. But if frightened out toward the end of an attentive period, she does not return until after her inattentive period is passed. This flux and ebb in her attentiveness is distinctly rhythmical and must depend upon a physiological or nervous property that is rhythmical on the same time schedule.

Relation between number and length of periods. The average number of attentive periods per day varies among different females (Table 6) from 24 to 70; the length of these attentive periods varies between the extremes of 6.7 and 22.3 minutes, and the length of the inattentive periods between 5.2 and 12.6 minutes. To determine what relation may exist between the different phases of attentive behavior, the records on length of attentive and inattentive periods, as given in Table 6, were averaged for each range of ten in number of periods per day (Table 10). It is at once apparent that as the number of periods per day increases there is a decrease in the length of both attentive and inattentive periods, and that the percentage of decrease in respect to the mean is greater in the attentive periods (+58 to —34) than in the inattentive periods (+ 35 to — 30). There is no significant variation in percentage of total

TABLE 10. Correlation of average number of periods per day with their average duration.

Average number per day	Number of records	*Attentive period* (min.)	*Attentive period* Percentage of mean	*Inattentive period* (min.)	*Inattentive period* Percentage of mean	Percentage of total time attentive
27.0	4	19.7	158	11.3	135	62.7
37.5	8	13.8	110	9.6	114	58.3
44.9	19	11.4	91	8.5	101	56.7
55.8	5	9.2	74	6.9	82	56.7
64.8	4	8.2	66	5.9	70	57.8

daylight time that the bird is active in regard to the number of periods per day.

There is also considerable variation in the number and length of attentive and inattentive periods in the same female on consecutive days

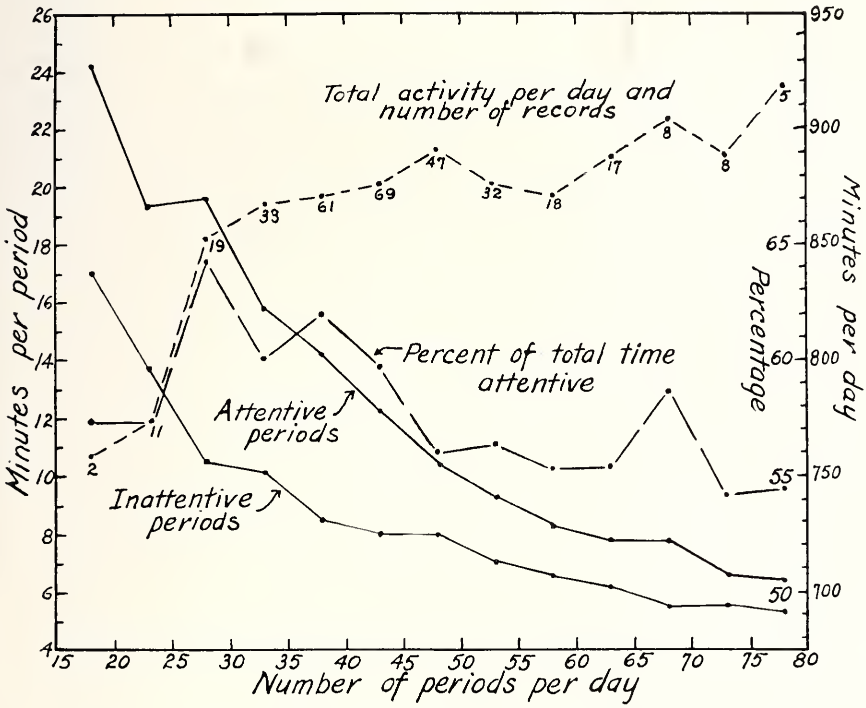

FIG. 6. Relation between different aspects of attentive behavior.

(Tables 4 and 5). In figure 6 the relation between number and length of periods is shown for averages of daily records irrespective of the female on which obtained, grouped in ranges of five periods per day. Although the length of attentive and inattentive periods decreases as the number of periods increases, the decrease is somewhat faster in the attentive periods than the inattentive. There is irregularity in the percentage of total time that the bird is attentive. The greatest percentage of attentiveness occurs when there are 28 to 43 trips per day. From 28 to 78 trips per day the trend in percentage of time attentive is a declining one. Why the percentage also declines at 23 and 18 trips per day is not clear.

The total time of attentive and inattentive activity per day increases with an increase in the number of periods and a decrease in their length. This increase is rapid in the lower ranges and then becomes more gradual and fluctuating. The difference in total activity on days with 18 and 78 periods amounts to over two and one-half hours. This is considerably more than the difference of 26 minutes of daylight between May 21 and June 21 and between June 21 and July 22 (Fig. 15) and hence cannot be explained by difference in the daily photoperiod. There is no relation between total daily activity and temperature (p. 43). Cloudiness may be a factor by affecting time of beginning and ending the day's activity. Perhaps also the number and length of periods is an index of the psychological or physiological state of the individual bird on a particular day. The more nervous the bird or the higher the pitch of its metabolic or physiological state, the more numerous and shorter are its periods, the earlier it begins activities in the morning and the later it ceases them in the afternoon.

There is also evident in figure 6 a positive correlation between the length of the attentive and inattentive periods. This relation is better shown when the average duration of each period is calculated for each range of ten minutes in the average daily duration of attentive periods. These calculations are as follows:

Range: 0-10 minutes; attentive period—7.9 minutes; inattentive period—7.5 minutes.

Range: 10-20 minutes; attentive period—13.8 minutes; inattentive period—8.5 minutes.

Range: 20-30 minutes; attentive period—22.3 minutes; inattentive period—10.8 minutes.

The attentive period varies in length considerably more than the inattentive periods. The extreme range in the length of the attentive period is 98 per cent of the mean of the three figures; the extreme range in the length of the inattentive period is only 37 per cent of the mean.

The analysis in this and preceding sections indicates that during incubation the length of the attentive period is very variable and the length of the inattentive periods is the least variable. Variations in the number of periods per day depend primarily on the length of the attentive periods. This is a statistical relationship. The relation between the length of the attentive and inattentive periods is probably a physiological one, however, since with shorter attentive periods, less rest and less food are required, while with longer attentive periods there needs to be more rest and more food. The duration of the attentive period is affected by air temperature and the individuality of the female. Probably there is a characteristic length of the attentive period for the species which is determined by heredity and is the result of evolution, and individual birds vary rather widely in their attentiveness around this figure as determined by their individual temperament, physiology, heredity, and as modified by the environment.

Brooding the Young

The female continues to brood the young after hatching, much as she incubated the eggs. The record of attentive periods becomes difficult to interpret, however, because the periods are often interrupted by the male coming with food for the young and because of the greater restlessness and activity of the female herself. The data compiled in Table 11 represent primarily the number and length of the periods spent in brooding. The attentive period, to be complete, should also include time spent in feeding the young as well as in brooding them. Brooding periods are nearly equivalent to attentive periods during the first one to three days after the young begin to hatch, as the amount of feeding is not great; but as the young get older, the amount of brooding becomes reduced and the rate of feeding is increased.

Attentive behavior is very irregular on the day that the young begin to hatch, as hatching may begin at any time and all attentive periods for the day, both before and after hatching, are averaged together. Hatching of the eggs normally occurs one at a time at intervals of a few hours, and may extend over two days. The most evident change to be noted, in comparison with attentive behavior during incubation for the same individuals, is the increase in number of periods per day and decrease in their length. The number of periods on the day of hatching increases 49 per cent, the attentive periods decrease in length 34 per cent, and the inattentive periods decrease 29 per cent. This increase in activity may be due in part to the excitement of the female but may also be due to an adjustment to the physiological needs of her newly hatched cold-blooded offspring.

The record of A94248 in territory 68 is of special interest. The male deserted this box before the young hatched, so the itograph record is uncomplicated and shows the brooding periods clearly. The first egg hatched on August 17 at 1030 hours, the second at 1445, the third at 1620, the fourth about 1700, and the fifth between 1330 and 1500 hours the next day. The number of brooding periods, beginning August 17, varied on consecutive days as follows: 48, 61, 75, 77, 72, 62, 49, 38. The total time per day spent at the nest varied: 529, 476, 525, 462, 382, 236, 211, 213 minutes. As indicated by this record, brooding ordinarily continues beyond the second day given in Table 11, but the registration of brooding time is only occasionally clear for the later days. B56490 brooded 57, 64, and 56 times on the third, fourth, and fifth days for totals of 371, 474, and 342 minutes. There is evidence in some records that brooding may continue to some extent until the young are ten days old.

An exceptional record is that for B96900 in territory 83 on the second day after hatching. The record indicates that the female spent relatively

Table 11. Brooding of young.

Female number	New (N) or return (R)	Year	Territory	Box	Number of young	Date of hatching	Temperature-recorder (TR) or itograph (I)	Number of periods	Brooding periods (min.)	Intervals (min.)	Number of periods	Brooding periods (min.)	Intervals (min.)	Number of periods	Brooding periods (min.)	Intervals (min.)
								0 Day (Hatching)			*1st Day*			*2nd Day*		
71653	N	1926	59	9	3	Aug. 4	TR	87	6.2	3.6	59	9.6	4.9	64	6.2	7.1
A94247	N	1927	65	9	4	July 18	TR	61	9.4	4.6	55	10.0	5.1	54	9.2	6.8
A94248	N	1927	68	30	5	Aug. 17	TR	48	10.4	6.4	...	...	...	...	...	...
A94248	N	1927	68	30	5	Aug. 17	I	49	10.8	5.7	61	7.8	5.4	75	7.0	4.3
B45348	N	1928	78	51	1	July 14	I	89	6.9	3.1	...	...	...	...	...	...
B45349	N	1928	73	74	5	June 12	TR	99	4.4	5.0	107	3.1	6.1	...	...	...
B56490	N	1929	86	25	4	June 21	TR	96	4.5	5.6	92	4.0	6.0	78	4.8	6.9
B96433	N	1929	85	30	3	July 19	TR	...	...	...	36	8.8	12.5	...	...	...
B96900	N	1929	83	75	4	July 29	TR	62	5.7	8.0	52	7.1	9.7	19	17.1	31.4
B97003	N	1929	81	47	2	June 29	TR	77	5.5	6.4	...	...	...	...	...	...
C68253	N	1930	96	25	5	July 3	TR	56	8.9	6.9	62	7.7	6.8	45	8.1	8.5
C68253	N	1930	96	25	5	July 3	I	53	10.6	5.6	...	...	...	...	...	...
C68257	N	1930	97	49	2	June 29	I	70	7.1	5.8	...	...	...	...	...	...
C68705	N	1930	93	43	4	July 18	TR	60	7.1	7.0	...	...	...	...	...	...
C94219	R	1932	120	53	6	June 25	TR	68	6.7	6.5	76	5.1	6.7	...	...	...
C94219	R	1932	120	53	6	June 25	I	70	7.5	5.2	...	...	...	...	...	...
L24987	N	1934	140	10	2	July 11	I	49	11.2	7.6	...	...	...	...	...	...
L24101	R	1936	166	21A	2	May 31	I	52	11.0	5.3	...	...	...	...	...	...
Average					3.5			69.6	7.5	5.8	66.7	7.0	7.0	55.8	8.7	10.8

few periods in the box, but these were exceptionally long and with long intervals between successive periods. The original recording shows great nervousness on the part of the bird during the brooding periods. She was up and down almost constantly. This was a hot day with maximum shade temperatures reaching 90° F. Since the box was exposed to the sun, temperatures inside the box were even higher. The heat produced a different response in the attentive behavior of the bird from that invoked during incubation, although during the middle of the day the bird remained away from the box entirely.

Since attentive behavior is similar on the first day of hatching and on the next two days, an average of all daily records except for the unusual one described above indicates typical behavior to involve 67 brooding periods, averaging 7.3 minutes each, spaced at intervals of 6.4 minutes. Brooding constitutes 52.9 per cent of the daytime activities, which is a lower percentage of time spent in this activity than the 58.2 per cent of the daytime spent in incubating the eggs.

Feeding the Young

Both adults may feed the young while in the nest; the female regularly does so unless disturbed, but the male often does not or may do so irregularly. There is no way, from the itograph record, to distinguish which sex enters the box nor to determine whether it feeds one young, several young, or none at all. Observations extending over many hours from peepholes in the back of boxes indicate that occasionally during the first few days the female may enter the box without feeding the young, but that later in nest life normally one, and only one, bird is fed on nearly every visit. As the young get older and larger, they may receive more food per feeding. However, and possibly also where the young are fed at a slow rate, they may receive more food each time. The data obtained are strictly on trips to the box, although there can be little doubt that they furnish a close approximation of the actual rate of feeding the young.

Table 12 is a detailed record of the total number of trips into the nest box from dawn to dusk each day, the number of young present, and which adult sex was observed active at the box during the day. Data for the day that the eggs began to hatch (marked "0") include visits to incubate the eggs as well as to brood and feed the first young to come out of the shell. Usually all young are hatched by the day marked "1st." When the female goes to the nest to brood, she usually brings food. If the young bird does not defecate after being fed, the female begins to brood immediately. When the young are very small, the female may swallow any excrement voided, but later she carries it out of the box and returns at once to brood, often without food. The itograph records this as two visits and they are counted as such, as they cannot be distinguished

TABLE 12. Record of number of trips to box per day during the nest life of the young. (See also Table 15 for description of nesting record of each female.)

Female	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips
	0 Day (Hatching)			*1st Day*			*2nd Day*		
664708	...	...	...	...	...	...	...	...	...
664751	FM	2	130	...	...	...	...	...	...
664751	...	...	...	...	...	...	...	...	...
A93513	FM	3	145	FM	5	190	FM	5	199
A94247	...	...	...	...	...	...	...	...	...
A94248	...	...	...	...	...	...	F	5	112
A94248	...	...	...	...	...	...	...	...	...
B5640	...	...	...	...	...	...	...	...	...
B5640	FM	5	209	...	...	...	...	...	...
B5640	...	...	...	...	...	...	...	...	...
B45348	...	...	...	FM	3	199	FM	3	260
B45348	...	...	...	...	...	...	...	...	...
B96001	FM	1	145	FM	2	165	FM	2	134
Unknown	...	...	...	...	...	...	...	...	...
C68253	...	...	...	...	...	...	...	...	...
C68253	...	...	...	...	...	...	...	...	...
C68254	...	...	...	...	...	...	...	...	...
C68257	...	...	...	F	3	107	F	3	124
C94216	...	...	...	...	...	...	...	...	...
C94219	...	...	...	...	...	...	...	...	...
C94331	...	...	...	...	...	...	...	...	...
F45942	...	...	...	...	...	...	...	...	...
F45942	...	...	...	...	...	...	...	...	...
F45947	...	...	...	FM	6	164	FM	6	160
F45947	FM	1	177	FM	3	220	FM	3	217
F58248	...	...	...	...	...	...	...	...	...
H18583	F	5	171	F	4	174	F	4	145
L24101	...	...	...	...	...	...	FM	4	191
L24101	...	...	...	FM	4	204	FM	4	263
L24101	FM	1	126	FM	2	164	FM	2	197
L24101	...	...	...	...	...	...	FM	6	138
L24987	FM	2	112	FM	2	147	FM	2	160
34-4445	FM	1	96	FM	1	73	FM	1	100
34-86072	...	...	...	FM	1	102	FM	1	99
35-13635	FM	5	153	FM	6	214	FM	6	220
35-13671	...	...	...	...	...	...	...	...	...

TABLE 12 *(cont.)*. Record of number of trips to box per day during the nest life of the young. (See also Table 15 for description of nesting record of each female.)

Female	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips
	3rd Day			*4th Day*			*5th Day*		
664708	...	...	...	...	...	...	F	2	285
664751	...	...	...	FM	5	223	FM	5	232
664751	F	?	83	...	...	...	F	1	113
A93513	FM	5	174	FM	5	210	FM	5	168
A94247	...	...	...	FM	4	201	FM	4	187
A94248	F	5	116	F	4	117	F	4	138
A94248	...	...	...	...	...	...	...	...	...
B5640	...	...	...	...	...	...	...	...	...
B5640	FM	5	276	FM	5	244	FM	5	271
B5640	...	...	...	...	...	...	...	...	...
B45348	FM	3	295	FM	3	271	FM	3	228
B45348	FM	7	185	FM	7	177	FM	7	259
B96001	FM	3	161	FM	3	152	FM	3	158
Unknown	...	...	...	...	...	...	...	...	...
C68253	...	...	...	...	...	...	...	...	...
C68253	F	5	155	F	5	149	F	5	233
C68254	...	...	...	...	...	...	...	...	...
C68257	F	3	104	Deserted		...	...	...	...
C94216	...	...	...	...	...	...	...	...	...
C94219	FM	6	237	FM	6	350	FM	6	373
C94331	...	...	...	...	...	...	...	...	...
F45942	...	...	...	FM	5	212	FM	5	213
F45942	...	...	...	...	...	...	...	...	...
F45947	FM	6	196	FM	6	187	FM	6	194
F45947	FM	3	214	FM	3	217	FM	3	210
F58248	...	...	...	...	...	...	...	...	...
H18583	F	4	140	F	4	125	F	4	139
L24101	FM	4	153	FM	4	184	FM	4	181
L24101	FM	4	260	FM	4	249	FM	4	235
L24101	FM	3	122	FM	5	167	FM	5	170
L24101	...	...	...	...	...	...	...	...	...
L24987	FM	2	165	FM	2	174	FM	2	172
34-4445	FM	1	105	FM	1	96	M	1	107
34-86072	FM	1	68	Destroyed		...	...	...	...
35-13635	FM	6	247	FM	6	252	FM	6	262
35-13671	...	...	...	...	...	...	...	...	...

Table 12 *(cont.)*. Record of number of trips to box per day during the nest life of the young. (See also Table 15 for description of nesting record of each female.)

Female	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips
	6th Day			*7th Day*			*8th Day*		
664708	...	...	...	F	3	294	...	...	...
664751	FM	5	263	M	5	377	M	5	391
664751	F	1	96	F	1	117	F	1	113
A93513	FM	5	174	FM	5	154	FM	5	174
A94247	FM	4	223	F	4	235	F	4	263
A94248	F	4	129	F	4	143	F	4	186
A94248	...	...	...	...	...	...	...	...	...
B5640	FM	3	176	FM	3	162	FM	3	171
B5640	FM	5	298	FM	5	270	FM	5	322
B5640	...	...	...	...	...	...	...	...	...
B45348	FM	3	279	FM	3	246	FM	3	335
B45348	FM	6	282	F	6	147	F	4	178
B96001	FM	3	213	FM	3	158	FM	3	198
Unknown	...	...	...	...	...	...	...	...	...
C68253	FM	5	178	FM	5	184	FM	2	112
C68253	F	5	246	F	5	191	F	5	174
C68254	FM	5	204	FM	5	263	FM	5	235
C68257	...	...	...	...	...	...	...	...	...
C94216	...	...	...	...	...	...	...	...	...
C94219	F(M?)	6	272	F(M?)	6	344	F(M?)	6	286
C94331	...	...	...	...	...	...	...	...	...
F45942	FM	5	245	FM	5	282	FM	5	273
F45942	...	...	...	...	...	...	...	...	...
F45947	FM	6	205	FM	5	241	FM	5	267
F45947	FM	3	201	FM	3	159	FM	3	233
F58248	FM	6	256	FM	6	307	FM	6	312
H18583	F	4	166	...	...	...	...	...	...
L24101	FM	4	181	FM	4	230	M	4	208
L24101	FM	4	272	FM	4	227	FM	4	226
L24101	FM	4	190	FM	4	199	FM	4	224
L24101	FM	5	167	FM	5	196	FM	5	231
L24987	FM	2	163	FM	2	147	FM	2	133
34-4445	Deserted		...	...	...	...	...	...	...
34-86072	...	...	...	...	...	...	...	...	...
35-13635	FM	6	262	FM	6	318	FM	6	281
35-13671	...	...	...	...	...	...	...	...	...

TABLE 12 *(cont.)*. Record of number of trips to box per day during the nest life of the young. (See also Table 15 for description of nesting record of each female.)

Female	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips
	9th Day			*10th Day*			*11th Day*		
664708	F	3	251	...	...	...	F	3	277
664751	M	3	289	M	1	116	Died	...	...
664751	Deserted		...	...	...	...	...	...	...
A93513	FM	5	204	FM	5	212	F	5	162
A94247	F	4	238	...	...	...	...	...	...
A94248	F	4	123	F	4	194	F	4	189
A94248	...	...	...	...	...	...	F	6	360
B5640	FM	3	198	FM	3	205	FM	3	238
B5640	FM	5	350	FM	5	349	FM	5	327
B5640	...	...	...	...	...	...	F	1	154
B45348	FM	3	297	FM	3	324	FM	3	290
B45348	F	2	131	F	2	173	F	2	210
B96001	FM	3	240	FM	3	180	FM	3	194
Unknown	...	...	...	...	...	...	M	3	209
C68253	FM	2	101	FM	2	97	FM	2	140
C68253	F	5	145	...	...	...	F	5	106
C68254	FM	5	281	FM	5	333	...	...	...
C68257	...	...	...	...	...	...	...	...	...
C94216	FM	5	217	FM	5	281	FM	5	227
C94219	F(M?)	5	346	F	5	365	F	5	327
C94331	...	...	...	...	...	...	...	...	...
F45942	FM	5	270	FM	5	263	FM	5	305
F45942	...	...	...	FM	3	210	...	...	...
F45947	FM	5	252	FM	5	298	FM	5	308
F45947	FM	3	226	FM	3	200	FM	3	190
F58248	...	...	...	FM	6	389	FM	6	396
H18583	M	4	263	Deserted		...	...	...	...
L24101	M	4	203	M	4	189	M	4	190
L24101	FM	4	223	FM	4	271	FM	4	322
L24101	FM	4	215	FM	4	272	FM	4	2[illegible]5
L24101	FM	5	253	FM	5	232	FM	5	254
L24987	FM	2	143	FM	2	219	FM	2	144
34-4445	...	...	...	...	...	...	...	...	...
34-86072	...	...	...	...	...	...	...	...	...
35-13635	FM	6	311	M	6	313	M	5	389
35-13671	FM	2	166	FM	2	178	FM	2	213

TABLE 12 *(cont.)*. Record of number of trips to box per day during the nest life of the young. (See also Table 15 for description of nesting record of each female.)

Female	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips	Sex feeding	Number of young	Number of trips	Hour of day young left nest
	12th Day			*13th Day*			*14th Day*			
664708	...	...	...	...	...	...	F	3	319	...
664751	...	...	...	...	...	...	...	...	...	...
664751	...	...	...	...	...	...	...	...	...	...
A93513	F	5	301	F	5	271	F	5	68	1130
A94247	...	...	...	...	...	...	...	...	...	...
A94248	F	4	152	F	4	145	F	4	132	...
A94248	F	6	294	F	6	333	F	6	200	...
B5640	FM	3	253	...	...	...	...	...	...	...
B5640	FM	5	356	FM	5	308	FM	5	241	...
B5640	...	...	...	F	1	150	F	1	163	...
B45348	FM	3	271	...	...	...	...	...	...	...
B45348	F	2	227	F	2	284	F	2	217	...
B96001	FM	3	179	FM	3	128	FM	3	103	...
Unknown	M	3	156	M	3	392	M	3	206	...
C68253	FM	2	163	FM	2	198	FM	2	145	...
C68253	F	5	116	F	5	122	F	5	182	...
C68254	...	...	...	...	...	...	...	...	...	...
C68257	...	...	...	...	...	...	...	...	...	...
C94216	FM	5	206	FM	5	201	FM	5	241	...
C94219	F	5	291	F	5	280	F	5	272	...
C94331	FM	6	491	FM	6	460	FM	6	400	...
F45942	FM	5	257	FM	5	223	FM	5	286	...
F45942	FM	3	339	FM	3	280	FM	3	307	...
F45947	FM	5	308	FM	5	331	FM	5	328	...
F45947	FM	3	237	FM	3	206	FM	3	219	...
F58248	FM	6	433	FM	6	405	FM	6	404	...
H18583	...	...	...	...	...	...	...	...	...	...
L24101	M	4	329	M	4	262	M	4	321	...
L24101	FM	4	317	FM	4	363	FM	4	377	...
L24101	FM	4	276	FM	4	266	FM	4	238	...
L24101	FM	5	244	FM	5	314	FM	5	286	...
L24987	FM	2	129	FM	2	130	FM	2	179	...
34-4445	...	...	...	...	...	...	...	...	...	...
34-86072	...	...	...	...	...	...	...	...	...	...
35-13635	M	4	340	M	4	351	M	3	252	...
35-13671	FM	2	175	FM	2	192	FM	2	123	1752

TABLE 12 *(cont.)*. Record of number of trips to box per day during the nest life of the young. (See also Table 15 for description of nesting record of each female.)

Female	Sex feeding	Number of young	Number of trips	Hour of day young left nest	Sex feeding	Number of young	Number of trips	Hour of day young left nest
		15th Day				*16th Day*		
664708	Young left		. . .	. . .	. . .	. . .	. . .	. . .
664751	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
664751	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
A93513	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
A94247	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
A94248	No further record			. . .	. . .	. . .	. . .	. . .
A94248	F	6	245	. . .	F	6	368	. . .
B5640	FM	3	101	1158	. . .	. . .	. . .	. . .
B5640	FM	5	126	1250	. . .	. . .	. . .	. . .
B5640	FM	1	110	. . .	FM	1	149	. . .
B45348	FM	3	249	. . .	FM	3	115	1223
B45348	F	2	258	. . .	F	2	224	. . .
B96001	FM	3	148	. . .	FM	3	172	. . .
Unknown	M	3	28	1130	. . .	. . .	. . .	. . .
C68253	FM	2	200	. . .	FM	2	204	1920
C68253	F	5	75	1307	. . .	. . .	. . .	. . .
C68254	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
C68257	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
C94216	FM	5	129	1130	. . .	. . .	. . .	. . .
C94219	. . .	. . .	. . .	. . .	Young left		. . .	. . .
C94331	FM	6	326	. . .	FM	6	384	. . .
F45942	FM	5	257	. . .	FM	5	38	0730
F45942	FM	3	171	1030	. . .	. . .	. . .	. . .
F45947	FM	5	309	. . .	FM	5	344	. . .
F45947	F	3	95	1215	. . .	. . .	. . .	. . .
F58248	FM	6	450	. . .	FM	6	488	. . .
H18583	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
L24101	M	4	240	. . .	M	4	234	. . .
L24101	FM	4	297	. . .	FM	4	301	. . .
L24101	FM	4	278	. . .	FM	4	285	. . .
L24101	FM	5	256	. . .	FM	5	324	. . .
L24987	FM	2	153	1525	. . .	. . .	. . .	. . .
34-4445	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
34-86072	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
35-13635	M	3	259	. . .	M	3	198	. . .
35-13671	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .

TABLE 12 *(cont.)*. Record of number of trips to box per day during the nest life of the young. (See also Table 15 for description of nesting record of each female.)

Female	Sex feeding	Number of young	Number of trips	Hour of day young left nest	Sex feeding	Number of young	Number of trips	Hour of day young left nest
		17th Day				*18th Day*		
664708	...	...	...	...	...	...	...	...
664751	...	...	...	...	...	...	...	...
664751	...	...	...	...	...	...	...	...
A93513	...	...	...	...	...	...	...	...
A94247	...	...	...	...	Young left		...	...
A94248	...	...	...	...	...	...	...	...
A94248	F	6	135	1130	...	...	...	...
B5640	...	...	...	...	...	...	...	...
B5640	...	...	...	...	...	...	...	...
B5640	Young died		...	...	...	...	...	...
B45348	...	...	...	...	...	...	...	...
B45348	F	2	205	...	F	2	178	...
				(*19th Day*:	F	2	119	1230)
B96001	FM	3	25	0705	...	...	...	...
Unknown	...	...	...	...	...	...	...	...
C68253	...	...	...	...	...	...	...	...
C68253	...	...	...	...	...	...	...	...
C68254	Young left		...	...	...	...	...	...
C68257	...	...	...	...	...	...	...	...
C94216	...	...	...	...	...	...	...	...
C94219	...	...	...	...	...	...	...	...
C94331	Young left		...	...	...	...	...	...
F45942	...	...	...	...	...	...	...	...
F45942	...	...	...	...	...	...	...	...
F45947	FM	5	376	...	FM	5	66	0630
F45947	...	...	...	...	...	...	...	...
F58248	FM	6	152	1000	...	...	...	...
H18583	...	...	...	...	...	...	...	...
L24101	M	4	129	1600	...	...	...	...
L24101	FM	4	77	0629	...	...	...	...
L24101	FM	4	210	1911	...	...	...	...
L24101	Young left		...	...	...	...	...	...
L24987	...	...	...	...	...	...	...	...
34-4445	...	...	...	...	...	...	...	...
34-86072	...	...	...	...	...	...	...	...
35-13635	M	3	18	0900	...	...	...	...
35-13671	...	...	...	...	...	...	...	...

from the record made when the male feeds the young just before the female arrives.

When the itograph record extends to the day on which the young leave the box, the time of their leaving is indicated and the number of visits is just for the portion of the day preceding their flight. When the itograph record is not complete, notation is made anyway as to the day on which the young leave.

Changes with growth of young. Ten records made by seven females and nine males are fairly complete in that they begin within the first two days after hatching and run continuously through at least thirteen full days of recording (territory 65—box 51; 68-30; 88-53; 119-49; 121-49; 140-10; 146-49; 153-25; 160-49; 164-49). The data in these records are averaged for each day to correlate variations in number of trips to the nest with the increasing age of the young (Table 13).

Omitting the day of hatching, the number of visits per day increases as the young birds get older and require more and more food and less and less brooding (Table 13). When plotted (Fig. 7), this increase is seen to follow a sigmoid growth curve. From the first to the fifth days the increase amounts to only about eight more trips per day. There was an

TABLE 13. Average number of trips to nest on each day of nestling life.

Day	Number of records	Number of young in nest	*Number of trips* Per nest	Per young bird	Corrected number of trips to nest	Percentage of mean number (217)
0 (Hatching)	(6)	(2.2)	(143)	(65)	. . .	. . .
1	8	3.8	184	48	184	85
2	10	3.9	185	47	184	85
3	10	4.1	181	44	185	85
4	10	4.2	191	45	187	86
5	10	4.2	189	45	192	88
6	10	4.1	200	49	197	91
7	10	4.0	199	50	206	95
8	10	4.0	213	53	210	97
9	10	4.0	216	54	218	100
10	10	4.0	235	59	225	104
11	10	3.9	230	59	233	107
12	10	3.8	257	68	240	111
13	10	3.8	246	65	246	113
14	9	3.6	240	67	251	116
15	6	3.8	255	67	255	118
16	6	3.8	255	67	256	118

increase in the average number of young in the nest from 3.8 to 4.2 during this time. This is the period when the young require frequent brooding to maintain their body temperature. During the early part of this period the unused yolk absorbed by the embryo from the egg may furnish considerable energy. Likewise, during these early days, the young birds are so small that the food brought by the parents on one visit furnishes rela-

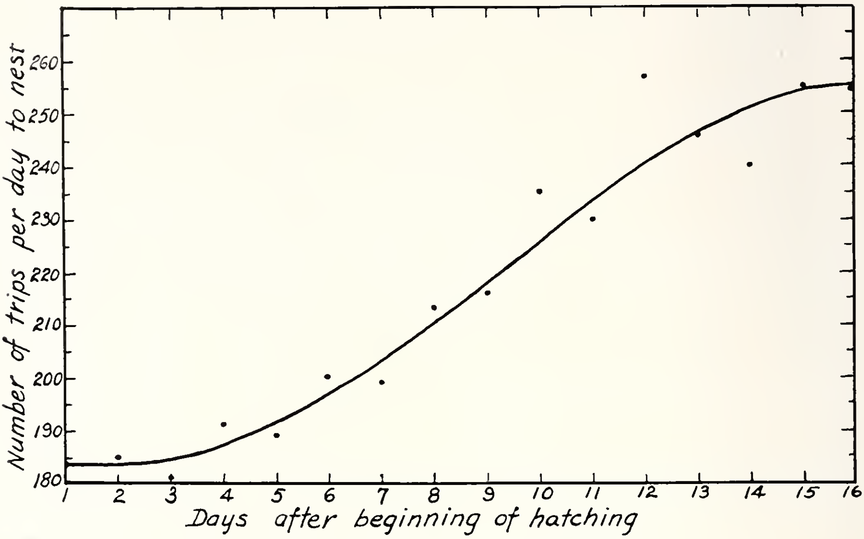

FIG. 7. Increase in feeding rate of young with increasing age.

tively more nourishment than it will when they have increased eight to ten times in size. Beginning with the sixth day, feeding becomes more frequent, and the daily increase averages about 6.8 visits or 1.7 more meals per bird until the thirteenth day— after which the daily increase becomes much less.

Because of the irregular fluctuations in the data from day to day, a column of corrected values for number of visits each day is given in Table 13 which were read off from the smoothed curve shown in figure 7. Probably this represents more nearly what the values would be for each day if a much larger number of records were available. The mean number of visits per day for the first through the sixteenth days is 217, or 56 per bird. On the first day after hatching, the number of visits is only 85 per cent of this mean. On the day before the young leave the box the number of visits has increased to 118 per cent of this mean. Since the period of daily activity is approximately 15 hours, the feeding rate averages 14.5 per hour or 3.7 per bird per hour.

Observations of others on the rate of feeding of nesting house wrens have produced varying results: 24.9 per hour (Shirling 1927), 23 per hour (Judd 1902), 19.5 per hour (F. E. L. Beal MS), 16.6 per hour (Common 1948). During 65 hours 4 minutes of observation during seven of the first nine days after hatching, Jones (1913) reports the young were visited by their parents 667 times, 560 times by the male and 107 times by the female. This is at the rate of 10 times per hour or about 150 times per day. The female spent much of her time brooding, and the male brought food to the female who would then feed the young. L. O. Howard (1890) calculated that the young were each fed 1,500 insects while in the nest. Densmore (1925) conducted an all-day observation of both adults feeding a brood of five young that were about seven days old. The adults made 491 trips to the nest. A most remarkable record is reported by Bayliss (1917), that in 15 hours 45 minutes on one day a brood of probably seven young, 13 to 14 days old, was fed 1,217 times by the male, who was caring for them alone. Probably this record is in error as it means a continuous rate without rest averaging 1.6 times per minute throughout the period. The highest number of feedings per day recorded in the present investigation is 491, which happens to be identical to that recorded by Densmore.

TABLE 14. Correlation of feeding rate with number of young in brood.

		Average number of trips per day						
Average number young per nest	Number of records	At nests with one adult feeding	At nests with both adults feeding	At all nests	Per nest per bird	Corrected number per nest	Percentage of mean number (213)	Corrected number per bird
1.0	4	121	110	115	115	115	54	115
2.2	3	. . .	. . .	163	74	156	73	78
3.0	8	208	227	220	73	197	92	66
4.0	8	179	249	222	56	237	111	59
5.1	10	168	261	252	49	272	128	54
6.0	3	309	359	326	54	300	141	50

Relation to number of young in nest. To compare the behavior of the adults at different nests having different numbers of young in the brood, all the data for each recording in Table 12 were averaged according to the number of young in the brood. Since there is a great variation in the number of days' recording at each nest and in the average age of the young, the average number of trips obtained for each record was corrected for the age factor. This was done by dividing the average number of visits by the percentage of the mean, given in Table 13, corresponding to the average age of the young during the time the recording was made. This permitted analysis of the data for the influence of other factors.

Table 14 shows that with an increase in the number of young there is an increase in the number of trips to the nest each day, as would be expected with more young to feed. In figure 8, the smoothed line indicates that the increase in trips to the nest is almost linear. Although the three records of broods with six young show a very high rate of feed-

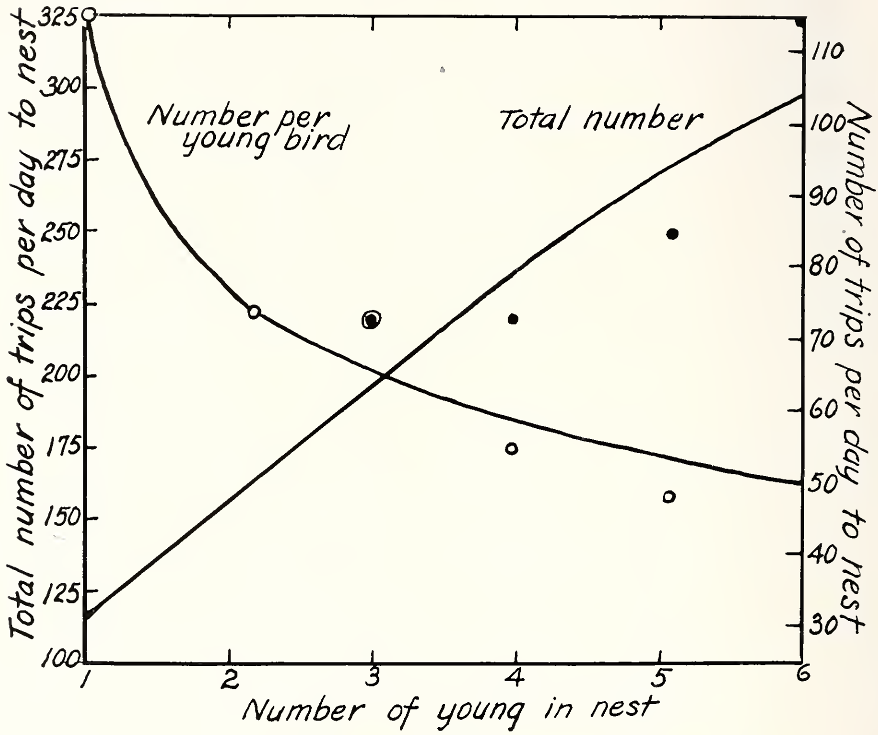

FIG. 8. Variation in feeding rate with number of young in brood.

ing, the more reliable data for broods of five young, based on ten records, makes it probable that the rate of increase in feeding obtained in broods with one to four young is not maintained in broods with five or more young. House wrens frequently raise seven young in a brood and occasionally eight or even nine, and it is very likely that the curve of increase in number of visits to the nest per day reaches an upper asymptote. Values have been read from this curve to give the corrected number of trips per nest, given in Table 14. The increase in number of trips to the nest per day is from 54 per cent of the mean with one young to 141 per cent of the mean with six young.

In spite of the increase in total number of visits, each young bird does not receive the same amount of attention when several young are present as when there are only a few. The progressive decline in number of visits per bird with increase in their number is shown in Table 14. Corrected values for the number of visits per bird per day have been read from the smoothed curve in figure 8. With six birds in the nest, each young would, according to these data, be fed less than half as often as when there was only one present. However, where there is only one young in the brood, it may not be fed on every visit of an adult to the nest. When the young bird is surfeited with food, its swallowing reflex becomes sluggish and it is unable to accept more food. The adult ordinarily consumes this rejected food. Under these conditions, the adult may visit the nest several times in the course of a day without actually feeding the young bird. In the case of large broods of young, the adult usually feeds the most eager young, and it rarely happens that she is unable to feed a young bird on each visit. The number of times that the young are fed is determined in part by their eagerness for food and the stimulus that they offer their parents, and in part by the ability and willingness of the parents to hunt food for them.

If the willingness or ability of both parents were identical and the only factors involved, one would expect that the young would be fed twice as often when both sexes participated as when only one did. This, however, is not the case. With only one young in the brood there was no significant difference in number of trips per day whether both adults were feeding or only one. No comparisons are available with broods of two young. With three young in the brood the rate of feeding was higher by 9.1 per cent in nests where both adults fed than in nests where only one did. In nests with four young the increase was 39.1 per cent; in nests with five young, 55.4 per cent; but in nests with six young, only 16.2 per cent. Probably the small percentage increase with broods of six young is not representative, as there are only three records available. The average increase with broods of three, four, and five young is 35 per cent.

It is apparent that with only one young in the brood, one adult can easily care for it alone. With three or more young in the brood, help from the other adult is more urgent and is more effective. When feeding alone, one adult increases its feeding rate with three to five young in the brood 53 per cent over its rate with only one young in the brood. With both adults feeding, the increase amounts to 103 per cent. The female is usually the more attentive sex in caring for the young, and if the male aids at all, his care of the young is simply added on to that of the female. But when the female deserts and the male takes over all the care of the young, he applies himself fully as assiduously as did the

Table 15. Behavior of individual birds while caring for their young in the nest.

Female	New (N) or return (R)	Male	New (N) or return (R)	Year	Territory	Box	Date beginning to hatch	Number days record	Days female active	Days male active	Average number of young	Average age of young in days	Average number trips to nest per day	Number of trips corrected for age of young	Number of trips corrected for age and number of young
664708	N	?	...	1928	81	75	July 15	5	5	0	2.8	9.2	285	279	317
664751	N	A94249	R	1928	75	6	July 4	7	3	7	4.1	7.0	270	284	251
664751	N	A94249	R	1928	75	10	Aug. 8	5	5	0	1.0	5.8	104	116	215
A93513	N	A94249	N	1927	65	51	July 24	13	13	10	5.0	7.0	199	209	163
A94247	N	A94249	N	1927	65	9	July 18	6	6	3	4.0	7.0	224	236	213
A94248	N	A94242	N	1927	63	6	July 10	6	6	0	6.0	13.5	300	263	187
A94248	N	?	...	1927	68	30	Aug. 17	13	13	0	4.2	8.0	144	148	130
B5640	R	B96418	N	1929	92	70	July 26	7	7	7	3.0	9.0	200	200	217
B5640	R	B97203	N	1931	109	74	June 12	12	12	12	5.0	8.5	301	307	240
B5640	R	?	...	1931	112	80A	July 25	5	5	0	1.0	13.8	145	126	233
B45348	N	A38398	R	1928	78	51	July 14	13	13	13	3.0	7.2	273	287	312
B45348	R	A38398	R	1930	98	51	June 3	16	16	4	3.6	10.5	208	198	192
Unknown	...	A93433	R	1929	91	59	July 22	4	0	4	3.0	13.0	241	213	232
B96001	N	B56491	N	1929	88	53	July 27	16	16	16	2.9	8.5	168	171	190
C68253	N	C68911	N	1930	96	25	July 3	11	11	11	2.5	10.5	157	150	183
C68253	R	C68801	R	1931	106	25	June 8	11	11	0	5.0	8.4	165	168	131
C68254	N	B97018	R	1930	97	53	June 11	5	5	5	5.0	8.0	263	271	212
C68257	N	B97018	R	1930	97	49	June 29	3	3	0	3.0	2.0	112	132	143
C94216	N	C94215	N	1931	105	3A	June 16	6	6	6	5.0	11.5	229	210	164

C94219	R	F45994	N	1932	120	53	June 25	12	12	7(?)	5.5	8.5	312	318	237
C94331	N	C68252	R	1931	111	80A	June 8	5	5(?)	5	6.0	14.0	412	355	252
F45942	N	F45946	N	1932	117	25	June 5	12	12	12	5.0	9.5	257	252	197
F45942	R	H18582	N	1933	128	25	June 8	4	4	4	3.0	12.2	284	256	278
F45947	N	C68910	R	1932	119	49	June 6	17	17	17	5.4	9.0	263	263	198
F45947	N	F45763	N	1932	121	49	July 28	14	14	14	3.0	7.5	211	220	239
F58248	N	C68910	R	1933	129	49	June 10	10	10	10	6.0	11.2	384	359	255
H18583	N	H18580	N	1933	126	10	June 13	7	6	1	4.0	4.3	165	190	171
L24101	R	L24996	N	1934	146	49	July 15	16	16	16	4.0	8.5	275	281	253
L24101	R	L24956	R	1935	153	25	June 8	15	6	15	4.0	9.0	220	220	198
L24101	R	L24996	R	1935	160	49	July 11	16	16	16	3.8	8.5	219	223	208
L24101	R	L24949	R	1936	166	21A	May 31	12	12	12	5.1	10.2	241	232	180
L24987	N	L24993	N	1934	140	10	July 11	14	14	14	2.0	7.5	158	165	226
34-4445	N	34-86085	N	1935	154	25	July 25	5	4	5	1.0	3.0	96	113	209
34-86072	N	34-86085	N	1935	154	21A	July 18	3	3	3	1.0	2.0	90	106	196
35-13635	N	35-13634	N	1936	164	49	June 16	16	9	16	5.1	8.5	279	85	221
35-13671	N	35-13670	N	1936	167	25	July 17	5	5	5	2.0	11.0	185	173	237

female. This is shown in a few cases in Table 12, particularly in the records of females 664751 (first), Unknown, L24101 (second), and 35-13635. The male will not brood nor will he stay on the nest overnight, so the young must be fairly well grown if they are to survive.

Relation to length of nestling period. With the young birds in large broods receiving individually less food per day, their development should be slower and a longer time required of them to remain in the nest before flight. In none of the four cases with only one young in the nest did the bird become fledged. One of the nests was destroyed by a snake; in two nests the adult deserted; in the fourth nest where a nestling long-billed marsh wren had been substituted for the house wren, the young bird died. In 10 of the 11 nests with two and three young present and receiving food about 73 times per day each, the average duration of nest life was 15.3 days. In 18 of the 21 nests containing four, five, and six young and when the young were fed about 49 times per day each, the average nestling period was 16.6 days or one and one-third days longer than in the small broods. Thus the rate of maturing of the young depends in part on the amount of food that they receive, which in turn depends on whether one or both adults are feeding and their energy and ability to do so.

Relation to other factors. To analyze the data for possible influence of other factors, the figures giving the number of visits to the nest corrected for differences in the age of the young were further corrected for the number of young in the nest (Table 15), using the percentages of the mean given in Table 14.

These data were then grouped according to whether the young hatched before July 1 or after July 1 to determine if change in rate of feeding occurred with the advance of the nesting season. Many females have second broods in July, and July is usually hotter than June. An average of 16 records for May and June gave 204 trips per day; a similar average of 20 records for July and August gave 221 visits per day. This difference is small and not statistically significant. A few records on the same females nesting in both periods showed no consistent differences.

The data were next analyzed to determine whether birds nesting during the first year behaved differently than when renesting in later years. Twenty-two records where the female was in her first nesting season gave the same average number of visits per day as 10 records for return females. Similarly, 17 records where the male was a new bird gave the identical average as 13 records when the male was a return bird. Apparently, with each sex this work is performed with the same efficiency the first time it is done as in later years.

It proved impossible to detect any significant influence of weather on the rate of feeding. The detailed analysis is not here presented. Since the young rarely hatch before the first of June, the temperature does not fall sufficiently low to affect them. Very high temperatures are energy-depressing on adult birds, but this is counterbalanced by the insects, on which they feed, which are then most active, abundant, and easy to find. Since the adult female does not need to brood the young during hot weather, she can seek out shaded areas for comfort, and her rate of feeding is not affected. The adults continue to feed the young at a normal rate during rainstorms, although they may be temporarily halted during very severe downpours. Cloudy weather, fog, and wind furnish no detectable handicaps of consequence.

Variations in the doubly corrected values for number of visits per day to the nest, given in Table 15, must be due to individual peculiarities on the part of the birds themselves, as they are not to be explained by any known influence of external factors. The mean of the 36 records is 213, with a standard deviation of 42 and a coefficient of variability of 20.

This variability is greater than what it is in the average behavior of an individual pair of birds at different times. There are listed in Table 15 eight females with from two to four records obtained either in the same season or in different years. Average values for number of visits per day for these females and their mates range from 156 in C68253 to 252 in B45348. Although average values for different individuals cover the whole range of variations for the species, yet the level of activity of each female is relatively fixed. In the case of no individual is the coefficient of variability as large as the variability of 20 given for the species as a whole. The average coefficient of variability for the eight birds is 13 ± 5. In B5640 with three records over three years it is only four; in L24101 with four records over three years it is 13; in the other birds, with two records each it ranges from 8 to 18.

How much influence the male's activities exerted in these comparisons is difficult to assess. In most instances the male was active at the nest throughout the nestling period, although there is no way of estimating what proportion of total visits with food was his share. In Table 14 above, it will be noted that on the average, two birds at a nest caused an increase of 28.8 per cent in the number of visits compared with the activity of one bird. When the total number of visits per day are reduced by this amount or by the proportion of this amount corresponding to the number of days when the male was active at the nest, there is no great change to be noted in the variability of the records between individuals. One arrives at the same conclusions. The cause, then, of these differences between individuals in average rate of feeding must lie in the innate psychological or physiological constitution of the birds themselves.

Attentive periods. When both male and female actively feed the young, the itograph record cannot be analyzed for attentive and inattentive periods because the trips of the two sexes cannot be distinguished. There are a number of records, however, where only one sex did all the feeding (Table 12). A close study of these records shows that frequently single feedings occur regularly at definite intervals over periods from a few minutes to an hour. However, it is much more common to have the feedings occur in groups with intervals between when few or no feedings of the young occur. When trips to the nest or feedings occur one immediately after the other, this may represent an attentive period, and the intervals between groups of feedings may be the inattentive period. The number of feedings in a group varies considerably, as shown both by the itograph records and from observations at the nest. Where there are isolated trips or groups of only two, these may not indicate the full length of the attentive period. Very commonly all the young are fed consecutively so that the number of visits in a group corresponds to the number of young, after which there is a pause. Occasionally more visits are indicated in a group than the number of young in the brood so that the young are fed more than once in a single attentive period, but this is not common. The groupings show the best when the appetite and eagerness of the young for food synchronizes with the attentive behavior of the adult. Because the young may often have their appetites fully satisfied while the adult continues to be attentive, or at other times the adult may lose interest temporarily in them before they are fully satiated, these groups of feedings are not very satisfactory indicators of the attentive behavior of the adult. Because of this, little attempt has been made to measure them except in the case of male 35-13634, at box 49, territory 164, in 1936. Beginning June 26 and until the young flew on July 3, his "attentive periods," as indicated by the grouping of visits to the box, averaged 99 per day and were 4.4 minutes in length; spaced at intervals, his "inattentive periods" were 4.9 minutes. Actually the time spent by the adults in searching for food for the young, if it were known, should be added to the period at the nest and subtracted from the period away from the nest to give the true length of the attentive and inattentive periods.

Undoubtedly another reason that periodicity of the attentive behavior is not better expressed is that the adults do some feeding intermittently while looking for food for the young. They are particularly apt to consume insects or insect larvae which are too small, too large, or not otherwise suitable for the young. The periodicity therefore tends to break down on its own accord and is not of as obvious an importance as during the incubation of the eggs. There is reason to believe, however, that a skeletal framework of periodicity persists even though it is not subject to as exact measurement.

There is some evidence that attentive periods on the part of the adults persist even after the young leave the box. Observations are difficult as the young, accompanied by a parent, move through the bushes and tangles, but ordinarily each time a young bird is approached by an adult with food it calls out vigorously. By timing these sound responses of the young, 15 attentive periods during the first week after the young abandoned the nest averaged 7.6 minutes in length and 20 inattentive periods between groups of feedings averaged 5.7 minutes. The rate of feeding averaged once every 3.1 minutes for the total time involved. After the first week the attentive periods begin to shorten and the inattentive periods to lengthen until the young become entirely independent of their parent for food between 10 and 15 days after leaving the nest. In certain respects the gradual manner in which the attentive behavior of the adults is lost at the end of the nesting cycle is just the reverse of the manner in which it is acquired at the beginning, as the eggs are laid and incubation develops.

Daily Rhythm in Attentive Behavior

To trace variations in activity during the daylight hours, data were compiled for each hour on number of visits to the nest and number of minutes spent at the nest. The data were plotted on the even hour as the time interval extended in each case from one half-hour to the next half-hour. Behavior at night will be given separate treatment. Eastern Standard Time is used.

Males. In figure 9 are two curves showing hourly variations in activity of the male before he attains a mate. The curve showing "ordinary activity" involves insertion of sticks into the box and inspection tours. It is based on averages of 29 daily records on 18 different individuals

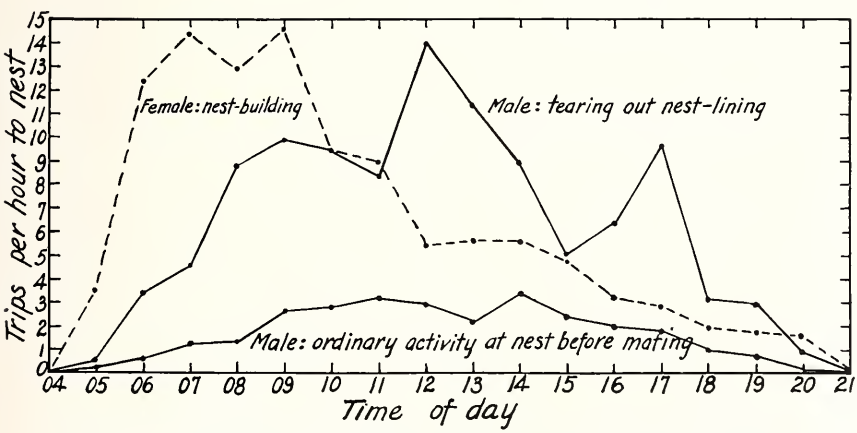

Fig. 9. Daily rhythm of adult activity at nest before eggs are laid.

obtained with the itograph. The curve of males' "tearing out nest lining" is an average of 15 days' records with the itograph on eight males and is concerned with preparing the nest for a second nesting after completion of a first. Both curves show an increase in activity in the morning reaching a peak in the middle of the day and followed by a decrease in the afternoon. Neither of these curves shows the total activity of the male as the frequency and vigor of singing were not measured. It is quite possible that a curve of singing activity would vary more or less inversely with number of visits to the nest and with a peak in early morning. In a study of the European wren, *T. t. troglodytes,* Clark (1949) found that the male began to sing 30 to 40 minutes before sunrise and to maintain a high level of song output for five or six hours, after which singing was reduced for the rest of the day. In April there was a well-marked afternoon song period, but this became less marked in May and June and disappeared in July and August.

Nest building by female. With the arrival of the female and her insertion of nest lining the male's visits decrease, and in many instances, he may not enter the box again until the young hatch. The curve of nest building in figure 9 is largely but not entirely representative of the female's activity. She becomes very active soon after daybreak and continues so until the middle of the morning, then decreases her activity during the rest of the day. This curve is based on 28 days of itograph records on 13 individuals.

Egg-laying. The egg-laying phase of nesting is one of rapid change in attentive behavior with the progressive establishment of full incubation. As shown earlier in this paper, the establishment of this behavior proceeds at a different pace when five eggs are laid than where there are six eggs in a set. Hence the data were averaged separately for each day and separately for the two sets of different sizes. All the available data obtained both with itograph and temperature-recorder were averaged, and these varied from four days' record for one curve to 11 days' record for another. Since the fluctuations and amount of behavior on the days that the first and the second eggs were laid were nearly identical in both five-egg and six-egg sets, they were combined into a single curve (Fig. 10). The females usually spend the night in the box so the maximum time shown at the nest is in the early morning and evening hours. Otherwise, the shape of this curve is similar to that of the female while nest building, in that it shows a progressive decline from mid-morning through the afternoon.

For those females which lay six eggs in a set, the curve of activity for the day the third egg is laid is so nearly the same as the curve for the first two days that it was omitted from the figure. A change begins on the day the fourth egg is laid. Somewhat more time is spent on the nest in the morning, and considerably more time is spent at the nest in the afternoon than during the first three days. Further increases in attentive time occurred with the laying of the fifth and sixth eggs. With the sixth egg, the last one laid, the daily rhythm curve coincides with the general curve for the incubation behavior that follows.

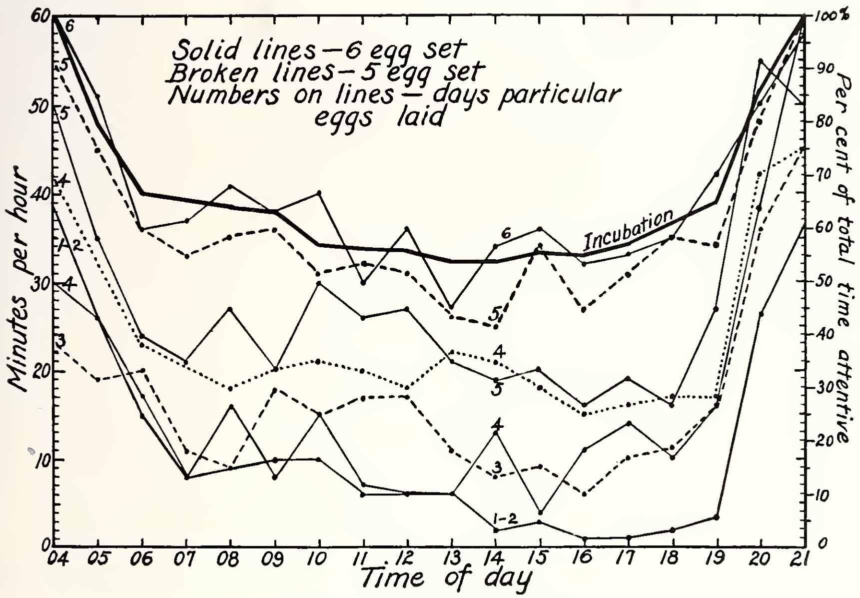

Fig. 10. Daily rhythm of activity during the egg-laying period.

With those females that lay five-egg sets, the curve of activity on the day of laying the third egg more nearly coincides with the curve for the fourth day in the six-egg set than with the first and second days. Likewise the activity on the fourth day of egg-laying in the five-egg set agrees with the fifth day in the six-egg set, and the day the last or fifth egg in the five-egg set is laid corresponds to, but is slightly lower, than the curve of full incubation behavior first obtained with laying the sixth egg in the six-egg set. All the curves show agreement in indicating greater attentiveness at the nest in the morning and a decrease in attentiveness during midday or afternoon.

In Table 16 the number of attentive periods begun each hour is averaged separately for the morning and the afternoon. This is of different significance than the actual number of minutes spent in attentiveness each hour. In general, the number of periods begun each hour is considerably greater in the morning than in the afternoon during the first few days. Beginning with the fourth day, there is still a difference between morning and afternoon but the difference becomes very much less. Apparently attentive behavior develops more easily in the morning and is more retarded in the afternoon. The actual deposition of the egg in the nest occurs during either the first attentive period in the morning or very soon afterwards. This attentive period may sometimes be longer than usual but often it is not. Normally the periods are longer at this time anyway, compared with midday, even when no egg is laid, and the actual deposition requires a very short time when the egg is ready.

TABLE 16. Number of periods per hour during egg laying and incubation.

Day	*0600 — 1200 hours*			*1300 — 1900 hours*		
	5-egg sets	6-egg sets	All sets	5-egg sets	6-egg sets	All sets
First	...	...	1.7	...	...	0.3
Second	...	...	1.3	...	...	0.5
Third	1.7	0.9	1.4	0.9	0.4	0.7
Fourth	2.1	1.1	1.8	1.9	0.7	1.5
Fifth	2.7	1.9	2.4	2.6	1.3	2.2
Sixth	...	2.8	...	...	2.2	...
Incubation	...	...	3.2	...	...	2.9

Incubation. To analyze the daily rhythm in attentive behavior of the female during incubation, all the data available were averaged separately for the first day of incubation (14 records on 14 birds), fifth day (22 records on 19 birds), ninth day (24 records on 22 birds), and last day before hatching (23 records on 21 birds). Since separate curves drawn from these data had the same form and characteristics, the four sets of data were again averaged and plotted to give the curves shown in figure 11. Records were combined from both itograph and temperature-recorder.

The curve of attentiveness begins and ends at 60 minutes per hour as all birds spend the night on the nest during incubation. Time spent on the eggs is fairly constant from 0600 to 0900 hours, when a decline begins that persists until about 1400 hours, after which there is a gradual increase in attentiveness until 1900 hours. The curve then rises rapidly as the birds start their night's stay on the eggs. The actual differences from hour to hour are small in number of minutes, with the extreme minimum at 1300 and 1400 hours being only about eight minutes less than the maximum at 0600 hours, although this difference amounts to about 20 per cent of the maximum amount of time per hour spent on the eggs. At no time does the time off the eggs in inattentiveness surpass the time on the eggs, although in early afternoon the time off approaches close to the time on the eggs.

The number of attentive periods started each hour fluctuates around a value of 3.2 until 1500 hours. This means that the number of attentive periods is not involved in the daily rhythm so much as is their average duration, which becomes shortened. From 1600 to 1900 hours, inclusive, this is not true as there is a slight decrease in number of periods at the same time as the total attentive time increases. Taking

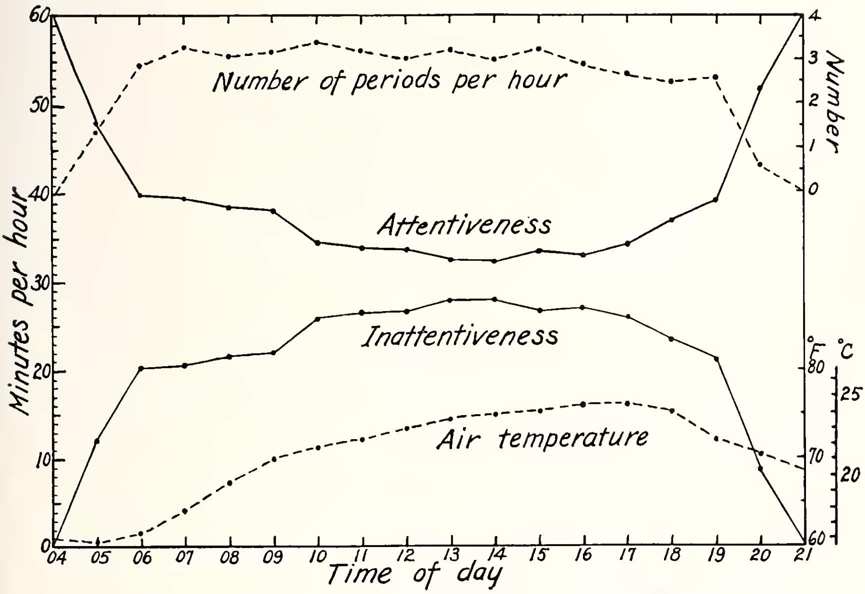

FIG. 11. Daily rhythm of activity during incubation.

values from these curves, the average length of the attentive period varies from 12.5 minutes at 0600 to 0900, to 10.4 minutes at 1300 to 1400, to 15.0 minutes at 1900 hours. Inattentive periods on the other hand vary at the same hours: 6.7, 9.0, and 8.1 minutes.

Influence of temperature. A curve showing daily rhythm in air temperature was computed for the same days on which the recordings of bird activity were made. A hygrothermograph, that recorded relative humidity and temperature in the open but with the instrument in a regulation weather-shelter, was operated for several years on the estate, and for days when original weather records were not available, data from the Cleveland Weather Bureau, some 12 miles distant, were used.

The curve of attentiveness varies inversely with this curve of temperature change, although the time of highest temperature and minimum incubation per hour do not exactly correspond. Probably the high air temperatures in the middle of the day prevent the eggs from cooling so rapidly during the female's inattentiveness so that the female does not need to apply as much heat to them. Perhaps also the female is less comfortable in the nest box when the box is very warm.

To test further the importance of daily temperature on the curve of attentiveness, an average was made of the amount of time spent on the

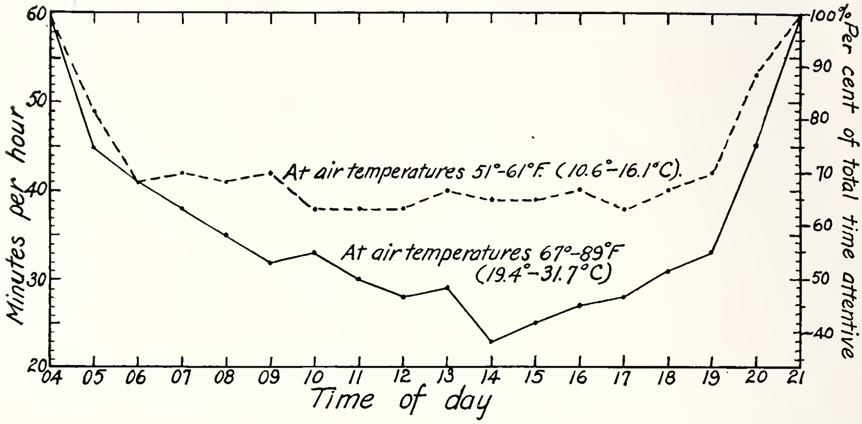

FIG. 12. Influence of air temperature on daily rhythm of attentiveness during incubation.

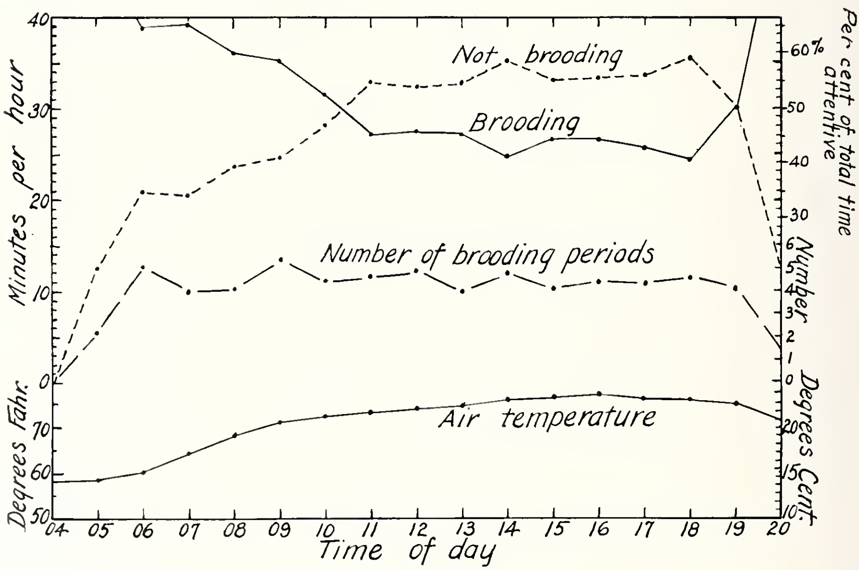

FIG. 13. Daily rhythm of activity while brooding newly hatched young.

eggs each hour for the three days of highest temperature and the three days of lowest temperature on the fifth, ninth, and last day of incubation. The first day of incubation was not included, since there were no records obtained at as low temperatures as on the other days, and because the incubation behavior is less perfectly established. The curves obtained are shown in figure 12. On days when the air temperature did

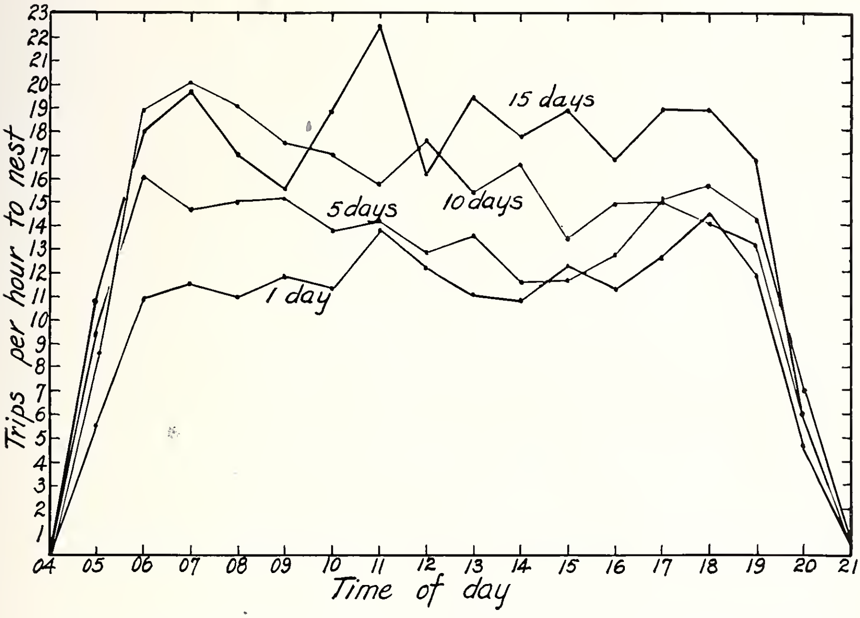

FIG. 14. Daily rhythm in the rate of feeding young of four different ages.

not become high, attentive time shows scarcely any drop in the afternoon. On very warm days, on the other hand, the daily rhythm is highly developed and during most of the afternoon more time is spent away than on the eggs. In extreme cases, the bird does not visit the eggs for several hours at a time. It appears, therefore, that high air temperatures are responsible for the decrease of attentive time in the middle of the day.

Brooding. Figure 13 is an average of data obtained at nine different nests. The daily rhythm in attentiveness while brooding one-day-old young follows the pattern already described except that the afternoon decrease is more extreme and less time is spent brooding than not brooding. The young birds are without doubt more resistant to heat loss than the eggs, even though they remain essentially cold-blooded for at least a week after hatching.

Feeding the young. The curves (Fig. 14), showing rate of feeding per hour, are based on number of visits to the box by both sexes as recorded by the itograph for four stages in the growth of the young. The young normally leave the nest soon after the fifteenth day. For the first day there were more trips to the box and probably more feeding done in the afternoon than in the morning. This curve is inverse to the one of brooding (Fig. 13), and the inference is that there may be more feeding of the young when less brooding is necessary and vice versa.

On the fifth and tenth days, brooding is much less extensive and the feeding curve is comparable to the curve for incubation, with generally a higher rate of feeding in the morning than in the afternoon. On the fifteenth day the young come to the entrance of the box for food and the adults are strained to their full capacity to keep them supplied at all hours. The curve is irregular but, in general, remains high throughout the day. Bayliss (1917), Densmore (1925), and Shirling (1927) have reported the hourly rate of feedings from all day observations, and their data agree with the above conclusions.

Time of Beginning and Ending the Day's Activities

Both the temperature-recorder and the itograph give the time that the female begins her morning's activities and ends her activities in the evening during the egg-laying, incubation, and brooding periods, and the itograph records it also during the rearing of the young in the nest. Normally the female spends every night in the box throughout the nesting cycle.

When a comparison is made of data obtained with the same recording instrument and on the same female before and after the eggs hatch, fifteen records indicate that the female begins her activities 8 minutes earlier in the morning and continues them 16 minutes later in the evening on the average when she is brooding and feeding young than when she is incubating eggs. In only three instances did she begin her activities later in the morning and in only two cases did she stop them earlier in the evening after the eggs hatched than before. Nice and Thomas (1948) found similarly that the female Carolina wren, *Thryothorus ludovicianus*, retired to the nest from 1 to 33 minutes *before* sunset during incubation, and from 4 to 17 minutes *after* sunset when there were young in the nest. Likewise, Kluijver (1950) found in the great tit, *Parus major*, that the female started morning activity 20 minutes after sunrise while incubating her eggs but only 6 minutes after sunrise after the young hatched. She retired into the nest in the evening 100 minutes before sunset while with eggs but not until sunset after hatching took place.

Using all the available records for the incubation period only, and omitting the first day when the last egg was laid and the last day when the eggs first began to hatch, averages were made of all the data for each day of time of beginning and ending of activities. From May 23 to July 31, inclusive, there was an average of 3.6 records on different females for each day. In August the number was reduced to only 1.3 records per day and after August 6 only one female was recorded. These

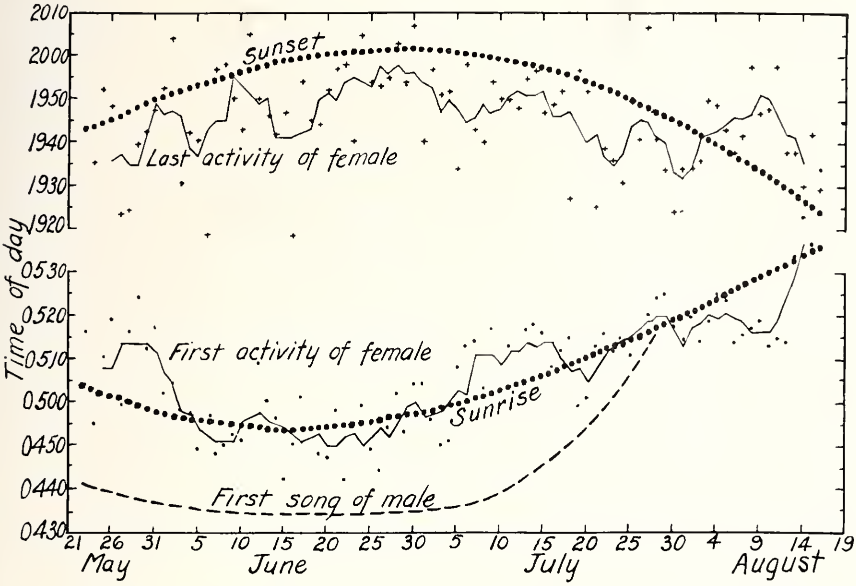

FIG. 15. Beginning and ending of daily activities of the female and the first morning singing of the male in relation to sunrise and sunset. Data for the first male's song is from Allard, 1930.

daily averages are plotted in figure 15 and compared with time of sunrise and sunset.

There is considerable variation in the averages from day to day and in the activities of different females on the same day. These variations could not be correlated in any definite manner with either temperature or relative humidity. There was some tendency for the period of daily activity to be shortened at both ends when there was considerable cloudiness, but it is not possible to demonstrate this tendency statistically. Females at boxes placed so as to get the early morning sun showed some tendency to begin activities a few minutes earlier than those in shaded boxes. The same may be said for females slightly prolonging their day's activities when their boxes were exposed to the sun in the evening. In neither case is the tendency very pronounced or indisputable. Many of the differences between females appeared to be inherent individual characteristics not correlated with any known external factor. Finally, the influence of the male must be mentioned as he may sing near the box early in the morning and influence the time that the female starts her activities.

In spite of these wide variations in the data, certain trends are discernible as the season progresses. To show these trends two lines are drawn (Fig. 15) based on moving averages involving five consecutive daily figures, i.e., the figure for any point on these lines is an average for that day, the two preceding days, and the two subsequent days. Such moving averages eliminate much but not all of the day-to-day variations. These trends may then be compared with time of sunrise and sunset.

The seasonal trend in time of beginning the day's activities varies around the time of sunrise. When all data are included, time of beginning activity averages 0.7 minutes after sunrise. When all data are averaged except those for August when the number of records is so few, daily activity begins 2.3 minutes after sunrise. This interval is small and within the limits of possible error of the recording instruments, although errors in the recording instruments may be either plus or minus and should mostly cancel out. Considering all records, the time of ceasing the day's activities averages 6.4 minutes before sunset.

No special study was made of the time that the male began and ended his daily activities, although incidental observations indicated that he began to sing in the morning before the female left the box and did not go to roost in the evening until after the female had entered the box for the night. Kluijver (1950) also found this to be true in the great tit, *Parus major*. Allard (1930) included the house wren in his extensive investigation of the first morning songs of birds. Compared with other common species, the male began singing relatively late, averaging about 21 minutes before sunrise from late May through early July and about 5 minutes later on cloudy mornings than on clear mornings. According to this information, the male begins his activity approximately 23 minutes earlier than the female during the incubation period but only 15 minutes earlier during the care of the young in the nest. A smooth line has been drawn through the data given by Allard and this line has been fitted into figure 15, to show the male beginning his activities at the corresponding number of minutes before sunrise. After July 10 the curve rises rapidly until at the end of the month the male and female are beginning their activity at the same time or approximately at sunrise. Kluijver found a similar phenomenon in the great tit. By July 10, most male house wrens have their second nestings well started, if they are going to have them, and the intensity and necessity for singing decreases. The gonads begin to atrophy and molting commences as soon as nesting is over. This change in physiological state from the reproductive condition of the preceding two or three months may mark a decrease in sensitivity to low intensities of light, as Allard postulates, or simply a change in behavior pattern. Allard does not give data on the time of cessation of song in the evening, but he states that birds often stop singing relatively earlier with respect to the time of sunset than they begin singing in the morning with respect to sunrise, although this is not invariable. Lutz (1931) found that the closely related *Troglodytes musculus* in the Tropics was able to detect a light intensity as low as 0.4 foot-candle. In the Carolina wren, Nice and Thomas (1948) found that during the incubation period the male started singing 21 to 38 minutes *before* sunrise and that the female started her daily activities 10 to 23 minutes *after* sunrise.

Activity at Night

Inspection of nesting boxes after dark has never revealed a male roosting in them. The male passes the night roosting in a bush, a hedge, in

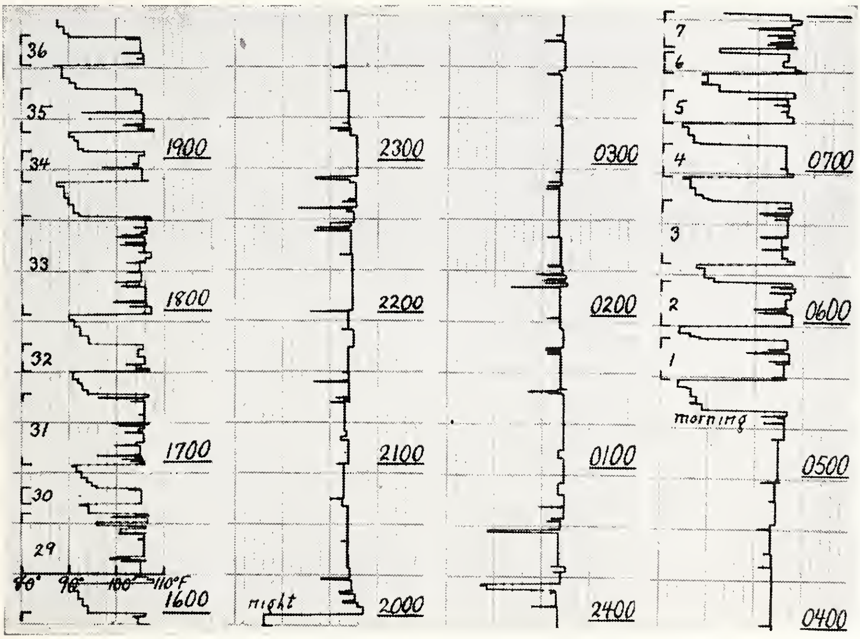

Fig. 16. Nest-temperature record of female No. B96433 on the fifth night after full incubation had started. Attentive and inattentive periods during late afternoon of July 11 (shown at the left) and during the early morning of July 12 (shown at the right) are also included. Each attentive period is numbered. When the line moves to the left and the nest temperature drops, the bird is away or is restless on the eggs. A straight vertical line indicates that the bird is sitting quietly on the eggs.

vines next to buildings, or in low branches of trees. The female doubtless roosts in similar places when she is not nesting, although there are few observations available. When she has a nest, however, she may regularly be found in the nest box at night.

In fourteen box inspections with a flashlight, when sticks were present which had been carried in by the male, no bird was found. In three inspections, where lining had been added to the nest cavity by the female, the female was found in at night two times. Six inspections out of eight revealed the female in the box at night when the nest contained an incomplete set of eggs. All inspections throughout the incubation period revealed the presence of the female. When nestling birds were in the nest, the female was always present except toward the end of the period of nestling life when the young birds were well feathered and about ready to fly. Then she was sometimes absent. There is no record of a female having spent the night in a box after her young had flown. These statements based on observations are fully substantiated by the records of the itograph which registers continuously all comings and goings at the box.

Changes in position of the female on the nest during the night, her restlessness, and how much heat she applies to the eggs are registered by the temperature-recorder (Fig. 16). These records become less perfect when the young increase in size as they, themselves, affect the temperature of the thermocouple. During the incubation period (Table 17) the female applies heat to the eggs all night, although her body and skin temperature are then somewhat lower than during the day. The female seldom sits quietly for long at a time before shifting her position. These shifts may occur every few seconds, in case of extreme restlessness, to intervals of 10 to 30 minutes. After midnight the intervals between movements often become still longer. There may be significance that the length of the intervals between periods of restlessness is comparable to the length of attentive periods during the day. The rhythm of activity established during the day is carried over into the night. Restlessness at night is usually associated with the same degree of restlessness during the attentive periods during the day. The temperature-recorder once registered the unusual absence of an incubating female from 2050 at night until 0104 hours the next morning (Baldwin and Kendeigh 1927).

In the few instances where the female was intensely and continuously restless, this may have been due partly to the annoyance of the thermocouple wire stretched across at the level of the top of the eggs, although most females quickly became adjusted to the presence of this foreign object in the nest.

There is a tendency for the female to be somewhat more restless before midnight than after, although in many records no such difference

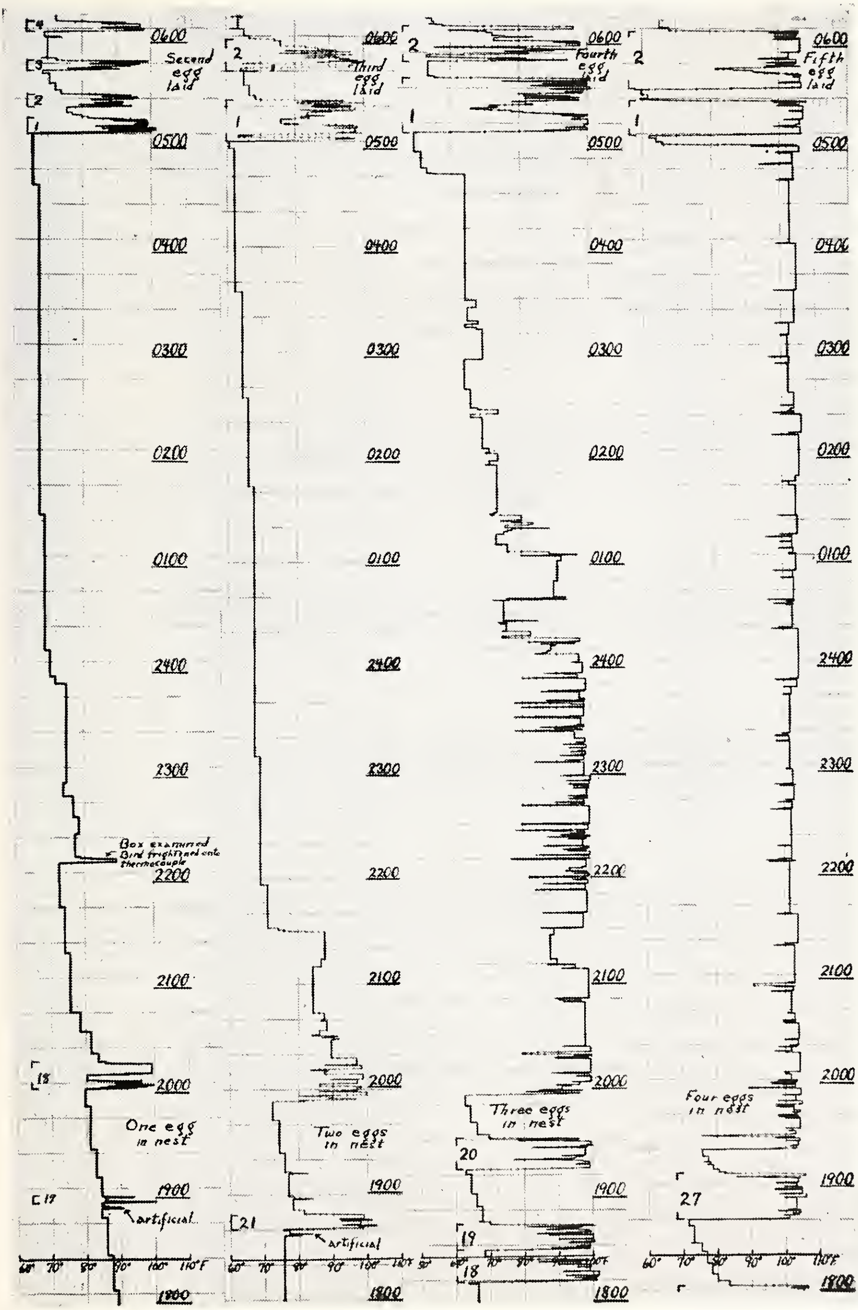

Fig. 17. Overnight records of nest temperature and the attentiveness of female No. A94247 on the nest during the egg-laying period.

TABLE 17. Activity of the female at night during the nesting period.

Band number	Territory	Date of first egg	Number of eggs laid	Night after first egg laid	Night after second egg laid	Night after third egg laid	Night after fourth egg laid	Night after fifth and later eggs laid	Incubation period
71653	59	July 19	5	...	Absent	Absent	Nearly full heat all night	Full heat all night	Somewhat restless first 1-3 hours, quiet rest of night
Unknown	58	June 4	5	...	Partial heat all night	Partial heat all night	Full heat to 2300 hours, partial heat thereafter	Full heat all night	Died
A38446	58	July 1	5	Absent	Absent	In box but no heat applied to eggs	Full heat all night	Full heat all night	Very uneasy all night during incubation period, maximum intervals of rest 15-20 minutes
A94247	65	July 1	5	Partial heat to 2015 hours	Partial heat to 2130 hours	Full heat to 0015 hours, partial heat thereafter	Full heat all night	Full heat all night	Usually quiet all night, restless some nights, slightly more restless before midnight than after
A94248	68	July 30	5	Intermittent full heat to 2230 hours, partial heat thereafter	Intermittent nearly full heat to 0100 hours, partial heat thereafter	Full heat to 2400 hours, partial heat thereafter	Full heat all night	Full heat all night	Restless all night, especially first 1-2 hours
B45321	73	July 5	5	Partial heat to 2200, 0100-0440 hours	Partial heat to 2200 hours	Full heat to 0400 hours, very restless	Full heat all night, very restless	Full heat all night, very restless	Intensely restless all night long throughout incubation period
B45349	73	May 24	6	...	Full heat to 2230 hours, partial heat thereafter	Intermittent full and partial heat all night	Nearly full heat to 0050 hours, decreasing heat rest of night	Full heat all night	Restless all night at intervals up to 15 minutes
B45536	71	July 10	5	Nearly full heat to 2330 hours, partial heat intermittent thereafter	Nearly full heat to 2400 hours, partial heat thereafter	Full heat to 0200 hours	Full heat all night	Full heat to 0030 hours, none thereafter	Full heat all night, at first but little restless and mostly only first 3 hours of night, later in incubation period intensely restless all night

B96433	85	July 2	5	Partial heat all night	Full heat to 2200, partial heat 2340-0200 hours	Full heat early in night, none after 2230 hours	Full heat to 0400 hours, partial heat rest of night	Full heat all night	Restless at intervals up to 30 minutes all night, slightly more restless later in incubation period
Unknown	87	July 30	5	Partial heat to 2100 hours	Partial heat to 2250 hours	Full heat to 2245 hours, partial heat thereafter	...	Full heat all night	Deserted
C68253	96	June 15	5	...	Absent	Absent	Absent	Full heat all night	Intermittently restless at intervals up to 40 minutes, greater restlessness later in incubation period
C68257	97	June 11	6	...	Partial heat to 2130 hours	Partial heat to 2230, also 0300-0445 hours	Nearly full heat to 0320 hours, partial heat rest of night	Full heat all night	...
C68705	93	June 29	5	...	Full heat to 2020 hours	Partial to full heat to 2100 hours	Full heat to 0150 hours, partial heat thereafter	Full heat all night	At first quiet for intervals up to 10 minutes, later in incubation period becoming intensely restless all night
C94219	120	June 7	6	Partial heat to 2145 hours, again after 0015 hours	Partial to full heat: 1945-2115, 2230-2250 hours	Partial to full heat to 2400 hours	Full heat all night	Full heat all night	More restless before midnight than after, at intervals up to 30 minutes, greater restlessness later in incubation period
Unknown	137	June 21	..	Partial heat to 2020 hours	Partial heat to 2100 hours	Partial heat to 2130 hours	Partial heat to 0130 hours	Deserted	...

can be noted. Likewise some birds are restless for the first one to three hours of the night, after which they settle down more quietly. There is no evidence that the birds become increasingly restless just before leaving the box in the morning, and their departure is usually abrupt. Some birds show a slight tendency and other birds a strong tendency to become more restless at night as incubation progresses. With still other birds no such change can be noted.

Of considerable interest is the amount of heat applied to the eggs at night before the set is complete, since the first ones laid would get some development before the last ones appeared (Fig. 17). There is only one record of a female (C68253) not being in the box at night until the set was complete. Some heat was applied to the eggs during the day, but the long incubation period of 15 days in this case may be due to the lack of this early development at night.

In Table 17 the amount of heat applied to the eggs as they were being laid is given in general terms for fifteen sets. The usual behavior pattern is for the first egg to receive partial heat the first night for a period up to two hours, although occasionally it may receive the full incubating temperature for the first part of the night and partial heat all night. The application of heat the second night is similar except that the heat may be applied somewhat longer the first part of the night and at times the temperature is higher. During the third night, full heat is applied in about half the cases and partial heat in the rest until around midnight, and occasionally partial heat is continued all night. On the fourth night the full incubating heat is given the eggs throughout the night in about half the cases. Finally, on the fifth night when sets of five eggs are complete, the incubating heat that is maintained throughout the incubation period becomes established in all sets with few exceptions. In the three sets with six eggs, the full incubating temperature was established on the fifth night, the same as in sets that contained only five eggs.

Only one incomplete record (territory 63) is available for a seven-egg set and this requires special consideration. The first egg was laid on May 23. The night after the fifth egg was laid showed full heat applied at the beginning of the bird's stay in the box, but this was followed by a steady decline in temperature until there was no extra heat at all at 0415 hours. The next day no egg was laid and that night full steady heat was applied until midnight and none thereafter. On the following day the sixth egg was laid, and full heat was given the eggs until 0045 hours and partial heat the rest of the night. It was not until the succeeding night with seven eggs in the set that full heat was given the eggs continuously all night.

These observations show that the working up to a full incubating behavior and the application of the full incubating temperature is a gradual process at night, the same as during the day, and that it is not completed until the set is completed or at the most not until one night before it is completed. This development involves both a change in behavior and a change in physiology. Although the female starts to spend every night in the box as soon as she accepts a male and begins carrying in nest lining, she does not spend all her time in the nest cavity itself. The itograph shows that at some nests during the egg-laying period the female spent considerable time on a perch at the front entrance of the box. A few observations after dark have found the female on the stick platform inside the box but in front of the nest cavity. In this position the thermocouple in the nest cavity as well as the eggs may pick up some heat radiated from the bird and accumulating within the enclosed space of the box, but this would be small. Even when resting on the eggs in the nest cavity, the bird may not always fluff out her feathers so that the eggs come in direct contact with her skin. This has not, however, been satisfactorily proven. During the incubation period it is rare for the female to uncover the eggs at night for any appreciable length of time.

It is probable that the loss of down feathers in the ventral apteria is due to hormone action. Along with the loss of feathers comes an increased vascularization of this area so that a brood patch is formed. At one box the female was captured at the beginning of egg-laying, midway through, and again when the set was first completed. At the first capture the brood patch had not developed, and the area was covered with feathers. When captured the second time, the brood patch was partly formed. When captured at the end of the egg-laying, the brood patch was fully formed. This slow development of the brood patch affects the amount of heat applied to the eggs and is more pronounced for the first sets early in the season than for later sets during the same season. In Table 17, the females in territories 120, 96, 85, 71, and 68 were known to have had a full set of eggs previously during the season, and it will be noted that the development of the full incubation heat and behavior occurred more rapidly than it did with the females in territories 58 (both records), 65, 73 (second record), and 93 which were probably nesting for the first time. Doubtless, the brood patch, after once developing during a season, would not regress completely between consecutive nestings. Tucker (1943) has reviewed in a general way the occurrence and development of the brood patch in various kinds of birds, and both Swanberg (1950) and Kluijver (1950) have described the gradual development of the incubation temperature during the egg-laying period.

Discussion

The evidence on the preceding pages establishes the fact that alternating periods of attentiveness and inattentiveness to the duties of reproduction is a prevailing pattern underlying all phases of behavior during the nesting season. It is by this rhythm of alternating phases that the bird responds to the drives of reproduction and self-maintenance. The first drive is for the existence of the species; the second is for the existence of the individual. The individual must maintain itself or reproduction is not possible; at the same time reproduction is indispensable or there would be no oncoming individuals to replace the adults upon their death. It would be interesting to know how this particular behavior pattern arose and how it is regulated.

House wrens are insectivorous in their feeding habits. They seek food in and under shrubs, on the ground, in crannies, under buildings, in rockpiles, and in other similar locations. The female searches for this food in the vicinity of the nest, usually within the territory established by the male. Normally, food is abundant and not difficult to find during the season of the year when the birds nest. The inattentive period, averaging 8.5 minutes for the female during the incubation period, is very likely determined in its length by the time required for the bird to fill its stomach with food. Insects are less active in cold weather and probably more difficult to find, hence the longer inattentive periods noted at temperatures of 53° F. (11.7° C.). When attentive periods average longer than usual regardless of temperature, the inattentive periods are also longer, perhaps due to greater fluctuations in the physiological rhythm, perhaps also due to the inherited peculiarities of the individual.

During the attentive period the food in the stomach is digested. This digestion takes place rapidly. Stevenson (1933) found that in sparrows a stomachful of cracked corn was completely digested with the elimination of undigested excrement in about 2 hours 30 minutes. The first appearance of undigested material in the excrement came in about 1 hour 30 minutes. The difference of one hour would represent the maximum possible time that the food could remain in the stomach, and the actual time may be shorter. There is no direct information on this point.

The attentive period of the song sparrow averages 28.5 minutes in duration (p. 161), which is about half of this one-hour period, but hunger contractions in the stomach may become intense before the stomach becomes completely empty. Rogers (1916) studied hunger contractions in the crop of pigeons and noted that they began even with a full crop but became more frequent as the crop emptied. Hunger was associated with marked restlessness on the part of the bird. The song sparrow and the house wren do not possess crops, but hunger contractions doubtless occur, possibly in the proventriculus, and they may furnish the primary stimulus for the termination of the attentive period and the search for more food. The average duration of 12.1 minutes for the attentive period in the house wren may mean that the house wren either digests its food more rapidly than the song sparrow or that the stomach can hold less food at a time. The house wren is entirely insectivorous, the song sparrow only partially so.

Incubation is an energy-demanding process since it requires the transference of heat from the adult to the eggs. The loss of heat energy requires a continual replenishment of the energy resources of the bird, which can be accomplished only from the ingestion of food. A greater transference of heat energy must occur at low air temperatures than at high, and this is reflected by the increase in length of attentive periods as air temperature drops. In order for this increase in average length of attentive periods to occur, there must be a greater food consumption, and this may be partly responsible for the longer inattentive periods at air temperatures below 55° F. (12.8° C.), to allow for the searching of this material (Fig. 5, p. 41).

At high air temperatures, particularly above 65° F., there is less demand for energy as the eggs can be kept warm more easily. Consequently, the attentive periods become shorter. The lengthening of the inattentive periods is then to be explained by the slower rate of physiological activity of the bird, by its loafing and resting, and at extreme high temperatures by the actual reluctance of the bird to enter the hot nest box or to remain in it for any length of time. It appears, therefore, that the regulation of attentive behavior and the length of the alternating phases of attentiveness and inattentiveness is primarily physiological.

Odum (1944) suggests that circulatory congestion of the venous blood flow, due to muscular inactivity during the inattentive period, may produce discomfort in the bird and bring about the termination of the period. He was impressed by the amount of muscular activity that the bird underwent at night which might alleviate this discomfort. Before this suggestion can be taken seriously, we need to know how much difference in rate of blood flow actually occurs during the periods of attentiveness and inattentiveness and whether a slowing up of flow through the veins actually causes restlessness on the part of the bird. It is interesting that Odum found an increase in rate of heart beat toward the end of the attentive period, while the bird was still inactive but which was anticipatory of the birds leaving for an inattentive period. Baldwin and Kendeigh (1932) found that there was usually also a rise in body temperature toward the end of the attentive period.

Daglish (1930) suggests that the rush of blood into the brood patch, with the resulting increase of skin temperature, produces an irritation at this part of the body. The birds tend to relieve this irritation by pressing their breasts against the hard smooth surfaces of the eggs. Presumably as the skin temperature dropped the irritation would stop, bringing about the termination of the attentive period. This idea is not subject to ready verification and would not explain the occurrence of alternating phases of attentive and inattentive behavior in other than the incubating and brooding phases of nest life.

If changes in physiological state are of primary importance in the regulation of attentive behavior, then psychological elements may be considered as secondary or superimposed factors. Actually, changes in physiological state exert an effect only by furnishing stimuli and thereby initiating a chain of nervous responses that result eventually in an overt action of the bird. After the stimuli are received, the central nervous system organizes the response. Repetition of stimuli at regular intervals with resulting identical actions may well establish a routine or habit which then becomes a secondary regulatory factor in maintaining the rhythm at a certain tempo.

Finally, external stimuli may also modify the rhythm. The appearance of a singing male near the box may excite the incubating female to leave sooner than she otherwise would. For the most part, however, the male adjusts his behavior to the rhythm already established by the female. These external factors are all of minor importance, superimposed on the basic physiological one that is chiefly responsible in determining the nature and development of the bird's behavior.

Summary

Attentive and inattentive periods may sometimes be detected and measured in the activities of an unmated male when he is singing or tearing out nest lining and these vary around 4 to 6 minutes in length. Unmated males commonly visit the boxes in their territories 29 times per day, often with sticks for the nest foundation, but the number of trips made is highly variable and may be increased three to five times when he tears out the old nest lining of his former mate, when he defends his possessions against an invading male, or when a potential female mate arrives.

After pairing occurs, the female immediately begins the insertion of lining into the nest cavity. The male does not aid in this task. Two or three days are required with the female visiting the box 118 times per day, more on the first days, less on the later days. The female's attentive periods at this time are 7 to 9 minutes long. The intervening periods are very variable, and become increasingly long as the nest lining becomes completed. Another one or two days lapse before the first egg is laid.

Five or six eggs are commonly laid; there may be as few as three or as many as nine. Each day as another egg in a five-egg set is laid, the female visits the box more frequently and for a longer attentive period. With six-egg sets this daily increase does not begin until the fourth egg is deposited. Full incubation behavior in either case is not reached until the last egg is laid. It appears that whether or not a sixth egg is to be laid is determined two or three days earlier and is associated with changes in behavior beginning at that time.

Only the female incubates the eggs and broods the young. Averages on 30 females over 332 days at 40 different nests indicate that 45 attentive periods, each 12.1 minutes in length and with inattentive periods 8.5 minutes long, are typical of the species. Although there are daily fluctuations, attentive behavior appears essentially uniform throughout incubation and constitutes 58.2 per cent of the daytime activity of the bird. No differences in attentive behavior are discernible correlated with age, change of mates, or advance of the nesting season.

As air temperature rises from daily averages of 48° to 88° F. (8.9° to 31.1° C.), there is an increase in the number of attentive periods per day and a decrease in the length of the attentive periods. This results in a decrease in total attentive time during the day and an increase in the total time of inattentiveness, even though there is no significant change in the average length of the inattentive periods.

The eggs tend to hatch in the order laid over a period of 26 hours. The length of the incubation period varies from 12 to 15 days and averages 13.9 days. Attentive periods average longer when incubation extends over 14 or 15 days than when it lasts only 12 or 13 days, but probably this correlation is incidental due to the effect of temperature on both.

The average number of attentive periods per day during incubation varies between different females from 24 to 70, the length of these periods varies between 6.7 and 22.3 minutes, and the length of the inattentive periods varies between 5.2 and 12.6 minutes. The male may influence the female's attentive rhythm slightly, but his own attentive behavior mostly becomes synchronized to hers. Differences between females appear due principally to the bird's individual temperament, physiology, and heredity and as modified by the environment. In general, the length of the attentive period is a very variable phase of attentive behavior and the length of the inattentive is much less variable. Variations in the number of periods per day depend primarily on the length of attentive periods.

With the hatching of the young, the tempo of attentive behavior increases to a faster pace. For the first three days there is an average of 67 brooding periods per day, each 7.3 minutes long, spaced at intervals of 6.4 minutes. The percentage of daytime spent brooding is 52.9, which is slightly less than for incubating the eggs. The amount of brooding decreases daily thereafter but may persist to some extent during the daylight hours until the young are ten days old.

Both adults feed the young, the female more consistently than the male, although with the death or desertion of the female the male will assume full responsibility, except that he will not brood. Normally only one young is fed on each trip to the box. With an average of four young in the brood, total trips to the nest per day increase from 184 on the first day to 256 on the sixteenth. The increase from day to day follows a sigmoid growth curve.

The rate of feeding per day varies with the number of young birds constituting the brood. With only one young in the nest the adults made 115 trips to the nest with food, but with six young present there were 300 trips. Each young bird receives less food in large than in small broods, the extreme variation is 115 trips with food for a single young to only 50 trips per young bird in broods with six young. One adult bird alone easily cares for broods with a single young. When the size of the brood increases to three, four, or five, a single adult increases its feeding rate an average of 53 per cent. The effectiveness of both adults participating in feeding the young in these larger broods is evident in the comparative increase of 103 per cent in the rate of feeding that occurs. Broods containing two or three young left the nest after 15.3 days; broods containing four to six young did not do so until they were 16.6 days old, which suggests that the slower individual rate of feeding in large broods brings a retardation in rate of development.

The rate of feeding the young did not vary significantly between the two breeding periods during the season. Similarly the rate of feeding was not influenced by the age of the adults nor by their previous experience. Weather conditions produced no obvious effect except that feeding was temporarily halted during severe rainstorms. Variations in the rate of feeding by the same bird at different nests were less extensive than were variations between different individuals.

The duration of attentive and inattentive periods is difficult to measure when the adults are feeding the young, but the periods nevertheless do occur. In one male bird feeding the young alone, "attentive" periods averaged 99 per day and 4.4 minutes in length with intervening "inattentive" periods of 4.9 minutes. The young birds are attended to for 10 to 15 days after leaving the nest, during which time the inattentive periods increase in length and the attentive behavior disappears.

Both males and females have a daily rhythm in the intensity of attentive behavior. For unmated males, ordinary activity and tearing out nest lining reaches a peak during the middle of the day. Insertion of nest lining by the female is most rapid during the early morning hours and then decreases during the rest of the day. Eggs are laid soon after the female begins her daily activities early in the morning. During the first two days of the egg-laying period there is very little attentiveness in the afternoons, but on each successive day thereafter until the set is complete there is increased attentiveness during all hours of the day until the typical daily rhythm of the incubation period becomes established.

This typical daily rhythm during incubation begins with the female on the eggs 60 minutes out of the hour at night, 39.8 minutes at 0600 hours, a minimum of 32.1 minutes at 1400 hours, a rise again to 39.0 minutes at 1900 hours, and 60 minutes when the bird retires. The length of the attentive period varies from 12.5 minutes at 0600 to 0900 hours, to 10.4 minutes at 1300 and 1400 hours, to 15.0 minutes at 1900 hours. Inattentive periods vary at the same hours: 6.7, 9.0, and 8.1 minutes. This curve of attentiveness varies inversely, although not exactly, with the daily curve of air temperature. On cool days, the curve of attentiveness shows scarcely any drop in the afternoon, but on every warm day the daily rhythm becomes highly developed and the bird may spend more time away than on the eggs.

The daily rhythm of the female while brooding the young follows the general pattern of the incubation period except that the afternoon decrease is greater, and less time is spent brooding the young than in incubating the eggs.

When the young are newly hatched, they are fed slightly more often in the afternoon, when there is less brooding, than in the morning. When the young are five and ten days old and there is little brooding, the feeding rhythm is similar to the incubating rhythm with greater activity in the morning than in the afternoon. When the young are 15 days old, the adults are strained to full capacity at all hours and the feeding rate is fairly uniform throughout the day.

During incubation, the female becomes active about 2.3 minutes after sunrise and ceases activity an average of 6.4 minutes before sunset. When the female is brooding young, she begins activity 8 minutes earlier in the morning and continues for 16 minutes later in the evening. During the nesting season, the male begins his daily activity several minutes earlier than the female and continues them for some minutes in the evening after she has retired to the nest.

There is no record of a male in the nest box at night. The female may begin spending the night in the box as soon as she starts the insertion of nest lining and before the eggs are laid. She may start roosting again outside the box when the young are nearly ready to leave the nest, and there is no record of her spending the night in the box after the young have flown. While incubating eggs, the female is often quite restless at night, more so before midnight than afterward. There is a relation between the degree of restlessness at night and the amount that she is restless during attentive periods during the daylight hours. There is a suggestion in some recordings that periods of quiet and restlessness at night vary at intervals simulating periods of attentiveness and inattentiveness during the day.

Although the female spends the night in the box during egg-laying, she is not always on the eggs. Furthermore, even if sitting on the eggs, she may not apply full incubating heat to them. The brood patch develops gradually during the egg-laying period so that the amount of heat that the eggs receive increases gradually from night to night. Usually full heat is applied beginning with the night after the fifth egg is laid.

The length of the inattentive period is probably determined by the time required to fill the stomach with food. The length of the attentive period is probably determined by the time required to digest this food. Superimposed on this physiological rhythm are psychological factors, such as habit formation. Changes in function may give a stimulus. The nervous system must respond before there is an overt act.

IV. Attentive Behavior of Miscellaneous Species

Now that the details of attentive behavior have been worked out for one species, it is desirable to see how uniformly this concept may be applied among different species of birds. There are bound to be variations in the way attentive behavior has evolved in species of different ancestral history, having different physiological potentialities, or with different adjustments to the environment. After attentive behavior has been described for various species in as much detail as is available, some general comparisons will be made.

Killdeer, *Charadrius (Oxyechus) vociferus*

The best accounts of killdeer behavior are by Nickell (1943), who had eight nests of three different pairs under observation, and Emma Davis (1943), who studied both wild birds and birds raised in captivity. After three weeks of seemingly aimless courtship performance by Davis' captive birds, one of the males began nest building and had the nest well formed, except for lining, by the same evening. The female later contributed some small stones for the lining. Copulation occurred repeatedly during the egg-laying period, and during this period the male was much more solicitous of the nest and eggs than the female. Nickell found that intervals between laying of successive eggs were irregular with often a day being skipped. He states that steady incubation began soon after the last egg was laid, but the fact that hatching extended over two or three days may indicate considerable incubation at night before the set was complete. There were seven sets of four eggs, one of five.

Nickell gives the incubation period as 24 to 26 days, with both sexes sharing the incubation duties. Ganier (1934) found at one nest that the incubation period was 29 days. Davis also found both adults participating in incubation. Pickwell (1930), however, found only one bird caring for the eggs at each of two nests, and when collected, each proved to be the male. It is probable that the male incubates more than the female.

Davis found that the young after hatching were taken care of for 23 days with the male assuming major responsibility. For the first two or three days the young killdeers were brooded by both parents for short periods at frequent intervals but thereafter only during the cooler parts of the day. Nickell also found both parents caring for the young after hatching and that this period in two instances extended to 39 and 42 days.

We were able to insert thermocouples into two different killdeer nests.

In one nest in late April, three full-day records and two part-day records gave an average attentive period of 32.6 minutes with 24 periods per day (Table 18). Intervals between successive attentive periods when no bird was on the eggs averaged 5.6 minutes. Although observations at this nest were limited, there is no doubt but that both adults shared incubation duties. The average inattentive period should be considered as 32.6 plus 5.6 minutes or 38.2 minutes. There was no indication that one sex had longer attentive periods than the other. It is not known which sex sat on the eggs at night, but the record indicates that the bird was a close sitter. Daytime activities began in the morning around 0522 (range: 0503-0555) and terminated in the evening around 2011 hours (range: 1943-2103). This is approximately 8 minutes before sunrise in the morning and 53 minutes after sunset in the evening.

TABLE 18. Attentive behavior of killdeers during incubation.

Date	Number of periods per day	Attentive periods (min.)	Interval between periods (min.)	Inattentive periods (min.)
1927				
April 25	...	26.0	6.9	32.9
April 26	27	30.0	4.1	34.1
April 27	...	37.8	4.7	42.5
April 29	21	36.5	5.6	42.1
April 30	23	32.5	6.5	39.0
1948				
June 23	...	25.5	7.3	32.8
June 24	21	39.2	8.8	48.0
June 25	30	28.3	4.4	32.7
June 26	26	32.7	3.3	36.0
June 27	...	47.3	5.0	52.3
June 28	...	48.6	3.1	51.7
June 29	27	28.1	2.8	30.9
June 30	...	26.9	1.8	28.7

At the other nest the thermocouple was inserted on June 20, the day the second egg was laid. The fourth and last egg of the set was deposited on June 22. Four attentive periods during the egg-laying phase averaged 36.2 minutes or approximately the same as the average of 34.6 minutes for the 8 following days of incubation. The interval between attentive periods, 12.3 minutes, was considerably longer, however, than the average of 4.6 minutes during the incubation period. The corresponding inattentive periods are 48.5 and 39.2 minutes. Exchange of adult birds was frequently observed at the nest. One of the two birds usually waited until the other appeared before it left, but the other bird often left a few minutes before its mate came around.

The attentiveness of the birds at this nest at night was quite irregular. Neither adult sat on the eggs at night until June 26 which was the fourth day after incubation began. On later nights there was considerable restlessness as the birds got on and off the nest and there appeared to be attentive and inattentive periods beginning as early as 0100 hour on at least one night. Likewise on another night, attentive behavior continued until 2248 hours.

The average lengths of the attentive and inattentive periods at these two nests were remarkably similar. Possibly the adults were the same during these two consecutive years. The average of the two records gives 33.6 minutes for the attentive period and 38.7 minutes for the inattentive period.

There was little consistent variation in attentiveness with time of day. Intervals between successive attentive periods decreased slightly around the middle of the day and lengthened again in the evening: 06-09 hours—5.3 minutes; 11-14 hours—4.2 minutes; 16-19 hours—5.4 minutes. In the 1927 nest there was also a significant decrease in length of attentive periods around midday: 38.6—25.9—55.9 minutes; but this variation did not occur in the 1928 nest: 31.8—37.0—35.9 minutes.

Chimney Swift, *Chaetura pelagica*

Four nests of the chimney swift were under observation at various times: 1925, 1932, 1938, 1939. All were located in a short brick chimney in an old maple-sugar house at the edge of a woods. The bird activities at the nest were observed at close range through a small peephole made by removing a brick from the opposite wall. A thermocouple was inserted in the 1938 nest and a record obtained throughout much of the incubating period. About 27.5 hours of observation were spent at the 1932 nest, approximately equally divided before and after hatching of the eggs. There are scattered references in the literature to attentive nesting behavior of this species, but no thorough study has been published.

Both sexes participate almost equally in the various phases of nest life. Actual nest building was not observed but at one nest six days before the young hatched, both adults were seen several times bringing sticks and fastening them to the nest. The two adults could be distinguished as one had a sooty throat, the other a white throat, but the sex of each was not known. While active in nest repair, they alternated in sitting on the eggs at intervals of 17, 13, 4, 17, and 31 minutes. These intervals are considerably shorter than the average length of attentive periods during full incubation. To place a stick in the nest, they first wet a spot on the nest thoroughly with saliva, put the stick held in the bill into the saliva, and then wet the stick all around thoroughly, usually at its center. Strands of the saliva run up over the adjacent part of the nest and wall so that when the saliva dries the stick is held firmly in position. When the bird's mate came in for the next attentive period, it tested the firmness with which the stick was fastened. On the chimney wall adjacent to the nest were eight small sticks or groups of sticks plastered firmly, as if the birds had tried several places before selecting the final nest site.

In a nest observed by Amadon (1936) the four eggs were laid on alternate days and incubation began with the third egg. At our 1938 nest, the four eggs were laid on consecutive days, and a bird was first observed sitting on the nest the day the third egg was laid. Hatching occurred 18 days after the last egg was laid or 19 days after the third egg was laid. The 1939 nest was two-thirds or more complete on June 12. The first egg came on June 17 and that night both adults were observed in the chimney but not on the nest. No birds were observed at the chimney on June 18 and 19, but on June 20 there were two eggs early in the morning. The prevailing cool rainy weather may well be responsible for retardation of the laying schedule. The third egg appeared on June 22 and incubation first began. In the late afternoon of June 23 there were still only three eggs and no adult was on the nest. On June 24, steady continuous incubation began with the appearance of the fourth egg.

The two sexes regularly alternate at incubation duties. At the 1932 nest, eleven complete attentive periods for "sooty throat" averaged over 34.8 minutes in duration. The full length of three periods was not determined but even then these three periods averaged 40 minutes. The shortest period was 4 minutes when "sooty throat" returned with a stick and forced "white throat" off the nest. The longest period was 65 minutes. Eight attentive periods for "white throat" averaged 29.4 minutes with extremes of 13 and 53 minutes. Often one bird on arriving had to push with its body to urge the other to leave, but the exchange of positions on the nest was rapid, and during the entire 13.3 hours of observation the eggs were never left uncovered for any appreciable time.

This was not true at the 1938 nest. The thermocouple record indicated that 12 times, on 8 of the 15 days recorded for the incubation period, the eggs were left exposed for periods of 19 to 84 minutes. The average of these absentee periods is 46.3 minutes which may indicate that one of the birds occasionally missed his turn. The thermocouple did not register the time of exchanging places, but 8.9 hours of observation give an average of over 32.3 minutes for 12 attentive periods with a variation from 7 to over 135 minutes for single periods. One period of only one minute is omitted from these calculations. An average of 31 attentive periods at both of these nests gives 32.4 minutes as the usual length of time a bird sits on the nest at a time.

The three young at the 1932 nest hatched within twenty-four hours of each other. During this period "sooty throat" had one measured attentive period of 49 minutes and "white throat" one of 25 minutes.

Brooding went on fairly regularly at the 1932 nest for the next five days with 10 periods of the two adults averaging 25.4 minutes. Both adult birds were absent for only 25 minutes during nearly five hours of observation. During the next seven days the brooding periods shortened to about 14 minutes, and there was an increasing number of times that the young were exposed without either parent present. Brooding was practically terminated during the daytime on the twelfth day beyond hatching. On the twenty-first day the nest washed down in a heavy rain, and the young were forced to cling to the walls of the chimney. On the twenty-third day the two young were banded after which one left the chimney and one remained. One or two birds were seen in the chimney until the twenty-eighth day, when for the first time all were gone from the chimney.

At the 1938 nest the young were found hatched on July 15. On August 5, the nest was loose and ready to fall and the young were clinging to the chimney wall. One got away in the sugar house but was returned to the chimney. The next day, 22 days after hatching, the young were gone.

Bent (1940) gives one record of 19 days for incubation and 26 or more days for the young to remain in the chimney. Amadon's (1936) records show the last young hatching 18 days after the last egg was laid which agrees exactly with our one record. He found the young off the nest at 21 days after hatching, but they did not leave the chimney until they were 23 days old. Macnamara's (1918) record of young hatching 16 days after the last egg was laid may have meant that steady incubation began with the laying of the next to the last egg two days previous. Baker (1948) observed brooding during the day until the 10th day, the young leaving the nest on the 19th day, and leaving the chimney on the 24th day after hatching.

The adults feed the young at the beginning of each brooding period or occasionally a few minutes after brooding has begun. Feeding was missed only once during the time the 1932 nest was under observation and that was on the day the first young hatched and was alone in the nest. Feeding is by regurgitation. During the first four days when there were three young in the nest, all were fed on each of four visits and either two or three on two other trips. One young bird later died. When the two surviving young were six and seven days of age, one or both of the birds were fed on each trip. On later days only one bird was observed fed on each trip. For the entire nestling period, the average of 2.5 young in the nest were fed at the rate of 2.5 times per hour. When usually all three young were fed on each trip during the first four days, the average rate was three times per hour. From then until the two young were 15 days old, and usually only one was fed per trip, the rate averaged nearly four trips per hour, but during the next five days the rate decreased to once per hour.

Amadon (1936) and Bent (1940) quote observations of others that the chimney swift may be active at night and that they may feed their young at that time, going out and in the chimney repeatedly. Amadon, however, was not able to verify these nocturnal activities during the nesting period. Our observations indicate that the birds may move around in the chimney and change positions, but we have no evidence of more extensive activity.

Forbush (1927) reports observations of Stella M. Davis of both birds sitting side by side on the nest at night with their throats pressed against the wall and their long wings and tails extending outward over the rim. This is the usual position of the birds while on the nest and we can confirm that often both birds occupy the nest at night. Fifteen observations between 2130 and 2300 hours on different nights during incubation revealed both birds on the nest seven times and only one bird on eight times. In the latter cases, the other bird was clinging to the wall of the chimney beside or below the nest. Two observations during the active brooding period showed both adults on the nest each time, but a week before the young left the nest, only one bird was on and it was uneasy and flew off when the flashlight was turned on. Three nights later both adults were found clinging to the wall, one on each side of the nest, which was now filled by the full-grown young. After the nest washed down, both adults and young clung to the wall at the place where the nest had been.

Belted Kingfisher, *Ceryle (Megaceryle) alcyon*

Bent (1940) has summarized what little is known of the nesting behavior of the belted kingfisher. The nest is almost invariably in a burrow in a sand, clay, or gravel bank, excavated by the birds themselves. From 3 to 14 or more days are required to dig the burrow, with each sex taking turns of two or three minutes. Sometimes the male excavates additional burrows nearby in which he retires to feed and pass the night. Normally six or seven eggs are laid and the incubation period is 23 or 24 days. There is a difference of opinion as to whether the male participates in actual incubation of the eggs. Doubtless the female does the major share, but the male enters the burrow and may possibly carry food to the female. After hatching, the young are fed by both parents and remain in the nest for 28 to 32 days. Mousley (1938) spent 42 hours in observation at one nest throughout the nestling period of the young and found that the six young were fed at the average rate of 1.6 times per hour by the male and 0.8 times per hour by the female.

An opportunity became available in 1942 to record the activity at a nest discovered at the Edmund Niles Huyck Preserve, Rensselaerville, New York. In a gravel bank, located a quarter of a mile from water, there were three short burrows and a longer one in which the nest was located. On June 7 flat-treadle electric contacts (Fig. 1) mounted on a narrow wooden block were buried in the entrance of the burrow so as to lie flush with the surface. The adults accepted the disturbance and started going into the nest shortly afterward. A complete itograph recording mechanism was installed the next day, and successful records of the visits of the adults were obtained during six days between June 9 and 16. There was some difficulty in keeping the electric contacts clean, but 73 visits were recorded over a total of 50.7 hours. The average daily rate of feeding, probably by both adults, varied between 1.1 and 1.6 with an over-all average of 1.4 times per hour. It was estimated that the young were in their second week after hatching. This rate of feeding is appreciably slower than that given by Mousley. Observations indicated that the adults were very timid around the nest. On three mornings the first visit to the nest came at 0410, 0422, and 0425 hours and the last visits on three evenings occurred at 0825, 0835, and 0852 hours. On three successful night recordings, the adult was shown to be present only once.

Flicker, *Colaptes auratus*

Both sexes of the flicker assist at excavating a nest cavity. Burns (1900) tells of one instance where the two sexes took turns, at five-minute intervals, chipping and carrying off pieces of wood. He also mentions one case where the female did all the excavating. From one to nearly three weeks may be required to construct a nest unless, of course, an artificial nest site is used when egg-laying may begin within a few days. Normally a single egg is laid daily between 0500 and 0600 hours (Sherman 1910), although there are two records where two eggs were laid in a day. There are commonly five to eight eggs in a set.

Incubation begins before the set is completed, as in three nests I had under observation. Hatching extended over three days in two instances and possibly over four days in one. Sherman states that beginning with the first egg one of the pair of adults customarily remains in the nest cavity as a guard. In one of our six-egg sets, steady incubation began with the laying of the fourth egg, and in another it began with the fifth egg. This was shown by the eggs, which were numbered, hatching on succeeding days 11 days and some hours after they were laid. For two eggs in different sets, Sherman also found that 11 days plus five to eight hours were required for complete incubation, while three number six eggs required over 12 days. At one nest box a thermocouple and temperature-recorder were connected, and they showed that heat was applied to the eggs for short intervals during the day that the second egg was laid, although not at night until after the third egg had appeared. Full incubation behavior became established during the day that the fifth egg was laid.

The fact is well known that the two sexes share incubation, brooding, and feeding the young and that the male, not the female, incubates or broods at night (Burns 1900, Sherman 1910, Skutch 1937b). We found no exception to this rule in our observations, although Sherman found on a few occasions that the female spent the night on the eggs while the male roosted in another box usually used by the female. Sherman states that the duties of incubation are shared about equally during the day and that they relieve each other at intervals of one and one-half to two hours. In one record extending over 24 hours, Skutch recorded two male attentive periods of 121 and 139 minutes and two female attentive periods of 186 and 132 minutes. For the 15-hour daylight period, the eggs were covered, on the average, 55 minutes during each hour, and the male was credited with 60 per cent of the total time that the eggs were actually covered. Unfortunately the thermocouple record does not indicate the time that the adults exchange places on the eggs. Neither adult bird sat very steadily but was up and down and at the box entrance at frequent intervals. Often this restlessness of the bird in the box makes a record that simulates attentive and inattentive periods, with "attentive periods" often 20 to 25 minutes long. The bird was also restless at night although never away from the eggs for so long at a time.

Sherman gives 25 to 28 days as the length of time that the young remain before leaving the nest cavity. In four nests recorded by us the time was 23, 24, 25, and 26 days, respectively. Sherman states that the young are brooded for two weeks and that the male stays in the box at night until the young are three weeks old.

Sherman found the seven young fed approximately 1.5 times per hour on the first day, while five young were fed 5.5 times per hour when 18 and 19 days old. During one all-day observation, Shirling (1927) reported well-developed young fed 2.9 times per hour. Observations during 1.3 hours at one of our nests when the young were 14 days old and again when they were 20 days old gave the same rate of 3.6 times per hour.

Skutch found that the male entered the box a little after 1900 hours on clear days and that he remained in or near the box in the morning until relieved by the female. One day she came at 0835, while on another day she had not yet come at 0930 hours. Very little can be said concerning the daily rhythm of attentive behavior. The eggs are covered nearly continuously except when the adults are restless. On hot days the adults appear at the box entrance more frequently but attentivity, as it is shared by the two sexes, is very highly developed.

Crested Flycatcher, *Myiarchus crinitus*

Both the male and female crested flycatcher are often mentioned as engaging in nest construction, but the close observations of Gillespie (1924) indicated that the female was chiefly responsible for it, although the male accompanied her back and forth on the trips for nest material. In this case 10 days were required for its completion, although there are records of even longer periods being required.

Gillespie gives the incubation period as 13 days, Bent (1942) lists 13, 14, and 15 days by different observers. In one nest we had under observation, all four young of the brood hatched 14 days after the last egg was laid. The adult was found in the box the afternnon before the last egg was laid. Gillespie mentions that the male may feed the female on the nest, but this was not observed by us and is probably not common. Only the female incubates.

We were successful in obtaining a record of attentive behavior of the female for five days at one nest (Table 19). The attentive rhythm is fairly slow with only 25 attentive periods per day, averaging 21.3 minutes, and with intervening inattentive periods of 13 minutes. The percentage of total daytime is normal, however, averaging 61.2. On June 23, with a marked drop in temperature, the attentive periods doubled in length, but the next day, with continued cold, they reverted to normal length again.

Both adults feed the young. Mousley (1934a) watched a nest for nearly 30 hours and found the average rate to be 5.3 trips per hour. The rate increased from four times per hour when the young were supposedly three days old to 7.5 times per hour when they were 18 days old. The female fed the young 74 per cent of the total times they were fed. Gillespie estimated that the female fed the young twice as often as the male. Mousley estimated that the brood he had under observation stayed in

Table 19. Attentive behavior of a female crested flycatcher during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	Mean daily temperature °C.
June 20	25	24.2	9.5	64	17.8
June 21	27	16.6	14.8	72	22.2
June 22	29	16.2	13.1	76	24.4
June 23	16	33.7	14.4	62	16.7
June 24	28	15.6	13.1	60	15.6

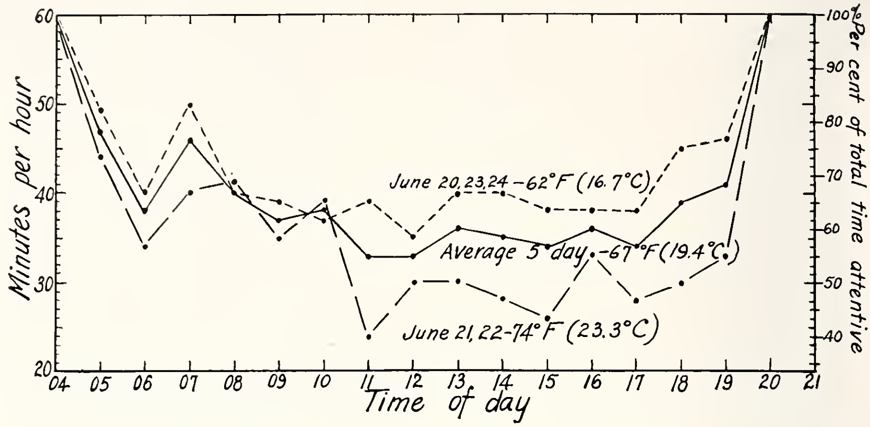

FIG. 18. Daily rhythm in attentiveness of a female crested flycatcher during incubation.

the nest for 18 days; Gillespie gives 15 days for one brood when there may have been some disturbance due to banding, and cites another record where the young remained in the nest for 25 days.

Figure 18 shows the daily rhythm of attentive behavior of the female during incubation. More time is spent on the eggs during the midday slump in cold than in warm weather. The female takes her first trip away from the eggs in the morning an average of six minutes after sunrise (range: 10 min. before to 27 min. after), but she retires exceptionally early in the evening, fully 63 minutes before sunset on an average (range: 86 to 44 min. before). Nice (1928, 1931b) recorded the first early morning songs of the male in late May and early June from 0424 to 0503 hours which would probably be a few minutes earlier than the first activities of the female. Gillespie observed the young to be fed from 0430 to 1912 hours. Our temperature record indicated that the female was usually very uneasy on the nest during the nighttime.

PHOEBE, *Sayornis phoebe*

There has been surprisingly little published concerning the nesting behavior of the phoebe. Henderson (1924) and Smith (1942) observed only the female engaging in actual nest construction, while the male accompanied her back and forth on her trips to gather nest material. Three or four days or sometimes as long as 10 days are required to complete the nest building. Bent (1942) quotes observations of Althea R. Sherman at 10 nests that the average length of the incubation period is 16 days and that only the female incubates. Henderson (1924) and Stoner (1939) also give the incubation period as 16 days at three nests that they had under observation. W. P. Smith (1942) found it to be

17, 16, and 14 days at three nests. In six nests under our observation, the incubation period was 16 days in one instance, definitely 15 days in another instance, while in four the hatch appeared to be late on the fifteenth day. If records of all observers were combined, the average would be 16 days. We have record of only the one adult incubating, presumably the female. Out of 10 cases recorded, all the young hatched on a single day in four instances, but these were all small sets or incomplete hatching of the set, the brood required 2 days in which to hatch in three instances and 3 days in three other cases. Thus the first eggs must receive a small amount of heat before the last of the four- to six-egg set is completed. Henderson did not often observe the adult on the nest during the egg-laying period, but she came on at night. Smith recorded some incubation beginning with the second egg, and steady incubation began with the next to last egg in two of his three nests.

A partial record of attentive behavior of the female during incubation was obtained by means of the itograph at nest No. 1 and by the temperature-recorder at nest No. 2. A record of the rate for feeding the young was also obtained with the itograph at nests No. 1 and 3.

As evident in Table 20, there is considerable difference in length and number of periods per day between the females at nests No. 1 and 2. At nest No. 2 the female had twice as many periods as at nest No. 1, and the periods were about half as long. However, the percentage of total daytime spent on the eggs at nests No. 1 and 2 was nearly the same, being 58.5 and 55.6, respectively. At a third nest, where observations only were taken, the female was observed to sit nearly motionless on the eggs from 0830 to 1030 when the watching was terminated. This was on the twelfth day of incubation and is a longer attentive period than any recorded by the instruments.

When the young birds of the nest No. 1 hatched, the number of periods greatly increased and their length decreased so that they were more nearly comparable to attentive periods at nest No. 2 during incubation. The percentage of total daytime spent brooding dropped, however, to 46.3.

Stoner gives 16 to 17 days as the length of the nestling period. Henderson observed the young to remain in two nests for 17 days and in one nest for 20 days. Smith found his young birds leaving the nest after 15, 16, and 17 days and parental care to last 22, 20, and 17 days, respectively, after the young left. Our records show the young leaving in 16 days in one nest, 17 days in seven nests, 18 days in two nests, and 18 or 19 days in one nest. Both adults share in feeding the young and Henderson observed that the size of the insects brought increased, as the young became older.

A complete record is available of the total feeding of four young at

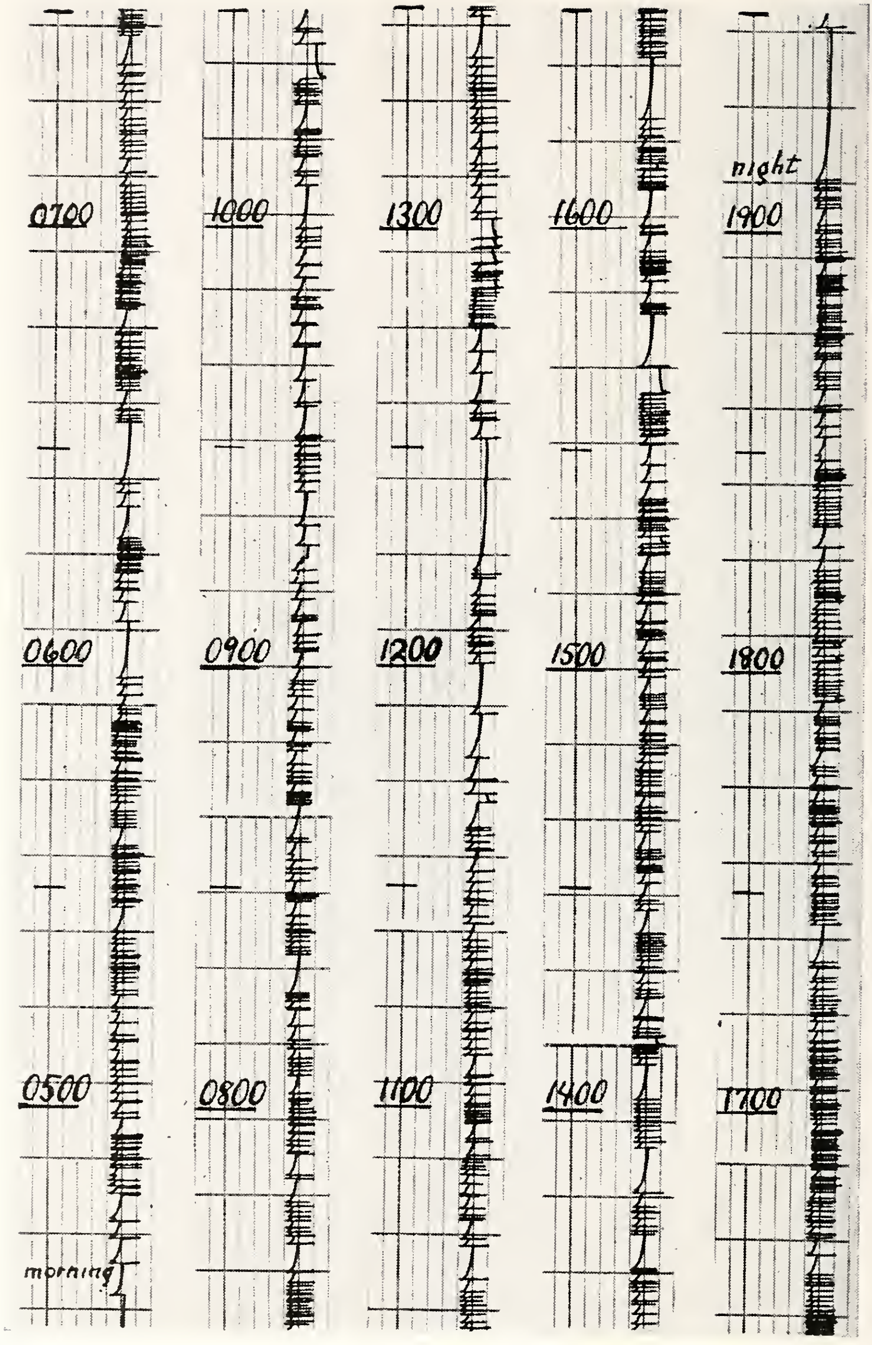

Fig. 19. Itograph record of the pair of phoebes feeding four young, 12 days old. Each transverse line represents one trip to the nest, of which there were 845 during the day.

TABLE 20. Attentive behavior of female phoebes.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.
Nest No. 1		*Incubation*			
June 18, 1932	45	13.4	7.2	76	24.4
June 19	48	10.1	9.2	74	23.3
Average	46.5	11.8	8.2	75	23.9
Nest No. 2					
July 3, 1928	61	8.9	5.8	79	26.1
July 6	85	6.2	4.4	68	20.0
July 7	118	4.1	3.8	75	23.9
July 8	124	3.5	3.8	81	27.2
July 9	80	5.9	4.9	79	26.1
Average	93.6	5.7	4.5	76	24.4
Nest No. 1		*Brooding young*			
June 20, 1932	68	6.4	6.9	76	24.4
June 21	129	3.0	4.0	74	23.3
Average	98.5	4.7	5.4	75	23.9

nest No. 1 from the beginning of hatching on June 20 until the last one left the nest after 17 days at 0622 hours on July 8 (Table 21). A remarkable total of 8,942 visits to the nest by the two birds was made which works out to be 2,275 trips per young bird, presumably with food each time. As the young grew older and required more food, the number of trips per day increased fairly regularly to a maximum of 845 when the young were 12 days old (Fig. 19), after which the number of trips was again reduced. According to Stoner's detailed data on growth of nestlings, increase in weight is more rapid up to 11 days of age after which further increase is slow and fluctuating. The rate of feeding the single young at nest No. 3, June 12 to 16, furnishes an interesting comparison. When this young grew from 7 to 12 days in age, the adults made 680 trips to the nest, probably with food each time. At nest No. 1 with four young, the adults made 4.05 times as many trips in the same period. In this comparison, the rate of feeding was directly proportional to the number of young in the nest.

Smith found nest building most vigorous between 0600 and 1030 hours. Egg-laying occurred usually between 0530 and 0630. The daily rhythm in attentiveness during incubation as shown by our records (Fig. 20) follows the usual pattern with a decline to the afternoon, although the period of minimum attentiveness from 1600 to 1900 hours

TABLE 21. Number of trips to nest made by adult phoebes.[a]

Average age of young (days)	Number of trips per day	Number of trips per young bird per day	Mean daily temperature °F.	Mean daily temperature °C.
		Nest No. 1, 1932		
0	68	45	76	24.4
0.5	129	43	74	23.3
1+	211	53	74	23.3
2	228	57	65	18.3
3	286	72	64	17.8
4	382	96	70	21.1
5	351	88	72	22.2
6	437	109	72	22.2
7	499	125	68	20.0
8	451	113	72	22.2
9	444	111	76	24.4
10	594	148	71	21.7
11	769	192	62	16.7
12	845	211	64	17.8
13	776	194	64	17.8
14	753	188	64	17.8
15	509	127	74	23.3
16	531	133	69	20.6
17	679	170	68	20.0
		Nest No. 3, 1929		
7	...	136	68	20.0
8	...	138	69	20.6
9	...	133	69	20.6
10	...	164	69	20.6
11	...	109	73	22.8

[a] There was in nest No. 1 an average of 1.5 young on 0 days, 3 young on 0.5 days, and 4 young the rest of the time. In nest No. 3 there was only one young on all days.

TABLE 22. Time of beginning and ending of daily activities of female phoebes.

Date	*Difference from* Sunrise (min.)	Sunset (min.)
Nest No. 1		
June 18, 1932	−18	+12
June 19	−19	+10
June 20	−10	− 4
June 21	− 3	+ 1
June 22	− 4	+37
June 23	− 6	+39
June 24	+27	+13
June 25	−10	+41
June 26	...	+10
June 27	− 6	+34
June 28	− 9	+34
June 29	−15	+24
June 30	−18	+22
July 1	−20	+25
July 2	+12	+18
July 3	−20	+ 3
July 4	− 7	+13
July 5	−24	+17
July 6	−11	+27
July 7	− 1	−32
July 8	−17	...
Average	− 8	+18
Nest No. 2		
July 3, 1928	− 6	− 1
July 6	− 8	0
July 7	−16	+16
July 8	−10	+15
July 9	− 3	−36
Average	− 9	− 1
Nest No. 3		
June 11, 1929	...	−24
June 12	−14	−13
June 13	+ 1	−22
June 14	+ 8	+17
June 15	− 8	− 3
June 16	− 6	...
June 18	...	−50
June 19	− 1	...
June 20	...	−35
June 21	+ 4	...
Average	− 2	−19

appears to be a little later in the day than usual. The daily rhythm in feeding the young at nest No. 1 shows two pronounced peaks coming in early morning and late afternoon, but the late afternoon peak does not show in the curve for nest No. 3. The largest single number of trips per hour (106) came at nest No. 1 between 1630 and 1730 hours when the young were 13 days old. The next largest number (89) is for the same hour of the preceding day. Although there is no actual information available, one would surmise that the adults must have been feeding the young very small insects and probably only one at a time.

Table 22 shows that during both incubation and care of the young, the female ordinarily left the nest a few minutes before sunrise, which came about 0458 hours. This averaged eight minutes at nest No. 1, nine minutes at nest No. 2, and two minutes at nest No. 3. The unusually late awakening of the female at nest No. 1 on June 24 and July 2, may have been due to cold damp weather. Wright (1913) found that the male began his early morning calling an average of 53 minutes before sunrise.

The cessation of the daily activities averaged 18 minutes after sunset, which came about 2000 hours, for the female at nest No. 1, and only twice during 20 days did this bird retire before sunset. The female at nest No. 2 varied considerably in her time of retirement, but the average is one minute before sunset. At nest No. 3 the female terminated her daily activities an average of 19 minutes before sunset and only once did she do so after sunset. An average of the three birds would make the time of retiring very close to the time of sunset. Wright had only two records for the cessation of the male's activities, and these averaged 22

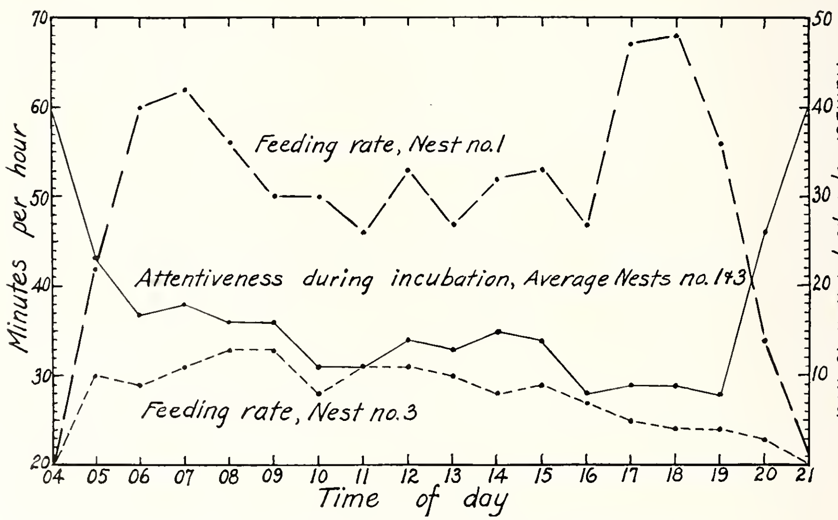

FIG. 20. Daily rhythm in activity of the phoebe.

minutes after sunset. The female at nest No. 2 showed some restlessness at intervals of several minutes for the first night or two after the thermocouple was inserted, but sat quietly on the nest at night thereafter.

Wood Pewee, *Contopus (Myiochanes) virens*

There is little published information on the attentive behavior of the wood pewee. In Bent's (1942) compilation of notes from various observers, it is stated that the male does not assist either in nest building or at incubation, but that he feeds the female more or less frequently while she incubates. The incubation period for the usual set of three eggs is given as 12 or 13 days. The young are cared for by both parents and may remain in the nest for 15, 16, or 18 days.

We had one nest under observation from the time of its construction until the young flew. Since it was situated 18 feet up on a horizontal limb of an elm, most of the observations were made at some distance. The nest was discovered on July 23 when already well begun and one or possibly both adult birds were carrying material to it. On July 24, during a short observation period, trips to the nest with building material were at the rate of 24 times per hour, on July 25 the rate was seven times per hour, and on July 26 it was 10 times per hour. On this last date it was evident that only the female was working at the nest which was then nearing completion. On July 30, there were two eggs in the nest, and on August 2, there were three eggs of a complete set. The exact time of laying the third egg is uncertain but presumably was July 31. The temperature-recorder was attached to the nest on August 2, but a satisfactory record was obtained only between August 5 and 15.

Table 23 shows that there normally are 32.1 attentive periods per day, averaging 19.6 minutes long with intervals between attentive periods averaging 6.8 minutes. This gives a high percentage of 73.5 for daytime activities devoted to incubation of eggs. On the two warmest days of August 10 and 11, the attentive periods were fewer in number and averaged longest in duration. The coldest day came on August 15, when it also was rainy all day. The number of attentive periods was greatly reduced and there were long periods when the nest was left uncovered. Perhaps the hunting of food was difficult and the adult bird was uncomfortable. The data for August 15 is omitted from the averages above given.

Hatching began about 0615 on August 16 and all three birds hatched the same day. The shortest possible length of the incubation period was, therefore, 14 days and more likely it was 16 days. This is three or four days longer than indicated by the observations compiled by Bent. It is possible that hatching would have started on August 15, had the adult covered the eggs more faithfully. It is obvious that more information is

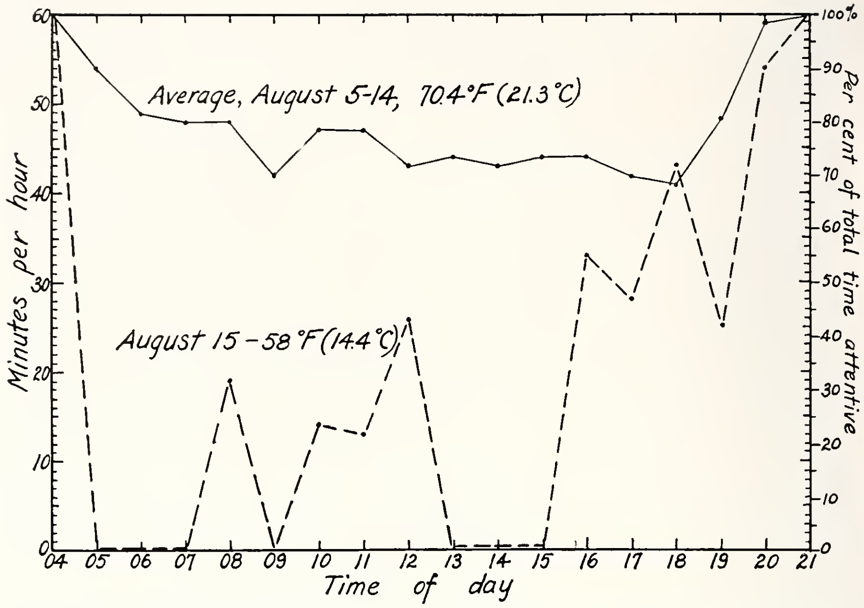

FIG. 21. Average daily rhythm in attentiveness of a female wood pewee during incubation and on a rainy day, August 15.

required for this species. The three young birds left on either September 1 or 2, after 16 or 17 days in the nest.

Figure 21 gives the average daily curve for the incubation period exclusive of August 15. The data for the two warmest days, August 10 and 11, fall so close to this line that no separate curve is presented. The reduced and spasmodic incubation on August 15 is in marked contrast with the steady incubation at other times.

The female began her morning activities an average of 22 minutes before sunrise, which came about 0530 hours, and terminated them not after sunset, as one might suppose, but 16 minutes before sunset, which came about 1933 hours. The data for August 15 are not included due to the distinctly unfavorable weather conditions. Likewise, the data for August 5 and 6 are not included in the average for time of arising. The temperature record indicates that on these days the female actually became active on the nest at 0532 (7 minutes before sunrise) and 0536 (10 minutes before sunrise), respectively, although she did not leave for a definite inattentive period until the times indicated. It is entirely possible that the male fed the female on the nest at these times, as he has been seen to do by other observers. We have no evidence that the male fed the female regularly at other times of day. Craig's (1943) data show that the first waking song of the male during June and July comes about

TABLE 23. Attentive behavior of a female wood pewee during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.	Difference from [a] Sunrise (min.)	Sunset (min.)
1929							
Aug. 5	35	16.8	4.8	64	17.8	+103	+ 7
Aug. 6	32	19.9	5.5	66	18.9	+ 22	−16
Aug. 7	38	16.6	8.6	67	19.4	− 33	−17
Aug. 8	37	15.6	6.2	68	20.0	− 34	− 5
Aug. 9	29	21.0	7.9	74	23.3	− 20	−18
Aug. 10	26	24.5	7.4	77	25.0	− 16	−23
Aug. 11	28	23.1	6.4	77	25.0	− 19	−26
Aug. 12	29	22.4	8.1	71	21.7	− 28	− 6
Aug. 13	30	19.1	6.8	74	23.3	+ 16	−38
Aug. 14	37	16.6	6.7	66	18.9	− 41	− 6
Aug. 15	16	13.6	29.9	58	14.4	− 5	+10

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

an hour before sunrise and the last evening song occurs about a half hour after sunset. The male is thus active earlier than the female in the morning and later in the evening. The temperature record indicates that the female is fairly quiet on the nest at night, sometimes motionless for 30 to 40 minutes at a time, but that usually she stirs around slightly at more frequent intervals.

Stanford (1942) recorded the feeding of three young during 37 hours of observation at one nest and found the rate per hour to vary as follows: just hatched—2.7, 2 days old—4.2, 3 days—2.3, 9 days—5.2, 11 days —2.4, and 12 days—5.5. The average rate for the entire period regardless of the age of the birds was 3.1 times per hour. The average of the daily rates, however, gives a higher rate of 4.5 times per hour. Of the total 116 feedings recorded, 90.5 per cent were made by the female, as the male was relatively inactive and was recorded feeding the young only when they were 9 and 12 days old.

BARN SWALLOW, *Hirundo rustica (erythrogaster)*

The discussion here will be limited to the North American race of barn swallow, *H. r. erythrogaster*. Comparative data on the European form, *H. r. rustica*, will be found in Table 45. In the observations of W. B. Smith (1933, 1937a) and Wood (1937), nest building begins in from 1 to 5 days after the birds first arrive and select a nest site in May or early June. From 6 to 9 days are required for nest building, in which work both adults share, although the female is the more active of the two sexes and appears to do most of the modeling of the nest. Wood calculated from the total weight of the nest and the size of individual mud pellets that 100 trips with nesting material per day for six days must have been made to the nest site. Herrick (1935) observed during 15 hours on 4 different days that the average rate of visiting the nest during its construction was 22 times per hour. From 1 to 3 days may intervene from the apparent completion of the nest until the first egg is laid. Bent (1942) reports observations wherein 12 days were required for nest building and two weeks elapsed after the nest was completed until the first egg was laid. Smith (1933) found in one case that 11 days lapsed between the time the last young of a first brood flew until the adults started repair on the same nest for a second brood and that the first egg was laid only 5 days later.

An egg is laid on consecutive mornings until the set of 3 to 5 is completed. The first eggs receive considerable incubation before the last is laid, as in the four nests observed by Smith and Wood and in two nests observed by myself, hatching extended over two or three days. The time intervals from the date the last egg was laid until the last young was hatched were 14, 15, and 16 days in the nests recorded by Smith. Seven-

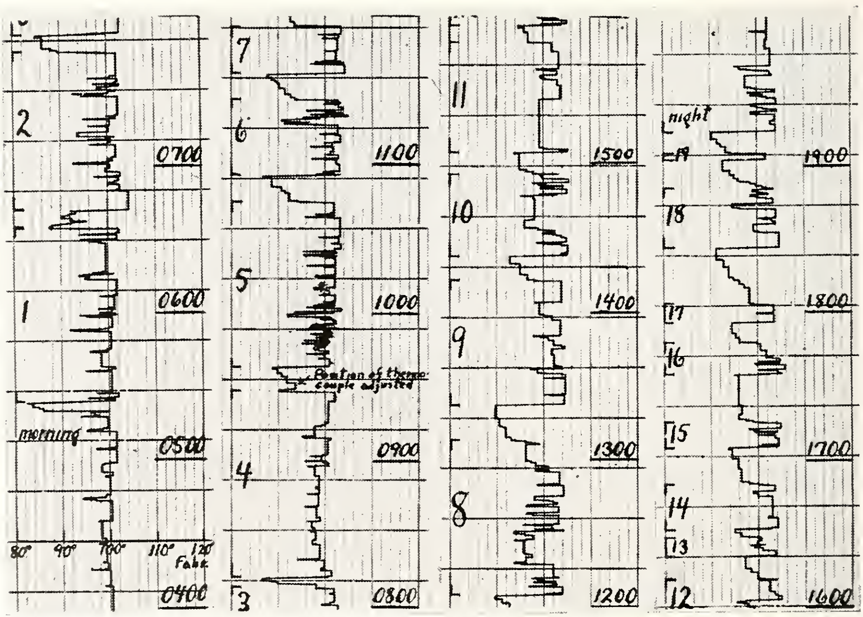

FIG. 22. Nest-temperature record of the incubating female barn swallow at nest No. 2 on July 4, 1935. The attentive periods are marked and numbered on the left side of each strip.

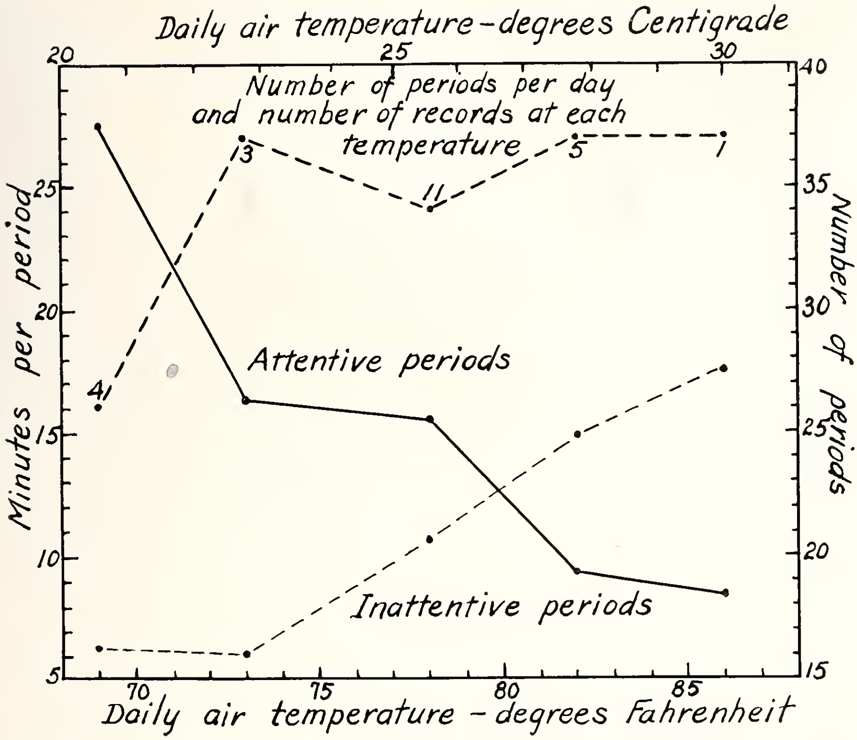

FIG. 23. Changes in attentive behavior of female barn swallows correlated with mean daily air temperature.

teen days elapsed in Wood's nest, but there was little or no incubation on the first day. It was either 15 or 16 days in one of my nests. Allen and Nice (1952) state that the incubation period is 14 to 15 days.

Smith (1933), Herrick (1935), Wood (1937), Brewster (Griscom 1938), and E. M. Davis (1937) all observed the male and female taking turns at incubating the eggs. Brewster noticed the exchange of birds on the nest at average intervals of 15 minutes. Wood found on the third day of incubation that the intervals on the nest varied from 4 to 15 minutes and on the eleventh day, the intervals came at 6 to 36 minutes. Davis gives the average time on the nest as 12 minutes on the basis of several hours of observation. Smith (1933, 1937) is not clear as to how much incubation the male performs. He states that at times the male is on the eggs during the female's absence but that frequently the female leaves without being relieved by the male. My observations at nests during incubation are limited, but I once saw the male come and stand in the nest over the eggs during the female's inattentiveness. He did not sit on the eggs and the recording potentiometer verifies that little or no heat was applied to them. Several days' records at two nests (Fig. 22) show typical attentive behavior of one bird only and will be analyzed, as in other passerine species, in the assumption that the female does all the effective incubation. The male cannot be considered as sharing in incubation unless he actually applies heat to the eggs. He may even sit on the eggs, but unless he arranges his feathers and applies vasculated skin to them, there is little heat transference. Davis (1937: 70) has handled living barn swallows for banding during the nesting period and states that in the male the brood patch "is not well developed and it is a good way to distinguish the sexes when they are caught."

Our two records on different birds, involving a total of 24 complete days (Table 24), give an average of 15.8 minutes for the attentive period and 10.6 minutes for the inattentive period with 34 periods coming each day. The percentage of total daytime spent on the eggs is 59.1. Except for a fewer number of periods at temperatures below 70° F. (21.1° C.), the average number per day is not greatly affected by differences in temperature (Fig. 23). However, with increase in air temperature there is a progressive decline in the length of the attentive periods and an increase in the length of the inattentive periods. The percentage of daytime that the bird is on the eggs at five-degree intervals of temperature from below 70° F. (21.1° C.) to above 85° F. (29.4° C.) is 80.5, 72.4, 58.6, 38.0, and 31.6.

Smith, Wood, Davis, Herrick, and I recorded the young remaining in the nest for 18, 18, 18, 19, 19, 20, and 23 days before they flew. Herrick and Smith found that the young roosted in the nest for several nights after first leaving it, and Smith noted that the parents continued to feed and care for the young for 9 or 10 days, after which the family group as a unit began to break up. Wood found that a family of four, which he had under observation, remained together from the time the young left the nest on July 16 until they departed August 13, presumably on their southward migration.

Little observation of brooding behavior has been noted, but Davis suggests it is less prevalent after the first 4 days. Wood states that on the tenth day the four young were fed on the average once every 53 seconds or at the rate of 68 times per hour. Short observation periods by Smith when five young were 8 days and 10 days old and by myself when three young were 7 days old give rates of 24, 53, and 15 per hour. Both parents share in feeding the young. Davis states that feeding is irregular, sometimes at the rate of once a minute for 15 or more minutes followed by a pause of perhaps 15 minutes.

Figure 24 gives the daily rhythm of attentiveness of the female during incubation. The average rhythm is based on records for 5 days each for birds No. 1 and No. 2 at medium temperatures. For contrast average

TABLE 24. Attentive behavior of female barn swallows during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.	*Difference from* [a] Sunrise (min.)	Sunset (min.)
Nest No. 1, 1933							
July 19	41	10.8	11.6	77	25.0	...	...
July 20	32	11.4	15.3	82	27.8	...	−36
July 21	44	9.5	10.5	83	28.3	−1	+ 9
July 22	37	8.9	15.2	81	27.2	+10	+38
July 23	37	8.3	17.5	86	30.0	−25	+50
July 24	35	17.8	5.6	72	22.2	−12	−65
July 25	25	27.8	5.6	69	20.6	−7	−42
July 26	36	17.9	5.1	69	20.6	+5	−35
July 27	42	12.0	7.6	74	23.3	+1	−40
July 28	50	8.9	8.5	78	25.6	−3	+ 3
July 29	31	9.3	19.2	81	27.2	+8	+42
Average	37.3	13.0	11.1	77.4	25.2	−2.7	− 7.6
Nest No. 2, 1935							
July 3	31	13.9	11.1	79	26.1	+31	...
July 4	19	33.4	10.0	77	25.0	+20	−47
July 5	26	18.9	11.8	80	26.7	+40	−50
July 6	23	12.8	19.0	80	26.7	...	−35
July 7	26	17.3	13.4	76	24.4	+33	−75
July 8	25	25.0	8.1	68	20.0	...	−19
July 9	34	18.9	4.8	72	22.2	+59	−27
July 10	40	11.1	9.0	76	24.4	+56	−25
July 11	39	7.4	14.0	82	27.8	+40	− 9
July 12	41	12.3	7.0	78	25.6	+28	−50
July 13	34	19.0	6.5	76	24.4	+15	−14
July 14	42	11.6	8.5	78	25.6	+34	− 6
July 15	18	39.4	7.0	69	20.6	+25	−23
Average	30.6	18.5	10.0	76.2	24.6	+34.6	−31.7

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

curves for the two hottest and the two coldest days for each bird are shown. These days of extreme temperature are not included in the curve showing the average rhythm. Both nests were placed on rafters in a hay barn close to the roof that was covered with wood shingles. On hot sunny days the nest temperature during midday was frequently over 100° F. (37.8° C.), when the adult was absent, and she spent very short

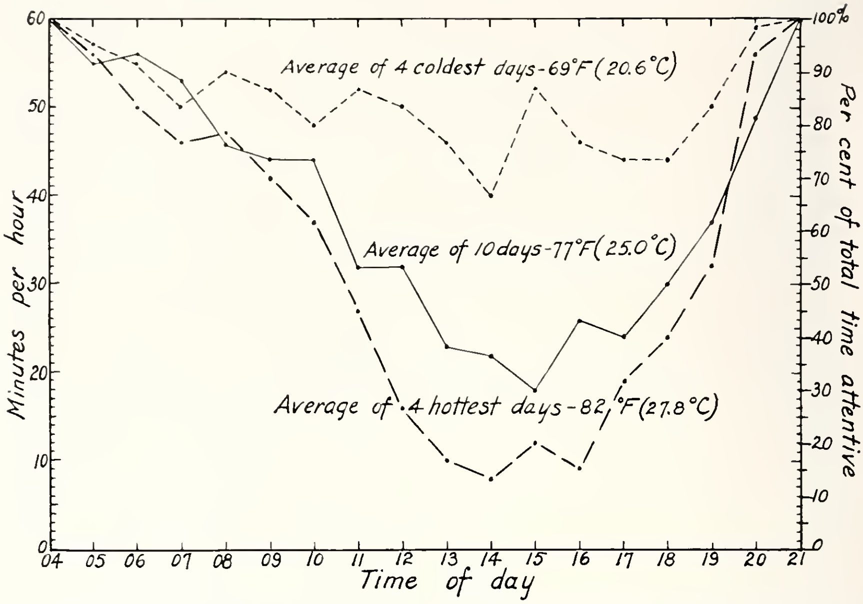

FIG. 24. Daily rhythm in attentiveness of female barn swallows during incubation.

intervals on the eggs. On colder days, a pronounced daily rhythm was not evident. On one such cold rainy day, July 15, the bird spent successive attentive periods of 65 and 155 minutes at the nest with an intervening period away of only 15 minutes. This behavior contrasts sharply with that of the wood pewee in similar weather (p. 110). On the other hand, during a storm in the hot afternoon of July 6, the bird spent successive periods of 2, 4, and 3 minutes on the nest with intervening inattentiveness of 52 and 57 minutes.

Wood noted that during incubation the female spent every night on the nest, settling down about 1950 hours. The male went elsewhere. When the parents were feeding young, they appeared with food at 0450, 0440, and 0444 hours on consecutive mornings after the young had awakened and started calling for food on these same days at 0445, 0440, and 0435 hours, respectively. Smith (1937a) found that the parent discontinued its regular night's stay on the nest when the young were 14 days old. He gives the time of first appearing on one morning at 0352 and of leaving in two evenings at 1946 and 2000 hours. According to Bent (1942), C. W. Townsend observed the young returning to the nest for 5 nights after leaving it; after this they roosted elsewhere.

Female No. 1 (Table 24) did not stay on the nest at night until July 20, which was the second or third day after the last egg had been laid.

She appeared somewhat restless at night throughout the rest of the incubation period. Female No. 2 spent every night on the nest and was fairly quiet until 4 days before the end of incubation when there was some evidence of increasing restlessness.

Female No. 1 showed considerable irregularity in the time of beginning and ending her daily activities, but an average of all records indicates that these times came slightly before sunrise (0515 hours) and sunset (1950 hours). Bird No. 2 exhibited an interesting contrast in beginning her activities over a half hour after sunrise and ending them before sunset so that her period of daily activity was about an hour less than that of bird No. 1. Wright's (1913) data indicate that the male becomes active in the morning before the female, as 14 records gave his first appearance as 61 minutes before sunrise. One record gave the last activity of the male as 27 minutes after sunset.

Purple Martin, *Progne subis*

According to Allen and Nice (1952), the female purple martin does most of the nest building and all of the incubation. Usually four or five eggs are laid. At one nest where a thermocouple was inserted, the male frequently entered the box during the female's inattentiveness but usually for short periods only. The temperature record indicates that the male may have contacted the thermocouple by standing in the nest, but there is no indication of any actual incubation on his part. The record is a typical one for only the female incubating. Allen and Nice give the length of incubation as 15 to 16 days.

Six days' recording was made with the thermocouple in one nest (Table 25). There were an average of 21.8 attentive periods per day, each period 32.0 minutes long and totaling 76.7 per cent of the daytime activities. The intervening inattentive periods averaged 9.3 minutes. The first day was the warmest and the attentive periods were only 24.6 minutes. As the air temperature fell during the next 3 days, the length of the attentive periods increased to 45.9 minutes; but then as the average air temperature remained constant during succeeding days, the attentive periods became progressively shorter as well as more numerous, as if the bird was becoming acclimated to the cold. The percentage of total time attentive varied from 67.6 on June 10 to 76.7 on June 12 and increased still further to 81.2 on June 16.

The young were found in the nest for 35 or 36 days. Both parents cared for the young, as is typical for the species. Allen and Nice say that brooding decreases to about 50 per cent when the young are 5 days old and usually stops on the ninth or tenth day. After first leaving the nest, the young may return to the box at intervals or to pass the night for several days. Allen and Nice believe the true nestling period is about 28 days.

Widmann (1884) says that young martins do not leave the box until they are 6 weeks old, as in the case of our birds, but Allen and Nice interpret this to mean permanent leaving.

TABLE 25. Attentive behavior of a female purple martin during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.	*Difference from*[a] Sunrise (min.)	Sunset (min.)
1927							
June 10	24	24.6	11.3	70	21.1	+27	− 4
June 11	20	34.6	8.1	65	18.3	+47	+ 5
June 12	15	45.9	13.1	56	13.3	+41	+ 5
June 13	...	...	...	57	13.9	+36	− 5
June 14	17	35.4	9.5	58	14.4	+42	+12
June 15	25	28.7	8.5	58	14.4	+11	+42
June 16	30	22.8	5.1	56	13.3	+ 7	−59

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

In a nest under observation for 63 minutes when the young were 2 days old, 79 minutes when they were 9 days old, and 78 minutes when they were 24 days old, the four young were fed at the rate of 19, 21, and 49 times per hour or 4.8, 5.1, and 12.3 times per bird per hour. Of the total visits to the box, there were 58 by the male and 59 by the female, and presumably at least one young bird was fed each time. Macnamara (1917) calculated on the basis of observations that extended over two weeks that the young were fed 3.3 times per bird per hour. Widmann (1884) watched 16 nests for an entire day. Most of the nests contained three young, 1 to 5 weeks old. Widmann observed not only an increase in the rate of feeding with older young but also that very young birds were given crushed insects, mostly small beetles. When they were 2 weeks old, they were fed insects the size of large flies; when they were 4 weeks old, they were fed large dragonflies, grasshoppers, and butterflies. In one of three nests with young 5 weeks old, there were only two young. These were fed 192 times during the day. If the day included 15.5 hours of activity, this would average 6.2 times per bird per hour. At the other two nests with three young, they were fed 280 and 284 times or at the rate of 6.1 times per bird per hour. For the entire colony with young at all ages, the average feeding rate was 4.4 times per bird per hour. Forty-four per cent of the feedings were by the male and 56 per cent by the female. Allen and Nice state that the parents may feed the young every few minutes for eight or ten minutes, then cease feeding for a similar period. This suggests attentive and inattentive periods.

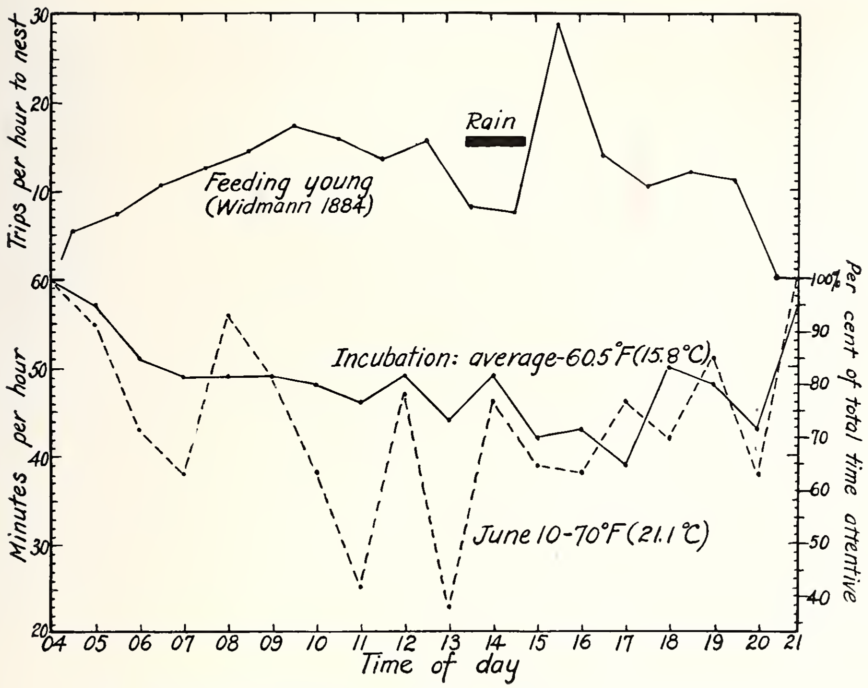

FIG. 25. Daily rhythm in attentive behavior of purple martin.

Figure 25 shows the average daily rhythm of attentive behavior during the six days of incubation. On June 10, with the highest air temperature, the depression of activity during the morning is pronounced compared with the average, but during the afternoon the rate is about the same.

In this same figure is shown the daily rhythm of feeding the young from the hourly records of Widmann made during one day. In general, the feeding curve is the reverse of the curve during incubation. Feeding is more rapid during midday than during early morning and evening. This was a warm day with the temperature varying from 74°F. (23.3° C.) at 0500 to 92° F. (33.3° C.) between 1200 and 1300 hours. Probably the adults spent relatively more time getting food for themselves in the early morning and evening and devoted less attention to the young at these times. Perhaps also there may have been some time spent in brooding the very young in the cooler portion of the day, but no record was made of this.

The one female recorded in Table 25 began its daily activities, on the average, 30 minutes after sunrise (0454 hours) and terminated them 1 minute before sunset (1958 hours). This female was restless on the eggs at night, noticeably more so before than after midnight.

Catbird, *Dumetella carolinensis*

In one nest building during mid-May that Herrick (1935) followed through to completion, 7 days were required from the insertion of the first crude material to the completion of the lining. The female did most of the work, but the male aided at least to the extent of bringing building material. Three more days elapsed before the first egg was laid. During this interval the birds usually kept away from the nest, although on the second morning the female was observed sitting in the nest at 0830 hours, as if about ready to lay. Herrick states that each of the four eggs was laid between 0900 hours and noon, during which time the female sat closely on the nest. During the afternoon, he found the female on and off the nest at intervals of one-half hour or longer. D. E. Davis (1942) states that at one nest the eggs were laid daily about 0800 hours.

At Herrick's nest steady incubation began on the day that the third of a four-egg set was laid, and lasted 13 days. Davis gives the incubation period as 12 days, but he must also have considered incubation as beginning with the third of a four-egg set. At 19 of our nests where time of hatching was recorded and where there were either three or four young, hatching of all eggs apparently occurred in a single day at six nests, and was spread over 2 days at ten nests, over 3 days at two nests, and over 4 days at one nest. We have no data on attentive behavior during egg-laying, but the wide spacing of hatching indicates that the first eggs received considerable incubation before the last were laid. Of six nests where data are available on time between laying and hatching of the last egg, there is one record of 12 days, four records of 13 days, and one record that was either 13 or 14 days. Most likely, the usual incubation period is 13 days.

Only the female incubates. D. E. Davis (1942a) makes a general statement that the female is on the nest for 20 minutes at a time and off the nest for about five-minute intervals. We obtained data on attentive behavior during incubation at four nests with the use of the recording potentiometer (Table 26). The attentive period for those four birds averaged 22.7 minutes and the inattentive period 7.0 minutes, with 33 attentive periods per day. Time on the eggs made up 75.9 per cent of the bird's daytime activity.

The chief variation in attentive behavior from day to day is due to temperature. The daily records are averaged for intervals of five degrees in mean daily temperature, Fahrenheit and plotted in Figure 26. At a medium temperature of 69° F. (20.6° C.), the attentive and inattentive periods were the longest and came at least frequent intervals during the day. Total time spent incubating the eggs during the daytime fluctuated only between 672 and 718 minutes (75.3 and 78.3 per cent of total day-

TABLE 26. Attentive behavior of female catbirds during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.	Difference from[a] Sunrise (min.)	Sunset (min.)
Nest No. 1, 1927							
July 3	...	...	...	...	...	...	−13
July 4	32	22.3	5.8	61	16.1	+ 1	+ 2
July 5	31	21.6	7.2	64	17.8	− 3	− 5
July 6	34	20.2	6.4	72	22.2	− 9	+ 1
July 7	29	24.3	5.9	70	21.1	+39	+21
July 8	28	24.0	7.1	64	17.8	+22	+ 3
July 9	...	...	...	...	...	+25	...
Average	30.8	22.5	6.5	66.2	19.0	+12	+ 2
Nest No. 2, 1930							
June 28	35	20.7	4.9	62	16.7	− 2	− 5
June 29	41	14.9	7.1	72	22.2	+ 1	+ 3
Average	38.0	17.8	6.0	67.0	19.4	0	− 1
Nest No. 3, 1931							
June 19	62	7.8	7.4	80	26.7	−26	+15
June 20	42	12.7	7.3	78	25.6	+20	+ 1
June 21	30	23.8	7.5	68	20.0	−23	+18
June 22	30	22.6	6.8	72	22.2	+ 1	−14
June 23	27	26.1	7.8	68	20.0	−15	+ 2
June 24	30	21.4	8.3	66	18.9	−21	+13
June 25	55	9.4	7.2	79	26.1	−22	+49
Average	39.4	17.7	7.5	73.0	22.8	−12	+17
Nest No. 4, 1931							
July 7	...	...	...	...	...	...	+16
July 8	28	23.1	8.3	74	23.3	− 1	+11
July 9	21	35.8	8.4	72	22.2	−22	+20
July 10	24	31.6	6.0	68	20.0	− 3	+10
July 11	21	32.8	9.0	70	21.1	+22	+ 1
July 12	17	41.3	9.4	70	21.1	+17	+ 4
July 13	...	...	...	...	...	+ 4	...
Average	22.2	32.9	8.2	70.8	22.1	+ 3	+10

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

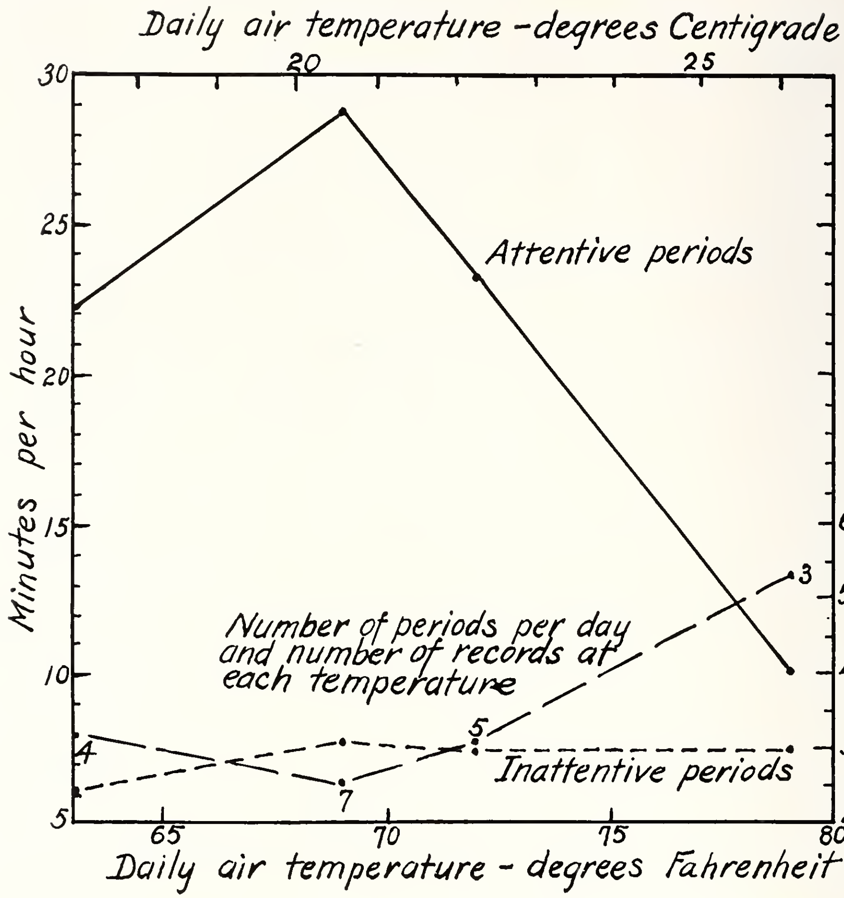

FIG. 26. Changes in attentive behavior of female catbirds correlated with mean daily air temperature.

time) at 63° F. (17.2° C.), 69° F. (20.6° C.), and 72° F. (22.2° C.), but fell to only 530 minutes (57.3 per cent of total daytime) at 79° F. (26.1° C.). At both 63° F. (17.2° C.) and 72° F. (22.2° C.) the length of the attentive and inattentive periods was less than at 69° F. (20.6° C.), and their number per day was greater. At 79° F. (26.1° C.), the total time spent on the eggs decreased 23 per cent, the average length of the attentive period decreased 60 per cent, the length of the inattentive period remained about the same, and the number of periods per day increased 82 per cent.

On the day that the young began to hatch, the number of attentive periods remained the same (Table 27), although the length of the brooding periods diminished and the intervals between them increased.

TABLE 27. Attentive behavior of female catbirds during brooding.

Nest	Number of periods	Brooding periods (min.)	Intervals (min.)	Number of periods	Brooding periods (min.)	Intervals (min.)	Number of periods	Brooding periods (min.)	Intervals (min.)
	0 Day (Hatching)			*1st Day (Brooding)*			*2nd Day (Brooding)*		
No. 1	42	11.9	7.7	32	14.6	14.3	17	11.6	41.4
No. 3	31	16.3	10.7	...	...	...	...	...	...
No. 4	25	23.4	12.2	29	14.9	12.6	...	...	...

Brooding periods decreased during the next 2 days either in number or duration or in both. The percentage of daytime spent brooding during the three days was 62.1, 51.7, and 20.9. In an intensive study at one nest, Gabrielson (1913) found that the adult spent 80 to 32 per cent of her time brooding the young throughout the period of their stay in the nest. However, a good share of this time was protecting the young from the intense solar radiation, and there was also an exceptional amount of heavy rain which required the parent to protect the young from getting wet. Gabrielson recorded a long, unbroken brooding period of 80 minutes and another of 180 minutes.

Of 12 records obtained by us, 10 days elapsed in eight instances and 11 days in three instances from the time the first young hatched to the time that the first young left the nest. In addition, there are two records of young leaving, probably prematurely, on the seventh and eighth days, and there is one record of a single young bird that remained 15 days in the nest.

A record of feeding the young was obtained at one nest. Two young hatched on July 25, and the third on July 26. Hardware cloth was placed partly around the nest on this latter date, but the itograph connections were not completed until July 29. With the young 5 to 11 days old, the rate of daily feeding varied 147, 113, 137, 136, 173, 130, 195, and averaged 147 times per day or 49 times per bird per day. The rate was fairly uniform from day to day. Although both adults share the duty of feeding the young, the relative amount of work performed by the two sexes is not known in this case. At two nests that Gabrielson had under observation at nearly all hours for a total of 12 days, the average daily rate per bird was 32. Gabrielson found that on 8.7 per cent of the trips to the nest, two young were fed instead of one.

Figure 27 shows the daily rhythm in various activities of the catbird during its nesting life. The average curve for incubation behavior at medium temperatures is for 8 days—two records from each of the four

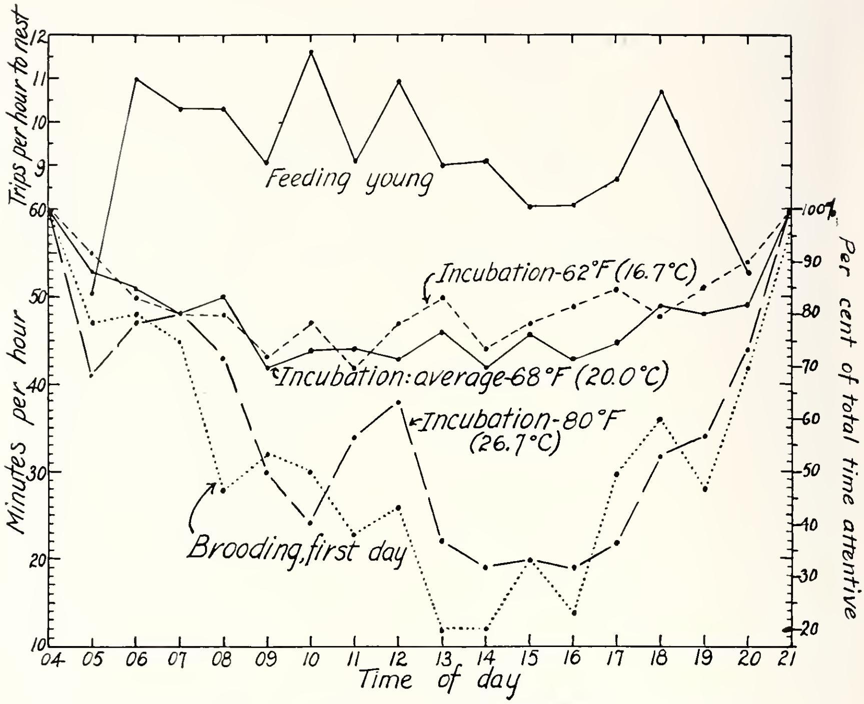

FIG. 27. Daily rhythm in attentive behavior of catbirds.

birds—and it shows a decrease in attentiveness until 0900 hours, a fairly uniform rate until 1700 hours, and a rise again in the evening. At the somewhat lower temperature of 62° F. (16.7° C.), an average of 2 days' records shows slightly more attentiveness. At the considerably higher temperature of 80° F. (26.7° C.), an average, again of 2 days' records, shows a great drop in amount of time spent on the eggs, especially in the early afternoon.

The curve for the first full day of brooding, an average of records for two different females, shows a pronounced decrease during the afternoon when air temperatures rose. In one record for the second day there was no brooding at all from 0900 to 1700 hours, although the average air temperature was only 72° F. (22.2° C.). The same behavior was evident also in the incomplete record of the following day. This daily brooding rhythm agrees, except for the exact times involved, with the manner in which Gabrielson divided the day into three parts: the first from 0430 to 0730 hours when the adult brooded the young to keep them from chilling, the second from 1030 to 1400 hours when she stood over them with outstretched wings to protect them from the heat of the sun, and the third from 1830 hours until dark to protect them from the chill of the evening. Although nests are ordinarily located in dense shrubs, they are frequently exposed to the direct sun at certain hours of the day. The shading of the young by the parents would not be registered by our recording instruments.

The curve showing the feeding rate during the day is an average of the last 7 days for three young in the nest. This shows a depressed rate of feeding from 1300 to 1700 hours, the hottest hours of the day.

The females at the four nests were very irregular in the time that they began and ended their daily activities during incubation (Table 26). The average of the records for the four birds gives the beginning of activities 1 minute after sunrise (about 0500 hours) and their cessation 7 minutes after sunset (about 2000 hours). Allard (1930) recorded the first singing of several male catbirds about 30 minutes before sunrise during June and July.

The recording instrument showed that the female at nest No. 1 was somewhat restless at night during incubation from the time that she settled on the nest until about 0100 hour the next morning and sometimes again from about an hour before she left the nest to begin her day's activity. At nest No. 3 the female was uniformly quiet all night. At nest No. 4 the female showed slight movements all night, although somewhat more frequently before than after midnight.

American Robin, *Turdus migratorius*

The nesting behavior of the robin has been most intensively studied by Schantz (1939) and Howell (1942), and summarized by W. M. Tyler (Bent 1949). Electrical apparatus was used by Schantz "to announce and record the arrivals at the two nests so that it was impossible for the adults to come to the nest without ringing an electric bell or making a recording on paper tape." Both he and Howell spent many hours in observation at the nest, and Howell has summarized the literature to date on many phases of the bird's behavior. Our own records of attentive behavior were obtained with thermocouple and potentiometer until the eggs hatched, after which the itograph was used at one nest.

Building of the first nest requires 5 or 6 days, but later nests may be completed in 2 or 3 days. The work is done almost entirely by the female. During this period the attentiveness of different males varies between nearly complete ignorance, accompanying the female back and forth, and bringing material for the female to incorporate into the nest structure. In one such latter case, Kelly (1913) reported the male making 86 and the female 108 trips to the nest during 11 hours of observation.

Schantz found that 5 days in one case and 3 days in another elapsed between the completion of the nest and laying of the first egg. During these intervals neither adult visited the nest more than once or twice

TABLE 28. Daily record of attentive behavior in female robins.

Nest	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
	2nd Day (Egg-laying)				*3rd Day (Egg-laying)*			
1	...	...	...	...	...	...	...	...
2	58°F.	27	21.2	12.2	52°F.	24	27.7	10.0
3	52	12	51.3	20.1	(Deserted)			
4	...	...	...	...	...	...	...	...
5	...	...	...	...	...	...	...	...
	1st Day (Incubation)				*2nd Day (Incubation)*			
1	...	...	...	...	...	...	...	...
2	55	33	19.7	8.1	53	27	18.6	6.3
3	...	...	...	...	...	...	...	...
4	...	...	...	...	...	...	...	...
5	80	37	18.0	7.1	82	37	17.0	8.5
	3rd Day				*4th Day*			
1	...	...	...	...	...	...	...	...
2	56	28	23.8	6.9	58	36	19.2	6.4
3	...	...	...	...	...	...	...	...
4	...	...	...	...	...	...	...	...
5	84	60	8.5	7.2	78	53	10.9	6.9
	5th Day				*6th Day*			
1	...	...	...	...	54	27	24.8	7.4
2	64	31	20.6	8.7	58	30	23.5	6.4
3	...	...	...	...	...	...	...	...
4	...	...	...	...	...	...	...	...
5	82	55	9.8	6.9	78	34	20.5	6.3
	7th Day				*8th Day*			
1	60	25	26.1	8.3	58	24	30.6	5.8
2	52	30	25.5	6.2	...	...	...	...
3	...	...	...	...	...	...	...	...
4	...	...	...	...	...	...	...	...
5	70	30	25.6	5.2	72	59	10.2	5.3
	9th Day				*10th Day*			
1	54	22	32.9	6.3	...	...	...	...
2	56	30	23.7	4.2	58	32	22.9	5.1
3	...	...	...	...	...	...	...	...
4	66	41	16.6	6.2	79	41	14.2	8.6
5	69	38	16.8	7.1	69	50	12.9	5.4

TABLE 28 *(cont.)*. Daily record of attentive behavior in female robins.

Nest	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
	11th Day				*Hatching*			
1	56	32	20.6	7.1	60	46	12.9	6.0
2	(Incubation only 10 days)				60	36	18.2	7.3
3	...	...	...	...	...	...	...	...
4	...	...	...	...	...	...	...	...
5	73	51	11.8	6.0	78	72	5.8	6.9
	1st Day (Brooding)				*2nd Day (Brooding)*			
1	...	...	...	...	...	...	...	...
2	62	41	15.4	6.7	60	41	14.5	7.3
3	...	...	...	...	...	...	...	...
4	75	37	11.0	11.2	...	...	...	...
5	...	...	...	...	...	...	...	...

a day. In eight records obtained by us, the interval between insertion of nest lining and the first egg varied as follows: one case, one day; two cases each of two, three, and four days; one case of eight days; average 3.5 days.

Schantz found that the female remained on the nest for 64 minutes before the laying of the first egg in the set and behaved similarly before the laying of the second egg, remaining away for the rest of the day. He states that incubation began the evening after the second egg was laid, but Howell says that some robins begin with the first egg, others not until the last is laid. Normally three or four eggs constitute a full set.

At both No. 2 and 3 nests (Table 28), the female was on the nest the night after the first egg was laid and every night thereafter. With female No. 2, the attentive periods during the second and third day of egg-laying were of average length, but there were not quite so many of them, and the inattentive periods averaged slightly longer. Since the first eggs laid get considerable incubation before the last one is laid, they tend to hatch in the order in which they are laid, usually over a period of 2 and often 3 days.

Howell gives the incubation period as 12 to 14 days. In our records at 21 nests, the interval between the last egg laid and last to hatch was 12 days in thirteen instances and 13 days in eight instances, giving an average of 12.4 days. Only the female as a rule incubates, although there are scattered references in the literature of the male also taking part. Since the male often stands on the rim of the nest or even in the nest cavity when the female is inattentive, it may appear from a distance that he is incubating. Actually he may be applying very little if any heat to the eggs. We have observations at one nest of the male occasionally feeding the incubating female on the nest, and there are a few other similar records (Grinnell and Storer 1924, Howell 1942, Common 1947), but this behavior is unusual.

Schantz (1939) found the female attentive to the eggs during incubation an average of 16.3 times per day. Forty attentive periods averaged 44.2 minutes, alternating with inattentive periods of 11.3 minutes. At a later nest (1944) he found on one day that the female had 32 attentive periods averaging 20.6 minutes and inattentive periods averaging 5.6 minutes. Schantz's records were made in April and mid-May. Our first record (Table 29) is intermediate between those of Schantz and our other three records were made much later in the season. In general, it appears that as the season progresses the female averages more attentive and inattentive periods per day with the attentive periods becoming of shorter duration. The percentage of daytime spent on the eggs varies only between 78.7 and 76.2 early in the season and drops only to 67.0 and 68.6 in June and July. The average of Schantz's and our records is 31.9 attentive periods per day, 24.1 minutes long, with inattentive periods averaging 7.4 minutes, and with 75.9 per cent of the daytime spent on the eggs.

This correlation with the time of year is indirect, however, and is brought about by the influence of rising air temperature (Table 30). With rise in temperature the average length of the attentive periods decreases, as they are broken up by more frequent inattentiveness. Although the average length of the individual inattentive periods does not change in any consistent manner, the number of periods and consequently the total time off the nest during the day increases considerably compared with what it is at lower temperatures, while the total time spent on the eggs decreases proportionately less. The percentage that the bird is attentive decreases from 78.1 at 58° F. (14.4° C.) to 60.7 at 83° F. (28.3° C.). The total time of attentiveness and inattentiveness during the

TABLE 29. Attentive behavior of female robins during incubation.

Nest	Number of eggs	Date last egg laid	Days record	Air temperature °F.	Air temperature °C.	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)
1	4	April 26	5	56	13.3	26	27.0	7.0
2	3	May 27	10	56	13.3	30	22.5	6.8
4	3	June 15(?)	2	72	22.2	41	15.4	7.4
5	4	July 14	11	76	24.4	46	14.7	6.6

TABLE 30. Relation of daily attentive behavior in female robins to temperature.

Average temperature °F.	Average temperature °C.	Number of records	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Total attentiveness (min.)	Total inattentiveness (min.)
54	12.2	5	28	23.9	6.9	669	200
58	14.4	8	30	24.0	6.5	720	202
64	17.8	1	30	22.0	8.7	660	270
68	20.0	4	40	18.0	6.0	720	246
72	22.2	2	55	11.0	5.6	605	314
79	26.1	4	41	15.9	7.2	652	302
83	28.3	3	51	11.8	7.5	602	390

day is shorter at the lower compared with the higher temperatures because the lower temperatures generally occurred earlier in the season when the photoperiods were also shorter.

With the hatching of the first egg the periods of the female at and away from the nest become more frequent. In all three records available the attentive periods decreased in length while in two of the three records the length of the inattentive periods increased. The same tendencies persist during the next few days of brooding, although the difference in attentive behavior while incubating and brooding is not pronounced.

One record of adults feeding two young was obtained in the latter part of July with the average daily air temperature varying only between 72° and 76° F. (22.2° and 24.4° C.). During five of the last six complete days the young were in the nest, the number of visits per day varied 84, 98, 94, . . ., 64, 102, giving an average of 88 per day. Schantz (1939) has the most complete data available and states: "For the first two days with both broods the young received between 81 and 84 meals per day; the third day they were given 89 and 90 meals, respectively. During the rest of the time the first brood of three young received 82 to 99 meals per day and the second brood with four young 92 to 113 meals." Observations of others, compiled by Howell covering shorter periods of observation, indicate the rate to be five or six times per hour. Richard Lasater (personal communication) observed three young 5 to 6 days old fed 10 times per hour by both parents during six hours. Copeland (1909) recorded two young fed four times per hour by the female alone. The averages of the three records obtained by Schantz and ourselves are at the hourly rates of 6.5, 6.7, and 6.1, respectively. During the first few days when the female is brooding, the male provides more food for the young than does the female, but when the young are further developed, both sexes share this duty on a more nearly equal basis. Common (1947) gives an unusual record where in 11 hours and five minutes of observation during one day the three young 5 days old were fed only 7 times by the male and 17 times by the female.

Only a slight increase in rate of feeding is apparent as the young become older. According to Schantz (1939), there is some increase, however, in the amount of food given the young on each trip as they grow older. Some data show that on approximately half the visits two or even three young may be fed. Hamilton (1935) states that the adults bring their young approximately two grams of food on each trip and feed their brood a total of 200 grams during the day regardless of whether the number of birds in the brood be three, four, or five. Using the average rate of feeding during the last six complete days in the nest from our record of a brood with two young and Schantz's records of broods with three and four young, the rate of feeding per day averaged 88, 94, and 98, respectively, or at the rates per bird per day of 44, 31, and 25. According to these figures, the larger-sized broods were fed slightly more, but not nearly enough to give each bird in the large broods the same amount of food as each bird obtained in the smaller broods. It is possible that the adults adjusted to the larger broods by bringing correspondingly heavier loads on each trip, but this appears doubtful. The inequality in rate of feeding was further exaggerated in that young of the second brood stayed in the nest until they were 15 to 16 days old while the third brood left when only 14 days old. One wonders if inequalities in feeding result in inequalities in development, and if these will be compensated for by the length of time the young are cared for by their parents out of the nest before they become entirely independent (see pp. 170-72).

Howell gives the time that the young spend in the nest as 13 days with extremes at 9 and 16 days. This agrees both for the average and the extremes, with our data on 31 nests where the time from first hatching to first leaving the nest was determined. Schantz found two broods cared for by their parents until 11 days after leaving the nest, with only minor attention thereafter. When another brood is raised, the male may assume the major task of caring for the young in this stage, as the female begins the next nest and set of eggs.

The daily rhythm of activity in the robin has several points of special interest. Very soon after the first robin begins to sing in the early morning, there is a chorus of singing by males which lasts from 30 to 45 minutes, according to Howell. After that, there is desultory singing for the rest of the day, with the low point coming about noon, until the evening chorus sets in just before the birds retire for the night.

Contrary to most other passerine species the time of egg-laying is during the late morning rather than soon after daybreak. Howell gives this time as normally around 1000 hours. On the day the first egg was laid,

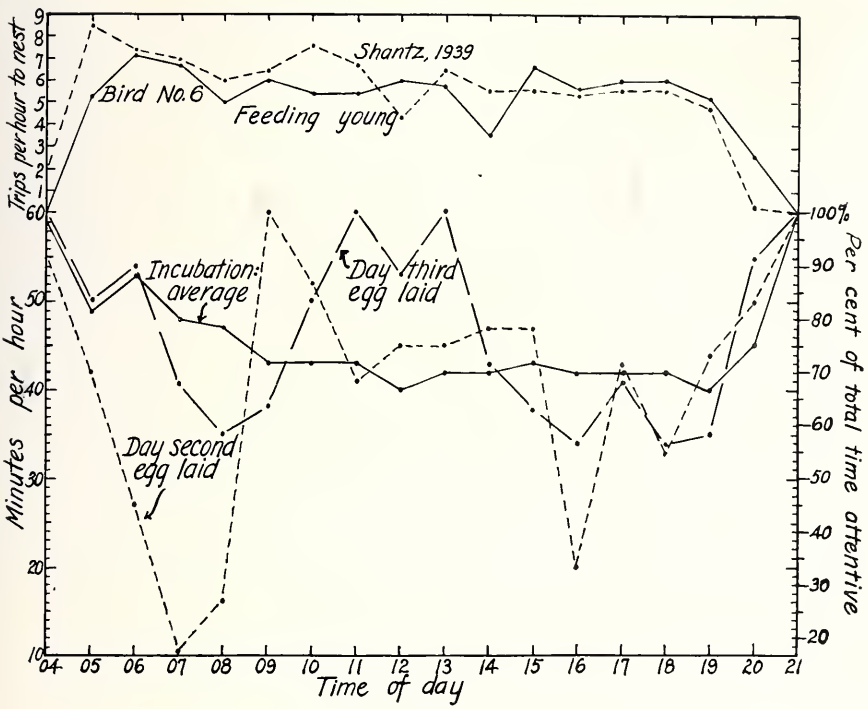

FIG. 28. Daily rhythm in attentive behavior of robins.

Schantz found the female visiting the nest five times between 0755 and 0846 hours, and then away until 0945 hours, when she returned to sit 64 minutes before the egg was deposited at 1058 hours. She left at once and did not return until the next day.

We have records on two females during the egg-laying period. At nest No. 3, she had been on the nest all night and left at 0538 the next morning. She returned 23 minutes later for a long attentive period of 89 minutes, the longest of the day. Her second egg was laid sometime before 0915 hours, possibly during the first long period. This bird showed a high degree of attentiveness with very long attentive periods all day long (Table 28). Her shortest period of 16 minutes came at noon.

The record of female No. 2 for the days on which the second and third eggs were laid is shown in figure 28. On both days, the attentiveness of this bird decreased from a high level soon after beginning the day's activities to a low point around 0700 and 0800 hours, and then rose to prolonged attentiveness which lasted beyond midday. It was during this time that the eggs were laid, the longest attentive period on the second day being 75 minutes while on the third day there were two consecutive long periods of 115 and 126 minutes with an interval of only 7 minutes between. Each day the attentivity became depressed during late afternoon but rose again in the evening. The daily rhythm of attentiveness during egg-laying differs strikingly from the average rhythm during incubation.

The daily rhythm of attentivity was determined for each of the four females for all the days of incubation, counting from the day after the last egg was laid until the day before hatching began. All four records were averaged to give a generalized curve for incubation (Fig. 28).

The level of attentiveness is fairly high in this species, dropping to its lowest between noon and 1900 hours. When air temperatures become high during the afternoon, this level is depressed to a greater extent than on cool days. The curve shows less attentiveness at 0500 than at 0600 hours. Actually, of the 26 days' records entering into this curve, the 0500 level was lower than it was at 0600 in 18 instances. This was due to the inattentive periods during the first hour averaging slightly longer in length after a night's stay on the nest than during the second hour when probably the bird's appetite had been appeased. However, the attentive periods also averaged longer during these two hours, as there were only 1.6 such periods per hour in contrast to an average of 2.5 periods per hour from 0700 to 1900 hours, inclusive. The decrease in attentiveness and increase in inattentiveness during these latter thirteen hours is due to changes in the length of the periods and not to an increase in their number.

It is of interest that in the daily rhythm of brooding the young by female No. 2 on the second and third days after the first egg hatched, the high point of attentiveness in early morning came at 0700 rather than at 0600 hours as during incubation. The low point came at 0500 one morning and at 0600 hours the next morning. For some reason this bird spent less time brooding her young from 0800 to 1400 hours (average, 36.3 minutes per hour) than during late afternoon (average 16 to 19 hours, 43.4 minutes), and this was true for each of the two days. For robin No. 4, the single day's record of brooding shows the female covering the young for an average of 29 minutes per hour from 0800 to 1800 hours, inclusive.

The daily rhythm in rate of feeding the young is shown separately for nest No. 6, covering five days, and for Schantz's record that included 11 days (Fig. 28). These records include the feeding by both parent birds. The two curves are similar except Schantz's birds fed more often in the morning than did our birds. There were four young in the nest of his bird and only two in ours. In both cases the rate of feeding was maintained fairly constant at all hours of the day.

Allard (1930) gives the time of the first morning song of the male robin at about 36 minutes before sunrise in mid-April, increasing to about 45 minutes before sunrise in June, then again regressing to 36 minutes before sunrise by mid-July. Shaver and Walker (1931) showed that the song continued after sunset about 9 minutes on March 1, 27 minutes on April 1, and 19 minutes on May 1.

In Table 31, data from Schantz (1939) are included with our own to show the time that the female begins and ends her daily activities. While incubating, she first leaves the nest after a night's stay about 25 minutes before sunrise. Probably the same is true when she is egg-laying, although the number of records is few and inconsistent. When brooding and feeding the young, she becomes active somewhat later, averaging 13 minutes before sunrise. The two records of Schantz and our nest No. 2 represent the time the female first leaves the nest after a night of brooding. The record at No. 6, however, is for the time the young were first fed in the morning, as the female did not spend the night on the nest, and in some cases the male may have fed the young first before the female. In general, it appears that the female does not begin her daily activities until 15 to 30 minutes after the male.

When egg-laying the female retires about the same time as the male. Schantz's two birds terminated their day during incubation about 16

TABLE 31. Time of beginning and ending of daily activities in female robins.

Nest	Median date	*Number of records* Morning	Evening	*Difference from* [a] Sunrise (min.)	Sunset (min.)
		Egg-laying			
Schantz	April 1	1	...	−85	...
Schantz	May 10	1	2	−14	+22
No. 2	May 26	2	2	−26	+ 4
No. 3	June 1	1	1	+41	+25
		Incubating			
Schantz	April 7	6	5	−26	−22
No. 1	May 5	6	5	−11	+25
Schantz	May 17	...	8	...	−11
No. 2	June 2	10	8	−22	+ 4
No. 4	June 24	3	4	−30	+11
No. 5	July 20	11	10	−34	+12
		Caring for young			
Schantz	April 20	3	10	−14	+ 5
Schantz	May 28	5	12	−24	− 4
No. 2	June 8	2	3	− 4	+ 4
No. 6	July 24	5	6	−11	+ 5

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

minutes before sunset, while our four birds did not do so until 13 minutes after sunset or not much earlier than the male. When caring for the young, activities cease earlier or approximately at sunset. The period of daily activity is shorter at beginning and end when caring for the young than it is when incubating eggs.

At nest No. 3 the robin applied full heat at night after the second egg was laid. At nest No. 2, however, she applied only partial heat, as compared to her attentive periods during the day, on the nights after the first and second eggs were laid, but full heat on the night after the third or last egg was laid. The mere presence of a bird on a nest is not certain evidence that full incubation is underway as the bird may vary the amount of heat given the egg, perhaps by the amount of feathering on her underparts or by the way she fluffs out her feathers so that her skin may become directly applied to them. After incubation begins, the birds sit closely on the eggs at night with little restlessness; but when the weather is hot, they get up and stir around at more frequent intervals. This difference in behavior at night was quite apparent with bird No. 5. When the nestlings become fairly well grown, the female stops brooding them at night. The female was on nest No. 6 only once during the last 6 nights before the young left. Schantz found at his two nests that the female remained away at night during the last 4 and the last 5 nights. By this time the nestling birds have acquired their temperature regulating mechanism, and their feathers are well along in development.

Wood Thrush, *Hylocichla mustelina*

Brackbill (1943) has made the most complete study of nesting behavior in the wood thrush, although many details are still lacking. The male possesses a territory, guards the nest, and aids in feeding the young. How much help he gives in nest construction is not known. Florence G. Weaver (1939) states that 5 days may be consumed in nest building, that the average size of the egg-set is three, and that there is no record of more than four eggs in a set. Incubation apparently begins gradually, as Brackbill found hatching to extend over two days at one nest and over three days at another. At our nest No. 2 (Table 32) one egg hatched on June 17 by 0800 hours, another by 1330 hours, the third by 0830 the next day. The incubation period has not been fixed with certainty but is probably 12 days. Only the female incubates the eggs and broods the young.

We obtained potentiometer records at two nests during June (Table 32). The attentive periods at nest No. 2 (52.5 minutes) averaged twice as long as those at nest No. 1 (26.4 minutes) although temperature conditions were very similar. The average number of trips per day was 13.7 at nest No. 2 and 24.0 at nest No. 1, and percentage of time attentive, 78.5 and 66.1, respectively. In contrast, the average inattentive period was about the same in the two birds (13.4 and 13.0 minutes, respectively). A few records of Brackbill give the average attentive period at two nests as 31 and 27 minutes with inattentive periods of 8.5 and 6.1 minutes. When the female is incubating, Brackbill observed the male to be inattentive but when the female is away from the nest, the male guards the nest closely, perching either on its rim, in the same tree, or nearby. He guarded somewhat less carefully during the second nesting than the first, and less when the female was brooding than when she was incubating.

On June 17, the day the eggs began hatching at nest No. 2, the attentive periods of the female decreased to 22.1 minutes and the inattentive periods increased to 15.3 minutes, while the number of periods during the day rose from 14 during incubation to 24. The bird brooded for 58.1 per cent of the daytime. There may be some significance that the excitement of her young hatching changed the very slow attentive rhythm of this bird to the faster one exemplified by bird No. 1 and Brackbill's bird. Brackbill observed the female at the nest about two-thirds of the time during the daylight hours and every night, although in very hot weather with temperatures of 93° F. (33.9° C.) and above, she did not cover the young but stood on the nest rim on the side where she did not shade the young. Also he found that there was no daily decrease in amount of brooding as the young increased in age.

TABLE 32. Attentive behavior of female wood thrushes during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.	*Difference from*[a] Sunrise (min.)	Sunset (min.)
Nest No. 1, 1931							
June 11	...	...	...	...	...	...	−12
June 12	24	29.5	11.7	72	22.2	−28	+13
June 13	20	29.0	16.8	74	23.3	−29	0
June 14	29	19.2	12.1	75	23.9	−30	−28
June 15	23	27.9	11.6	65	18.3	−28	...
June 16	...	...	...	...	...	−14	...
Nest No. 2, 1929							
June 13	...	...	...	...	...	...	−13
June 14	13	55.9	11.4	69	20.6	−18	−37
June 15	13	56.3	14.0	66	18.9	−18	+ 4
June 16	15	45.3	14.7	73	22.8	−14	− 6
June 17	...	...	...	...	...	−23	...

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

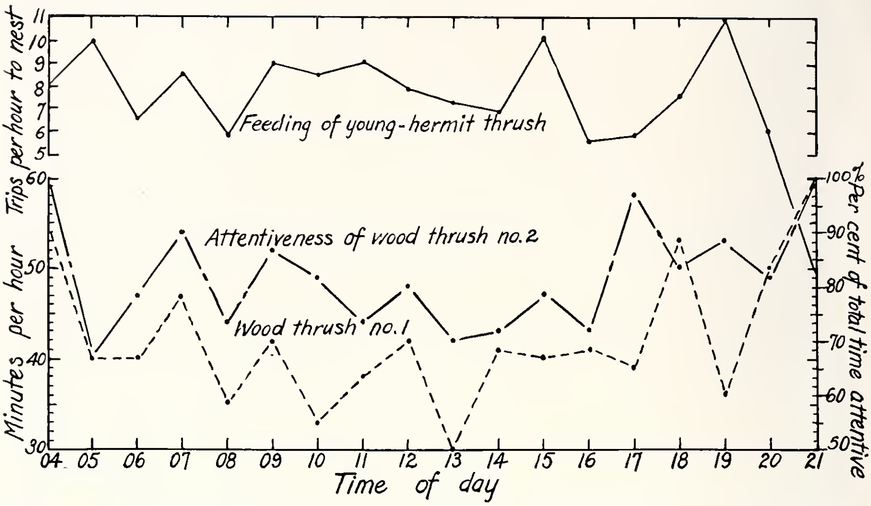

FIG. 29. Daily rhythm in attentive behavior of wood thrush and hermit thrush.

Brackbill reports the adults making 8.7 trips per hour with food for three young in 13.8 hours observation on different days at one nest and 4.5 trips per hour in 13.6 hours observation at another nest also with three young. On 11 trips of the 181 observed, two young were fed instead of one. The male was responsible for about two-thirds of the feedings of the young while in the nest, and for practically all of the feedings of the young after they had left the nest. He found no increase in the rate that the young were fed as they became older. The young remained in one nest until 12 and 13 days old, and he noticed that fledged young continued to receive some food from their parents until they were 25 to 32 days of age. Copeland (1909) reports one all-day record when the young were fed 8.6 times per hour.

Figure 29 shows the bird at nest No. 1 with the more frequent but shorter attentive periods, incubating considerably less than the bird at nest No. 2. Bird No. 1 incubated 67 per cent of the time between 0500 and 2000 hours, in contrast to bird No. 2 which incubated about 80 per cent of the time. Brackbill reported one bird incubating 78 per cent and another bird 80 per cent of the time during observations extending over 15.8 and 16.9 hours, respectively. Incubating tends to be least between 0800 and 1600 hours, although there is considerable variability. During early morning the slowing up of the attentive rhythm is rapid. From 0430 to 0530 hours birds No. 1 and 2 start 2.2 attentive periods per hour, between 0530 and 0630 hours they start 1.8 periods, while during the rest of the day they average only 1.1 periods per hour. The length of the attentive periods increases during these three time intervals: 24, 30, 43 minutes, and the length of the inattentive periods also increases: 10, 9, 14 minutes. There is no reverse speeding up of the attentive rhythm during the hours preceding retirement for the night.

Wright (1913) recorded the first singing of male wood thrushes throughout May, June, and July from about 32 to 38 minutes before sunrise. Florence G. Weaver (1939) reports the males beginning to sing during June near Ithaca, New York, at 0345 hours and continuing in the evening until about 2000 hours. These times would be approximately 45 minutes before sunrise and 20 minutes after sunset, respectively. As shown in Table 32, females No. 1 and 2 left their nests after a night's stay on the eggs an average of 26 and 18 minutes before sunrise (0453 hours). This is not quite so early, apparently, as the male wood thrush begins his daily activities. There is considerable variation in the time that the female retires at night, although the average for the two females is 7 and 13 minutes before sunset (1958 hours) rather than after sunset, as it is for the male.

Bird No. 1 was restless at intervals of 18 to 90 minutes during the night of June 11-12. On following nights she was slightly restless but at indefinite and irregular intervals. Bird No. 2 was usually very quiet throughout the night until 15 to 20 minutes before beginning activities in the morning. On June 17, she became restless 80 minutes before leaving the nest. This may have been due to her first young pipping the shell, as it was found hatched at 0800 hours.

Hermit Thrush, *Hylocichla guttata*

Stanwood (1910b) wrote concerning the hermit thrush as follows: "The time of incubation . . . is twelve days; the young remain in the nest twelve days, and leave early in the morning, as a general thing. One egg is laid each day about ten o'clock in the morning (1000 hours), and the birds begin to incubate by 12 o'clock (1200 hours) of the day the clutch is completed. I have found the number of eggs to vary from four to two. I should judge from the nesting dates I have gathered that the Hermit Thrush . . . raises two or three broods during a season."

Since only the female broods the young after hatching, she probably also does most, if not all, of the incubating, although observations at the nest during the incubation period are scarce. At a nest with three eggs, found near Rensselaerville, N.Y., on July 15, one bird, presumably the female, was watched on the nest from 1333 to 1512 hours, during which time she scarcely stirred. This was seven days before the eggs hatched and may indicate that attentive periods are very long in this species.

This nest was three feet off the ground on a horizontal branch of a

TABLE 33. Attentive behavior of the hermit thrush while caring for young.

	Duration of record at Kendeigh's nest		*Brooding periods*		*Trips per hour to nest*			*Difference from* [a]	
Days after hatching	(hours)	(min.)	Number per hour	Duration (min.)	Kendeigh's nest	McClintock's nest	Stoner's nest	Sunrise (min.)	Sunset (min.)
0	3	31	4.0	5.2	7.2	...	...	...	+32
1	1	44	2.9	6.6	8.7	...	...	−11	+40
2	15	59	1.8	7.1	4.9	...	2.5	−27	+50
3	6	17	1.3	12.0	5.6	...	4.3	− 1	...
4	...	...	...	...	...	...	4.6	...	...
5	8	56	0	0	7.1	...	6.3	...	+31
6	15	39	0	0	7.7	...	5.3	−50	+13
7	8	41	0	0	8.2	12.7	6.3	−24	...
8	4	34	0	0	12.9	13.5	3.0	...	+20
9	10	40	0	0	10.6	8.2	3.2	−40	+27
10	15	35	0	0	9.2	[b]	[b]	−42	+26
11	16	32	0	0	11.5			−53	+74

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

[b] Young left nest prematurely, due to disturbance.

small spruce, an unusual location. To get the recording of an itograph at this nest, a piece of hardware cloth was placed around back of the nest, 6 days before hatching. The next day a tunnel, open at the top, was made on the front side. Two days later a stake was driven into the ground so that the top was level with the bottom of this tunnel. The following day the itograph perches were fastened on top of this stake and wires run to it. The next day, the recorder and batteries were connected and the record started. Probably greater care and time was taken to get the apparatus established than was necessary, but since the hermit thrush is supposedly a shy bird around its nest, the adults were permitted ample time to get adjusted to each step in the procedure before the next one was taken. No record of incubating behavior was made.

On July 23, at least two of the three eggs hatched, and the top of the tunnel was covered with more hardware cloth; the third young was found hatched on July 24. The three young left before 0650 hours on August 4 after 12 days in the nest. The record of the adult in caring for the young is given in Table 33. Observations indicated that only one bird, probably the female, was active in feeding the young, but of this there could be no certainty.

There are three other records of observations at nests of this species. In each case both adults took part in feeding the young. In McClintock's (1910) nest there were three young and from 89 to 205 minutes were spent each day in watching. Stoner's (1920) nest had four young and from 121 to 498 minutes daily were devoted to observations. These records are incorporated in Table 33. In a nest observed by Perry (1918), three young were fed six times per hour on the average and left the nest when 12 days old.

Brooding mostly ceased when the young were 3 or 4 days old, although there may have been one short period on the sixth day. Rain fell on the day that the young were 3 days old, which may account for the longer brooding periods then. McClintock found the female brooding a little on the sixth day, but Stoner does not record any brooding after the fourth day.

The hourly rate of feeding was greater in the latter half of the nest life than in the first half although the day-to-day increase was irregular. The data obtained by Stoner do not show any such increase in rate of feeding. Stoner's data are unusual also in the very low rate of feeding attained. For the seventh, eighth, and ninth days, the adults at Kendeigh's nest and McClintock's nest fed their young at the average rates of 3.5 and 3.8 times per bird per hour, respectively, but at Stoner's nest the adults fed four young only 1.4 times per bird per hour. Stoner found that in 161 visits to the nest, the male and female shared nearly alike or 82 and 79 times, respectively. He likewise observed that from one to all four young were fed on each trip to the nest for an average of 1.5 young per visit, and that this did not vary significantly as the young got older.

The curve (Fig. 29), showing average number of feedings at Kendeigh's nest for the various hours of the day, is based on the complete records for only the second, sixth, tenth, and eleventh days and exhibits considerable irregularity. However, there appears a progressive decline in the rate of feeding during the afternoon except for peaks at 1500 and 1900 hours.

The female sat on the nest every night until the young left with no apparent uneasiness. She left the nest, on the average, 31 minutes before sunrise, which came about 0444 hours, and returned for her next night's stay 35 minutes after sunset, which came about 1918 hours. Wright (1913) states that the male's first song comes 53 minutes before sunrise, although he may start calling five minutes or more earlier. Thus the male begins his activities earlier than the female; but in the evening, the last song and call of the male averages 33 minutes after sunset which is almost identical to the time recorded for the female to retire.

Bluebird, *Sialia sialis*

Nearly all of the nest building of the bluebird is performed by the female and requires from 4 to 12 days. Occasionally the male may participate. Two or three days elapse between completion of the nest and laying the first egg, according to W. P. Smith (1937b), or one week, according to Thomas (1946). This interval, according to our records, is quite variable and at five nests was 1, 4, 4, 5, and 8 days.

Smith gives the time of egg-laying as before 0600, between 0630 and 0800, and once at 0900 hours. We have one record of egg-laying between 0730 and 0830, another between 1000 and 1600, a third between late afternoon one day and 0530 hours the next, but most egg-laying, not otherwise timed, appeared to occur in the early morning. Three to six eggs make up the set.

Smith lists two sets requiring 13 days incubation, four sets 14 days, three sets 15 days, and two sets 16 days. Thomas gives the incubation period as 13 to 15 days, commonly 14. The intervals between the last egg laid and the last to hatch in three nests observed by Brodrick (1938) were 13, 14, and 15 days. The similar interval in 11 nests observed by ourselves was 14 days in all instances. In five cases the eggs all hatched the same day; in six cases hatching extended over 2 days. Smith states that the young generally remain in the nest for 18 days, but he gives one instance of 17 days. Brodrick's young birds left at 17, 18, and 19 days after the first one hatched. Records at 10 nests studied by us give this interval at 17 days in five cases and 18 days in the other five.

Recordings of attentive behavior are not available for the egg-laying period, but in view of the relatively long incubation period and that all eggs frequently hatch on the same day, it is doubtful if the first eggs laid get very much incubation before the last one is laid.

There is no question but that the female is responsible for incubating the eggs, although the male may be more or less attentive. W. P. Smith (1937b), Brodrick (1938), and Laskey (1939) all give instances where the male appeared to share this duty. Observation of the male's entering the nest box or even sitting on the eggs is not positive evidence, however, that he is applying any significant amount of heat to them. This needs to be determined by either noting whether he has a brood patch or measuring the egg temperature with thermocouple or other device. Smith and Thomas observed the male feeding his mate at intervals, but this seems not to be the general rule. Often he stands guard near the nest while the female is inattentive.

Twelve days of recording at one nest and 2 days at another with thermocouple and potentiometer indicate 34.4 attentive periods per day averaging 14.1 minutes in length alternating with inattentive periods of

12.4 minutes (Table 34). This is a relatively low proportion of attentiveness, making up only 52.5 per cent of the daytime activity. The record for bird No. 2, beginning 2 days after laying the last egg, suggests that the attentive periods shorten somewhat and the inattentive periods lengthen toward the end of the incubating period. This is probably correlated, however, with the higher temperatures prevailing during the last 4 days.

Brooding of the hatched young is performed only by the female, although both sexes usually share in feeding the young. One record of feeding by both adults was obtained with the itograph at one nest for 10 days beginning the sixth day after the single nestling hatched. The total times during the day that the adults visited the nest were 77, 71, 65, 100, 99, 74, 92, . . ., . . ., 104, 69, 76. The bird left the nest the next day. The average is 82.7 trips per day. There was no increase in number of trips with development of the young bird, but the one bird in the brood was doubtless supplied with a surplus of food at all times. Nice (1931a), Wetherbee (1933), and Laskey (1939) have reported grown young of a first brood helping to feed nestlings of a later second brood, but this was not observed in this study.

TABLE 34. Attentive behavior of female bluebirds during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	Mean daily temperature °C.	*Difference from*[a] Sunrise (min.)	*Difference from*[a] Sunset (min.)
Nest No. 1, 1931							
April 17	41	10.9	8.4	66	18.9	−16	−12
April 18	38	13.2	8.6	68	20.0	−14	+22
Nest No. 2, 1931							
June 23	20	27.5	18.1	72	22.2	−15	+10
June 24	37	15.3	9.1	66	18.9	− 6	+ 1
June 25	40	14.6	9.2	67	19.4	−45	+ 3
June 26	32	18.4	9.7	61	16.1	− 3	0
June 27	35	14.0	10.7	66	18.9	+ 4	+ 5
June 28	31	16.3	12.1	68	20.0	+ 9	− 2
June 29	34	14.9	10.9	68	20.0	+ 8	− 9
June 30	40	12.2	10.2	68	20.0	+ 3	+ 4
July 1	35	10.3	14.0	72	22.2	+20	−17
July 2	38	9.8	13.9	76	24.4	+ 1	+15
July 3	32	10.8	17.7	79	26.1	+ 6	+32
July 4	29	9.7	20.7	79	26.1	+ 8	+ 9

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by — if before.

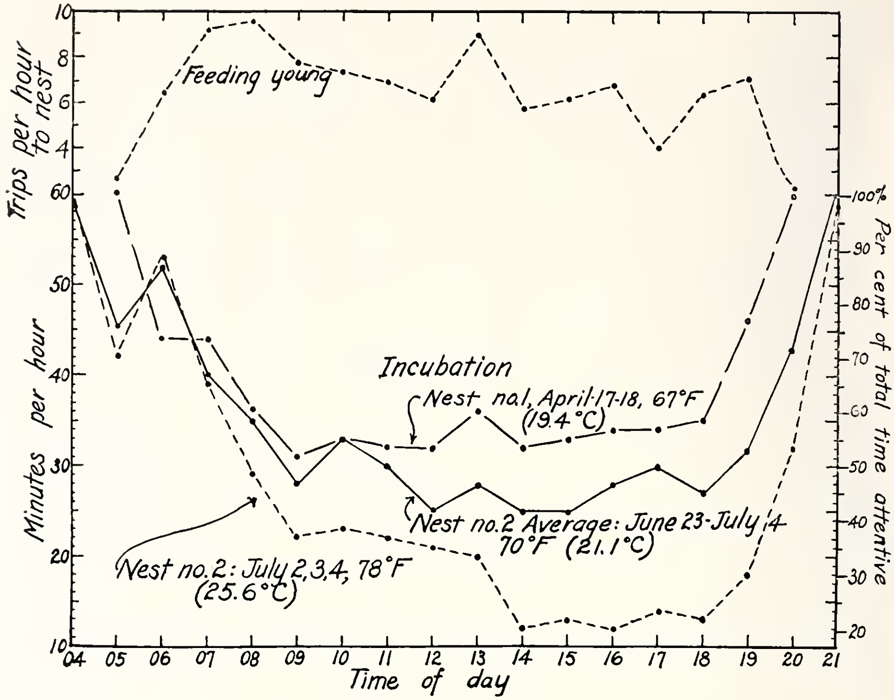

FIG. 30. Daily rhythm in attentive behavior of bluebirds.

The daily rhythms of incubating attentiveness for the female at nest No. 1 in April and nest No. 2 in late June and early July contrast in showing the later beginning and earlier ending of the daytime depression correlated with the difference in time of sunrise and sunset (Fig. 30). The higher level of attentiveness maintained during the middle of the day for the April bird is probably a response to the lower temperature. Perhaps this species is more than usually sensitive to temperature change as the three days' average curve at 78° F. (25.6° C.) shows a drop in attentiveness to a remarkably low level. The average maximum temperature on these three days was 85° F. (29.4° C.).

The greater attentiveness at 0600 compared with 0500 hours in the curve for female No. 2 is identical to one at the same hour in the robin. Of the 12 days entering into this curve, this fluctuation occurred eight times, while on 3 days the record at 0600 hours was less than at 0500 hours, and on one day it was the same. Apparently the bird usually spends a longer time away from the nest during the first hour after arising in order to replenish energies used up overnight.

The number of attentive periods per hour increases from 1.1 at 0500 hours to a maximum of 2.8 at 0900 hours, after which it fluctuates between

2.1 and 2.7 until evening. The greater amount of inattentiveness during the middle of the day is due not to any marked change in the length of the inattentive periods but to these periods occurring more frequently. This causes a pronounced decrease in the length of the attentive periods or the length of time the female sits on the eggs at a stretch.

With hatching of the young and feeding by both adults, it appears that the rate is greatest at 0700 and 0800 in the morning, perhaps after the adults have satisfied their own hunger, and then decreases in a fluctuating manner the rest of the day.

The time of beginning and ending of the day's activities by the female is remarkably inconsistent. The summary of all records indicates that on the average the bird rose three minutes before sunrise, which occurred at about 0546 in April and 0452 in late June and early July, and retired four minutes after sunset, which occurred at about 1906 and 2001 during the two periods. On individual days she departed widely from this schedule.

Female No. 2 sat very closely on the eggs at night and was very quiet at all times. Female No. 1, however, behaved quite differently. She was very restless, stirring around on the eggs and getting up and down. Her periods on and off the eggs at night were reminiscent of attentive and inattentive periods during the day, although the periods on the eggs were longer and the periods off the eggs shorter than in the daytime. The itograph recording was somewhat imperfect, but the female apparently brooded the young bird at night until 4 days before it left the nest.

Cedar Waxwing, *Bombycilla cedrorum*

Both cedar waxwing adults share in nest building. Probably the female does more of the work than the male. One or two trips per minute may be made during the peak of the nest-building activity. From 5 to 7 days are required before the nest is completed, although with renesting the time may be shortened. The first egg is laid as soon as the nest is completed or may be delayed for as long as three days. Additions to the nest lining may be made during the egg-laying period. These observations were made by Saunders 1911, Post 1916, W. A. O. Gross 1929, Crouch 1936, Lea 1942, and Putnam 1949.

Putnam states that the eggs are laid between 0500 and 0800 hours. Lea had data on 18 marked eggs and states that the incubation period averages 11.7 days with variation from 11 to 13 days. James (1946) gives 11 days and Saunders and Putnam, 12 days, for the incubation period. At two of my nests the period was 12 days, at three nests it was 13 days. Gross gives 14 days and Post gives 15 days as the incubation period for the nests they had under observation. Doubtless the incubating attentiveness develops gradually as the female is sometimes observed sitting on the eggs before the set is complete and the hatching period extends from 1 to 3 days. Putnam found the adult incubating at night after the third egg was laid.

Although Gross records both adults sharing incubation at one nest, most students who have paid special attention to this species agree that incubation is ordinarily performed entirely by the female. The male feeds the female during incubation either on the nest or on some nearby perch. Gross states that this feeding was at half-hour intervals, Crouch gives it as 10 to 15 minutes, Lea observed it every 20 minutes. Putnam found this rate to be variable between 0.4 and 1.4 feedings per hour. Crouch found that the female left the nest to get this food from the male in inattentive periods of 3 to 5 or, rarely, 10 minutes.

Table 35 gives a record of attentive behavior at two nests, possibly of the same female with successive broods, both obtained with a thermocouple inserted just above the eggs. At the first nest, due to hot weather, the bird's attentiveness during the middle of the day was so irregular that definite periods could not be identified. Likewise at the second nest, the bird did not incubate steadily during the attentive periods in the middle of the day, although there was less difficulty in recognizing the limits of the periods. An average of the two nests makes the attentive period 29.4 minutes long and the inattentive period 5 minutes. The attentive periods not infrequently extended to over one hour in length, and one period was nearly three hours. It is quite likely that during these extra long periods the male fed the female on the nest, while at other times she left the nest to receive the food. Putnam found the mean attentive period to be 45 minutes in 402 hours of observation at 11 nests and the inattentive period about 5.6 minutes. Apparently the percentage of daytime that the bird is attentive to incubation varies between 85 and 89.

Only the female broods the young after hatching, but both adults feed the young. Hatching occurred on July 4 at the first nest and on August 6 at the second nest. At this latter nest the number of attentive periods on the day of hatching rose to 40, their average length dropped to 16.6 minutes while the length of the inattentive periods remained about the same, 3.8 minutes. The bird thus spent 81 per cent of her time in attentiveness which compares well with 87 per cent given by Lea for attentiveness of the adults at his nest when the young were one to two days old. Much of this time is spent in brooding. Lea records the percentage of the time of the female at the nest when the young were 4 to 5 days old as 59, 7 to 8 days old as 38, and 11 to 12 days old as 25. Of course, less time is spent brooding and more time is spent in feeding the young as they get older. Putnam states that the female broods 75 per cent of the daylight hours during the first 5 days.

Lea found the average nestling period was 15.5 days with extreme

TABLE 35. Attentive behavior of female cedar waxwings during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.	Difference from[a] Sunrise (min.)	Sunset (min.)
Nest No. 1, 1931							
June 30	40	15.5	7.6	82	27.8	−12	+14
July 1	...	23.0[b]	6.1[b]	86	30.0	− 7	−31
July 2	...	27.8[b]	5.7[b]	83	28.3	− 7	−13
July 3	...	19.7[b]	4.7[b]	76	24.4	− 5	+ 7
Average		21.5	6.0	81.8	27.7	− 8	− 6
Nest No. 2, 1931							
July 29	26	28.0	3.3	83	28.3	+ 4	−46
July 30	24	31.5	5.0	76	24.4	− 4	−17
July 31	29	25.7	2.8	74	23.3	− 6	−43
Aug. 1	21	38.3	3.0	74	23.3	− 7	+ 2
Aug. 2	22	33.4	3.5	83	28.3	+50	+ 3
Aug. 3	14	57.1	3.3	76	24.4	+ 5	− 5
Aug. 4	16	46.7	6.3	78	25.6	− 4	− 6
Average	21.7	37.2	3.9	77.7	25.4	+ 5	−16

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by — if before.

[b] Length of periods determined only in early morning and evening.

variations of 14 and 18 days. James (1946) found it to vary from 13 to 16 days at five nests and average 14.8 days. Putnam gives the nestling period as 16 days. Two records of mine are for 17 days in the nest. Saunders found the young usually remaining 16 or 17 days. One brood that left in 14 days he recorded as being fed by the parents four times per hour, while another brood that stayed for 18 days were fed only once an hour. The usual interval of feeding was between three-quarters and one hour. Gross recorded feeding of the young three times per hour. Post observed feeding to be less frequent on hot than on cooler days. Lea found a progressive increase in the rate of feeding five young with increasing age. At ages of 1 to 2, 4 to 5, 7 to 8, and 11 to 12 days the adults at one nest made 26, 33, 46, and 41 trips, with food or at the hourly rates of 2.1, 2.7, 3.8, and 3.4. The male was not observed feeding on the twelfth day, but he did 69 per cent of the feeding on the first day as the female spent time in brooding. For the four days as a whole, he made 46 per cent of the trips with food. Up to 7 days of age, each of the five young in the brood were fed on each visit; later an average of 3.5 young were fed on each trip. At first the food was all crushed, but small whole

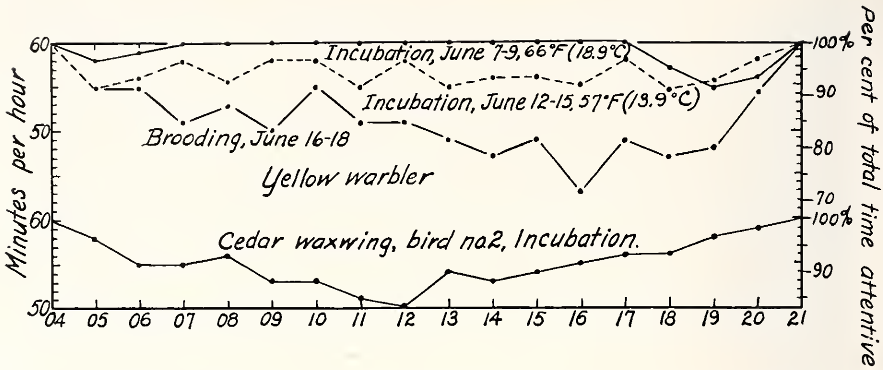

FIG. 31. Daily rhythm in attentive behavior of a female cedar waxwing and a yellow warbler.

pin cherries were fed to the 4-day-old young, and whole June berries and blueberries were fed to the young when 7 to 8 days old. Doubtless the slow rate of the feeding trips to the nest is due to the adult bird's ability to carry a large supply of food in its gullet and regurgitate it to feed most or all the young on each trip. Putnam found that the feeding rate by both sexes averaged between 2.4 and 3.9 times per hour while at the nest, and that the young were fed by the parents for 7 or 8 days after fledging.

Figure 31 shows the daily rhythm in attentive behavior at our second nest during incubation. This is calculated from the full length of the attentive period during the middle of the day, although large portions of these periods were not spent actually on the eggs. If only the time on the eggs were included, the depression of the curve in midday would be more pronounced. In nest No. 1 only brief but frequent intervals were recorded for the bird on the eggs as the nest temperature soared to 100° and 102° F. (37.8° and 38.9° C.) in the heat of the sun. Lea found that feeding of the young ceased during the middle of a very hot day, although the female remained at the nest for one hour and forty minutes to shade the 5-day-old young. Post, however, found that ordinarily the young were fed more frequently during the middle of the day than toward evening.

Bird No. 1 left the nest in early morning consistently a few minutes before sunrise (0457 hours), and her last inattentiveness fluctuated around sunset (2001 hours). Bird No. 2 varied considerably in the time of beginning and ending her daily trips away from the nest, but they also came about sunrise (0521 hours) and sunset (1943 hours). Some of this irregularity may have been due to the male feeding her on the nest so that there was no break in her attentiveness to the eggs. At both nests the female sat very quietly at night, although at the earlier nest the record shows the female was quite restless the night of July 3. This may have been due to her young starting the hatching process, since they appeared the next day. Wright (1913) has recorded the male's first notes one minute after sunrise and his last notes seven minutes before sunset, so it appears that in this species the two sexes are well coordinated in the time of beginning and ending of their daily activities.

Yellow Warbler, *Dendroica petechia (aestiva)*

The nesting behavior of the yellow warbler may be pieced together from the writings of Bigglestone (1913), Mousley (1926), W. P. Smith (1943), Schrantz (1943), and the present investigation.

Smith and Schrantz agree that only the female builds the nest, although the male remains nearby singing at intervals. In about three hours observation during active building, the female brought material to the nest approximately 10 times per hour. Schrantz observed at three nests that 4 days elapsed between the beginning of nest construction and the laying of the first egg, but at another nest 5 days intervened between the completion of the nest and the first egg. Smith states that 3 to 5 days are required for nest building and 2 more days elapse before the first egg appears. Normally four eggs occur in a set with variations from two to six. A day is frequently skipped in the egg-laying process. The time of laying is between 0400 and 0500 hours in the morning. Only the female is known to incubate.

Smith states that incubation begins with the laying of the third egg in four-egg sets, but in one set of six, steady incubation did not begin until the last egg appeared. We were successful in recording attentive behavior at one nest with the use of a thermocouple from late on the day the second of a four-egg set was laid, June 3, 1927, until after all had hatched (Table 36). The female sat on the eggs throughout every night from the laying of the second egg until all hatched. The nesting was disturbed on the day the second egg was laid, by the setting up of the recording equipment, but incubation was under way the next day when the third egg appeared. The exact time of appearance of the fourth egg is uncertain but was probably the following day. The fact that incubation behavior begins before the last egg is laid is further shown by two eggs hatching on June 16, one on June 17, and one on June 18. This makes the incubation period 13 days, which is exceptionally long. At another nest it was only 11 days. Bigglestone and Schrantz give the average incubation period as 11 days, but Smith found the interval between the last egg laid to the last one to hatch as only 10 days at three nests.

The male feeds the female on the nest during incubation and because of this, her attentive behavior is somewhat modified. In 4.5 hours obser-

TABLE 36. Attentive behavior of a female yellow warbler.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.	*Difference from* [a] Sunrise (min.)	Sunset (min.)
1927			*Egg-laying*				
June 4	27	23.7	5.6	66	18.9	+51	+11
June 5	...	...	...	58	14.4	...	...
			Incubation				
June 6	18	34.9	2.7	52	11.1	+21	−23
June 7	(Periods not differentiated)			59	15.0	+56	−12
June 8	(Periods not differentiated)			67	19.4	+ 8	+ 3
June 9	(Periods not differentiated)			73	22.8	+ 7	+18
June 10	18	43.2	3.2	70	21.1	+16	+11
June 11	21	33.2	3.3	65	18.3	− 3	−15
June 12	21	26.7	3.4	56	13.3	− 3	−31
June 13	18	37.9	3.2	57	13.9	+22	−20
June 14	24	30.1	2.9	58	14.4	+ 7	−43
June 15	20	44.1	2.5	58	14.4	− 7	+22
			Brooding				
June 16	29	25.3	3.8	56	13.3	− 3	− 1
June 17	32	22.0	5.5	60	15.6	+17	− 5
June 18	32	20.8	5.1	58	14.4	+ 9	− 2

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by — if before.

vation scattered over 7 days at our nest, this feeding of the female was at the rate of 5.6 times per hour.

Schrantz does not present his statistical data but simply states that the female left the eggs at intervals of fifteen to twenty minutes, presumably for feeding. At our nest (Table 36), during 7 of the 10 days, the average number of attentive periods per day was 20, their average length, 35.7 minutes, the percentage of time attentive, 91.9, and the inattentive periods, 3.0 minutes. The female exhibited considerable uneasiness during her periods on the eggs and may have been annoyed by the thermocouple across the top of the eggs. This getting up and down and stirring on the nest may have cooled the eggs and since air temperatures were considerably below normal, this may explain the unusually long incubation of 13 days already noted. However, at night she sat fairly quiet in spite of the thermocouple and her skin temperature was always quite high. The unusually long attentive periods are doubtless due to the male's feeding her so that she did not need to leave so frequently to get food. It will be noticed that her attentive periods were shorter, but more frequent, and her inattentive periods somewhat longer before the set of eggs was completed. During her inattentive periods the female often did not go far away, sometimes feeding in the same tree in which her nest was located.

On June 7, 8, and 9 it is not possible to recognize more than two or three inattentive periods each day and these occurred after 1700 hours. The bird exhibited her usual restlessness on the nest and may have secured food from the tree or immediate vicinity during periods too short to register as inattentiveness on the record. About 1⅔ hours of observation on these days did not indicate that the male was feeding her more frequently than usual. The only correlation to be made is with a rapidly rising air temperature from the minimum of 52° F. (11.1° C.) on June 6, to the maximum for the entire incubation period of 73° F. (22.8° C.) on June 9. Perhaps with the rise in temperature, there was a decrease in physiological requirement for food compared with the demand at lower temperatures when metabolism becomes increased.

With the hatching of the young, the number of attentive periods per day rose to an average of 31, their length decreased to 22.7 minutes, and the length of the inattentive periods rose to 4.8. Brooding required 82.2 per cent of the daytime. I did not observe the male to feed the female while she brooded, which agrees with Schrantz's experience. Bigglestone and Schrantz observed the male passing food to the brooding female who then fed the young, or the male fed the young directly. Bigglestone observed considerable variation in the length of brooding periods, which generally varied between 1 minute and 10 or 12, and sometimes was longer. After the fifth day, brooding greatly decreased. Mousley gives the average length of the brooding period as 6.2 minutes. The longer attentive periods observed by us were computed from the recording. During these periods, brooding was frequently interrupted, and during these times the female may have left the nest. These interruptions were never as long as those designated as inattentive periods, but if they were so considered, the attentive periods would probably be as short as those observed by Bigglestone and Mousley.

The number of days that the young remain in the nest after hatching varies between the different individuals since their hatching may extend over three days. The most common interval is 10 days after the first hatching, at which time the last young hatched may be only 8 days old. Schrantz found that large broods sometimes left earlier than small broods because the crowding made them more restless.

Mousley spent 29 hours in observation of adults feeding young in the nest at various stages in their development. During this time the young were fed 112 times by the male and 277 times by the female or at the rate of 13.4 times per hour. If five young remained in the nest throughout this period, the average feeding rate per bird per hour would be 2.7.

Bigglestone's record of feeding young is most complete and detailed. Until the young were 4 days old, the male fed them more frequently than the female, doubtless because she spent considerable time in brooding. The average rate of feeding of the three young during the first 6 days was 16 times per hour. On the seventh day there was a disturbance at the nest after which the male no longer took part in feeding the young. During the following 4 days, the female by herself maintained the average rate of 16 times per hour, although during the 2 days preceding the male's desertion of his duties, her feeding rate had been only about 7 times per hour. In nearly 145 hours of observation the average feeding rate per bird per hour was approximately 6, which is over twice the rate reported by Mousley. In both instances the young left 10 days after hatching. Smith observed both adults caring for the young out of the nest for at least 17 and possibly 21 days before they became independent.

Mousley found that the male, after the young hatched, sang 1,800 times in 29 hours or at the average rate of 62 times per hour. He never found the male singing more often than 6 times per minute over short periods. During egg-laying and incubation and early in the morning, Smith found the usual rate of the male's singing to be 4 or 5 times per minute with a maximum of 7 times per minute.

There is very little daily rhythm in the activity of the female during incubation (Fig. 31). On cool days, contrary to what is found in other species, she is away from the nest more than on warm days when the male is able to keep her appetite appeased by bringing her food while she remains on the nest. During brooding, her curve of activity is more like that of other species, as the male no longer feeds her and she must search for all of her food. The least amount of time is spent brooding during mid-afternoon when the air temperatures are highest.

The time that the female begins and ends her daily activity is quite irregular (Table 36). Doubtless some of this irregularity is due to difficulty in interpreting from the record the exact time of beginning and ending the day's activities. An average of all the records indicates that she first becomes active 12 minutes after sunrise (0453 hours) during incubation and 8 minutes after sunrise while brooding the young. Likewise, the termination of her daily activity averages 9 minutes before sunset (1956 hours) during incubation and 3 minutes before sunset while brooding. The differences in time between these two phases of nesting activity is probably not significant. Five records of the earliest morning song of the male, obtained by F. Allen (1913), average 33 minutes before sunrise.

According to the potentiometer record, the female sat more quietly on the nest at night than she did during the day. Yet these quiet periods seldom lasted more than 10 to 20 minutes before they were interrupted by some movement. On one or two nights, she was seldom quiet for more than 5 or 10 minutes. The impression gained throughout this study is that the female is quite restless in temperament.

Goldfinch, *Spinus tristis*

One fairly complete record of attentive behavior in the goldfinch was obtained with the temperature-recorder from midway in the egg-laying period through incubation and hatching (Table 37). The nest was found about one-third built on July 2, but the first egg was not laid until July 17. Each new egg was numbered as laid until the set of six was completed on July 22. Egg No. 1 disappeared and No. 2 was slightly crushed. Egg No. 3 hatched first on August 2, 11 days after the last egg was laid, Nos. 4 and 5 hatched on August 3, and No. 6 hatched either late on August 3 or more probably early on August 4. This makes the incubation period 13 days long. All four young left the nest on August 16 which is 14 days after the first one hatched. Both adults shared in feeding the young while in the nest.

Various phases of the nesting behavior of this species have been studied by Bruce (1898), Mousley (1930a, b, 1932, 1935), A. O. Gross (1938b), Walkinshaw (1938-1939), and Stokes (1950). The female does all of the nest construction. The male is generally nearby, singing, and accompanies the female on her trips. He may rarely bring nest material for the female to insert into the structure. Thirteen days are required to construct the nest in early July but only 5.6 days in late August. Copulation is probably frequent during this period. There may be a lapse of 2 days between the completion of the nest and the laying of the first egg early in the season but none later. The eggs are laid daily early in the morning, although Gross found the first egg of one set to be laid between noon and 1600 hours. Five eggs is the most common number in a complete set, although Walkinshaw gives the average of all sets as 4.5 eggs. Stokes found the size of sets to be 5.3 in July and then to decrease to 3.7 in late August.

All authorities agree that steady incubation begins before the set is completed, and this is further substantiated by hatching extending over 2 or commonly 3 days. Walkinshaw (1938-39) states that in four-egg sets the female begins incubation and is on at night for the first time after laying the second egg, while in five-egg sets she does not do so until the third egg is laid, but there are variations from this schedule. At the nest which we studied, the female was observed on the nest in the morning after the first egg was laid but not in the afternoon or at night. The female was frequently seen on the eggs in the morning after the second egg was laid and was on twice in the afternoon, for periods of 19 minutes each, after the thermocouple was inserted in the nest at 1530 hours.

Table 37 shows that the attentive periods became longer and the inattentive periods shorter with the laying of successive eggs and during the first 3 days of incubation. The bird went on and off the eggs more frequently at this time than when she settled down for incubation at a slower routine. In this case the first night that the bird spent on the nest was the night before the last egg in the set was laid, when she was fairly quiet and applied full heat to the eggs.

Walkinshaw has the most extensive data and places the average length of the incubation period for 33 sets at 13 days. All authorities agree that incubation is performed entirely by the female and that the male regularly feeds the female at the nest. Mousley (1935) has evidence that the female sometimes raises a second brood in which case she does so alone, while the male takes full responsibility for caring for the young of the first brood after they fly and does not come at all to the female's second nest. Gross found that the male started feeding the female at the nest at intervals of one-half hour as soon as incubation began during the egg-laying period.

The attentive periods of the female during incubation are very long, averaging 2.2 hours. Doubtless this is because the male feeds the female at the nest. There is one record on July 29 of the female staying continuously at the nest for nearly 10.5 hours and another record of 9.5 hours on August 1. There may be some question whether the female exhibits attentive and inattentive periods at all during incubation. However, she does leave the nest and eggs for intervals that average 8.7 minutes which are convenient to recognize as a vestige, at least, of inattentiveness. The total time away from the nest during the day and night averages only about one hour. Sitting on the eggs takes up 92 to 100 per cent of the time. There is a little evidence that on cool days she leaves the nest more frequently than on warm days although not for very long at a time. The female does not sit quietly during these long attentive periods but shifts around on the eggs, jumps back and forth to the rim of the nest, rises up to receive food from the male, and may leave the nest entirely for several seconds at a time while she moves around nearby.

Hatching extended over 3 days. In general, the attentive or brooding periods are better differentiated than during incubation and they are less than one-third as long, averaging 15.7 per day, 37.1 minutes long. Brooding requires 76.5 per cent of the daytime. Inattentive periods average 10.7 minutes. The short time spent in attentiveness during these 3 days may have partly been due, however, to the higher air temperatures that prevailed. Mousley found at one nest that the brooding periods averaged 18.5 minutes during the first 7 days and at another nest they averaged 14.9 minutes. There is a progressive decrease in amount of time spent brooding until it nearly ceases after the young are 6 or 7 days old. On

TABLE 37. Attentive behavior of a female goldfinch.

Date	Phase of nesting cycle	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Average temperature °F.	Average temperature °C.	Difference from [a]: Sunrise: First restlessness (min.)	Sunrise: First inattentiveness (min.)	Sunset: Last inattentiveness completed (min.)	Sunset: Last restlessness (min.)
1928										
July 19	3rd egg	15	30.3	24.2	76	24.4	...	...	...	...
July 20	4th egg	12	37.5	13.8	79	26.1	...	...	...	...
July 21	5th egg	16	43.9	10.2	74	23.3	...	...	−28	+32
July 22	6th egg	7	102.0	16.8	76	24.4	−13	0	−33	...
July 23	Incubation	5	144.2	8.8	72	22.2	−18	+58	−47	+13
July 24	Incubation	4	198.5	8.8	72	22.2	−19	+6	−33	+27
July 25	Incubation	4	158.5	12.2	74	23.3	−29	+39	−142	+ 8
July 26	Incubation	5	147.0	5.3	75	23.9	−16	+63	−44	+ 9
July 27	Incubation	...	...	...	72	22.2	− 6	+249	...	...
July 28	Incubation	...	...	...	66	18.9	...	...	−62	+12
July 29	Incubation	7	119.3	5.8	63	17.2	...	−16	− 3	...
July 30	Incubation	10	79.0	6.6	64	17.8	...	+ 5	+ 2	...
July 31	Incubation	7	110.1	5.2	71	21.7	−22	+ 4	−53	...
Aug. 1	Incubation	...	...	...	72	22.2	...	− 1	−90	+15
Aug. 2	Hatching and brooding	11	45.4	7.9	80	26.7	−24	+196	−16	+ 3
Aug. 3	Hatching and brooding	15	43.5	9.2	83	28.3	−25	+54	− 4	...
Aug. 4	Hatching and brooding	21	22.5	14.9	82	27.8	−17	+ 2	+ 5	...

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

hot days the female may devote her attentive period to standing on the rim and shading the young from the direct rays of the sun rather than in keeping them warm. During rain or cold weather the female may cover the young at least up to 11 days of age.

When the female is brooding the young, the male continues to feed her at the nest. Some of this food she keeps for herself, the rest she hands over to the young. When the female is away and after brooding is over, both male and female feed the young directly. When the female ceases to brood, the male no longer feeds her even though she begs for it. Feeding is by regurgitation of food previously ingested and perhaps partly digested. This permits the adults to bring more food at a time and to feed it at intervals. Mousley (1932) observed the female leaving the nest twice in three hours to search for food, yet she was able to feed the young nine times during this period. A. O. Gross (1938b) observed that the male fed each of six young on each visit, sometimes repeating the round more than once; however, the female fed only two to four of the young at a time. Doubtless this manner of feeding is responsible for the slow rate of feeding the young customary in this species.

Bruce found at one nest that the young were fed at the rate of about once per hour by the male and female. Mousley spent over 164 hours in observation at four different nests and found that the rates of feeding at the different nests varied between 1.1 and 1.6 times per hour for a general average of 1.4. The rate is no faster with both adults feeding the young than with the female feeding them alone. At one nest the rate of feeding tended to decrease as the young got older, but at another nest the rate remained about the same throughout. Walkinshaw found during 10.5 hours of observation that the young were fed about twice per hour by the male and female. Due partly to hatching being prolonged, the young leave the nest at ages varying from 11 to 15 days, but the average is 13 days. Both adults may continue to feed the young periodically for several more days, or the female may start a second nest leaving the care of the young of the first brood to the male (Mousley 1935).

Gross observed that when the construction of the nest was nearing completion the female made her visits only in the early morning and again one to two hours before sunset. Figure 32 shows the daily rhythm of activity of the female at various stages in her nesting cycle as shown by our temperature-recorder. To simplify the figure and because the record for the third and fourth days of egg-laying are nearly the same, the hourly data for these 2 days have been averaged together. The same was done for the fifth and sixth days. The curve for the incubation period is an average for 7 days and the curve for brooding is an average for 3 days.

The incubating behavior exhibits a progressive development during the egg-laying period. On the days that the third and fourth eggs are laid

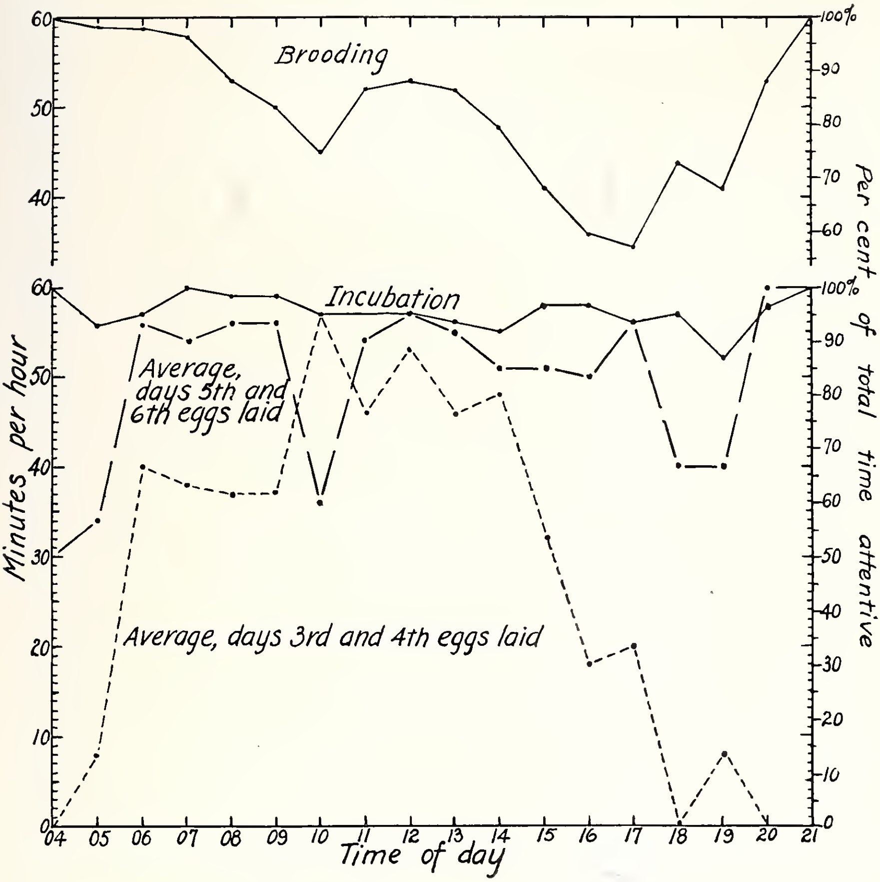

FIG. 32. Daily rhythm of attentiveness of female goldfinches.

attentiveness is most pronounced from 0600 to 1400 hours. On the days that the fifth and the last eggs are laid, attentiveness is well sustained throughout the day. With full incubating behavior established, the curve shows a tendency to drop slightly in the late afternoon. Differences in daily temperature produced a negligible effect during incubation, but the pronounced drop in the curve for brooding after the middle of the day may have been accentuated by the prevailing heat. If the female were standing on the rim, shading the young from the sun in the afternoon, her attentiveness would be longer than the record showed. The various curves indicate, however, that through most of the nesting cycle there is decreased activity in the afternoon. No data are available to show the daily rhythm in rate of feeding.

The first inattentiveness of the female in the morning during incubation, but excluding July 21 and 22, averaged 45 minutes after sunrise (Table 37). Sunrise occurred at about 0518 hours. This is not a true index in this species of the commencement of the day's activities as the female becomes active on the nest long before this time. Gross (1938b) states that the male makes his first visit to the nest at dawn. Actually the temperature record indicates that restlessness of the female began 18 minutes before sunrise on all except two mornings. Probably this is the time that the male starts feeding the female on the nest.

Gross (1938b) also states that the male continues to feed the female at intervals well after sunset. This may well be the case, as the last inattentive period was completed 52 minutes before sunset (1947 hours). On 6 evenings the female continued to be restless until 14 minutes after sunset. On some evenings, however, there is no certainty that the male continued to feed her until this late. While brooding the young, the female does not leave the nest until much later in the morning but may be off at a later time in the evening. Except for the early morning and evening restlessness already noted, the female usually spent a quiet night on the nest.

Chipping Sparrow, *Spizella passerina*

Although several attempts at detailed studies of the chipping sparrow were made, only once were we able to get a successful recording of nest activity with potentiometer and thermocouple. The birds, especially the female, seemed unusually sensitive to disturbance, and this species proved to be one of the most difficult with which we have worked. It is fortunate that Walkinshaw (1944) has summarized his observations so that the nesting history of this bird may be pieced together.

According to Walkinshaw, the male sings in defense of territory almost continuously during the daylight hours from the time of his arrival in migration until mating is completed, but sings very little between mating and the beginning of incubation. The female does all the nest building, although the male usually accompanies her on her trips back and forth. The nest is completed in 3.4 days, on the average.

The eggs are laid daily between 0500 and 0700 hours until three or four are laid. Only the female regularly incubates the eggs, although Walkinshaw once saw the male covering them. Only 10 days elapsed between the last egg laid and the first young to hatch in the four nests where this was determined. Walkinshaw found the female on the eggs the night before the last one was laid and computes, therefore, the incubation period at 11 days. At five nests of ours, 11 days (10-12 days) elapsed between the last egg laid and the first to hatch, and since the hatching extended over 1, 2, and even 3 days in one instance, the incubation period was more nearly 12 days long.

TABLE 38. Attentive behavior of a female chipping sparrow during incubation.

Date	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Mean daily temperature °F.	°C.	*Difference from* [a] Sunrise (min.)	Sunset (min.)
1931							
July 16	...	...	...	82	27.8	...	+ 2
July 17	38	10.3	12.3	84	28.9	+ 7	−19
July 18	44	11.6	8.6	78	25.6	− 6	+10
July 19	...	...	...	82	27.8	...	−15
July 20	34	17.1	8.6	78	25.6	−12	−15
July 21	32	21.8	6.2	70	21.1	−20	0
July 22	...	...	...	72	22.2	−22	...

[a] The time that the daily activity began and ended in respect to sunrise and sunset is indicated by + if after and by − if before.

Table 38 summarizes one record of attentive behavior. There were 37.0 attentive periods per day, averaging 15.2 minutes in length, with the inattentive periods 8.5 minutes long. The bird sat on the eggs 66.0 per cent of the daytime. The table indicates a possible increase in length of the attentive periods and decrease in length of the inattentive periods with progress of incubation, but more probably this is correlated with the decrease in mean daily temperature. We did not observe the male to feed the female at the nest, but Rudolphi (1935) and Bradley (1939) found that the male brought food about two times per hour "sometimes feeding her while she remained on the nest and sometimes coming to a nearby tree or bush where she met him and received the food."

Walkinshaw found that the female did most of the brooding of the young, but on cool mornings the male occasionally brooded for a very few minutes. Nearly 10 hours of observation early in the morning on the day the young hatched and the next two days showed a steady decrease in average length of the brooding period from 41.1 to 14.2 to 11.1 minutes with intervals between brooding increasing from 3.8 to 12.0 to 13.7 minutes. Brooding ceased entirely during the daytime after the young were 6 or 7 days old.

Walkinshaw spent over nine hours in observation of feeding the young at one nest and seven hours at another nest. Both nests contained three young. At the first nest the rate of feeding increased with the age of the young as follows: just hatched—2.0 times per hour; one to two days—8 times per hour; and six to seven days—11.2 times per hour. At the other nest the rate varied: one to two days—6.4 times per hour; two to three days—6.5 times per hour; and four to five days—13.3 times per hour. Both male and female took nearly equal parts in feeding the young. The young left the nest when they were 7 and 8 days old, which is before they were able to fly. F. E. L. Beal watched two nests with four young each at ages of 4 and 6 days for 14 hours and found the adults feeding at the rate of 19 and 17 times per hour. In five records of ours, an average of 9 days elapsed (8-10 days) between the first young to hatch and the first to leave the nest. Walkinshaw observed the young fed by their parents when 24, 33, and perhaps 35 or 40 days old.

Most of the nest building is done in the early morning hours. The daily rhythm of activity during incubation as obtained by the recording potentiometer is shown in figure 33. Less time is spent incubating on warm than on cool days. On July 21 when there was rain and cool weather, the female stayed on the eggs for one long period of 129 minutes and several other periods of one-half to three-quarters of an hour. The record on all 4 days, regardless of the temperature, shows a secondary rise sometime between 1000 and 1200 hours before dropping to the afternoon low. Perhaps this was a peculiarity of this particular individual. The number of periods per hour increases steadily from 1.5 at 0500 hours to a maximum of 3.3 at 1500 and 1600 hours and then regresses. The length of the inattentive periods does not show any consistent variation with time of day, but the attentive periods vary as follows: 0500 to 0800 hours, inclusive—21.8 minutes; 0900 to 1200 hours—26.4, although the average would be 12.1 if the rainy July 21 is omitted; 1300 to 1600 hours—11.1; 1700 to 2000 hours—13.4. The relatively long brooding periods recorded

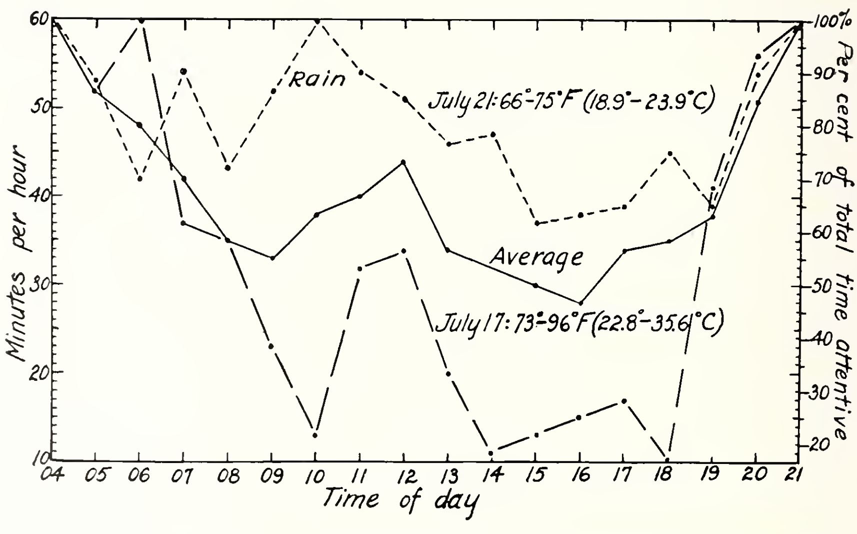

FIG. 33. Daily rhythm of attentiveness of female chipping sparrows during incubation.

by Walkinshaw are probably to be explained by the time of day, as all of his observations were made between 0500 and 0930 hours.

This bird showed the interesting trait of beginning her daily activities earlier on cool than on warm mornings, although no such relation with temperature is evident in the time her daily activities terminated in the evening (Table 38). On the average she left the nest 11 minutes before sunrise (0510 hours) and retired 6 minutes before sunset (1954 hours). Allard (1930) registered the first morning song of the male about 30 minutes before sunrise or close to 20 minutes before the female becomes active.

The potentiometer recorded the female somewhat restless on 3 out of 5 nights. Twice the bird became more restless just before leaving the nest in the early morning, on one occasion for one-half hour, on the other for 15 minutes. Near midnight on July 21-22 there was a severe thunderstorm. The bird had been quiet on her nest previously, but beginning at 0015 hours she left the eggs for two periods totalling 33 minutes. Perhaps the eggs and nest got soaked, because when the bird returned she was restless the rest of the night. The eggs, however, hatched successfully.

Song Sparrow, *Melospiza melodia*

The potentiometer and thermocouple were used to record the activity of five female song sparrows over a total of 35 days during incubation and brooding. No detailed observations were made at the nest nor of the male's activities. The male is chiefly responsible for the establishment and defense of the nesting territory and helps to feed the young. The female does all the nest building, incubation, brooding, and part of the feeding of the young.

Singing of the male. Nice (1943:119) obtained records on the rate of singing for eight males over 500 hours and found that the rate varied under different conditions as follows:

Times per hour	*Stage of nesting cycle*
0-20	Prenuptial, preliminary nest building and coition, feeding young, molt
30-70	Building, egg-laying, incubation, late afternoon
90-160	Competitive singing between males, proclaiming territory in summer, cold days in spring
180-300	Proclaiming territory in spring, competitive singing between males.

One male while proclaiming territory sang 4.8 times a minute for the first two hours in the morning with only one-half minute inattentive periods. During the next hour he was inattentive and not singing for only 12.5 minutes. During the afternoon, however, his singing was less intense and continuous (Fig. 35).

Nest building of the female. A few observations by Nice (1943:210) of one female during nest building gave attentive periods of 15, 20, and 23 minutes with intervening inattentive periods of 5, 7, and 8 minutes. The nest is nearly completed within 2 days and lined by the third or fourth day, with the first egg commonly coming on the fifth day. Normally three to five eggs occur in a set. The brood patch begins to develop 4 to 6 days before the egg is laid so that with the first egg the

TABLE 39. Daily record of attentive behavior of female song sparrows.

Nest	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
	1st Day (Incubation)				*2nd Day*			
1	...	...	...	...	...	...	...	...
2	.....	...	...	...	...	...	...	...
3	...	...	...	...	...	...	...	...
4	...	...	...	...	...	...	...	...
5	72°F.	20	29.2	11.7	69°F.	20	32.0	8.8
	3rd Day				*4th Day*			
1	...	...	...	...	...	...	...	...
2	...	...	...	...	...	...	...	...
3	...	...	...	...	...	...	...	...
4	...	...	...	...	...	...	...	...
5	70	16	34.0	10.2	...	...	...	...
	5th Day				*6th Day*			
1	...	...	...	...	52	38	15.2	6.1
2	...	...	...	...	...	...	...	...
3	...	...	...	...	...	...	...	...
4	...	...	...	...	...	...	...	...
5	61	25	26.2	7.2	60	27	22.2	8.6
	7th Day				*8th Day*			
1	46	35	18.5	5.3	52	29	20.1	7.5
2	...	...	...	...	...	...	...	...
3	...	...	...	...	72	18	39.7	8.6
4	75	13	48.9	10.4	...	...	...	...
5	66	33	16.9	9.5	64	30	19.5	7.3
	9th Day				*10th Day*			
1	...	...	...	...	43	31	22.4	4.1
2	...	...	...	...	67	27	21.0	12.2
3	80	20	36.3	8.9	78	17	39.4	10.9
4	...	...	...	...	83	15	41.1	19.5
5	68	28	21.0	8.3	77	27	20.9	9.5

TABLE 39 *(cont.)*. Daily record of attentive behavior of female song sparrows.

Nest	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)	Air temperature	Number of periods	Attentive periods (min.)	Inattentive periods (min.)
		11th Day				*12th Day*		
1	44°F.	32	21.0	4.5	55°F.	33	18.4	6.6
2	68	26	26.5	7.3	66	22	32.6	7.9
3	68	23	28.7	7.2	72	17	36.2	11.1
4	84	20	32.3	14.8	78	13	47.2	17.7
5	70	26	24.0	7.3	62	23	27.5	7.3
		0 Day (Hatching)				*1st Day (Brooding)*		
1	56	58	9.2	5.6	52	73	7.4	4.6
2	...	...	...	...	...	...	...	...
3	...	...	...	...	...	...	...	...
4	83	29	16.1	16.1	73	?	23.5	7.6
5	62	37	18.1	5.9	64	38	14.1	6.9
		2nd Day						
1	51	56	8.7	6.5				
2	...	...	...	...				
3	...	...	...	...				
4	72	48	11.3	5.8				
5	67	39	11.4	10.5				

patch is entirely bare and vascularized (Nice 1937:122). Eggs are laid in the early morning on succeeding days. The incubation period is most often 12 or 13 days in length.

Egg-laying. Nice is correct in stating that incubation begins before the set is complete, since normally two days are required for all the eggs to hatch (1937:122). Only one record was obtained in the present study during the egg-laying period. At nest No. 5 the female had six attentive periods totaling 43 minutes from 1430 hours until dark on the day that the first in a two-egg set was laid, compared with six attentive periods totalling 219 minutes over the same time the next day. She did not spend the night on the eggs on the first day, although she did thereafter throughout incubation.

Incubation. During incubation, the attentive periods of the female average 28.5 minutes, her inattentive periods average 8.8 minutes, and there are 23 attentive periods per day (Table 40). Thus the bird is attentive 75.6 per cent of the daytime. There is considerable variation between different birds and with the same individual at different times. Only the record at nest No. 5 extends throughout the incubation period (Table

39). The number and length of her periods are somewhat greater during the first three days than later during incubation. Considering all these records and Nice's observations (1937:124), there is probably, however, no consistent variation in attentive behavior with progress of incubation.

There appears to be a definite correlation between average number and length of periods with average temperature. This correlation was also evident when the daily records, irrespective of the individual on which they were obtained, were considered. Since the increase in length of attentive period with rise in temperature is contrary to what occurs in other species, since it does not agree with similar data obtained by Nice, and since it is not supported by the curves of daily rhythm on hot and cool days (Fig. 34), the apparent correlation requires further scrutiny.

When the daily averages for individual sparrows are considered separately, the length of the attentive periods decreases with rise in temperature at nests No. 1 and 4, increases at nest No. 3, while at nest No. 5 the trend is uncertain since it decreases as temperatures rise from 60° to 68° F. (15.6° to 20.0° C.) but is greatest at temperatures of 69°

TABLE 40. Attentive behavior of female song sparrows.

	Number of eggs in set	Date of last egg	Days' record	Air temperature °F.	Air temperature °C.	Number of periods per day	Attentive periods (min.)	Inattentive periods (min.)	Total attentiveness (min.)
				Incubation					
Nest									
1	4	May 6	6	49	9.4	33	19.3	5.7	637
2	4	June 8	3	67	19.4	25	26.7	9.1	668
3	3	June 11	5	74	23.3	19	36.1	9.3	686
4	4	July 16	4	80	26.7	15	42.4	15.6	636
5	2	July 29	11	67	19.4	25	24.9	8.7	622
Bird				*Data compiled from Nice, 1937, p. 123*					
K7	...	April	17 hours	57	13.9	...	30.5	6.0	...
K2	...	April	30 hours	55	12.8	...	30.0	7.8	...
K2	...	June	21 hours	70	21.1	...	27.0	9.0	...
K3	...	June	24 hours	69	20.6	...	20.0	8.0	...

	Number of young	Date first hatched	Air temperature °F.	Air temperature °C.	Number of periods	Brooding periods (min.)	Intervals (min.)	Total brooding (min.)
			Brooding (first two days after hatching)					
Nest								
1	3	May 18	52	11.1	64	8.0	5.6	512
4	3	July 28	72	22.2	...	17.4	6.7	...
5	2	Aug. 10	66	18.9	38	12.8	8.7	486

to 72° F. (20.6° to 22.2° C.). Female No. 3 was an exceptional bird in that high temperature appeared to make her nervous. The record shows that during the middle of the day she would spend long periods at the nest. One such period was three hours long, another nearly four hours long. She did not incubate steadily. The nest temperature was in almost continual flux as if she were hopping on and off the eggs. There was never a period of more than three or four minutes when she was away from the nest, but she may have picked up occasional tidbits to eat in these intervals. As the air temperature moderated in late afternoon, her behavior became normal again and her attentive and inattentive periods became typical of the species. The unusual relation between length of attentive periods and temperature in our records for this species is apparently due to the nervous idiosyncracies of one or two birds.

Further study of the daily records of individual birds showed no consistent change in the number of periods per day with increase in temperature. Considerable irregularity occurred from day to day. On the other hand, all four birds (nests 1, 3, 4, 5) showed without exception an increase in the length of the inattentive period as the air temperature increased. The daily records for all birds in each range of temperature show that the length of the inattentive period varied: 4.6 minutes at 44° F. (6.7° C.), 7.2 minutes at 55° F. (12.8° C.), 8.4 minutes at 67° F. (19.4° C.), 11.1 minutes at 76° F. (24.4° C.), and 17.2 minutes at 84° F. (28.9° C.). This is in harmony with the relation between inattentiveness and temperature found in other species. The total attentive time during the daylight hours averages nearly the same for all five birds regardless of the temperature, so that the manner in which this time is divided between attentive and inattentive periods is peculiar to the individual.

The male may have an influence in determining the behavior of individual females. Nice (1937:124) noted that the similarity in length of attentive periods of K7 and K2 may be due to their being mated in different years to the same male. She also found that the female, two-thirds of the time, terminated her attentive period in answer to signal-songs of the male given within 20 feet of the nest. While the female is inattentive, the male guards the nest for a few minutes, then leaves to join his mate and often accompanies her back. While the female is on the nest, the male sings and has his inattentive period for feeding just before the female is due to leave the nest.

When total attentive time per day is averaged for days with different numbers of attentive periods, it fluctuates around a constant value of 638 minutes regardless of whether the average number of periods is 14, 18, 23, 28, or 33 per day. Likewise the total inattentive time varies around 204 minutes. The increase in number of periods per day is correlated with a proportionate decrease in the length of both the attentive and inattentive periods.

Brooding young. From Table 39, it is evident that as soon as the eggs begin to hatch there is a marked increase in number of attentive periods per day, as measured by the time spent brooding, and a decrease in the average length of these periods. The inattentive periods may remain of the same length as before or may decrease. The data on brooding behavior are averaged for the first and second days after the one on which the eggs hatch (Table 40), as on the day of hatching part of the time is spent in incubating the eggs. During these two days, 64 per cent of the time is spent in brooding the young, there are 51 brooding periods per day, their average duration is 12.7 minutes, and the intervals between brooding periods average 7.0 minutes. For the corresponding two days Nice (1937:130) records the female brooding only 52 per cent of

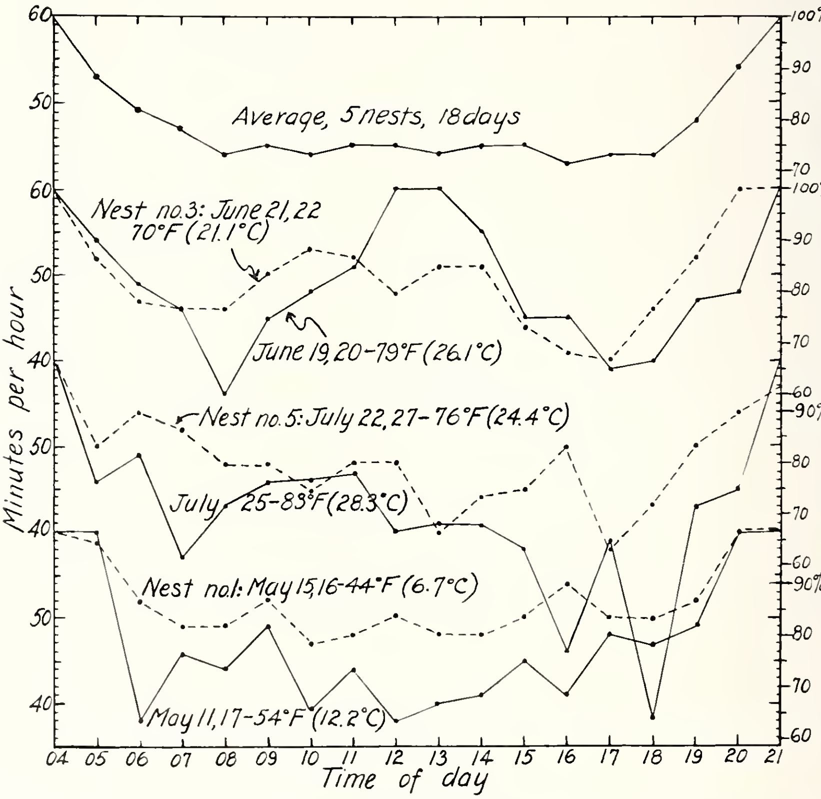

FIG. 34. Daily rhythm in attentiveness of female song sparrows during incubation.

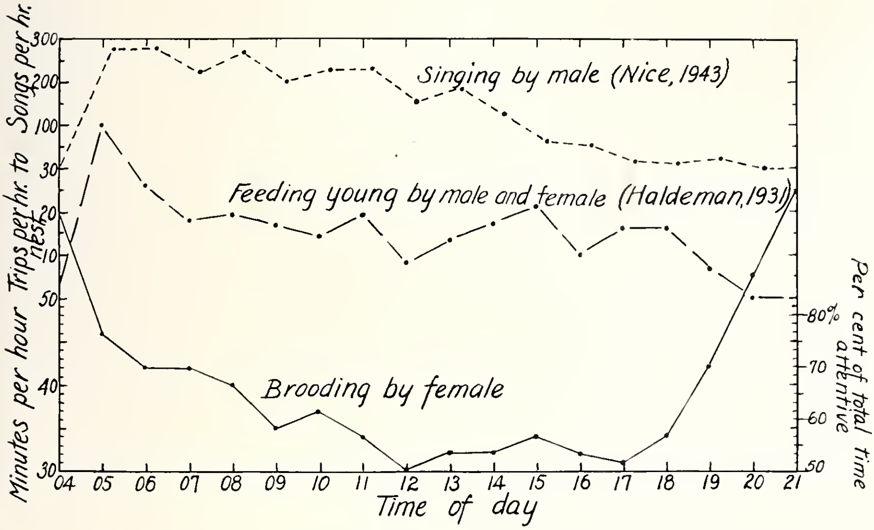

FIG. 35. Daily rhythm in attentive behavior of song sparrows.

the time, but her observations probably did not include the early morning and the evening when a greater proportion of time is devoted to this activity. She found, however, that a similar proportion of time spent brooding persisted into the third or fourth day, and then dwindled to almost none after the sixth day. The young stay in the nest for 10 days and are cared for after leaving for another 18 to 20 days.

Feeding young. No records were made in the present investigation on the rate of feeding the young. Nice (1943:231) has summarized her own observations and those of Haldeman and Mousley. For the first 5 days of nest life the young are fed, on an average, 7.2 times per hour, 5.2 times by the male and 2.0 times by the female. During the second 5-day period they are fed 17.8 times per hour, 9.7 times by the male and 8.3 times by the female. At three out of five nests during the second period the females fed more frequently than the males since they did not then need to devote time to brooding. The rate of feeding by both adults was 2.5 times more rapid during the second 5 days than during the first 5 days, corresponding to the increased requirements of the young as they grew older. The average rate for the entire nesting period, obtained by averaging the two rates given above, is 12.5 times per hour. As there was an average of 3.7 young per nest, the number of trips to the nest was at the rate of 3.4 per young bird per hour. Haldeman (1931:399) found that when the young were approximately 5 days old an average of 1.4 young were fed on each visit by the parents to the nest, but there is no information available whether this rate is maintained throughout the nest life. In one all-day record, Copeland (1909) found an average rate of only 5.5 feedings per hour.

Daily rhythm. Nice (1943:122) recorded the number of times an eight- to nine-year-old male sang each hour throughout the day when proclaiming territory and seeking a mate. Her data are plotted in figure 35 and they show that he was most actively singing early in the morning, at a slightly decreasing rate until 1300 hours, and then at a considerably decreased rate the rest of the day. There was no resurgence of active singing in the evening.

The daily rhythm of incubating activity is shown for three birds in figure 34, both for warm and cool days. The greater depression of attentiveness on hot days is evident for females No. 1 and 5, and the peculiar behavior of female No. 3 has already been mentioned (p. 163). An average curve for all five females under various conditions of weather shows a constant level of attentiveness from 0800 to 1800 hours. There were no consistent changes during these hours in number of periods nor in length of the attentive and inattentive periods.

A record of two females brooding over 4 days (Fig. 35) shows a typical curve of decreasing time spent on the young until noon, a continuance of brooding for only 30 to 35 minutes during each hour until 1800 hours, and then an increasing amount again in the evening.

The curve for hourly feeding rate is taken from Haldeman (1931:396) and is for young which she estimated to be in their fifth day after hatching but which Nice (1943:231) believed may have been 6 or 7 days old. Haldeman found that the female fed at a rapid but decreasing rate all morning and at a slow rate in the afternoon. The rate of feeding by the male was the reverse, and during two hours in the afternoon he fed the young more often than did the female. Of the total feedings during the day, the female gave 198, the male, 63.

Beginning and ending of day's activities. In considering time of beginning and ending of the birds' daily activities, it is again necessary to separate the various phases of the nesting cycle. When caring for young birds in the nest, the female arises 28 minutes earlier and retires 9 minutes later than when incubating eggs (Table 41).

During incubation the female first leaves the nest after a night on the eggs at 2 minutes, on the average, after sunrise and returns to the nest in the evening 5 minutes before sunset. While brooding she anticipates sunrise fully 26 minutes and retires 4 minutes after sunset. There is considerable variation between different females and in the same female on different days. Arising late and retiring early is the rule on cloudy and rainy days, but the necessary data are not at hand to analyze this modification of behavior in detail.

Nice (1943:101, 107) obtained 11 records on three females and found that they arose 23 to 25 minutes before sunrise and retired about sunset. She does not state the nesting activity of the birds at the time, but the records would agree with ours for the period after the young hatch. Allard (1930:440) and Nice (1943:102) agree that during the breeding season the males begin singing about a half-hour before sunrise and Nice (1943:107) finds that he does not go to roost until 14 minutes after sunset. Cloudiness shortened the day's activity at both ends. Wright (1913), on the other hand, recorded the male's first song an average of 73 minutes before sunrise and his last song 23 minutes after sunset.

TABLE 41. Time of beginning and ending of daily activity in female song sparrows.

Nest	Median date	*Number of records* Morning	Evening	Hour activity began	Hour activity ended	*Difference from* Sunrise (min.)	Sunset (min.)
			Incubating eggs				
1	May 14	6	7	0530	1917	+19	−17
2	June 17	4	4	0455	2000	+ 2	+ 1
3	June 20	6	5	0452	1944	− 2	−16
4	July 25	6	5	0504	2015	−10	+25
5	Aug. 4	11	12	0523	1920	− 1	−20
			Brooding and feeding young				
1	May 18	3	3	0444	1929	−22	− 9
2	June 19	. . .	1	. . .	1957	. . .	− 3
4	July 29	1	2	0445	2002	−33	+16
5	Aug. 11	2	3	0507	1944	−23	+13

Activity at night. The temperature record shows that at nests 4 and 5 the females were usually fairly quiet all night long, although in the early part of the night of July 31, the female at No. 5 left her eggs. From 2040 to 2125 hours she was probably perched on the nest rim as the thermocouple recorded some heat, but from 2125 to 2300 hours she was away from the nest entirely. After 2300 hours she settled down on the eggs for the rest of the night. The female at nest No. 3 was very restless at night, but this may have been due to the experimental use of two thermocouples in the nest instead of one. Females Nos. 1 and 2 showed some restlessness at more or less definite intervals of 15 to 30 minutes and 10 to 20 minutes, respectively. No bird showed any consistently greater restlessness at one hour of the night than another. Females Nos. 1 and 5 were considerably more restless the first 2 or 3 nights after the young hatched than they were when incubating eggs.

Discussion and Summary

The analysis of attentive behavior in different species indicates that considerable variation occurs. The general rule is for both sexes to share nesting duties but in greatly varying proportions. In species having a low taxonomic position, such as killdeer, chimney swift, and flicker, both sexes share incubation as well as the care of the young. In species of more advanced ranking, the male commonly does not incubate or brood, but he helps to feed the young. In some species, as the cedar waxwing, yellow warbler, and goldfinch, the male has not only lost the incubating behavior but has developed a new trait of keeping the incubating female supplied with food so that she seldom needs to leave the nest and search for food for herself.

Coincident with the loss of incubating behavior in the male has been the loss of a brood patch, such as the female retains and such as males of the lower orders also possess. Without a brood patch the male does not truly incubate even if he sits on the eggs during the female's absence. In addition to instances noted for some of the above species, Ryves (1943a) cites several others where the male may "sit on eggs without the production of the requisite temperature to further their development," and he also points out that this behavior on the part of the male should not be considered true incubation. He proposes that this male behavior be called "brooding," but we prefer to limit this term to the application of heat to young birds after hatching.

There are several other important variations between species in attentive behavior, but the analysis and interpretation of these various types of behavior patterns will be postponed to the next section.

A common characteristic of all behavior patterns is the gradual way in which they develop and then recede during the yearly reproductive cycle. The earlier recrudescence of reproductive behavior in the male than the female is doubtless conditioned by the earlier development of the testes in response to the lengthening photoperiods of early spring. After migration is completed, the male then establishes his territory and may start nest construction. When the female arrives and mating is consummated, nest building proceeds in earnest, followed by egg-laying and onset of incubation. Reproductive behavior undoubtedly depends on hormones liberated from the maturing gonads and may also require stimulation from the opposite sex as well as a proper environment. After reproduction has run its full course, there is regression again to the quiescent winter condition. This is also a gradual process with the male, and he usually precedes the female in returning to the nonbreeding condition. This gradual retrogression occurs along with the atrophying of the gonads and the progressive gaining of independence by the young.

Doubtless the time will come when it will be known how each stage in this cycle is controlled and coordinated with all the other stages and the relative roles played in this regulatory mechanism by hormones, weather, companions, energy resources, and other factors. It may well be that each stage in the reproductive cycle serves as the stimulus to initiate the next, as Herrick (1910b) maintained long ago.

Nest building commonly proceeds vigorously from the very start, once the female and male have definitely become mated. Usually the nest is essentially completed sometime before the female is ready to lay her first egg. As a result the nest may not be visited during this interim of one or more days and attentive behavior may appear at low ebb. In passerine species, 5 or more days may elapse between first copulations between sexes and the laying of the first egg. Usually not all of this time is required for nest building.

Considerable evidence has been presented in this paper that incubation attentiveness develops gradually. Ryves (1943a) discussed the problem several years ago and Swanberg (1950) more recently. Purchon (1948) showed that as the four eggs were laid, a female *Hirundo rustica* spent daily increasing percentages of time on the nest: 16.7, 20.1, 45.0, and 58.1. Only on the last day did the average length of the attentive period exceed the inattentive period. In the avocet, *Recurvirostra avosetta,* P. E. Brown (1949) found that with successive eggs in the four-egg set the avocet incubated 75, 89, 97, and 100 per cent of the time. It is probable that the incubating attentiveness is initiated by hormones, but it may also require a contact stimulus from a full set of eggs and be correlated with the development of a brood patch. Full incubating attentiveness is normally developed by the time the set is completed and in some species may occur well before the last egg is laid. The amount of incubation that the first eggs receive before the last eggs are laid affects their intervals of hatching.

Once incubation is well established, it tends to remain more or less uniform until the young hatch. In the studies here reported there is no evidence that the incubating birds consistently spend more time on the eggs during the latter days just before hatching. Air temperature affects the attentive rhythm, however, and the coincidence of cold weather with the latter days of incubation may explain observations reported in the literature where the incubating birds appeared to sit more closely as incubation progressed.

An increase in tempo of the attentive rhythm commonly occurs with the hatching of the eggs. Attentive periods tend to be shorter and to come more frequently. As the young get older and mature physiologically, brooding attentiveness progressively declines, but the rate of feeding usually increases. With full active feeding of the young, attentiveness may be just as intense as during the incubation phase of the reproductive cycle, even though definite periods of attentiveness and inattentiveness are more difficult to discern. However, after the young become fledged, leave the nest, and become progressively more independent of their parents, the attentive behavior of the adults gradually disappears, and the birds have completed their reproductive cycle for the year.

Changes in air temperature cause important changes in the rhythm of attentiveness from day to day. With a rise in air temperature, our data show that there is almost always a decrease in the average length of the attentive periods. There is simultaneously an increase in the total time of inattentiveness, but this may be brought about either by lengthening the inattentive periods or by increasing their number. Nice and Thomas (1948) have summarized the literature for five passerine species and make this same generalization in regard to the influence of temperature on incubating attentiveness.

The effect of temperature on attentiveness is also evident in the daily rhythm of attentiveness or the variations that occur from hour to hour. In general, incubating and brooding attentiveness decreases until early or mid-afternoon and rises again in the evening. The drop in attentiveness during the afternoon may be scarcely noticeable on cool days but becomes pronounced on hot ones. The same rhythm of hourly variations in attentiveness occurs in the feeding of the young, although it may be less pronounced, and the late afternoon rise may not always appear. Information is accumulating fairly rapidly on the daily rhythm of attentive behavior in many species with the increasing tendency for bird students to use automatic recording devices or to take all-day observations. Palmgren (1949) has recently made a useful summary of much of this literature.

In those species where the female does all the brooding of the young after hatching, the male may bring more food to the young than does the female. As the young grow older and they need to be brooded less frequently, the female is commonly the more attentive of the two sexes to their feeding.

The rate at which the young are fed is affected by various factors, especially by the age and number of young in the nest. There is general agreement among most observers that the rate of feeding increases as the young get older, but there is difference of opinion as to how much the size of the brood affects the feeding rate and the length of the nestling period.

Paynter (1949) found that herring gulls *(Larus argentatus)* feed broods of three young just as easily and as efficiently as broods of one or two because a surplus of food is always brought to the nest. Skutch (1949a) transferred young between nests of the song tanager *(Ramphocelus* *passerii)* and found that broods of one, two, and three were fed at rates of 7, 15, and 21 times per hour or about seven times per young bird per hour regardless of the number in the nest. However, this study was for a very limited period. We found (p. 105) phoebes feeding a brood of four young four times as rapidly as a brood of one young. Kluijver (1950) found no relation between size of brood and rate of feeding in the great tit, *Parus major* nor did Moreau (1947) find any differences in the rate at which each young bird was fed in broods of different size in the white-rumped swift *(Apus (Micropus) caffer)* and red-throated rock martin *(Ptyonogrogne fuligula)*. However, Moreau found from the study of other species that "as a rule, the more young in the nest the more frequent the parents' visits, but not in proportion to the increase in the number of young." This conclusion is concurred in by Kluijver (1933), Lack (1947-48, 51), Lack and Silva (1949), and Gibb (1950), and was found with the house wren (p. 61) and robin (p. 130) in the present study. Skutch (1949a) suggests that "the existence of an innate rhythm, adjusted to the normal brood, would explain why each nestling in a smaller brood is fed more often than each one in a family of the usual size." One adult house wren can easily care for small broods, but the effectiveness of both adults participating increases greatly as the size of the brood becomes larger.

There is evidence that the nestling period of the house wren is shorter for small broods which are fed more frequently, than for large broods. This relation has also been demonstrated for violet-eared hummingbirds *(Colibri thalassinus)* by H. O. Wagner (1945) and for the paradise flycatcher *(Tchitrea perspicillata)* by Moreau (1947). Karplus (1949) found that the nestling period of robins *(Turdus migratorius)* in Arctic Alaska was reduced to 8.8 days compared with 18 days which is common for temperate regions. He correlates the shorter nestling period of Arctic birds to their being fed for 21 hours per day rather than 14 to 15 hours per day farther south.

On the other hand, Paynter (1949) found no relation between nestling period and size of brood in the herring gull, but this would hardly be expected since he found no difference in the rate at which each young was fed. In Moreau's (1947) study of nine species, the paradise flycatcher, already referred to, was the only one that showed a relation between the size of the brood and the length of the nestling period. Although no substantiating data are presented, Moreau suggests that although large broods may leave the nest after the same nestling period as small broods, they may weigh less at this time. Lack and Silva (1949) found in the European robin *(Erithacus rubecula)* that undernourishment caused a decrease in the weight of the birds at the time of leaving the nest and that the nestling period was not prolonged. Lees (1949) records that in this species broods of four or five sometimes average greater in weight than broods of either two and three or six and seven. Gibb (1950) found in *Parus major* and *P. caeruleus*, however, that individuals in large broods averaged less in weight than individuals in small broods. It would seem, therefore, that individual nestlings in large broods may often receive less food than individual nestlings in small broods. As a consequence their growth in weight is retarded. This may result in either a prolonged period in the nest or in a lower weight, if the nest is vacated at the normal time. There are characteristic differences between species in the manner in which these variations occur.

Koskimies' (1950) studies on the swift, *Apus (Micropus) apus*, are of interest in this connection. The nestling period in this species varies between extremes of 33 and 56 days dependent on the weather, although it is more usually 40 to 43 days. This great variability is due to the rate of feeding the young and consequently the time required for them to attain normal final weight being directly correlated with air temperature.

V. Evolution of Parental Care

Introduction

The foregoing analyses of details in the parental care of several species of birds demonstrate that important variations in behavior pattern exist. One immediately wonders how these variations in behavior came about and their relation to each other. Perhaps they show a phylogeny in the same manner as do structural characteristics of the body. Possibly, different behavior patterns of parental care develop in different environmental situations.

Curiosity in regard to these possibilities led to a summarization of the literature on the known parental behavior for the bird families of the world. This has been no small undertaking, but I have had the help of various assistants, particularly Dr. Frank A. Pitelka, Dr. J. Murray Speirs, and Dr. Ben J. Fawver. Attempt was made to cover completely the literature on North American birds. A systematic search was made through all important journals and other available literature as far back at least as 1930 for the rest of the world. For still earlier data on foreign birds, reliance has been placed on the summaries of Witherby *et al.* (1938-1941), Niethammer (1937-1942), Groebbels (1932-1937), Stresemann (1927-1934), and Knowlton (1909). For North America the summaries of Burns (1915) and especially Bent (1919-1950) have been most helpful. The present summary should bring information on parental care up to date to the year 1950. At this point, we wish to make special acknowledgment of the splendid studies of Alexander F. Skutch on Central American birds, of R. E. Moreau on African birds, and of L. E. Richdale on marine birds, which in many instances have been the only sources of information for some of the less widely distributed families. I wish also to acknowledge the special help given by Mrs. Margaret M. Nice in correcting incubation periods given in Table 51 as a result of her thorough review of the literature on this problem.

The most critical information in establishing the parental behavior pattern for a species or for a family has been the share of the sexes in nest building and incubation, the length of attentive periods on the eggs, and the care of the young. For many families the information is very general. For families of higher phylogenetic rank the information is both more complete and more detailed. Data on length of time required for nest building, number of eggs laid, length of the incubation period, and the length of the nestling period are compiled mainly for those species where information is available on parental care, and usually, then, only when given by the author in his particular study. This should render correlations between these two sets of factors more trustworthy than if the compilation were of a more general sort. Furthermore, to render such a general compilation of greatest value one would need to distinguish differences due to race, latitude, climate, seasonal and yearly variations, and other factors which are extraneous to the present objectives. Incidentally, topics not touched on at all in the present work are the roles of the two sexes in the selection of nest sites (Nethersole-Thompson, 1943) and in nest sanitation (Blair and Tucker 1941, Tucker 1941).

The term "nestling period" rather than fledgling period will be used to designate the time that the young bird remains in the nest (Moreau 1946). There seems to be considerable confusion as to the use of "fledgling period," since "almost as much development toward complete fledging takes place after the nest is quitted as during the stay in it" (Ryves 1944). Fledging commonly means to become fully feathered and able to fly, but this more often than not fails to coincide with the time the young bird leaves the nest.

We have used Peters' *Check-List of Birds of the World* (1931-1948) for arranging and classifying the data on nonpasserine species, and we have similarly used Wetmore's *A Revised Classification for the Birds of the World* (1951) for the Passeriformes. Nomenclature follows Peters for the orders below the Passeriformes, and Witherby *et al.* (1938-41) and the A. O. U. *Check-List of North American Birds* (1931), along with its later supplements in *The Auk*, for the Passeriformes. When the name given by the author of a paper does not agree with these authorities, it is shown in parentheses, so that there should be no confusion concerning the species concerned. Observations are included on all living orders of birds except the Coliiformes, although the information available on some groups is scant.

Comparative psychologists commonly organize their information in an evolutionary sequence (Washburn 1923; Warden, Jenkins, and Warner 1934). Likewise, there have been attempts to outline the stages in the evolution of certain types of behavior (e.g., Allee 1938). Nevertheless, the actual tracing and analysis of behavior patterns as they develop from one group of animals into another have not been frequent. This has been done for social insects by Wheeler (1928), and Emerson (1938) has been able to do this for termites, using the nest structures in these latter insects as the morphological expression of behavior patterns. Emerson found the nest-forming behavior to be predominantly an inherited species pattern, and sequences of species patterns indicated evolutionary progress within the genus or related genera that could be correlated with the known morphological evolutionary relationships of the species. Astonishing examples occurred of adaptive modification of the nests together with convergent evolution of nest structure in certain environments which gave evidence of the force of selection upon inherited patterns. K. Lorenz (1941) and Delacour and Mayr (1945) have used behavior patterns as evidence for showing the proper relations and classification of the Anatidae.

The objectives of this study are to trace the evolution of the behavior pattern concerned with parental care through the class, Aves; to attempt to find underlying trends that will enable us better to correlate the behavior of related species; and to interpret the forces and influences that were and are effective in bringing about the patterns as we now see them in the various groups.

SUPERORDER: PALAEOGNATHAE; ORDER: STRUTHIONIFORMES

Family: STRUTHIONIDAE. Watson (1905) has described the nesting behavior of captive ostriches, *Struthio camelus,* in Arizona. The nest is a round hole in the ground which the male scoops out with his feet. At first the female may not take to the nest but may lay her eggs on the ground, whereupon the male will roll them into the nest. Generally, after the male has put three or four eggs into the nest, the female will lay there. In about thirty days she will lay twelve to sixteen eggs and will commence incubation. The incubation period is about 42 days. The male takes a prominent part, covering the eggs 15 or 16 hours a day. He usually goes on the nest about 1700 and remains until 0800 or 0830 hours the next morning; the female takes her turn during the day. According to Schneider (1949), the male does all the incubation. The male usually begins sitting three or four days before the female stops laying. If the weather is cold during the laying period, the male may often be found covering the eggs at intervals during the night. The birds are also very watchful in the warm season to prevent the eggs from becoming overheated by the sun. Often one of the adults will be found sitting on its ankle joints with both wings extended to shade the eggs. At the time of hatching, the parent bird is described as cracking the shell with its breastbone and sometimes taking the young bird by the head and pulling it out. Sometimes three or four days elapse between the hatching of the first and last eggs in the set. During this time one of the parents takes care of the precocial chicks while the other is attentive to the nest.

ORDER: RHEIFORMES

Family: RHEIDAE. Headley (1895) states that the female rhea, *Rhea americana,* lays a great number of eggs and that several females may lay in one nest. Adams (1908) noted that a captive female laid every three days. When a certain number of eggs have accumulated, one of the males takes over, and the female starts another nest. Incubation requires five or six weeks. The male not only does all the incubating but also takes care of the precocial young. Portielje's (1925) observations on captive birds showed that the male began incubation at one nest after the female had laid her fourth egg. The male occasionally left the nest to drink and feed during the middle of the day, and while the male was away the female was seen visiting the nest.

ORDER: CASUARIIFORMES

There are two families of living birds in this order. Detailed information on the nesting behavior of Casuariidae is not available, but supposedly only the male incubates.

Family: DROMICEIIDAE. The behavior of captive emus, *Dromiceius n. hollandiae,* has been studied by Crandall (1929) and Fleay (1936), and birds under natural conditions have been studied by Gaukrodger (1925). Sometimes two or three females will lay in the same nest, and there may be seven or eight eggs. The male incubates, beginning with the last egg, and he rarely leaves the nest. The incubation period is 58 to 61 days. The male also cares for the young.

ORDER: APTERYGIFORMES

Family: APTERYGIDAE. The most complete information on the kiwi, *Apteryx sp.,* was obtained by Robson (1948) from a pair of birds which he held captive several years. This species under natural conditions excavates a burrow for nesting. Robson states that both sexes dig, not just the female as is frequently stated in the earlier literature. The male bird, however, does almost all of the nest building.

The female laid two to five eggs in different years, but apparently not more than three were incubated at one time. The regular incubation period was found to be 75 days, although 77 days may be required for the first egg in a two-egg set. In one instance, the female sat on a freshly laid egg for 3 days, going out for food only at night. The male took exclusive charge of incubation thereafter. The second egg was not laid until 11 days after the first. The male incubates steadily, and may not go off the nest for a week at a time. When he is inattentive he covers the eggs, and when he returns he brings additional nesting material.

The chick is precocial at hatching, but its feathers do not become free of a slimy material for 4 or 5 days, and it does not leave the nest until the sixth day. During these 6 days the male blocks off the opening to the nest cavity and takes exclusive charge of the young. The chick loses weight while confined to the nest, but when it becomes free it eats an enormous amount, both day and night. The old birds feed only at night.

ORDER: TINAMIFORMES

Family: TINAMIDAE. According to Seth-Smith (1907) and Daglish (1930), the male tinamou takes charge of the eggs as soon as they are laid and incubates them. His mate goes off to court another male, only to leave him in due course with another potential family. The female tinamou is more brightly colored than the male, and the usual sexual courtship role is reversed. Beebe (1925) found an average sex ratio of four males to one female in *Crypturellus (Crypturus) variegatus.* No nest is made except for a slight depression on the forest floor. In this species the female, after courting the male, lays a single egg and then leaves the male to do all the incubating. The incubation period is about 21 days, and the young bird leaves within a day after hatching. The male takes care of the chick. Very soon, however, he may start incubating another egg, and this cycle may continue even for a third egg. Seth-Smith (1907) found *C. tataupa* and *Calopezus elegans* also polyandrous under aviary conditions. The behavior pattern in *Tinamus* is different in that the male incubates only one set, but this may contain from four to twelve eggs.

SUPERORDER: NEOGNATHAE; ORDER: SPHENISCIFORMES

Family: SPHENISCIDAE. Richdale has made detailed studies of the penguins, *Eudyptula minor* (1940), *Megadyptes antipodes* (1941b, 1949b, 1951), and *Eudyptes sclateri* (1941a); Bagshawe (1938) and B. Roberts (1940b) have studied *Pygoscelis papua* and Levick (1914), *P. adeliae.* Murphy (1936) has summarized information on several species. The group as a whole is very colonial in its nesting behavior, although in some species (*M. antipodes,* two species of *Eudyptula,* and perhaps others) the nests are somewhat scattered. Both sexes aid in nest building, and the nest may be composed of debris or stones or it may be a burrow in the ground. Usually two eggs are laid within 2 to 5 days. Incubation is shared by both sexes and may begin with either the first or second egg. The incubation period varies from 5½ to possibly 8 weeks in different species. Attentive periods between 6 and 12 hours are reported in *Spheniscus magellanicus, S. demersus,* and *Eudyptes sclateri,* but between 1 and 5 or more days in *Eudyptes crestatus, Eudyptula minor, Megadyptes antipodes, Pygoscelis papua,* and *P. adeliae.* Bagshawe (1938) found the male *P. papua* on the nest for periods of 1 to 2 hours and the female for 3 to 14 hours before the first egg was laid, both sexes on for periods of 5 to 15 hours between the laying of the first and second eggs, and for periods of 6 to 31 hours after the second egg was laid. In *P. adeliae,* Levick (1914) reported the female on the egg for 13 days followed by the male for 14 days, but the accuracy of his recognition of the sexes has been questioned.

After hatching, the young are brooded for 2 to 4 weeks and are fed once or twice a day. The nestling period varies from 8 to 16 weeks. The young are constantly guarded during the daytime for only part of this period—6 to 7 weeks in *M. antipodes,* 4 to 6 weeks in *E. minor.*

In several species, such as *Aptenodytes patagonica, Pygoscelis adeliae, P. papua,* and *Eudyptes crestatus,* a communistic arrangement appears to develop for the care of the young as they get older. From 12 to 20 young birds are grouped together into "crèches" and are guarded and shepherded by a few adult birds. This permits both parents of many of the pairs to hunt food at sea at the same time. When the parents return, it is uncertain whether they recognize and feed only their own young, but they may come back each time to the same area. In *Aptenodytes forsteri,* the communistic system is different in that there appears to be a surplus number of broody adults in the colony. No sooner does a parent leave its egg or young than a scrimmage takes place between many free adults to determine which will have its turn at caring for it. Thus old birds, other than the two parents, take turns at attending the egg and chick. Richdale (1951) questions the whole concept of crèches: He believes that the parents feed only their own young and that the extra adult birds present are nonbreeding individuals.

Order: Gaviiformes

Family: GAVIIDAE. Surprisingly little attention has been paid to the nesting behavior of loons or divers. A nest is built and two eggs are laid with an interval of at least two days between them; incubation begins with the first egg and lasts 28 to 30 days. Both sexes usually alternate at incubating and taking care of the precocial young (Bent 1919, Witherby *et al.* 1940), but in *Gavia (Colymbus) stellata,* Van Oordt and Huxley (1922) and Keith (1937) found only the female on the nest.

Order: Colymbiformes

Family: COLYMBIDAE. Huxley (1914) found in the grebe, *Colymbus (Podiceps) cristatus,* that the nest is built in a few hours. Both sexes took part, averaging between them more than two loads of weeds to the nest every minute, maintaining this rate for a half hour or an hour at a stretch. Three to seven eggs make up a set in various species. Sometimes two days elapse between consecutive eggs, and incubation commonly begins with the first egg (Niethammer 1938). Both sexes alternate at incubating. Deusing (1939) found in *Podilymbus podiceps* that the male's attentive periods on the eggs averaged 29 minutes and the female's 40 minutes. The eggs were left unattended an average of only 8 minutes at a time, and were usually covered with vegetation. The female continued to add nesting material through the incubation period. Witherby *et al.* (1940) record that in *Colymbus auritus* the sexes were observed changing on the eggs at intervals of four to five hours. In *Colymbus (Podiceps) nigricollis* the interval is one to three hours (Groebbels 1937), in *Colymbus (Podiceps) ruficollis* about 40 minutes (Hartley 1933) or 20 to 30 minutes (Mountfort 1934). The incubation period in several species appears not to have been accurately determined for natural conditions, but it is believed to be 21 to 23 days; Harrisson and Hollom (1932) give it as 27 to 29 days in *C. cristatus;* Mountfort (1934) found it very variable, 18 to 26 days in *C. ruficollis.* The young grebes leave the nest very soon after hatching and are attended by both parents. Probably the female is somewhat more solicitous in their care, especially as they grow older. Bird (1933a) observed that young *Colymbus ruficollis* would return to the nest until almost fully fledged. E. Ashby (1933) and Littlejohns (1936) give additional observations on this species.

ORDER: PROCELLARIIFORMES

Family: DIOMEDEIDAE. Richdale's (1939, 1942a, b) observations on the royal albatross, *Diomedea epomophora,* indicate a very slow rhythm of nesting behavior. The birds breed only every other year unless there has been a nesting failure. Both sexes aid in the building of a simple grass nest. One egg is laid. Both sexes incubate with very long attentive periods varying from 1 day to as long as 14 days. The average length of 43 attentive periods that were measured (30 given by Richdale 1942b: 253; 13 more obtained through correspondence with him) is 5.3 days. The incubation period is 78-80 days. The chick may require 3 days to get out of the shell. The young bird is fed daily by regurgitation in its very early days, even though the parent may not have left the nest for several days. The usual rate of feeding for the first three months is twice per week, once by each parent. The chick is guarded and brooded for 33 to 42 days after hatching by one or the other parent in attentive periods that average 3.4 days, a little shorter than during incubation. When the feathers begin to grow, the young bird is fed five times a week and may be left alone for long periods of time. Considerable food is given at a time, often 1.5 pounds; occasionally up to 6.5 pounds when both parents feed it. Feedings take place during the daytime. The chick stays aground until its wings have reached an adequate length, which may be 229 to 251 days after hatching. When fledged, during the last two weeks the feeding rate is again reduced to twice per week. Probably the nesting behavior of other albatrosses is similar. In *D. bulleri,* Richdale (1949a) records that nest building may be performed by either sex but usually by the male. The first attentive period of the female after the egg is laid averages 5.9 days, but subsequent periods by both sexes are equal and average 10.8 days. The longest observed period of a female was 24 days.

Richdale (letter) cites a still more remarkable record for the Laysan albatross (*D. immutabilis*) where the average attentive period subsequent to the first span by the female from 64 records is 21.8 days, range 5 to 32 days!

Family: PROCELLARIIDAE. In the subfamily, Fulmarinae, Richter (1937) found the incubation period of the fulmar, *Fulmarus glacialis,* to be 57 days. Each parent sits on the one egg in its shallow nest for attentive periods that average 1 to 2 days in some cases or 4 days in others. The young are brooded continuously for two weeks but are largely left alone in the nest after 5 weeks. The nestling period is 57 days, and the young is fed once each day until nearly ready to fly. In a personal communication, Richdale states that the young is fed during the daytime.

Richdale (1944b, c) found the incubation period of the one egg in the nest burrow of *Pachyptila turtur* and *P. forsteri (vittata)* to be 56 days and the nestling period about 49 days. The attentive periods for the two parents alternating on the nest are 6 or 7 days long. During the first 3 to 5 days after hatching, the young are sometimes fed during the daytime, but after that, only at night. Occasionally both parents feed the chick on the same night, but some nights are skipped by both adults. Considerable food is regurgitated each time, and the chick may sometimes receive an amount equal to its own weight.

In the subfamily, Puffininae, Lockley (1942) has studied the Manx shearwater, *Puffinus puffinus,* Richdale (1944a, 1945b) the sooty shearwater, *P. griseus,* and Glauert (1946), the little shearwater, *P. assimilis.* These birds nest in underground burrows which both sexes excavate. One egg is laid, and the incubation period is 51 to 58 days. The male and female take turns incubating at intervals of about 2 days in *P. assimilis* and 4 days in the other two species, although an occasional attentive period in *P. griseus* may be as long as 13 days. Brooding is required for only a very few days. For the first 3 to 7 days after hatching, the young chick may be fed during the daytime, but after that, only at night as these birds, like *Pachyptila,* are largely nocturnal in this habit. In *P. assimilis* the young bird is fed usually every second night. The adult birds spend the daylight hours in activities far out at sea. Sometimes both parents may feed the young on the same night; then again the bird may not be fed for periods up to 10 nights. Individual feedings are considerable and the young chick may sometimes consume its own weight of food. The young bird is usually not fed for 7 to 13 nights before it finally takes flight, 70 to 95 days after hatching.

Family: HYDROBATIDAE. Of the storm petrels, *Oceanites oceanicus* has been studied by B. Roberts (1940a), *Hydrobates pelagicus* by Lockley (1932), *Pelagodroma marina* by Richdale (1943-44), and *Oceanodroma leucorhoa* by Gross (1935) and Ainslee and Atkinson (1937). Both sexes participate in excavating the nesting burrow, although in Leach's petrel, *O. leucorhoa,* the male takes the major part and about 3 days are required. Only one egg is laid and incubation may begin immediately or after a lapse of 24 hours. Both male and female incubate in relays of 1 to 5 days. Nest relief occurs at night. There may be periods as long as 4 days when neither bird is on the egg; on the other hand, one parent may occasionally be attentive for as long as 9 continuous days. The incubation period is between 38 and 50 days long. After the young bird hatches, it is brooded for only 1 to 5 days. The down on these chicks is long. While brooding, the chick may be fed during the day as well as at night, but thereafter the parents usually visit and feed it only at night. Feeding is somewhat irregular, as frequently the young bird may not be fed for several nights in succession, especially near the end of nest life. In *O. leucorhoa* the average rate is once per night. The nestling period lasts about 8 weeks.

Family: PELECANOIDIDAE. In the diving petrel, *Pelecanoides urinatrix,* Richdale (1943, 1945a) found both sexes digging the burrow. He estimates the incubation period to be 8 weeks with the male and female relieving each other nightly. After hatching, the young bird is fed nightly and often also in the daytime during the 7- to 15-day brooding period. This longer brooding period may be correlated with shorter down than in the storm petrels. After brooding is over, one or both parents feed the chick only at night, until it is ready to leave the burrow after about 54 days from hatching.

Summary. Both sexes construct the nest, incubate, brood, and feed the young. Only one egg is laid, and the incubation period is from 7½ to 9 weeks except in Diomedeidae where it is over 11 weeks. The young bird is brooded for only a few days except in Diomedeidae, but it stays in the nest 7 to 12 weeks, except in Diomedeidae where it may not leave until eight months old. Average attentive periods during incubation commonly vary from 1 to 7 days in length. After the young bird hatches it is usually fed by both parents at night except in Diomedeidae and Fulmarinae and possibly some petrels, but there is considerable irregularity. These species are largely nocturnal in their nesting activities and spend the daylight hours out at sea. The slower rhythm of the larger Diomedeidae is evident as the young is fed only two to five times per week. This group is also more diurnal in its activities, so in several ways its behavior does not conform exactly to the procellariiform pattern.

Order: Pelecaniformes

Suborder: PHAETHONTES; *Family:* PHAËTHONTIDAE. In the yellow-billed tropic-bird, *Phaëthon lepturus,* a single egg is laid and both sexes alternate in its incubation (A. O. Gross 1912). An adult was once observed feeding its incubating mate, and apparently this interfeeding of the adults also occurs in *P. aethereus* (Bent 1922). Twenty-eight days are required for incubation, and the young bird remains in the nest for 62 days. The adult birds spend considerable time with the young for the first 10 days, but after 20 to 25 days they feed the young two or three times in the early morning and do not appear again until the next day.

Suborder: PELECANI; *Superfamily:* PELECANOIDAE; *Family:* PELECANIDAE. The pelicans lay two or three eggs. Incubation has been estimated at 4 to 6 weeks. Both sexes share the incubating duties, and there is a ceremony of nest relief (Bent 1922). The young stay in the nest for 2 to 5 weeks. According to Murphy (1936), the young of *Pelecanus occidentalis* may be fed at any hour but particularly between 0700 and 0800 hours, shortly before noon, and during the two hours before sunset. The young of *P. conspicillatus* become gregarious as soon as they leave the nest, occurring in flocks of 10 to 50 birds (Macgillivray 1923).

Superfamily: SULOIDEA; *Family:* SULIDAE. In the boobies, *Sula,* and in the gannet, *Morus bassana,* only one egg is laid, or a second may be deposited after an interval of several days. Both sexes share nest building, incubation, brooding, and feeding the young. Griffin and Hock (1949) record that the attentive period on the eggs in *Morus* is 24 hours, with variation between 7.5 and 30 hours. One bird, whose mate was removed, stayed on the eggs for 3 days. As nests of *Sula* are often fully exposed to the sun, incubating and brooding may be more a matter of keeping the eggs and young cool through shading than of keeping them warm (Murphy 1936). At night, the mate of the brooding *Sula* stands alongside the nest. After the young bird becomes too large to brood, it may pass the night on the ground between the two parents (Chapman 1908). The length of incubation is probably 42 to 45 days. The period that the young are fed by their parents is as long or longer. The young of *Morus* are fed more frequently in late afternoon, and not often during the middle of the day (Wodzicki and McMeekan 1947). Some 10 or more days before the young leave, the parents stop feeding them, and apparently the lack of food is a stimulus for the birds to begin shifting for themselves.

Family: PHALACROCORACIDAE. In the double-crested cormorant, *Phalacrocorax auritus* (H. F. Lewis 1929, Mendall 1936), the males bring nest material, and the females shape it into a nest in from 2 to 4 days. Usually one egg is laid each day, until the set of about four is complete. Incubation may begin with the first egg or irregularly with any subsequent egg. The incubation period is 24 to 25 days, the young are brooded until the third week after hatching, and fed until they are 5 or 6 weeks old. Both sexes incubate, alternating on the nest during the day at one- to three-hour intervals. Both sexes brood and feed the young. Two or three young are fed on each trip with trips about once every hour.

Family: ANHINGIDAE. Not much is known about the nesting of *Anhinga anhinga.* The four eggs are laid at irregular intervals and both sexes take part in their incubation. Both male and female care for the young.

Suborder: FREGATAE; *Family:* FREGATIDAE. Both sexes of *Fregata magnificens,* the man-o'war-bird, share in nest building, incubating the one egg, brooding, and feeding the young. There is no information, however, on the length of the attentive periods (Murphy 1936).

Summary. The nesting cycle of these colonial birds is long, since it frequently extends over three months. There is considerable uniformity in behavior in that both sexes share more or less equally in all the duties of nesting. In the *Phalacrocorax* the attentive period is only 1 to 3 hours long while incubating, but in *Morus* it may be 24 hours long. One to four eggs are laid, separated often by intervals of several days. It is usual for most of the brood to be fed on each trip. These trips may be as frequent as once per hour in *Phalacrocorax,* but as the young get older they tend to be limited more and more to early morning and late afternoon.

ORDER: CICONIIFORMES

This is a varied order that has been divided into four suborders. The Ciconiae is the largest and is again subdivided into three superfamilies each with a single family. No data are available for the suborder Balaenicipites, with its single family, nor for the family Cochleariidae of the Ardeae.

Suborder: ARDEAE; *Family:* ARDEIDAE. The herons or Ardeinae commonly nest in colonies. Both sexes take part in nest building. Three to five eggs are laid, usually at 2- or 3-day intervals. Incubation begins with the first egg. Estimates as to the length of incubation vary from 18 to 28 days, but the exact time is not known for many species. Both sexes alternate at incubating at intervals of two to six hours during the day, and an elaborate ceremony has developed when one sex relieves the other. Probably the female is on the eggs at night. Brooding may last 2 or 3 weeks, and the young may remain a few weeks longer before leaving. Both sexes bring food to the young at the rate of 6 to 14 times per day. Feeding is most active in early morning and evening. *Nycticorax, Nyctanassa,* and *Ardea herodias* are more or less active at night as well as during the day (Bent 1926, Witherby *et al.* 1939, Gersbacher 1939, Steinfatt 1934b, 1935, 1939e, Allen and Mangels 1940). The rhythm in the African green heron, *Butorides striatus (atricapilla),* is faster than above outlined. Cowles (1930b) states that the incubation period is about 18 days, the nestling period is only 2 weeks, and the young are fed three times per hour at first but that later this rate slows down. Hindwood (1933), however, found the incubation period of *Butorides javanica* to be 21 days and the nestling period about 4 weeks. Wheelock (1906) observed a feeding rate in *Butorides virescens* of about three times per hour for young 7 days old but only for the early morning and evening hours.

The behavior of bitterns, Botaurinae, is similar to that of herons. The four or six eggs are incubated by both sexes in *Ixobrychus* but apparently only by the female in *Botaurus* (Bent 1926, Groebbels 1937). Groebbels (1935) recorded four attentive periods for the female *Ixobrychus minutus* averaging 2 hours 23 minutes and five periods for the male averaging 1 hour 6 minutes. Incubation in this species lasts 16 to 17 days, and in *Botaurus stellaris*, 25 to 26 days. Young *Ixobrychus* may leave the nest in 7 to 12 days (Niethammer 1938). Young *Botaurus lentiginosus* stay in the nest for 14 days (Mousley 1939). Gabrielson (1914) found two young fed at the rate of 0.6 times per hour, but both young are fed on each visit of the adult. Niethammer (1938) records the nestling period of *B. stellaris* as 4 to 5 weeks, which seems very long.

Suborder: CICONIAE; *Superfamily:* SCOPOIDAE; *Family:* SCOPIDAE. Cowles (1930a) describes the nest and development of young of the hammerhead, *Scopus umbretta*, but does not tell much concerning their attentive behavior. It appears that both sexes are involved in various phases of nest life. The incubation period is about 21 days, and the young stay in the nest about 7 weeks.

Superfamily: CICONIOIDEA; *Family:* CICONIIDAE. According to Niethammer (1938) and Witherby *et al.* (1939), the nests of both storks, *Ciconia ciconia* and *C. nigra*, are build by both sexes, the male bringing most of the material and the female arranging it. The building of a complete nest may require 8 days. The three to five eggs are laid at 2-day intervals. Incubation begins with the first or second egg and lasts 30 to 38 days. In the former species the female incubates all night, while during the day, the male assumes the greater part of this duty. The two sexes alternate at one to four and a half hours (Nice 1933, Schüz and Schüz 1932, Schüz 1938). The nestling period is about 63 days. Both sexes brood and care for the young. In *C. nigra* the parents relieve each other at intervals of two and a half hours when the young are 3 weeks old. Five meals are brought to the young daily, two in the early morning and three late in the day. In *C. ciconia*, Schüz (1943b) found the feeding rate of young 5 to 15 days old to average 0.7 per hour but often with long intervals between consecutive feedings. Both sexes also incubate in *Jabiru mycteria* (Bent 1926).

Superfamily: THRESKIORNITHOIDEA; *Family:* THRESKIORNITHIDAE. Baynard's (1913) detailed study of the glossy ibis, *Plegadis falcinellus*, shows that both sexes aid in the construction of the nest which is added to throughout the incubation period. An egg is laid each day until three or four eggs are laid. Incubation does not start until a day after the last egg has been laid and lasts 21 days. The female sits on the eggs at night and until 0830 or 0900 hours in the morning. The male relieves the female for about six hours during the day. During the first 4 weeks after hatching, the adults feed the young 12 to 20 times per day. By the sixth week the young are leaving the nest during the daytime and feeding in the shallow water but returning to the nest to roost at night. The glossy ibis belongs to the subfamily Threskiornithinae.

The behavior of the roseate spoonbill, *Ajaia ajaja,* of the subfamily, Platoleinae, is very similar (R. P. Allen 1942). The average clutch is less than three eggs, probably one laid every other day, and the incubation period is 23 to 24 days. There is a ceremony at nest relief which occurs at least two or three times during the day. Incubation is not regular until the last egg is laid.

Suborder: PHOENICOPTERI; *Family:* PHOENICOPTERIDAE. Only one egg ordinarily is laid by flamingos, *Phoenicopterus ruber.* Chapman (1905) says that the two sexes exchange places on the eggs in the early morning and late in the afternoon. There is considerable irregularity as to which sex is on the nest during the daytime and at night. Bent (1926) indicates that the incubation period is 30 to 32 days. The young are brooded for 3 or 4 days and then they leave the nest. They are fed by the adults for about 2 weeks (Gallet 1948).

Summary. There appears to be considerable uniformity in attentive behavior in this order of colonial nesting birds. Both sexes share all phases of nesting duties. During incubation and brooding the sexes relieve each other with elaborate ceremonies at intervals of one to several hours. Feeding of the young is largely by regurgitation and all the young may be fed on each visit. The length of the incubation period varies greatly between species as does the nestling period.

ORDER: ANSERIFORMES

Quite a little general information is available for this order. In the family, Anatidae, of the Anseres, only the subfamilies, Plectropterinae, Cereopsinae, and Merganettinae cannot be included in the discussion, but they are small groups.

Suborder: ANHIMAE; *Family:* ANHIMIDAE. Stonor's (1939) observations on the nesting of the screamer, *Chauna torquata,* in a zoological garden are of interest here. Both sexes participated in nest construction and in incubation. Eggs were laid on alternate days, and there were as many as six eggs in a set. The female incubated from late afternoon, 1630 or 1730 hours, overnight or until 0900 or 1100 hours the next day, when the male took over for the rest of the day. There was a ceremony of nest relief. The incubation period was 6 weeks, and the young left the nest soon after hatching.

Suborder: ANSERES; *Family:* ANATIDAE. Swans, in the subfamily Cygninae, lay four to six eggs on alternate days in a nest which both sexes have been concerned in preparing. Incubation may not begin until the set is complete; it lasts 35 days or longer and is performed chiefly by the female. Ruthke (1941) observed incubation to begin with the fifth of a seven-egg set in *Cygnus olor.* Groebbels (1937) records both sexes incubating in *Chenopis (Cygnus) atrata* and *Cygnus melanocoriphus.* Both sexes care for the young, and the family group may retain its identity for several months (Bent 1925, Witherby *et al.* 1939).

With the geese, Anserinae, the set in *Branta canadensis* is commonly composed of four to six eggs, laid on consecutive days or at average intervals of 1.5 days. Incubation begins when the set is complete and lasts from 24 to 28 days in various species. The female makes the nest, but the male sometimes will bring material for it. Only the female incubates, although Soper (1942) believes that the male may take part in *Chen caerulescens.* In nearly all species the male remains close to the nest and is attendant on the female during incubation. Both adults care for the young. During the nonbreeding season, geese commonly feed during early morning and late afternoon and roost at night (Bent 1925, Kortright 1942, Kossack 1950, Manning 1942, Sutton 1932, Witherby *et al.* 1939).

Little is known concerning the nesting behavior of the tree ducks, Dendrocygninae. According to Bent (1925), *Dendrocygna autumnalis* commonly nests in tree hollows, but *D. bicolor* mostly nests on the ground. The former species has 12 to 16 eggs per set, but the number in the latter species may reach 36. There is some possibility that several females may lay in the same nest. Delacour and Mayr (1945) state that the male shares in incubation; in fact, in *D. viduata* and *D. bicolor* he may do the greater share. J. C. Phillips (1922) gives the incubation of the former species as 28 to 30 days. Both sexes take care of the young.

In the surface-feeding ducks, Anatinae (Bent 1923, Kortright 1942, Girard 1939, 1941, Bennett 1938, Munro 1944, Witherby *et al.* 1939), the female prepares the nest, commonly lays 7 to 12 eggs for a set, depositing one each day, and begins steady incubation when the set is completed. The incubation period varies between 21 and 28 days. The female does all the incubation, although rarely a male has been known to take a turn. Usually the male deserts the female after incubation gets well underway so that the female must care for the young alone. In *Anas (Querquedula) cyanoptera, Anas crecca, Aix, Spatula, Tadorna,* and *Casarca,* however, the male is more faithful and may aid the female in caring for the young. The same has been observed for *Anas platyrhynchos* (Lloyd 1937). Bennett (1938) says that the female blue-winged teal, *Anas (Querquedula) discors,* during incubation is inattentive once or twice a day for 20 minutes to two hours around 0700 and 1900 hours. Each time she leaves she covers the eggs with nest down, and during the last 48 hours of incubation may not leave at all. Girard (1941) found that the female mallard, *Anas platyrhynchos,* had a feeding period of about two hours between 0630 and 0830 hours and again in the afternoon or evening. During the migratory and wintering seasons, these ducks along the Illinois River in Illinois roost on the water during the day and feed during the night. D'Ombrian (1944) had black ducks *(Anas superciliosa)* nesting under captive conditions. The female made the nest and took full care of the eggs and young. She left the eggs for average inattentive periods of 20.6 minutes, 0.9 times per day. There were no regular times when she was inattentive, but they were equally divided between morning and afternoon. Four months after the young hatched, the female lost interest in them. Frank Bellrose (personal communication) has observed two inattentive periods, in early morning and late afternoon, in the wood duck, *Aix sponsa. Heteronetta atricapilla* is unique in that it does not build a nest and has become entirely parasitic, laying its eggs in the nests of a variety of other species (Phillips 1925).

The behavior of the diving ducks, Nyrocinae, is similar to Anatinae (Bent 1925, Kortright 1942, Witherby *et al.* 1939). Sets of eggs are often smaller, sometimes only five or six eggs. The incubation period is commonly 25 to 28 days. The male usually deserts the female soon after the eggs are laid, or at least by the time the young hatch. Murphy (1936) states, however, that in *Tachyeres branchyptera* both sexes lead the brood to sea, forming a family group which does not break up until autumn. In the eider, *Somateria mollissima,* the female may be inattentive for about two hours soon after daybreak (A. O. Gross 1938a), but some individuals apparently stay on their eggs continuously (Goodwin 1948). Gudmundsson (1932) maintains that during her early morning inattentiveness the female drinks and bathes but does not eat throughout the period of incubation. *Bucephala (Glaucionetta) islandica* females are to be observed feeding between 0900 and 1100 hours. Low (1945) used an itograph arrangement on the redhead, *Nyroca americana,* and found that the eggs were unattended during the laying period and that incubation usually began within 24 to 48 hours after the last egg was laid. Inattentive periods of the incubating female came at irregular intervals during the day and night. The birds left the nest from 3 to 26 times, averaging 6 times, during the 24-hour period. Prevailing temperatures affected the time on and off the nest; as much as seven hours per day were spent off the nest for first nests and nine hours for later nests. Hochbaum

(1944) also found in the canvas-back, *Nyroca valisineria*, that the female had no fixed hours off the nest. Short rest periods during morning and evening were regular, but the female also left at intervals during the day. Departures became less frequent as incubation proceeded. All species cover their eggs with down when they leave the nest.

The ruddy duck, *Oxyura jamaicensis,* represents the subfamily, Oxyruinae. According to Low (1941), the nests are built by the female. About eight eggs are laid, and the female may begin incubation before the last egg is laid. The incubation period is 25 or 26 days. Although the male does not incubate, he does not desert the female and aids in the raising of the brood (Bent 1925). According to Friedmann (1932), ruddy ducks deposit eggs in the nests of other species more frequently than do other ducks and may be in the process of evolving a parasitic nesting behavior pattern.

The behavior of Merginae is similar to that of other ducks. The 7 to 12 eggs are incubated by the female. Niethammer (1938) records the incubation period as 31 to 32 days in *Mergus serrator* and *M. merganser*. Weber (1946) gives it as 34 to 35 days in *M. merganser*. In *M. serrator,* Törne (1940) found that on sunny days the female left the eggs between 0500 and 0600 hours, a short time about 0800 hours, and between 1100 and 1500 hours and again between 1800 and 1900 hours. On rainy days she left for a half-hour at 0500 and again at 0900 hours and for an hour at noon and at 1800 hours. The male accompanied the female during these inattentive periods.

Summary. There are four types of nests (Delacour and Mayr 1945): open nests on the ground, open nests raised above the ground on ledges or stumps, concealed nests on the ground under rocks or in holes, and nests located in tree hollows. One may suppose that originally the male and female shared the duties of nest building, incubation, and care of young, as in the Anhimidae, but in various groups the male has lost more or less of his attentiveness. In the Cyginae and Anserinae, he does not usually incubate; in the Oxyurinae and Merginae he is not concerned with nest building either; in the Anatinae he is beginning to lose interest also in the young birds after hatching, while in the Nyrocinae he commonly deserts the female during the incubation period. In his summary of parental care in the ducks, Phillips (1922) states that in "nearly all those species in which the female and the male have similar plumage . . . the males are very pugnacious and active guardians of the family. . . . There seems to be some rather important relation between the early desertion of the females by the males and the presence of an eclipse plumage. . . ."

The female restricts her inattentiveness to an hour or so in the early morning and late afternoon and to occasional shorter periods during the day. In Nyroca she is alternately attentive and inattentive several times throughout the day. Usually she covers the eggs with down on leaving the nest, and commonly she is accompanied by the male on her inattentive periods. Incubation does not usually begin until the set is complete.

Order: Falconiformes

Of the living members of this order, there is no pertinent available information on attentive behavior in the superfamily Sagittarioidae, nor in some of the subfamilies. There are two suborders.

Suborder: CATHARTAE; *Family:* CATHARTIDAE. Two eggs constitute a normal set in the vultures, *Cathartes* and *Coragyps*, and these are laid on consecutive days inside a hollow log or cave or on the ground in a sheltered spot. Incubation begins with the second egg and lasts 39 to 56 days. The young stay in the nest or in its vicinity for 8 to 10 weeks. Both parents take part in incubation and feeding the young. Coles (1944) states that even when incubation is at its height, both birds may be simultaneously inattentive for periods in the morning and evening. E. S. Thomas (Bent 1937) observed in *Cathartes* that there were 17 feeding periods during nearly twelve hours of observation on one day.

Suborder: FALCONES; *Superfamily:* FALCONOIDEA; *Family:* ACCIPITRIDAE. The family is divided into nine subfamilies. In the Elaninae, the white-tailed kite, *Elanus leucurus*, has been intensively studied by Hawbecker (1942). Nest building requires about 7 days, both sexes participating, and at one nest the first egg was laid about 10 days after the nest was completed. Four eggs are laid on consecutive days, and incubation begins with the first egg. Incubation lasts 30 to 32 days, and both sexes take part. The male spends only a small share of time on the eggs, but he feeds the incubating female. The young are brooded by the female, and at first the male brings the food for both female and young, but when brooding is no longer required the female also searches for food. The young leave the nest in about a month but return to it for a time longer to be fed by their parents.

The best study in the Perinae has been of the honey buzzard, *Pernis apivorus* (Wendland 1935, Thiede 1938). Two eggs are laid nearly 2 weeks after the nest is ready; incubation begins with the first egg and lasts 30 to 31 days. Both sexes share nest building and incubation about equally; one attentive period of the male was at least three and a half hours. The young are brooded about 3 weeks, at first about equally by both sexes, but later more by the female. The young are fed wasp larvae, at first by regurgitation, later from the bill. Green leafy twigs are brought to the nest, and eggs or young may be covered with them during the absence of the adult (Thiede and Zänkert 1932a, Gentz 1935). The nestling period lasts 40 to 46 days.

In the kites, *Ictinia misissippiensis* (Sutton 1939) and *Milvus migrans* (Schuster 1936a) of the subfamily, Milvinae, both sexes share the incubation of the one or two eggs, although the male's share is irregular and sometimes questionable. Observations on *M. migrans* gave one complete attentive period of nine hours for the female and eleven hours for the male. In *M. milvus* (Niethammer 1938) the three eggs may be incubated entirely by the female, beginning with the first egg, and the male may bring her food. The nestling period is 40 to 50 days. The male supplies both the female and young with all their food during the first 14 days. He is especially active during the early morning hours (Thiede and Zänkert 1935). Skutch (1947a) observed both adults feeding insects to one young *Ictinia plumbea.* The feeding rate was very irregular, depending on the weather, but averaged 2.4 times per hour. This high rate is doubtless correlated with the type of food that is used.

In the European species of *Accipiter* of the subfamily Accipitrinae, the female is chiefly responsible for nest building and incubation, although the male may sometimes help. In *A. nisus,* Bal (1950) states that the ratio of the female to the male in nest-building activities is 9 to 1. In *A. gentilis* the male may relieve the incubating female four times daily (Niethammer 1938) for periods of one to two hours (Siewert 1933). The two to four or sometimes six eggs are laid at intervals of 2 or more days and incubated for 5 to 5½ weeks. Incubation begins before the set is complete. The nestling period is from 4 to 6½ weeks. The male brings most of the food for the young at first, but later the female also helps. In *A. nisus,* the male also feeds the incubating female who performs this duty alone (Siewert 1930). In this species, L. Tinbergen (1946) found an increase in number of trips to the nest with food from 2.1 per day when the young were 2 and 3 weeks old to 9.8 per day when they were 10 weeks old.

In the subfamily, Buteoninae, both sexes usually share in nest building, incubation, and care of young (Bent 1937). Two eggs per set are common, laid at intervals of 2, 4, or more days. Incubation begins with the first egg and in the smaller species lasts 28 days. In the eagle, *Haliaeetus leucocephalus* (Herrick 1934), it is 35 days and in *Aquila verreauxii* (Rowe 1947) and in *A. chrysaëtos* and *A. pomarina* (Niethammer 1938) it may be as long as 43 or 44 days. In *A. verreauxii* and *H. leucocephalus* the attentive periods are from one to three hours long. However, in *H. albicilla,* Schuster (1935) found the female incubating overnight until 0540 hours, the male on then until 0956 hours, after which the female stayed on the rest of the day. During an all-day watch at a nest of *B. buteo,* the male relieved the female twice for periods averaging about four hours each. In *A. chrysaëtos, A. pomarina* (Siewert 1932), *Aquila (Hieraäetus) fasciata* (Rivoire and Hue 1949), and in *Buteo jamaicensis* (*borealis*) and probably *B. lineatus,* the female takes much the greater share of the incubation duties but is brought part of her food by the male. In nearly 43 hours observation at a nest with two young *A. chrysaëtos,* food was brought five times by the female and seven times by male or at the rate of 0.3 per hour (H. A. Gilbert 1934). Stewart (1943) found the female alone feeding a brood of three *B. lineatus* which she did at intervals of one hour. In *H. leucocephalus* the average rate is 2.5 to 4 times per day, most usually before 0900 and after 1500 hours. Rowe (1947) records in *A. verreauxii* that during two different years a single nestling, 3 to 9 days old, was fed at rates of 0.47 and 0.33 per hour. Young eagles often stay in the nest 8 to 13 weeks, but in the smaller hawks the time may be reduced to 6 weeks.

In the marsh hawk, *Circus cyaneus (hudsonius),* of the subfamily Circinae, the female takes the greater share of nesting duties. Breckenridge (1935) found only the female incubating and brooding, although the male brought the young the greater part of their food. Other observers indicate that the male may occasionally incubate. He gives the incubuation period as 30 to 32 days. Witherby *et al.* (1939) and Haas (1939) record that in *C. pygargus* and *C. cyaneus* the incubating female is fed by the male. This takes place in the air away from the nest. The three or five eggs are laid at intervals of 2 or 3 days; incubation begins before the set is complete and it lasts 28 to 30 days. The nestling period is 5 weeks or longer. Hennings (1936) spent 73 hours observing the growth of five young in the nest, and during this time they were fed 77 mice and birds or at the rate of 1.1 per hour. Claudon (1935) observed only the male *C. pygargus* bringing food for the young. This he did at the rate of 1.1 per hour, when the young were small, but at the rate of 4.0 per hour toward the end of nest life. Thiede and Zänkert (1932b) observed four young *C. aeruginosus* fed about 0.6 times per hour by both sexes during the last 14 days of nest life.

In the subfamily, Circaëtinae, Niethammer (1938) states that *Circaëtus gallicus* lays one egg. The male relieves the incubating female one or two times daily, but she is chiefly responsible for incubation. The incubation period is 35 days and the nestling period very long, 9 to 11.5 weeks. The male may bring food to the nest for the young four times daily. Moreau (1945) found that one young *Terathopius ecaudatus* required nearly 19 weeks to fledge. When it was one month old, it was fed once every eight hours; during its last week in the nest it was fed three times as frequently. Only one adult was concerned in caring for this young.

The Pandioninae is represented by the osprey, *Pandion haliaëtus.* Both sexes participate in nest building. The male may take an occasional turn on the nest, but for the most part the female is responsible for the incubation duties, during which time she is brought food by the male. The two or three eggs may require as long as 35 to 38 days to hatch, and the young may remain in the nest for over 7 weeks (Siewert 1941). The male brings most of the food for the young which is fed to them at first by the female. Later both sexes bring food at a rate of two or three times a day (Bent 1937, Niethammer 1938).

Family: FALCONIDAE. In the subfamily, Polyborinae, Bent (1937) gives the incubation period of Audubon's caracara, *Polyborus cheriway,* as 28 days with both sexes sharing the duty.

In the Falconinae (Bent 1937, 1938, Witherby *et al.* 1939, Lawrence 1949b) three or four eggs are commonly laid at intervals of 2 or 3 days. In *Falco cenchroides,* however, Sharland (1931) observed that five eggs were laid in 6 days. Groebbels (1937) records that both sexes are involved in nest building in *Falco subbuteo* and *F. tinnunculus.* Incubation begins before the set is complete, lasts 28 to 31 days (Niethammer 1938), and is performed chiefly by the female. The nestling period commonly varies between 25 and 35 days (Niethammer). The male may take some part in incubation in *Falco subbuteo* (D. Nethersole-Thompson 1931), *F. peregrinus, F. columbarius, F. vespertinus, F. naumanni,* and *F. tinnunculus* (Groebbels 1937), but usually he is more concerned in supplying the incubating female with food. In *F. peregrinus,* he starts feeding the female during the laying period, alternates with her on the eggs at half-hour to five-hour intervals, takes some part in brooding, and feeds the female and the young again after hatching occurs (Schuster 1931a, 1932a, Gugg 1933, Demandt 1939, 1940). Labitte, Languetif, and Debu (1950) believe that in this species incubation does not start until the set is complete. In most species the male brings most of the food for the female and the young after hatching, and not until brooding is no longer needed does the female help in hunting food for the young (Beebe 1950). In *F. tinnunculus,* the male brought food to the incubating female about once every 2 hours 13 minutes, but when there were young he brought food once every 1 hour 24 minutes. Variation in number of young from two to four did not affect the feeding rate, but the tempo of feeding increased as the young got older. The female often left the eggs to get food from the male, and during these periods the male would sometimes cover them. The female brooded the young 7 to 10 days, and the young left when 28 to 32 days old (L. Tinbergen 1940). In observations that extended throughout the nestling life of *F. subbuteo,* Schuyl, Tinbergen, and Tinbergen (1936) found that when only insects were brought, both adults fed the young at the rate of 5.8 times per hour, but when larger prey, as small birds and mammals, were also brought, the rate decreased to about 1.2 per hour. The male fed insects directly to the young, but often gave larger prey to the female who then fed the young. Scholze (1933) did not observe any insects brought to the young, but birds were fed to them at intervals of two and a half to three hours.

Summary. Both sexes may participate in building the nest, incubating, and caring for the young. When both sexes incubate they commonly alternate in shifts of three to four hours, but in certain species there is only a single attentive period for each sex per day. The evolutionary trend is for the female to assume an increasing share of incubating and brooding and for the male to keep her supplied with food. Incubation usually begins before the set is complete, often with the first egg. The incubation period is commonly about 4 weeks long and the nestling period somewhat longer, in some species it is considerably longer. After hatching, the male commonly brings all the food to the female who takes what she needs and feeds the young. After the young become 2 or 3 weeks old, the female decreases her brooding and takes her turn at searching for food. Both sexes may then feed the young directly.

Order: Galliformes

There are two suborders: Galli and Opisthocomi. Very little information on attentive behavior is available for the latter group. Of the Galli, no data are available for the family Numididae.

Suborder: GALLI; *Superfamily:* CRACOIDEA; *Family:* MEGAPODIIDAE. The artificial incubation of their eggs practiced by the megapodes in this family is well known (Mayr 1930, Barrett and Crandall 1931). In *Alectura lathami* studied in the Melbourne Zoo, Fleay (1937) states that a mound of decaying vegetable material was built by the male. During rains the mound was opened at the top and a crater made to catch the water. The temperature of the mound varied between 29° and 35° C. Both the male and female appeared to test the temperature by digging a hole in the mound and inserting their heads. The male tolerated the female near the mound only while the eggs were being laid. The first egg was laid 18 days after the mound was started. The eggs were laid in depressions, 18 to 19 inches deep. A total of 18 to 24 eggs was laid, 2 or 3 days apart, with their small ends down. The incubation period was 9 to 10 weeks. The young birds hatched in an advanced stage and were able to flutter up into trees upon emerging from the mound. The male aided the young bird to escape by digging a hole in the mound where the chick was scratching its way out. Delacour (1935) has also compiled considerable information on this species.

According to Ashby (1922) and F. Lewis (1939, 1940), *Leipoa ocellata* builds its mound in the sun. The nest is composed of sticks and leaves mixed with sand. One or the other adult visits the mound daily, opening it up on sunny days and closing it on cool days so that heat is supplied partly by decaying vegetation, partly by solar radiation, and partly by the heated sand. The usual set of 10 eggs is laid in 18 to 20 days and requires at least 57 days to hatch. The young chick may require two hours to escape from the mound and is not assisted by the adults.

Pycraft (1910) records some mounds of very large size in other species, which may be the accumulation of several years' work or of more than one pair. He also described another type of incubator for *Macrocephalon (Megacephalum) maleo* in the use of burrows near hot springs or in black volcanic sand that absorbs solar radiation very readily. *Eulipoa wallacei, Megapodius eremita (brenckleyi),* and *M. pritchardii* have similar habits. Pockley (1937) and Sibley (1946) have described how *M. eremita* and *M. freycinet* use burrows in the side of active volcanos where the soil at one to three feet depth is noticeably warmer than at the surface.

It appears then that the birds in this family have lost their incubating and brooding behavior and have become specialized in the use of artificial incubation of various sorts: heat of decomposition of decaying vegetation, solar radiation, soil heated by volcanic action or hot springs. Armstrong (1947:42) makes the suggestion that artificial incubation evolved in this group out of the habit of throwing leaves and other debris over the eggs to conceal them when the adult bird left the nest unattended. This decaying humus from the moist tropical forest floor would have kept the eggs warm and been an aid to their incubation. E. Ashby (1922) believes that solar radiation was forced upon some species as a source of heat when the climate changed from a humid one that permitted development of a lush vegetation to a dry one that eliminated the obtaining of heat from decaying vegetation.

Family: CRACIDAE. Bent (1932) has summarized information on the chachalaca, *Ortalis vetula.* A small frail nest of sticks and leaves is built by both male and female at heights of four to ten feet in bushes and trees. Three eggs are laid, incubation lasts 22 to 24 days and is probably performed by the female alone. The young are precocial and leave the nest as soon as their down is dry.

Superfamily: PHASIANOIDEA; *Family:* TETRAONIDAE. Detailed accounts of nesting of ruffed grouse, *Bonasa umbellus,* are available (Bump *et al.* 1947, Edminster 1947). Nest building is by the female. The nests are merely hollows in the ground lined with whatever materials are available. There is then an interval of about a week before the first egg is laid. An average 11-egg set requires about 17 days for laying. Incubation is about 24 days and is performed entirely by the female. It does not begin until the last egg is laid, so all hatch about the same time. The female sits constantly except for 20- to 30-minute inattentive periods twice a day. These periods have been observed between 0400 and 0500, at 0950, at 1347, and between 1700 and 2000 hours. The early morning and evening hours are most characteristic. After hatching, the precocial young continue to be brooded and fed by the female alone. This lack of attentiveness by the male is also characteristic of *Dendragapus obscurus (fuliginosus)* and *Canachites canadensis* (Bent 1932). Walkinshaw 1948b) observed one inattentive period of a female off her eggs between 2043 and 2106 hours in the latter species.

Attentive behavior is similar in the ptarmigans, *Lagopus lagopus* and *L. mutus (rupestris),* in that the female does the major share of the work (Bent 1932), but the male guards the nest and young. Six to 12 eggs are laid. Nethersole-Thompson (1939) found in *L. scoticus* that incubation began with the next to last egg, lasted 23 days, and was performed by the female alone. The hen left the eggs three times during one day at intervals of six hours for inattentive periods of 45 to 60 minutes. The young stay in the nest only a few hours and begin to fly within 14 days. The male guards the nest and young but otherwise takes little part in their care.

In *Tympanuchus cupido* and *Pedioecetes phasianellus,* the male takes no part in nesting duties after the eggs are laid (A. O. Gross 1930, C. W. Schwartz 1944, Lehmann 1941, Grinnell, Bryant, and Storer 1918). Lehmann (1941) states that the female prairie chicken may dispense with her early morning inattentive period when incubation becomes advanced. The young are brooded much of the time until they are a week old but in decreasing amounts thereafter. *Centrocercus urophasianus* lays a set of only seven eggs on the average, one egg being laid each day. The incubation period is a little shorter, 20 to 22 days, and the female is not assisted by the male in any phase of the nesting cycle. At one nest the female was regularly inattentive during incubation between 0930 and 1130 and again between 1400 and 1500 hours during 5 days of observation (Girard 1937, Rasmussen and Griner 1938). Other European species described by Niethammer (1942) have very similar behavior to those forms specifically mentioned.

Family: PHASIANIDAE. The attentive behavior of the various quail in the subfamily, Odontophorinae, is based essentially on the same pattern. There have been detailed studies of several species: *Colinus virginianus* (Stoddard 1931, Klimstra 1950), *Lophortyx californica* (Sumner 1935, Glading 1938), *L. gambelii* (Gorsuch 1934), and *Odontophorus gujanensis* (Skutch 1947b). In the bobwhite, *C. virginianus*, nest building is normally by the male. Incubation lasts 23 days and is performed either by the male or by the female, more frequently by the latter, and the two may very rarely alternate at this duty. During early incubation, an inattentive period may be taken by the incubating bird both during early morning and late afternoon, but later only one period is normally taken, usually in the afternoon, and varies in length from one to nine hours depending on the weather. The 14 to 15 eggs hatch within an hour, indicating that incubation begins with the last egg. Both adults brood considerably during the first 2 weeks and direct the feeding of the precocial young. The main feeding periods are early and late in the day.

Observations on *Alectoris,* quoted by Stresemann (1928) and Niethammer (1942), indicate that the female lays two sets of 8 to 12 eggs in different nests. The male incubates and cares for the young at one nest, the female at the other. The incubation period is 24 days. Both sexes share incubation in Mearns's quail, *Cyrtonyx montezumae* (Bent 1932), but it is uncertain whether the male takes full responsibility for a nest.

Both male and female participate in nest building in *L. californica* with the female taking the lead. Twenty-two days are spent in incubation with the female on the eggs all the time except for a short period before 0830 and for a somewhat longer period, sometimes several hours, after 1530 hours. Workman (1943) cites a case where the male performed all the duties of incubation when the female deserted after the set was complete. Brooding is carried on by the female. The male accompanies the female during her inattentive periods and after the hatching of the young.

Incubation in *L. gambelii* requires 21 to 23 days and is performed by the female. The male may assume these duties if the female is killed. Gambel quail normally take two inattentive periods each day, one in the morning and one in late afternoon or evening. These are from one to two hours duration, or longer in hot weather. Hatching occurs in a few hours, and the young are brooded during the first week. The male remains near the nest and, after hatching, accompanies and guards the female and brood.

Odontophorus is of tropical distribution and has some variations in nesting activities. Only 4 eggs are laid instead of 12 to 16 found in north temperate species. Likewise in *Odontophorus* several days may elapse between successive eggs. In other quail, days may be skipped, but many eggs are laid on successive days. Incubation is 24 to 28 days by the female only. There is only one inattentive period per day, in the early morning when the female is called off the nest by the male, but it may last one and a half to three hours. All hatching occurs within 22 hours, and the young birds are accompanied away by both male and female.

Beebe (1936) states that nesting behavior of pheasants in the subfamily Phasianinae is essentially similar to that of other gallinaceous species. Incubation lasts from 3 weeks to a month in different species. The males do not share in nesting duties except to stand guard over the female and young; particularly males with brilliant plumage never go near the nest. Kozlowa (1947) found the inattentive periods of the incubating female ring-necked pheasant, *Phasianus colchicus*, to come shortly after sunrise to about 0900 and again from 1800 to 2030 hours. In *Perdix perdix* the incubating female has two regular inattentive periods, in early morning and late afternoon, and may leave for short intervals during the day. As incubation proceeds, she leaves the eggs for shorter periods. The male guards the nest and helps to direct the activities of the brood after hatching (Yeatter 1934, Yocum 1943, Nagel 1945, McCabe and Hawkins 1946). Goodwin (1948) found in captive golden pheasants, *Chrysolophus pictus*, that the female sat almost motionless on the eggs without leaving for food or rest throughout the period of incubation.

Family: MELEAGRIDIDAE. The female turkey, *Meleagris gallopavo*, requires 28 days to hatch her clutch of 9 to 15 eggs. Egg-laying may be somewhat irregular and incubation begins slowly, yet all eggs hatch within 24 to 36 hours. The female does all the nest building, incubating, brooding, and caring for the young. The male may call the female off the nest at first for feeding periods but later loses interest in her. He has been accused of destroying the eggs of any nest that he may find. Occasionally two or even three hens may lay in the same nest and simultaneously incubate a large number of eggs. The females leave the eggs for a short interval in the morning for feeding and possibly again at midday for water, but toward the end of the incubation period they may sit steadily without leaving at all during the day. Brooding during the day may persist for 2 weeks after hatching, especially in rainy weather and in early mornings, as the young are very sensitive to exposure and wetting (Blakey 1937, Mosby and Handley 1943).

Suborder: OPISTHOCOMI; *Family:* OPISTHOCOMIDAE. Beebe (1909) states that both sexes of the hoatzin, *Opisthocomus hoazin*, participate in the building of the nest. Usually two eggs are laid per set. Apparently the species is not polygamous.

Summary. The basic behavior pattern in this order is for the female to do all the nesting duties alone. The male stands guard but seldom gives any help. In *Colinus*, *Alectoris*, and possibly *Cyrtonyx* he has retained more attentiveness than in other species, in that he often takes responsibility for incubation and rearing a brood, but this is exceptional. The incubating bird sits steadily from the time that the set is complete but has one and often two inattentive periods per day, in the early morning and in late afternoon or evening. The Megapodiidae are remarkable in having evolved a very specialized type of behavior involving artificial incubation. This results in increased development of the chick in the egg so that it is exceptionally precocious at the time of hatching.

Order: Gruiformes

There are eight living suborders in this diversified order, but very few species have been subjected to detailed studies of their nesting behavior. No information on attentive behavior has been found for the suborders Heliornithes and Cariamae, or for the families Aramidae and Psophiidae.

Suborder: MESOENATIDES; *Family:* MESOENATIDAE. Rand (1951) found in *Monias benschi* a preponderance of males and the males performing the duties of incubation and care of young. However, in *Mesoenas*, only the female is known to incubate.

Suborder: TURNICES; *Families:* TURNICIDAE, PEDIONOMIDAE. In the bustards or hemipodes, the more brightly colored and larger sex is the female. The duller male performs the duties of incubation and caring for the young. Four eggs are laid in a grass-lined depression in the ground that serves as a nest. The young are precocial (Knowlton 1909). Groebbels (1937) records that in *Turnix sylvatica* the female may incubate a little during the first few days and that both sexes are concerned in nest building. Seth-Smith (1907) found in his aviary that the male *T. varia* and the male *T. tanki* alone incubated and cared for the young. The incubation periods were 13 and 12 days, respectively.

Suborder: GRUES; *Superfamily:* GRUOIDEA; *Family:* GRUIDAE. Walkinshaw (1947) studied the sandhill crane, *Grus antigone*, in captivity. Both the male and female were concerned in nest building, which required 1 to 3 days. Two eggs were laid, and incubation lasted about 32 days. Both adults incubate during the day with attentive periods about 44 minutes long. The female sits on the eggs at night. The young are able to fly when four months old but continue to be fed by the parents for six months. In *Grus canadensis*, Walkinshaw (1949, 1950) states that the two eggs are laid two days apart and that the incubation period is 28 to 30 days. Ten attentive periods on the eggs by both sexes averaged 165 minutes long but varied between 10 and 384 minutes in length. In another related species, *Grus (Megalornis) grus*, Witherby *et al.* (1938) state that the two eggs are also laid at intervals of 2 days or longer; incubation begins with the first egg, is 29 or more days long, and is shared by both sexes. According to Niethammer (1942), the eggs are apparently resistant to cold and may be left uncovered for several hours by the adults. Schuster (1931b) found either the male or the female may incubate at night. The young leave the nest in a few days and are able to fly in 9 to 10 weeks. During 2 full days of observation the average attentive period of the male was 94 minutes and of the female, 69 minutes. Christoleit (1939) has also made an intensive study of this species.

Superfamily: RALLOIDEA; *Family:* RALLIDAE. The nest is often a platform or clump of marsh vegetation on which 6 to 12 eggs are commonly deposited at the rate of one per day. Skutch informs me that three or four eggs are common in tropical rails, that the nest in *Laterallus* is oven-shaped, while in *Aramides* the nest is a bulky basket high up in a tangle of vines. Incubation sometimes begins before the set is complete so that hatching may extend over several days, or the onset of full incubation may be delayed until the set is nearly or quite complete. One adult may care for the young as they hatch while the other continues incubation. The incubation period of the various species is commonly 19 to 21 days. The young leave the nest as soon as they hatch and dry off. Both sexes incubate and care for the young, except in *Crex crex* and *Rallus aquaticus* where the female does most or all of the incubation and is fed on the nest by the male (Bent 1926, Witherby *et al.* 1938, Walkinshaw 1937b, 1940, Ruthke 1939, Sooter 1942). With *Laterallus leucopyrrhus* in captivity, Meise (1934) observed three eggs laid on alternate days with incubation beginning with the last egg. Both adults were on the nest at night, but after hatching, the female brooded during the day and the male at night. The male feeds the female on the nest, but the female may also leave occasionally to get her own food. In the gallinule, *Gallinula chloropus,* both sexes have been observed to share in nest building, and extra sleeping nests are sometimes made for the young (Steinbacher 1939). According to Holstein (1938), the male of this species is the principal nest builder and occasionally feeds his incubating mate. Howard (1940) observed the male and female relieving each other on the eggs at intervals of about 38 minutes. There appears to be no essential differences between the three subfamilies sometimes recognized.

Suborder: RHYNOCHETI; *Family:* RHYNOCHETIDAE. Knowlton (1909) reports that in captivity both male and female kagu, *Rhynochetos jubatus,* share in nest building and incubation, and that the incubation period is 36 days.

Suborder: EURYPYGAE; *Family:* EURYPYGIDAE. According to Riggs (1948), this family of sun-bitterns contains a single species, *Eurypyga helias,* which inhabits dense tropical forests. The birds are not gregarious. The nest is sometimes on the ground but may often be placed several feet above ground in trees. Both sexes build the nest and take turns at incubating the two eggs. The incubation period was 27 days in one nest recorded in captivity, and the young bird stayed in the nest for 21 days, and was fed by both parents. This long nestling period is unusual, as the young birds are covered with natal down as in precocial species.

Suborder: OTIDES; *Family:* OTIDAE. In the bustards, *Otis tarda, O. tetrax,* nests are placed in grassy fields, two to four eggs are laid, incubation begins with the last egg and lasts 20 to 28 days, and the female alone incubates. The female is also responsible for the care of the precocial young which begin to fly after 5 or 6 weeks (Witherby *et al.* 1940, Niethammer 1942).

Summary. The basic behavior pattern is for both sexes to share in all the duties of nesting. A nest is built, a variable number of eggs is laid, and the young are precocial. The Otidae show evolution in one direction, i.e., the female takes over the preponderant or total duties of incubating and rearing young, and the Turnices show it in the other direction in that the male assumes these responsibilities.

ORDER: CHARADRIIFORMES

This is a large and varied order. The Charadrii is especially complex, having seven superfamilies, twelve living families, and several subfamilies. No information is available on the superfamilies of Dromadoidea and Thinocoroidea, each one of which has a single family.

Suborder: CHARADRII; *Superfamily:* JACANOIDEA; *Family:* JACANIDAE. In *Jacana spinosa*, A. H. Miller (1931b) found the role of the sexes reversed to the extent that the female was decidedly active in courtship and the male performed most if not all of the incubation and care of the young. Sets usually consist of four eggs. According to Hoffmann (1949), the female *Hydrophasianus chirurgus* is polyandrous, laying seven to ten sets of four eggs per year. The male begins incubation with the first egg and performs these duties alone, and also the care of the young. He may raise two broods per season. Incubation lasts 22 to 24 days; the young are precocial and are tended by the male at least 2 weeks after leaving the nest. During 14 observation periods coming at various times of day, the male sat on the eggs only 52 per cent of the time, although on one cool rainy day this percentage was raised to 82. The female is vigorous in defense of the territory.

Superfamily: CHARADRIOIDEA; *Family:* ROSTRATULIDAE. In the painted snipes, the female is the more brightly colored of the sexes and the roles of the sexes are, in many ways, reversed. There is some evidence for polyandry in this group (Pitman 1912).

Family: HAEMATOPODIDAE. E. J. M. Buxton (1939) states that nest material continues to be added by the oyster-catcher, *Haematopus ostralegus*, after egg-laying starts. Webster (1941) found the eggs to be laid at intervals of 1 to 3 days. Keighley and Buxton (1948) found incubation to start usually with the last of a two- to four-egg set. They give the incubation period as 26 to 27 days, but in other species it may be shorter. Both sexes incubate; Buxton states that the male does so for shorter periods than the female. Webster believes that the adults change places every 12 hours at the time of low tide and that this regime continues as they care for the young. Webster found considerable brooding of the young during the first week after hatching, but only during rainy weather for the next 2 weeks, and none thereafter. The young are precocial and leave the nest in a few hours after hatching. Webster states "one parent stands guard and feeds himself while the other feeds the chick (and, probably, eats a little); then they change off at the turn of the tide and the second parent stands watch or eats while the first feeds the chick." Dircksen (1932) states that both sexes care for the young, but Buxton claims that the young are fed only by the male; the female stops brooding to get food for herself but not for the young.

Family: CHARADRIIDAE. Peters (1934) recognizes two subfamilies. In the subfamily, Vanellinae, and in the lapwing, *Vanellus vanellus*, Laven (1941) states that there are usually 30 to 45 hours between laying successive eggs in the four-egg set. Niethammer (1942) gives the incubation period as 24 days. R. H. Brown (1926) found steady incubation to begin with the last egg. Incubation is almost entirely by the female at first, but the male takes some share later in the incubation period. The young are precocial and able to fly when about 33 days old. The female, and occasionally the male, broods frequently during the first 5 or 6 days and during bad weather until the twelfth day. She broods the young at night until the sixteenth day. Both adults feed the young.

The subfamily, Charadriinae, includes the several species of plovers. In the killdeer, *Charadrius (Oxyechus) vociferus* (pp. 93-95), both sexes share nest building, incubation, and care of young with probably the male taking the greater share. Attentive periods during the 24 to 26 days of incubation averaged 33.6 minutes. At one of the two nests under observation the incubating adult was a close sitter at night between 2000 or 2100 hours in the evening and 0500 or 0600 hours in the morning. At the second nest, however, there was considerable nighttime activity. The thermocouple record indicated continuation of daytime attentive behavior until 2248 one night and its beginning at 0100 hours on another night. This is of considerable interest since Spingarn (1934) records in *Charadrius hiaticula (semipalmatus)* that the male and female alternate on the eggs during both day and night at intervals ranging from 31 minutes to two hours 19 minutes. He believed that the male was the more active of the two sexes in performing these duties. Ohlendorf's (1932) measurement of the length of attentive periods in this species over three days averages 64 minutes. Laven (1940) states that the male incubates at night and both sexes alternate during the day. Krösche (1936) found the male doing the greater share of incubating in *Charadrius dubius*. Walkinshaw (1948a) timed two attentive periods of a male black-bellied plover, *Squatarola squatarola*, at 35 and 30+ minutes and of a female at 65+ minutes. L. H. Brown (1948) found two or three eggs per set in *Charadrius (Afroxyechus) forbesi* which were laid on alternate days. Both male and female incubated, brooded, and cared for the young.

In other species of Charadriinae (Bent 1929, Witherby *et al.* 1940, Niethammer 1942), three or four eggs make a complete set with the eggs laid at one or two day intervals. The incubation period varies commonly from 23 to 28 days. Both sexes alternate at incubating the eggs in varying proportions of time. In *Eudromias morinellus,* the male does all of it; in *Charadrius (Pagolla) wilsonia,* the female is chiefly responsible.

The general tendency in this family, then, is for both sexes to share the nesting duties with variation between species as to which takes the major responsibility.

Family: SCOLOPACIDAE. In the subfamily, Tringinae, both sexes share the incubation and brooding. The male apparently takes the major part in *Limosa limosa, L. lapponica, Tringa erythropus, Xenus cinereus, Actitis macularia* (Nelson 1930), *A. hypoleucos* (Niethammer 1942), and *Catoptrophorus semipalmatus* (Wetmore 1921). In *Numenius tenuirostris, Tringa (Totanus) melanoleuca, T. ocrophus,* and *Heteroscelus incanus,* the female may do more than an equal share (Bent 1927, 1929; Witherby *et al.* 1938).

In Arenariinae, the male surfbird does most if not all of the incubating in *Aphriza virgata,* although both sexes may tend the young (Bent 1929). In the turnstones, *Arenaria interpres* and *A. melanocephala,* both sexes share incubation. In *A. interpres,* the four eggs are laid at intervals of 15 to 80 hours, the incubation period is 23 to 27 days, incubation begins with the third egg, and the female commonly incubates during the day from sunrise until 1500 to 1700 hours while the male incubates overnight (G. Bergman 1946).

In the subfamily, Scolopacinae, containing the woodcock and snipe, the female does most of the incubation and brooding (Witherby *et al.* 1938, O. S. Pettingill 1936, Steinfatt 1938c). Steinfatt states that *Scolopax rusticola* leaves the nest for 17 to 30 minutes in the early morning and again in late evening in order to get food. Incubation begins with the last egg and lasts 22 days. Rowan (1936) observed an unusual situation in the dowitcher, *Limnodromus griseus,* where only the female incubated and only the male cared for the young.

In the Eroliinae, the male takes the greater share of incubation and brooding in *Erolia (Pisobia) bairdii, E. minutilla, Erolia (Calidris) temminckii,* and *Eurynorhynchus pygmeus.* On the other hand, the female does so in *Erolia (Pisobia) melanotes, E. fuscicollis* (Sutton 1932), *Tryngites subruficollis,* and *Philomachus pugnax* (Bent 1927, 1929; Witherby *et al.* 1938). Swanberg (1945) found in the purple sandpiper, *Erolia (Calidris) maritima,* that the attentive period was 15 hours long.

In this family, a nest of some sort is usually formed, which may be a hollow in the ground, lined to a varying extent with dried grass or other material. Four eggs are commonly laid, and the incubation period is usually 20 or 24 days but may vary a few days either shorter or longer. Either or both sexes may incubate. The young are precocious and commonly leave the nest a few hours after hatching. One or both adults will care for the young.

Family: RECURVIROSTRIDAE. According to P. E. Brown (1949), both sexes in the avocet, *Recurvirostra avosetta,* are involved in the building of the nest and in incubation. The average of 55 attentive periods during incubation was about 66 minutes, but there was considerable variation. Often there was a ceremony of nest relief, but not always. Four eggs are laid. The incubation period is 23 days and the young are prococial within a few hours after hatching, but are brooded by one parent for 11 days. Yeates (1941) found the attentive periods on the eggs to be very short in *Himantopus himantopus,* ranging from 5 to 15 minutes, but these may not be normal.

Family: PHALAROPODIDAE. The reversed sexual dimorphism in this group is well known. The female phalarope has the more colorful plumage and is the more aggressive in courtship. The dull-colored males build the nest and, after the eggs are laid, take over the major duties of incubation, brooding, and caring for the young. Occasionally the female *Phalaropus fulicarius* and *Lobipes lobatus* sit on the eggs, and they may share with the male the care of the young. In *Steganopus tricolor* the male receives no help from his mate. Nothing is known as to how the attentive periods are regulated. Four eggs make up the usual set and the incubation period has been variously estimated at 20 to 21 days (Bent 1927, Sutton 1932).

Superfamily: BURHINOIDEA; *Family:* BURHINIDAE. Bird (1933) states that *Burhinus oedicnemus* lays two eggs on alternate days with incubation beginning with the second egg. Incubation lasts 26 to 27 days and is shared by both sexes. The young leave the nest within a day after hatching. According to Banzhaf (1933), the male incubates during the middle of the day and the female the rest of the time.

Superfamily: GLAREOLOIDEA; *Family:* GLAREOLIDAE. According to Witherby *et al.* (1938), *Cursorius cursor* lays two eggs which are incubated by the female. In *Glareola pratincola* both sexes incubate the three eggs (Yeates 1948). Groebbels (1937) gives a short incubation of 17 to 18 days. Stresemann (1928) records that *Pluvianus aegyptius* buries its eggs 10 cm. in the sand and allows them to develop in the heat of the sun. Moreau (1937b) describes how the male and female of *Rhinoptilus africanus* alternately shaded the egg, placed in full sunlight, at intervals of about one hour during the day. At night the egg was incubated in the ordinary way.

Superfamily: CHIONIDOIDEA; *Family:* CHIONIDIDAE. Murphy (1936) states that *Chionis alba* may lay two or three eggs more than a week apart. Incubation begins with the first egg to keep it from freezing. Consequently the young hatch at so widely separated intervals that seldom more than one survives.

Suborder: LARI; *Family:* STERCORARIIDAE. A simple nest is made by the skuas, *Catharacta skua*, and jaegers, *Stercorarius* sp., often a mere hollow in the tundra moss. Two eggs constitute a set with a possible interval of two days between layings. Incubation is estimated at 23 to 26 days. Both sexes share the duties of incubating and care of the young. The young may leave the nest soon after hatching (Sutton 1932, Murphy 1936).

Family: LARIDAE. The subfamily, Larinae, includes the gulls. Kirkman (1937) found in the black-headed gull, *Larus ridibundus*, that the male selected the nest site and began the nest building. Incubation began with the first egg of the three-egg set and was shared by both sexes. The male fed the female with regurgitated food from a month before nest building until after the eggs hatched. Both adults fed the young.

According to the summaries of Bent (1921) and Witherby *et al.* (1938), the general rule is for both adults to incubate about as soon as the first egg is laid. The time that incubation starts varies, however, with species, as Steinbacher (1938b) states that in *L. argentatus* incubation does not begin until the last egg is laid. Both Goethe (1937) and Kozlova (1938) found the female more attentive than the male in this species. According to Kozlova, the female may sit on the eggs four to five hours but the male for only a half-hour or less. The adults exchange places six to eight times a day and several times during the night. Two or three eggs are laid in a crude nest, often a day apart or more. Both adults may be concerned in nest building. The incubation period is variously estimated in different species of gulls at 20 to 26 days. After hatching, the young may leave the nest as soon as they are dry, may remain a few days, or may stay until fledged. Most commonly they leave after a few days, when they no longer need frequent brooding. Both adults feed and care for the young until fully fledged which may require from 3 weeks *(L. minutus)* to 8 weeks *(L. argentatus,* Niethammer 1942). The species nest in colonies on islands or along the shores of oceans and lakes.

In the Sterninae, some little attention has been paid to the nesting behavior of *Sterna hirundo* by Palmer (1941), Austin, Jr. (1932), Noll (1943), and others. The male common tern scrapes out depressions in the sand, and the female chooses one to complete as a nest. Usually three eggs are laid at intervals of two days. The incubation period begins with the first or second egg and lasts 21 to 23 days, and is participated in by both sexes, with the female doing the major portion of it. Attentive periods may be 20 to 40 minutes but vary with the insolation and the weather (Bent 1921). Huggins (1941) found that when exposed to a full sun, tern eggs on a rocky island had a higher temperature when the adult was absent than when the adult was present. Actually the chief function of the adult's attendance was to shade the eggs and prevent their overheating. It may be that the adults are sufficiently sensitive to the temperature of the egg and of the surroundings as to regulate the length of their attentive periods accordingly. Marshall (1942) has recorded the regular desertion of their eggs at night by an entire colony of terns, but this lapse of attentiveness is abnormal and was accompanied by a high rate of nesting failures. Both adults feed the young which will flee to the water at 12 days of age and can fly at 30 days.

In the noddy and sooty terns, *Anoüs stolidus* and *Sterna fuscata*, both sexes take part in nest building, incubating, and feeding the young. In *Anoüs* the male and female relieve each other at intervals of 30 minutes to five hours, the average attentive period being about two hours. The incubation period is 32 to 35 days. During the building of the nest, sticks and other materials may be brought at the rate of three to six times per hour. During this time, the male feeds the female at the nest, but this ceases with the laying of the eggs and the assumption by the adults of equal turns sitting on them. During the attentive periods the bird may leave at intervals to drink and to wet the breast feathers which may have some value in keeping the egg at the proper temperature. The parent birds alternately feed the young at intervals of one to four hours (J. B. Watson 1908).

In *Sterna fuscata* the attentive periods at incubating are much longer as shifts are made at night, each bird remaining on the eggs for 24 hours except for occasional short trips for water. Although the young may be fed at any hour of day at intervals of four to seven hours, feeding is most prevalent at dusk. The male may feed the female before the eggs are laid but not afterward.

Behavior in other species of terns is essentially similar. Most species are colonial. Bent (1921) records that in *Sterna dougallii* the attentive periods of the roseate tern on the eggs were 40 to 60 minutes, with the male's periods shorter than the female's. Witherby *et al.* (1938) state that the bridled tern, *Sterna anaethetus*, may have 24-hour attentive periods, with the shifts on the nest occurring at night as in S. *fuscata*. In *Chlidonias nigra*, only the female incubates at night but both sexes alternate during the day (Niethammer 1942). As a rule, eggs in this species are laid at intervals of one day (Haverschmidt 1945). One adult has been observed feeding the incubating bird in *Chlidonias nigra*, *Thalasseus (Sterna) sandvicensis*, *Sterna hirundo*, *Sterna albifrons*, and *Sterna fuscata*. Usually the female is more attentive than the male. One to three eggs make up the set, and these are laid on consecutive days or occasionally at 2-day intervals. The incubation period varies from 20 (Haverschmidt 1945) to 26 days. The young leave the nest in a few days but are fed by their parents until after they are able to fly. O. S. Pettingill (1939) gives the feeding rate of the young in *Sterna paradisaea* as 2 to 12 times per hour.

Family: RYNCHOPIDAE. The nest of the black skimmer, *Rynchops nigra,* is only an unlined depression in the sand or in the ground. There are commonly four or five eggs in a set, and incubation is performed by the female. Both sexes feed the precocious young. The length of the incubation period appears to be unknown (Bent 1921).

Suborder: ALCAE; *Family:* ALCIDAE. Most species in the family breed in colonies and have very little or no nest, although some of the puffins and auklets dig burrows, at the ends of which they place their eggs. Most species lay their single egg in rock crevices or on narrow ledges of steep cliffs. The black guillemot, *Cepphus grylle,* commonly has two eggs laid at intervals of 3 days, and incubation begins after the second egg is laid (Winn 1950). The incubation period is variously given for different species as 3½ to 5 weeks. In some of the auklets, the young enter the water within 2 or 3 days, but in most other species, not for several weeks after hatching, until they are at least half grown and partially feathered, even though they may not yet be able to fly.

Both sexes dig the burrow, when one is prepared, and incubate the eggs and care for the young. Observations indicate in *Brachyramphus (Endomychura) hypoleucus, Ptychoramphus aleuticus, Lunda cirrhata* (Bent 1919), and *Cerorhinca monocerata* Bailey (1927) that there are two daily shifts at incubating, one in the evening and the other in the early morning. The bird on at night would have the shorter shift due to the long daylight hours of northern regions where these birds are commonly found. There is some uncertain evidence that on his return, the male may feed the female on the nest. Lockley (1934) made an intimate study of *Fratercula arctica,* and found that only the female puffin incubates, that she incubates chiefly at night with occasional attentive periods during the day, that she leaves her burrow for feeding during most of the day, that the incubation period is 40 to 43 days long, that both parents feed the young and this feeding is most vigorous at the two flood tides each day, and finally that the young are fed for 40 days until they become fat after which they are deserted and find their own way out to the sea. The entire nestling period may be 47 to 51 days long.

Summary. The basic pattern of attentive behavior in *Charadriiformes* is for a scant nest to be formed in slight hollows in the ground, in burrows, in rock crevices, or on ledges of cliffs. One to four eggs are laid, usually at intervals of one to several days. Incubation often begins before the set is complete and lasts 2½ to 4 weeks or longer. The young may be precocial and leave the nest as soon as they are dry or they may stay for several weeks. In the Laridae an intermediate condition occurs in that the young may leave the nest soon after hatching but continue to be fed by their parents until they become fledged. Both adults take turns at incubating, brooding, and feeding the young. It is uncertain whether the primitive behavior pattern during incubation involved long attentive periods with only one or two shifts between adults per day as in the oyster-catcher *Haematopus ostralegus,* purple sandpiper *Erolia maritima,* turnstone *Arenaria interpres,* in the noddy, sooty, and bridled terns *Anoüs stolidus, Sterna fuscata,* and *S. anaethetus,* and in most of the Alcidae, or whether the attentive periods were shorter and came more frequently as in other species. The birds are more active at night than in many orders.

Superimposed on this basic pattern are two divergent trends in the evolution of specialized behavior patterns. One trend is for the female to assume an increasing proportion of the work, which is manifested to a certain extent in several families but probably best developed in some species of Scolopacidae and Sterninae. There are scattered references of the male bringing food to his incubating mate. The other trend is the reverse, in that the male assumes an increasing amount of the work. This is evident in some Charadriidae, in several species of Scolopacidae, in the Jacanidae, Rostratulidae, and Phalaropodidae.

Order: Columbiformes

Suborder: PTEROCLETES; *Family:* PTEROCLIDIDAE. Witherby *et al.* (1940) state that in the Pallas sand grouse, *Syrrhaptes paradoxus,* the birds lay three eggs and incubation is by both male and female. Niethammer (1942) records the incubation period as 28 days. Groebbels (1937) states that in two species of *Pterocles* the female incubates during the day and the male at night and that the incubation period is 22 to 23 days. Bowen (1927) differentiates between species that are diurnal and nocturnal. Diurnal species come to drink with clock-like regularity between 0700 and 0900 hours, after which they go far out into the desert, to return again about two hours before sunset. Other species do not come to their watering places before sunset but often continue to come well into the night and possibly also in the morning before sunrise. Seth-Smith (1907) recounts how adult *Pterocles alchata* soak their breast feathers with water, fly back to their young in the nest who suck off the water to supply their needs.

Suborder: COLUMBAE; *Family:* RAPHIDAE. Knowlton (1909) quotes from an early account of François Leguat in 1691 that the solitaire, *Pezophaps* *solitaria*, laid but one egg, that both sexes incubated, that the incubation period was 7 weeks, and that the young did not become independent for several months.

Family: COLUMBIDAE. There are four subfamilies of pigeons and doves recognized, but nesting data are available for only the Columbinae. Information concerning several other species is taken from Bent (1932), Witherby *et al.* (1940), and Niethammer (1942); in addition more detailed data were obtained on *Columba fasciata* from Neff and Niedrach (1946); *C. livia* from Levi (1941) and Oskar and Käthe Heinroth (1948); *C. oenas* from Steinfatt (1941a); *Zenaidura macroura* from Nice (1923, 1938), McClure (1943), and Pearson and Moore (1939); *Ectopistes migratorius* from Brewster (1889), French (1919), and Mitchell (1935); *Zenaida (Melopelia) asiatica* from Neff (1940); *Columbigallina passerina* from D. J. Nicholson (1937), *Scardafella inca* from Heilfurth (1934b) and Anderson and Anderson (1948); *Streptopelia decaocto* from Keve (1944); and *Oreopeleia montana* from Skutch (1949b).

There is considerable uniformity in the behavior pattern of attentiveness in this subfamily. Both sexes share in nest building, but the female does the major portion of arranging the materials. Normally only one or two days are required to complete the nest but occasionally a week or longer is taken. Usually two eggs are laid. In *C. livia* they are laid with an intervening interval averaging 44 to 45 hours. In band-tailed pigeons, *C. fasciata*, one-egg sets are more common than two-egg sets, and in the passenger pigeon, *E. migratorius*, one-egg sets occurred frequently. Stresemann (1933:760) states that the larger species lay one egg, others two. Some incubation begins as soon as the first egg is laid, but at least in *C. livia* and *O. montana* it is not continuous until the second egg appears. *E. migratorius* was colonial in its nesting and was reported as going many miles away from its nest to obtain food for itself and the young (Brewster 1889).

Incubation is shared by both sexes in probably all species. Each sex has one attentive period per day, the male is commonly on the eggs from about 0930 to 1600 hours and the female the rest of the time, although the exact time varies between species and individuals, and from day to day. The male's attentive period in *S. inca* is unusually short, from 1100 to 1500 hours, but the female may break her long period on the nest by a short period off in early morning and again in late afternoon. Skutch (personal communication) observed in Guatemala that the male white-winged dove, *Z. asiatica*, sat on the eggs from 0832 to 1715 hours. A day may be skipped occasionally in various species, so that one bird remains on the eggs without relief. Goodwin (1947) records a case in *C. livia* of the female incubating almost continuously throughout the incubation period after the desertion of the male.

The incubation period is commonly 16 to 19 days long in *Columba,* 14 days or a little longer in most other genera, but only 11 days in *Oreopeleia.* This latter genus is also exceptional in the family and also for a tropical species in having the nestling period only 10 days long. The period that the young remain in the nest is commonly 12 to perhaps 18 days in other genera except for *Columba* where it is 27 to 35 days.

The young are brooded by both sexes, in much the same manner as the eggs are incubated, for 7 to 15 days. They are fed with "pigeon milk" by both sexes for the first week or more but are usually given solid food before leaving the nest. The rate of feeding the young varies greatly. Skutch found in *O. montana* that the young were fed 22 times when one day old and only three times per day when they were a week old. However, they were fed more copiously as they grew older, and both nestlings were fed on each visit. Only one nestling was fed at a time when they were very young. In observations that extended from daylight to dark, Neff and Niedrach (1946) reported that in *C. fasciata* the male fed the young three times daily the first week and twice daily the second week. The female did not feed the young until they were 20 days old, then each sex fed them once per day.

Summary. The basic behavior pattern in this order is for both sexes to share in all phases of the nesting duties, with each sex having one long attentive period per day.

ORDER: PSITTACIFORMES

This is a large and varied order of parrots and their allies, but containing only one family which is divided into six subfamilies. Very little study has been made of their nesting behavior except in captivity.

Family: PSITTACIDAE. In species of *Agapornis* the female does most of the nest building. Incubation begins with the first egg and lasts 21 days, during which the male supplies the incubating female with food. In *A. pullaria,* the male fed the incubating female only once or twice a day (Hampe 1937a). The behavior of *Loriculus* is similar except the incubation period is 17 to 21 days. Macgillivray (1927) and Hampe (1937b, 1938, 1939, 1940, 1941, 1942) have made studies of *Platycercus eximius, P. icterotis, P. adscitus, Neophema bourkii, N. elegans, N. chrysostomus, Psephotus varius,* and *P. haematonotus* in captivity. These species belong to the subfamily, Psittacinae, native in Australia. The birds have a nest and lay three to six eggs in a set, usually on alternate days. Incubation may begin before the set is complete and lasts 17 to 20 days; the young are brooded for 7 to 12 days or longer and leave the nest at the age of 28 to 36 days. The female incubates and broods almost continuously while being supplied with food by the male. Both adults bring food to the young after they become older. In *P. eximius* and *N. bourkii* the female begins to feed herself when the young reach 8 days of age, in *P. adscitus* not until they are 14 days old. The female will, however, search for food for herself and her young during these first few days if the male is killed or deserts. In the records compiled by Groebbels (1937), the male supposedly takes some share of the incubation duties in *Nymphicus (Calopsittacus), Conuropsis, Agapornis,* and *Melopsittacus.* Large parrots may take 30 to 31 days for incubation (Heinroth 1924-33).

Order: Cuculiformes

There are two suborders of Cuculiformes but no information is available on the plantain-eaters, Musophagi, Musophagidae. The suborder, Cuculi, contains but the one family.

Suborder: CUCULI; *Family:* CUCULIDAE. This family is a heterogeneous one. Six subfamilies are recognized, and there is considerable differentiation of behavior between them. No information is on hand for one subfamily, Couinae.

The Cuculinae includes the European cuckoo, *Cuculus canorus,* and a large number of oriental and African species that are parasitic (E. C. S. Baker 1942, Friedmann 1949a, b). *Cuculus* is parasitic on a large variety of small birds; *Clamator* often parasitizes species of Corvidae. No nest is built, although the female *Cuculus* is sometimes seen carrying nest material during the mating period (Chance 1922). An egg of the host species is removed when the cuckoo lays its own. As many as 12 eggs are regularly laid per season by *Cuculus canorus,* but this depends somewhat on the number of available nests of the host species. Occasionally even 25 eggs are laid in one season. Eggs may be laid every other day. Incubation requires 12 to 13 days, and the young bird remains in the nest 20 to 23 days. The young bird is continued to be fed for another 3 weeks after leaving the nest.

In the subfamily, Phaenicophaeinae, the two species of *Coccyzus* occurring in North America have essentially the same behavior (Table 42). A nest is built. Egg-laying is irregular, and incubation begins with the first egg of the two to four that form the egg-set. As a result, hatching extends over several days, and there may be young of different ages and eggs in the nest at the same time. The two species frequently lay their eggs in each other's nests and occasionally in the nests of other species. Social parasitism, as in *Cuculus,* has not, however, developed; in one nest where both species had laid eggs, both were observed to incubate and brood at different times (Allison, MS). Bent (1940) gives the incubation period as 14 days; Spencer (1943) found two marked eggs to hatch in 10 and 11 days. Both sexes share in incubation and brooding with long attentive periods. C. H. Johnson (1942) found an average brooding period of 49.3 minutes throughout the nest life of young *Coccyzus ameri-*

canus. The nestling period is only about a week, at the end of which the young leave the nest, still unable to fly, and enter into a climbing period. During this period they scramble around through the bushes, and another two weeks may lapse before they can fly (Herrick 1935). The feeding rate is low. In addition to the records in Table 42, Herrick (1910a) found an average of 1.0 times per hour for four young at one nest and 2.4 times per hour for 3.8 young at another nest. His observation covered many hours over six different days at each nest.

In the Crotophaginae, studies of nesting behavior are available for *Guira guira* and *Crotophaga ani* (Davis 1940a, b) and *C. sulcirostris* (Bent 1940), the latter account based largely on observations by Skutch. These birds have developed a remarkable communal behavior in territorial defense, in having one nest used by several pairs, and in other phases of nest life. Occasionally a single pair may have a nest to itself, at least in *G. guira* and *C. sulcirostris,* but commonly two or three pairs join together. Davis found some indication in *C. ani* that monogamy, polygyny, and polyandry may all occur in different situations. Alvarez (1948) actually observed in *C. sulcirostris* a male copulating repeatedly with two different females. Both sexes of all pairs in a group aid in building the nest, usually the females arrange the materials that the males bring to them, and they themselves may gather some material. In *C. ani* the set laid by one female is commonly six eggs, in *C. sulcirostris,* three or four, in *G. guria,* five to seven. Several females may lay in the same nest, and all birds, both male and female, take turns at incubation. In *C. ani* and *C. sulcirostris* a single male incubates at night (Skutch). Sometimes a female will lay eggs in a nest but not help to incubate. Davis noted considerable irregularity in that different females in a group would lay eggs at different times, sometimes eggs were laid before the nest was ready so that they had to be deposited on the ground. Incubation lasts 13 to 14 days. The young remain in the nest for only 5 or 6 days, when they begin the climbing period also noted for other cuculids. They are commonly brooded during the day for the whole period in the nest and will also return to the nest at night during the climbing period. Skutch noted in *C. sulcirostris* the longest attentive periods during incubation at 30 to 60 minutes, and he observed the young fed at the rate of 12 times per hour. Davis recorded the rate of feeding the young in *G. guira* in two nests at 0.8 and 6.0 times per hour. All of the adults of both sexes may participate in feeding the young.

The roadrunner, *Geococcyx californianus,* is in the subfamily, *Neomorphinae.* Its nesting behavior is not well known (Bryant 1916; Sutton, see Bent 1940). A nest is built but the number of eggs varies between wide limits, 2 to 12. Where large numbers of eggs occur, probably they are laid by more than one female. The incubation period appears to be 18 days, which is long. Incubation begins with the first egg, and since the eggs are deposited at intervals of several days, by the time the last young hatches, the first young may be half the size of the adult. Bryant states that both sexes incubate and care for the young, but Sutton cites some evidence that only the female incubates. Sutton gives some observations to indicate that, like *Coccyzus,* young roadrunners may leave the nest after a week or so and have a climbing period before they become independent of their parents. Peters (1940) classifies *Tapera naevia* also in the Neomorphinae. However, this species has a pattern of behavior quite different than *Geococcyx* in that it is parasitic on other species, more nearly like the Cuculinae (Friedmann 1933).

In the Centropodinae, Spennemann (1928) believes that only the male builds the nest, incubates, and feeds the young in *Centropus bengalensis (javanicus).*

Summary. One cannot give any general pattern of attentive behavior in the Cuculidae that will fit all groups. The occurrence in several genera and different subfamilies of a short nestling period, followed by a period of climbing through the bushes and trees near the nest, is, however, of special interest in this regard. Perhaps this behavior characteristic is typical of the order as a whole, as Moreau (1938) reports similar behavior also for species in the family Musophagidae, suborder Musophagi. Evolution of behavior has been relatively rapid in the Cuculidae. It would seem that the behavior of the genus, *Coccyzus,* in the subfamily, Phaenicophaeinae, adheres most closely to an expected behavior pattern such as is found in other orders. In this group both sexes participate in all phases of nest life, which follows the usual sequence of courtship, nest building, egg-laying, incubation, brooding, and feeding the young. However, two irregularities may be noted in the behavior of *Coccyzus.* Eggs are laid at intervals of 1 to 3 days and with incubation beginning with the first egg, there are often considerable differences in the ages and development of the young. In other words, the various phases of the reproductive cycle are not as definitely defined as in other species. This may indicate a weakness in the timing of the reproductive behavior pattern that, if present in the ancestors of modern cuckoos, could have foreshadowed the evolution of the parasitic behavior. The other irregularity is the occasional laying of eggs in the nests of other birds. When other species are concerned, this would have forecast the development of parasitism; when the eggs are laid in the nests of other cuckoos, either the same or related species, and sometimes the joint care of them and the young, the first beginning of a social reproductive behavior pattern would have been suggested.

Friedmann (1933) believes that the cuckoo family is of ancient origin, probably in southern or southeastern Asia. Apparently the family branch that dispersed into the Americas did so before the parasitic behavior had become established as it later developed elsewhere over the world. If this is true, then the parasitic behavior in *Tapera* of South and Central America must represent an independent and convergent evolution. There is evidence in some species of parasitic cuckoos, that the adult bird may still occasionally feed the young (Friedmann 1949a, Moreau 1949b, Chisholm 1950).

Darwin (1859) long ago postulated the evolution of parasitism in *Cuculus* from progenitors with behavior patterns like *Coccyzus*. He recognized that the 2- or 3-day intervals between laying of the eggs and the consequent diverse ages of the young birds in the nest was a handicap for the raising of a full complement of vigorous and healthy offspring. He postulated as a consequence that the occasional raising of young by foster parents may have proved advantageous for the species and that this directed an evolutionary trend in behavior until it became the sole means of reproduction. Herrick (1935:105-6) seems to agree with Darwin when he states ". . . it seems to me probable that this lack of harmony between nest-making and egg-laying may be the 'loosened screw' that makes the acquisition of such a habit possible."

E. C. S. Baker's (1942) ideas as to the origin of parasitism appear conflicting. He believes that the first birds laid their eggs in various places and that nest-building behavior evolved later in the various groups. He states (p. 98): ". . . parasitism seems to have been acquired not by birds which were originally nest-builders, but by those who had never acquired the art of nest-building." Later in this discussion, however, he states (p. 99): ". . . our most primitive cuckoos are not parasitic, they make their own nests, hatch their eggs and rear their young." These statements would seem to mean that parasitic and nonparasitic cuckoos must have evolved independently from very early ancestors. We cannot agree with this hypothesis.

D. Davis (1942b) is probably correct in stating that social nesting is not a stage in the development of parasitism, but it is a distinct side branch in the evolution of a peculiar nesting behavior. Note has already been made how *Coccyzus* species may lay in each other's nests and both species care for the eggs and young in one nest. In *Geococcyx*, it is not uncommon for several females to lay their eggs in one nest, but there is no evidence available that the duties of incubation and raising the young are shared by more than one pair. In *Crotophaginae,* D. Davis (1942b) traces the phylogeny through three levels: I, *Guira guira,* II, *Crotophaga major,* and III, *C. ani* and *C. sulcirostris,* with increasing specialization at each level. He describes three primary factors conducive to the development of social nesting behavior: a) breakdown of territorial defense by individual pairs due to weak sexual fighting, lack of song, poorly developed courtship performances, and the appearance of composite territorial defense by the colony; b) aberrant breeding behavior involving only sporadic attentiveness to nest and eggs and young, lack of attunement between egg-laying and nest building, and spontaneous ovulation without complicated courtship; and c) type of habitat in that the birds originally occurred in savannahs where they could scatter to feed but they were compelled to concentrate in isolated groves of trees to roost and nest. It would seem that here again, the loss of precise definition and timing of the various phases in the reproductive cycle was prerequisite for the evolving of a new type of attentive behavior.

Perhaps the aberrant behavior of *Centropus bengalensis,* where the male asumes all the nesting duties, is still another evolutionary compensatory pattern for the loss of attentiveness. This species may indicate that it was in the female rather than the male that the main disturbance occurred in the reproductive cycle.

Order: Strigiformes

This order contains two living families. Probably because of their nocturnal habits, few detailed studies have been made of their attentive behavior.

Family: TYTONIDAE. The barn owl, *Tyto alba,* nests in old buildings, cliffs, trees, or walls. Often no nest is built or only a crude pile of sticks or broken-up regurgitated pellets. There are commonly six or seven eggs laid at intervals of 2 days (Wallace 1948); Niethammer (1938) gives four to six eggs as the usual set. Incubation may begin soon after the first egg is laid, as broods of young are obviously of different ages, depending on time of hatching. Incubation time has been variously determined, but is probably 30 to 34 days (Wallace 1948, Witherby *et al.* 1938). Forbush (1927) states that "the female while incubating is steadily supplied with food by the male, but occasionally she leaves the nest, and he takes her place thereon, and probably in some cases he assumes some part of the duties of incubation, as both male and female have been seen sitting side by side on the eggs." Niethammer states that only the female incubates. After hatching, the young remain at the nest site about two months. Bussman (1935) attached a terragraph to a nest containing four young. An average over several nights, when the weather was clear, gave 11.3 feedings in an average hunting period of 5 hr. 33 min. per night (2.0 per hour). In 1937 he obtained another record at a nest with six young. Here he found the female doing the brooding for 10 to 11 days. Over 28 nights, food was brought to the young eight times per night. Most observers agree that both parents share this duty.

Family: STRIGIDAE. The best studies of the nesting behavior of owls are those of Sherman (1911) and A. A. Allen (1924) on the screech owl, *Otus asio;* Gugg (1934) on the eagle owl, *Bubo bubo,* F. M. Baumgartner (1938) on the great horned owl, *Bubo virginianus;* Sutton (1932) on the snowy owl, *Nyctea scandiaca (nyctea);* Haverschmidt (1946) on the little owl, *Athene noctua;* Hosking (1941) on the long-eared owl, *Asio otus;* Kuhk (1943, 1949) on the Tengmalm owl, *Aegolius (Cryptoglaux) funereus;* and Santee and Granfield (1939) on the saw-whet owl, *Aegolius (Cryptoglaux) acadicus.* Bent (1938), Niethammer (1938), and Witherby *et al.* (1938) have summarized much miscellaneous information.

Nests are not ordinarily built (Schuster 1930). *Bubo virginianus, Strix (Scotiaptex) nebulosa,* and *Asio otus (wilsonianus)* utilize old hawk or crow nests and in some areas may add more sticks; apparently in *Bubo* this repair work is participated in by both sexes. Other species commonly nest in natural cavities or old woodpecker holes; *Speotyto cunicularia* may enlarge an old prairie dog or ground squirrel burrow; *Nyctea scandiaca* and *Asio flammeus* nest in slight depressions made in ground vegetation. Usually there is little or no lining, but occasionally there are feathers from the bird's breast or, in *Speotyto,* dried chips of mammal excreta.

The number of eggs per set varies from two to three in *Bubo, Glaucidium, Micrathene (Micropallos),* and *Strix,* to as many as seven or eight in *Nyctea* and *Speotyto.* The eggs are laid at intervals of 2 days or more, and incubation begins with the first or second egg.

Incubation and brooding in all species are done chiefly by the female. There is considerable difference of opinion as to how much incubating the male does, but in *Bubo, Micrathene, Speotyto, Strix,* and *Asio flammeus* he is supposed to take some part. In several genera, *Otus, Nyctea, Glaucidium, Athene,* and *Aegolius* and in *Asio otus* (Niethammer 1938) and *Bubo bubo* (Gugg 1934), the male is largely responsible for supplying the incubating female with food, so that she leaves the nest only at infrequent intervals. In *Aegolius funereus,* the male feeds the female four or five times in the night and the female leaves the nest for only three to nine minutes in early morning. Fleay (1942) states that in *Ninox connivens* the incubating female leaves for only a few minutes after dusk to get food. It may well be that some reported cases of males' incubating may be based on these visits of the male to the nest with food for his mate. After the young hatch, the male continues to supply the nest with food, the female taking what she needs and passing on the rest to the nestlings. Apparently it is only after the need for brooding is over that the female searches for food for the young, so that, in general, her role in this duty is a reduced one.

Bendire (1892) reports that the incubation period is only 2 weeks in *Micrathene,* but this should be reinvestigated. It is commonly 3½ to 4 weeks in other species or 5 weeks in *Nyctea* and *Bubo*. Brooding of the young may last 2 to 3 weeks and the young commonly remain in the nest for 3 to 5 weeks altogether.

A. A. Allen (1924) has seven nights' observations of male and female screech owls, *Otus asio*, feeding two young. Feeding periods lasted 6.0 to 7.5 hours each night, and the average feeding rate was 7.7 visits to the nest per hour. Santee and Granfield (1939) have similar observations of both adults feeding five young saw-whet owls, *Aegolius (Cryptoglaux) acadicus*, over three nights when the young were 19, 25, and 28 days old. The feeding periods were from 5.0 to 5.9 hours long, and the number of visits to the nest averaged 1.1 per hour. Haverschmidt (1946) recorded both adults of *Athene noctua* feeding two young, 16 to 23 days old, at the rate of 7.0 times per hour, and feeding one young, 24 to 35 days old, at the rate of 4.4 times per hour. During incubation he observed inattentive periods of the female at all hours of the day and night, but after hatching, the young were fed chiefly at night. Bussman (1931) recorded 21 to 48 comings and goings per day in this species, mostly at night but some by daytime.

All genera mentioned above belong to the Buboninae except *Strix*, *Asio*, and *Aegolius* which are placed in the Striginae. There appear to be no differences in behavior between these subfamilies.

Summary. The basic pattern for the order as a whole is for the female to sit nearly continuously on the eggs and the newly hatched young. The male may occasionally take a turn, but his usual duty appears to be to supply the female and young with food. Most species are nocturnal. Incubation in this order commonly begins with the laying of the first egg, with the result that the young hatch at intervals and maintain a marked difference in size through the nestling period.

Order: Caprimulgiformes

There are two suborders and five families in this order, but data are available on only the one family.

Family: CAPRIMULGIDAE. No nest is built. There are two eggs, and these are laid on alternate days.

In the whip-poor-will (Table 42), only the attentive behavior of the female is averaged for the incubation period. Raynor (1941) observed the male on the eggs three times, between 2045 and 2325 hours, for periods that averaged only eight minutes. Arnold (1937) believed only the female incubated, and she observed absences of 15 to 25 minutes. The female sits steadily on the eggs during the daylight hours, as this species is largely nocturnal in its habits. Both adults feed the young at night, and the male participates with the female in brooding them at this time. The young have no true nestling period as they move from one location to another at frequent intervals. The behavior of *Caprimulgus europaeus* is similar (Lack 1932, Stülcken and Brüll 1938) except for being more crepuscular. The male relieves the female on the eggs for 15 to 20 minutes in the evening and possibly also at dawn and participates in brooding and feeding the young. The incubation period is given as only 16 to 17 days and brooding as 16 to 20 days. The young begin to fly at 16 days but remain dependent on the adults for food for 31 days or longer. Both sexes take turns at incubating and brooding in the poor-will, *Phalaenoptilus nuttallii* (Orr 1948).

In *Nyctidromus albicollis,* Skutch (Bent 1940) found the male and female taking turns on the eggs and brooding the young, relieving each other every two or three hours *during the day.* At night only the female covered the eggs.

Although there are some records of the male nighthawk, *Chordeiles minor,* incubating, this behavior is exceptional as nearly all of this duty is performed by the female (Sutton and Spencer 1949). The female sits on the two eggs steadily day and night except for short inattentive periods of about 15 minutes soon after sunset in the evening and again in the morning before sunrise (Collet 1934; Fiorucci 1941; Gilreath 1934; Gross, see Bent 1940; Rust 1947). Collet once observed the male feed the incubating female. The incubation period is 18 to 19 days long. After hatching, the young are brooded about 23 days and become largely independent after 30 or 34 days (Gross; Bowles 1921). They first begin to fly short distances when 17 days old (Sutton and Spencer 1949). The brooding is done mostly by the female, but the male may do so briefly when he feeds the young. Both adults feed the young to varying proportions in late evening and early morning (Bowles 1921, Pickwell and Smith 1938, Wilson 1938).

Summary. The attentive behavior pattern in this family, which for lack of further data, must be taken as representative of the order, includes no nest building, usually crepuscular habits, nearly continuous incubation and brooding by the female except for short inattentive periods in late evening and early morning, and joint responsibility of male and female for feeding the young. *Nyctidromus* is exceptional in the diurnal changeover of the sexes on the nest and participation by the male more extensively in incubation.

Order: Apodiformes

There are two suborders here that need separate treatment, the swifts, Apodi, and the hummingbirds, Trochili. Data are available on only one of the two living families of swifts—the family Hemiprocnidae not being included. There is only one family of hummingbirds, and it is limited to the Western Hemisphere.

TABLE 42. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Proportion by sexes: Male	Nest building: Proportion by sexes: Female	Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Order: CUCULIFORMES; Family: CUCULIDAE								
1. Yellow-billed cuckoo	*Coccyzus americanus*	Johnson, 1942	...	...	...	...	...	...
2. Black-billed cuckoo	*Coccyzus erythropthalmus*	Spencer, 1943	...	...	...	0	3	1
Order: CAPRIMULGIFORMES; Family: CAPRIMULGIDAE								
3. Whip-poor-will	*Caprimulgus (Antrostomus) vociferous*	Raynor, 1941	0	0	0	0	2	2
Order: APODIFORMES; Family: APODIDAE								
4. Chimney swift	*Chaetura pelagica*	See pp. 95-98	...	++	++	0	4	3–4
5. White-rumped swift	*Apus (Micropus) caffer*	Moreau, 1942a	...	++	++	...	2	1
6. Palm swift	*Cypsiurus (Cypselus) parvus*	Moreau, 1941	10	++	++	...	2	2+
Family: TROCHILIDAE								
7. Mexican violet-ear	*Colibri thalassinus*	H. O. Wagner, 1945	...	...	...	...	2	1+
8. Rufous hummingbird	*Selasphorus rufus*	DuBois, 1938	...	...	...	...	2	...
9. Allen hummingbird	*Selasphorus sasin*	Dyer, 1939	11	0	++++	0	2	...
Order: TROGONIFORMES; Family: TROGONIDAE								
10. Quetzal	*Pharomachrus mocino*	Skutch, 1944c	...	++	++	...	2	...
11. Citreoline trogon	*Trogon citreolus*	Skutch, 1948a	6+	++	++	7	3	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 42 (*cont.*). Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Proportion by sexes: Male	Nest building: Proportion by sexes: Female	Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
12. Mexican trogon	*Trogon mexicanus*	Skutch, 1942	...	...	...	...	2	...
Order: CORACIIFORMES; Family: ALCEDINIDAE								
13. Belted kingfisher	*Ceryle (Megaceryle) alcyon*	See pp. 98-99	13–14	++	++	...	6–7	...
14. Half-collared kingfisher	*Alcedo semitorquata*	Moreau, 1944	...	...	...	...	2–4	...
Family: MOMOTIDAE								
15. Blue-throated green motmot	*Aspatha gularis*	Skutch, 1945e	...	++	++	8–9 months	3	2–3
16. Turquoise-browed motmot	*Eumomota superciliosa*	Skutch, 1947	5+	+	+++	...	4	...
Family: BUCEROTIDAE								
17. Silvery-cheeked hornbill	*Bycanistes brevis (cristatus)*	Moreau, 1937a, 1937b; Moreau & Moreau, 1941	...	++	++	...	2	1

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 42 (*cont.*). Summary of attentive data by species.

Common Name	*Incubation* Duration (days)	Proportion by sexes: Male	Proportion by sexes: Female	Male feeds female	Attentive periods (min.)	Inattentive periods (min.)	*Feeding young in nest* Duration (days)	Number of young	Age of young (days)	Trips per hour: Male	Trips per hour: Female	Trips per hour: Total
1	...	...	...	0	...	...	7–8	2	0–7	++	++	1.5
2	10–11	++	++	0	90	...	6–7	2.5	2–6	++	++	2.8
3	20	+	+++	0	82.3	24.5	0	2	1	2.5	1.2	3.7
4	18–19	++	++	0	32.4	32.4	19–21	2.5	0–21	++	++	2.5
5	21	++	++	0	75±	...	42	1.8	21–42	++	++	0.9
6	20	++	++	0	38	56	31	1.4	0–31	++	++	1.0
7	16–17	0	1.9/hr.	0	24.2	7.8	23–25	2	2–22	0	3.3	3.3
8	...	0	2.0	0	20.0	10.8	...	1	2–6	0	1.1	1.1
9	17	0	++++	0	...	...	...	2	1	0	2.5	2.5
10	17–18	+	+++	0	2.6-8.1 hrs.	8.1-2.6 hrs.	30	2	17, 19	1.9	0.3	2.2
11	19	+	+++	0	7.8-15.5 hrs.	15.5-7.8 hrs.	16–17	3	2, 4, 12	0.6	1.8	2.4
12	19	+	+++	0	1.8-13.6 hrs.	13.6-1.8 hrs.	15–16	2	3	1	1	2.0
13	23–24	+	+++	+	...	...	28–32	...	0–31	++	++	1.9
14	16+	0.6	0.6	0	102	103	27	3	1–27	++	++	3.4
15	21	++	++	0	240–360	...	29–31	3	15	++	++	4.8
16	17	++	++	0	60+	...	28	4	6–7	++	++	4.0
17	40	0	++++	1.3/hr.	continuous	0	70–80	1–2	0–80	1.6	0	1.6

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

Suborder: APODI; *Family:* APODIDAE. There is general agreement among the various species studied in that both adults share about equally in nest building, incubation, brooding, and feeding the young (Table 42). In *Apus apus* it happens occasionally that only the female incubates (S. B. Smith 1946). Nests are commonly made of sticks or other materials fastened together with saliva. Even in *Apus caffer,* where use is made at times of old swallow nests, the interior of the nest is covered with saliva. Commonly a day elapses between laying of consecutive eggs. In the black swift, *Nephoecetes niger,* there is record of the male feeding the female on the nest (Michael 1927), and in *Apus (Micropus) apus* Koskimies (1950) reports that the free adult may occasionally feed the incubating bird, but this behavior is not common in the family. Incubation is very irregular in the amount of time the adult birds spend on the eggs, and there are frequent periods, sometimes two or six hours in duration, when neither bird is present. Either or both birds may incubate at night when it is not uncommon to find both birds sitting side by side on the nest sharing the duties of incubation. If only one bird is on the eggs, the other bird will usually be roosting close by. In a personal communication, Moreau mentions that this is a family in which there is probably no parental care after the young leave the nest. Koskimies verifies this for *A. apus.* Moreau also states that in African species attention to the young is as irregular as it is to the eggs. He points out that a long period in the nest is inevitable when long flight feathers have to be matured. In an all-day observation Bartels (1931) found that two young *Apus (Micropus) melba* about three weeks old were fed at the rate of 1.9 per hour. Bloesch (1931) reported observations at four nests with two or three young each, varying from two days to four weeks of age, where the average feeding rate was 0.7 per hour. Koskimies recorded two young *A. apus,* three to four weeks old, fed during three days at an average rate of 0.6 per hour but quotes observations of others of 1.0 per hour and 1.5 per hour. Each feeding consisted of a mucous ball containing several hundred small insects which the adult accumulated in its aerial flights. Lack (1951) gives the average rate of feeding in 25 broods of *A. apus* over 920 hours as 1. 1 per hour. The rate of feeding the young and the consequent length of time they spend in the nest vary directly with weather conditions. Lack (1951) found the nestling period to vary between 38 and 56 days in *A. apus.*

Suborder: TROCHILI; *Family:* TROCHILIDAE. In hummingbirds, the male takes very little or no part in nesting after mating is consummated (Table 42). Pitelka (1942) believes that recorded observations of the male driving away intruders from near the nest is due to the chance location of the nest in or near the male's feeding territory. Moore (1947), however, has collected the male of *Colibri coruscans* while incubating eggs, and Cottam (1941) observed the male *Stellula calliope* feed the incubating female by regurgitation on a number of occasions.

Nest construction may require a week (Skutch 1931), and additions may be made after the eggs are laid. Normally there are two eggs, and these are laid on alternate days (Aldrich 1945, Berlioz 1944, Clabaugh 1936, Skutch 1931). Incubation starts after the first egg is laid but may not be fully established until the second egg appears. Hatching of the second egg may occur twenty-four hours after the first (Berlioz 1944, H. O. Wagner 1945). The incubation period is commonly 16 or 17 days and the nestling period 19 to 25 days (Skutch 1945d).

In *Selasphorus sasin*, Aldrich's observations (1945) indicate the attentive period during incubation averages 18.2 minutes and the inattentive period, 4.3 minutes. Orr (1939) found the periods to average only 4.6 and 1.4 minutes, respectively, in the morning, but both he and Aldrich agree that attentive periods become longer in the afternoon. DuBois (1938) observed also in *Selasphorus rufus* that the female sat steadily most of an afternoon except for an absence of one or two minutes in the middle of the period. Skutch (Bent 1940) found in one female, *Hylocharis leucotis*, the average attentive period during the entire day to be about 9.7 minutes and the inattentive period, 5.0 minutes. In four other species, however, he found the attentive period more than an hour, the longest attentive period of 99 minutes being in *Phaeochroa cuvierii* (personal communication). Bené (1940) found brooding in *Archilochus alexandri* to continue for at least 10 days and attentive periods to average about 5.9 minutes. Skutch noted young *Hylocharis leucotis* brooded until they were 17 to 18 days old. Orr (1939) states that brooding practically ceased when the young were 12 days old in *Selasphorus sasin*.

It appears that both young birds are fed by the female on each trip to the nest (Common 1933, H. O. Wagner 1945). Nickell (1948) records an unusual case of a female ruby-throated hummingbird, *Archilochus colubris*, alternately feeding young at one nest and incubating eggs at another nest. Additional feeding rates than those given in Table 42 are: 1.4 per hour for two young, 21 days old, in *Topaza pella* (E. M. Nicholson 1931); 2.6 per hour in *Archilochus alexandri* (Bené 1940, 1945) and 1.3 per hour (Common 1933) and 1.6 per hour in *Archilochus colubris*. The latter figure is an average from four nests studied by students of Dr. O. S. Pettingill, Jr., at the Michigan Biological Station.

Summary. There is agreement between the two suborders in that two eggs are the usual number in a set and that the eggs are laid on alternate days. In most other respects the behavior pattern for the two groups differs widely. In the *Apodi*, both sexes share almost equally in all phases of nest life; in the Trochili, the female does it all alone. In spite of that the incubation and nestling periods are shorter in Trochili, and the attentive and inattentive rhythm is faster during incubation as is also the feeding rate.

ORDER: TROGONIFORMES

There is only one family in this order, and it is of tropical and subtropical distribution. Skutch (1942, 1944c, 1948a) has made the only worth-while nesting observations on this group.

Family: TROGONIDAE. Nests are usually excavated in the rotten wood of a decaying trunk or stub; *Trogon citreolus* and sometimes *T. massena,* however, make their burrow in a termite nest in a tree. *T. caligatus* occupies a wasp's nest. There is no nest lining deposited. Both sexes share nest building, incubation, brooding, and care of the young (Table 42). The female is in the nest at night during the incubation period. The male took a single long attentive period during the day in *T. citreolus, T. curucui,* and at one nest of *T. mexicanus.* At another nest of *T. mexicanus,* the male was on for three short periods during the day and the female for the alternate periods and at night. In *Pharomachrus,* the male had a long morning and a shorter afternoon attentive period; the female was in the nest overnight and again for about four hours in late morning and early afternoon. The attentive periods of both birds are sometimes interrupted by absences of several minutes. It almost seems that in this species, and perhaps also in *T. mexicanus,* that the behavior pattern is in the process of changing to a more accelerated rhythm of shorter more numerous attentive periods with more frequent alternation of the two sexes.

ORDER: CORACIIFORMES

This order includes many tropical and subtropical families. There are four suborders, and fortunately there are nesting data for representative species in each. The only families not here included are the Todidae, Leptosomatidae, and Phoeniculidae.

Suborder: ALCEDINES; *Superfamily:* ALCEDINOIDEA; *Family:* ALCEDINIDAE. These birds commonly nest in burrows dug in the side of banks. Some tropical kingfishers nest in old swallow nests, in tree holes, or holes excavated in insect nests in trees (Moreau, personal communication). Both sexes share nearly equally in all duties of nesting (Table 42). Skutch (1933a) records that in *Chloroceryle amazona* and *C. americana,* the females incubate at night while the males do the major share of the incubation during the day. In *Ceryle torquata* the routine was very different. The two sexes alternated in the burrow once a day at 0700 or 0800 hours, so each bird incubated for a complete 24-hour period, with the exception of a brief period during the afternoon when the eggs were left uncovered. This behavior has not been reported, however, in *Ceryle alcyon,* although there are no very detailed observations available for the incubation period. Rivière (1933), R. L. Brown (1934), and Clancey (1935) state that both sexes share in incubation and feeding the young in *Alcedo alcedo.* The incubation period was found to be 19 to 21 days and the nestling period usually 22 to 26 days. Although both sexes participated in nest building, the male did the greater share of the digging. Brown observed the male to be very energetic in feeding his sitting mate, especially for a period after incubation commenced and again when the young were newly hatched. Rivière found after the first day that the average rate of feeding the young throughout the nestling period was 3.8 per hour. As the young grew, the size of the fish given them became greater, and there was consequently no increase in the rate of feeding. The attentive behavior pattern followed by *Dacelo novaeguineae (gigas)* appears typical of the family as far as observations have been made (Hindwood 1947).

Superfamily: MOMOTOIDEA; *Family:* MOMOTIDAE. The only data available on the life history of birds in this family are two studies by Skutch (1945e, 1947c; Table 42). Apparently both sexes participate in all phases of the nesting duties. In *Eumomota* the female did the major share of excavating the earthen nest burrow, but the male occasionally gave her something to eat. In *Aspatha* underground burrows are used as sleeping quarters throughout the year. Even while eggs and young are present, both adults spend the night together. In *Eumomota,* however, only one bird was observed on the eggs at night, and the burrow may be used only during the nesting season.

Suborder: MEROPES; *Family:* MEROPIDAE. Witherby *et al.* (1938) state that in the bee eater, *Merops apiaster,* both sexes dig the nesting tunnel and incubate the eggs. Koenig (1951) gives further details (Table 51).

Suborder: CORACII; *Family:* CORACIIDAE. The same authors record incubation in the roller, *Coracias garrulus,* as 18 to 19 days and the nestling period as 26 to 28 days. Incubation and care of young are shared by the male and female. Nests are commonly in holes in old timber, mud banks, crevices.

Family: UPUPIDAE. Nesting behavior in the hoopoe, *Upupa epops* (Witherby *et al.* 1938, Skead 1950), differs from the above families in that incubation is performed by the female alone. The female may be inattentive for 30 minutes in early morning and late afternoon but is ordinarily well supplied with food by the male. In three instances the male fed the female three, five, and eight times per hour. Nests are located in tree holes or other crevices. Four to eight eggs are laid, one daily, and the female begins staying in the nest when the first egg is laid. The incubation period is uncertain, but data accumulated at two nests by Skead would make it between 12 and 15 days. In the same article Hinde gives it as 16 days. The nestling period varies from 26 to 32 days. When the young hatch, the male brings food to the brooding female who then feeds the young. This continues for seven to eight days, after which both male and female feed the young directly. Four young were fed by three adults at an average rate of 22 times per hour, but this rate appears unnaturally high. Bussmann (1934) recorded a feeding rate for two young, 14 to 23 days of age, of only 1.9 times per hour.

Family: PHOENICULIDAE. In the wood-hoopoe, *Rhinopomastus cyanomelas,* Hoesch (1933a) observed nesting behavior after the young hatched. For the first day or so the female continued to stay in the nest, and the male brought food for her and the young; thereafter both adults sought food and brought it to the young about three times per hour.

Suborder: BUCEROTES; *Family:* BUCEROTIDAE. The hornbills are unique in that the female, with the male's help, plasters up most of the entrance of her nest hole after entering, and remains throughout the period of egg-laying, incubation, and at least part of the young's developmental period (Table 42). The total length of this time varies from six to eight weeks in *Tockus (Lophoceros) deckeni* to as long as four months in *Bycanistes brevis.* During all this time the female and her young are fed by the male through a small opening in the plastered wall. In the genus *Tockus* the female undergoes a sudden and complete molt while confined in the nest, but this is not generally true of the family as a whole (Moreau and Moreau 1940). The incubation period is probably about 40 days long in *B. brevis* and 28 to 36 days in various species of *Tockus.* The females of *Tockus,* unlike *Bycanistes,* break out of their nest 2 to 4 weeks before the young are ready to leave and aid the male in bringing food to the young until they are fully grown. Although the male *Bycanistes'* trips to the nest are not frequent, he commonly regurgitates as many as 25 items of fruit on a single trip. *Tockus* males, on the other hand, are more insectivorous and bring only a morsel at a time. North (1942) observed the male *Tockus (Lophoceros) erythrorhynchus* feeding its mate at the rate of 30 to 40 times per hour. This may be the reason why the females of this genus leave the nest sooner and assist in the searching of food for the young. Hoesch (1933) noted in *Tockus (Lophoceros) flavirostris* that the male supplied the female and two young with food for the first several days after hatching. Later the female left the nest to feed the young almost alone at the rate of twice per hour, with the male taking part only occasionally in the evenings. Furthermore, a brood of *Bycanistes* may consist of only one or two young birds, while the brood size in various species of *Tockus* varies from two to six (Moreau 1937, Moreau and Moreau 1941).

Summary. The basic behavior pattern in this order is for both the male and female to share more or less equally in nest building, incubation, brooding, and feeding the young. The attentive behavior pattern in the Upupidae and the Bucerotidae has evolved at a tangent, and in the Bucerotidae this tangent has become developed to an extreme. In a wide variety of families, including the Upupidae, belonging to different orders, the male often brings food to the incubating female who does all the incubation. In the Bucerotidae, however, the male brings all her food, and she is confined to the nest for periods of one and a half to four months. Along with this confinement has developed the special behavior of plastering shut all but a narrow crevice of the entrance hole, complete molting of feathers in the female while in the nest cavity in at least certain species, the male exclusively feeding the female and the young during the early part of their nest life, and other modifications of normal behavior.

Order: Piciformes

There are two suborders. The suborder, Galbulae, is further subdivided into three superfamilies containing five families. The suborder, Pici, however, contains but the one family.

Suborder: GALBULAE; *Superfamily:* GALBULOIDEA; *Family:* GALBULIDAE. Skutch (1937a) has the only available information on this family (Table 43). In the black-chinned jacamar he found the female taking the lead in excavating the kingfisher-like nest burrow in the ground, but the male later assumed nearly equal share of the duties. They worked for long periods, and the male fed the female at frequent intervals. Both sexes shared incubation, brooding, and feeding the young on nearly equal terms, except that the female was the one on the nest at night. Since the two sexes alternated on the nest during the day, the female secured most of her own food.

Family: BUCCONIDAE. Observations are available at only one nest of a puffbird, that of *Notharchus pectoralis* (Skutch 1948c, Table 43). Both sexes excavated the nest cavity in a tree at a leisurely rate, although one sex was more active than the other. The three eggs are laid at intervals of 2 days. Both sexes share incubation duties; the attentive periods are irregular in length, varying from 7 to 162 minutes; and during the seven hours of observation the eggs were covered only 70 per cent of the time.

Superfamily: CAPITONOIDEA; *Family:* CAPITONIDAE. In the prong-billed barbet, *Semnornis frantzii,* Skutch (1944b) found both sexes participating in nest building, incubation, and feeding the young (Table 43). This is the only study of attentive behavior that has been found for this group. Moreau (personal communication) states that there is a tendency for some African barbets to approach the habits of *Melanerpes* (pp. 227, 231).

Family: INDICATORIDAE. The trait of parasitism has developed in this small tropical family of honey guides, in at least *Indicator indicator* and *I. minor* (Groebbels 1937).

Superfamily: RAMPHASTOIDEA; *Family:* RAMPHASTIDAE. In addition to studies on toucans made by Van Tyne (1929) and Skutch (1944a), given in Table 43, H. O. Wagner (1944) has a little information on *Aulacorhynchus prasinus*. In both genera, *Aulacorhynchus* and *Ramphastos*, the sexes share the duties of incubation, brooding, and feeding the young, although Wagner did not observe the male feeding the young. When brooding two newly hatched young, Wagner states that "at each such visit it remained inside some 20 or 30 minutes, which is about the same length of time that it stayed away from the nest looking for food." Skutch found only one parent in the nest at night during incubation and through most of the nestling period. In two subspecies of aracaris, *Pteroglossus torquatus*, however, male and female may sleep in the nest cavity before the eggs are laid; during incubation a single parent attends the eggs at night; but after the nestlings hatch, both parents sleep with them. The long nestling period compared with the incubation period is worth noting for this family.

Suborder: PICI; *Family:* PICIDAE. Both sexes participate in the excavating of the nest, although to a variable extent. In *Melanerpes (Centurus) carolinus*, the red-bellied woodpecker, S. V. Wharram (personal communication) watched nest building for 16 days and found that the birds worked about 15 minutes at a period. Schuster (1936b) found *Dendrocopus (Dryobates) minor* working in periods of 30 minutes, and Steinfatt (1940) observed the male *D. medius* working in periods of 9 to 23 minutes. Skutch (1948) recorded *Melanerpes chrysauchen* excavating the burrow in 30-minute periods. In *Dendrocopos (Dryobates) major* (Pynnömen 1939), *D. medius* (Steinfatt 1940a), *D. minor* (Schuster 1936, Labitte 1945), *D. martius* (Niethammer 1938), *D. pubescens* (Thoms 1927), *Sphyrapicus thyroideus* (Michael 1935), *Picus canus* (Bussmann 1944), *P. viridis* (Steinfatt 1944a), and *Melanerpes rubricapillus (Centurus subelegans)* (Skutch 1943) the male does most of this work. Eygenraam (1947) reports that nest building in *Dryocopus martius* lasts almost a month. At first both sexes share equally in the task, but later the male works alone. Niethammer (1938) states that in *Picus viridis* 14 days are required to excavate the nest cavity.

Both sexes take turns during the daytime in incubating the eggs. The attentive periods commonly vary from one and a half to two and a half hours in length; in *Melanerpes chrysauchen* and in *Dendrocopos major*, the periods average only 23 minutes (Table 43). *D. major* may sometimes adhere to the time rhythm of other Picidae as Tracy (1938) found the adults changing places about every two hours. In *C. principalis* Tanner (1942) found the female relieving the male on the eggs between 0535 and 0730 hours in the morning and the male retiring in the evening between 1530 and 1745 hours. This allows an active day of only about

10 hours. During the day the female incubated 6.5 hours and the male 3.5 hours, the sexes relieving each other on the eggs eight times. According to Eygenraam (1947), the female *D. martius* takes only three attentive periods per day, 1.5 to 3.0 hours each. Likewise in *Picus canus* the female is attentive only in the morning and in the afternoon, the male is on the eggs during the middle of the day and at night (Bussmann 1944). The male *D. medius* is more attentive to incubation than the female (Steinfatt 1940a).

There is nearly unanimous agreement, and Skutch (1933b) has discussed the fact, that the male incubates at night. One exception is that Bussmann (1941) and Steinfatt (1941b) found the female *Jynx torquilla* on at night. In *Melanerpes chrysauchen, M. cruentatus, M. pucherani, Picumnus olivaceus,* and *Picumnus aurifrons (lafresnayei),* both the male and female spend the night on the nest. In these cases it is probably the male that actually sits on the eggs. The general rule in other orders is for the female to incubate at night. Since in woodpeckers the male and female both sleep in cavities throughout the year, and since the male is usually the more energetic in making fresh cavities, Skutch (1943) suggests that his cavity is the one the female selects for the nest and he simply keeps on using it at night. Observations of Sherman (1910) on *Colaptes auratus* support this contention in that male and female roosted in separate but similar boxes before egg-laying but nested in the box that the male had used.

The incubation period in many woodpeckers is short, 11 to 14 days. It is longer in large species, as the pileated, *Ceophloeus pileatus* (18 days—Hoyt) and ivory-billed, *Campephilus principalis.* Likewise in the genus *Picus,* Niethammer (1938) gives it as 15-17 days in *viridis* and Bussmann (1944) gives it as 18 days in *canus.* The usually short incubation period contrasts with a long period for the young to remain in the nest, 19 to 35 days. Both adults share in the feeding of the young, but the male is often more active in this duty than the female. In addition to the data in Table 43, the following rates of feeding have been recorded: *Dendrocopos (Dryobates) minor*—21.0 per hour (Pynnönen 1939), 5.3 per hour (Steinfatt 1939d), 8.0 per hour (Haverschmidt 1938); *D. medius*—5.0-13.7 per hour (Steinfatt 1940); *D. major*—9.0 per hour (Haverschmidt 1938), 24 per hour (Tracy 1933), 6.0 per hour (Ris 1936); *D. leucotus*—6 per hour (Franz 1937), 2.0 per hour (Pynnönen 1939); *D. pubescens*—29.8 per hour (Thoms 1927); *Picoides arcticus*—9.6 per hour (England 1940); *Picus viridis* and *P. canus*—1+ per hour (Bussmann 1933, 1944, Steinfatt 1944a); and *Sphyrapicus varius*—10.9 per hour (R. A. Johnson 1947), 15.9 (Shirling 1927). Owen (1925) found *D. major* feeding young 20 times per hour with occasional inattentive periods of 30 minutes. Gebhardt (1940) recorded an exceptional case in *Dryocopus martius* when only the female fed the young, in which she averaged 0.6 times per hour over 16 days of nest life.

Leach (1925) and Ritter (1938) have described the very unusual communal behavior of *Melanerpes (Balanosphyra) formicivora.* These birds occur in small flocks throughout the year, and several birds may roost together in the same cavity. Only one bird, however, stays on the eggs at night. Three, four, or five birds of both sexes may work in relays at excavating the nest hole, incubating, and feeding the young. If this is not true communal breeding, then it may be that a nesting pair is simply being assisted by unmated, possibly immature, birds of both sexes. The behavior of *Picumnus lafresnayei* may represent a stage of evolution toward communal behavior not quite so far advanced as in *M. formicivora.* Skutch (1948b) describes how one male and two females roosted in the nest hole that contained two eggs. During the day the male and at least one female took turns at incubation.

Summary. In this order the male usually takes a preponderant part in nest building, incubation, brooding, and feeding the young. At least in the Picidae he also does most of the incubating and brooding at night. The basic pattern is an alternation of male and female in all the nesting duties, and it is probable that the evolutionary trend toward a greater male load is from an older, more equal division of duties. The reason for believing this is that in *Galbula,* the genus lowest in the taxonomic series, the female takes the lead in nest building, incubates at night, and the two sexes share nearly equally in incubating the eggs during the day, while in *Dendrocopos,* and possibly *Dryocopus,* which are near the top of the taxonomic series, the relation is reversed. Eygenraam (1947) states that in *Dryocopus martius* the female takes the leading role in courtship which is in harmony with the reversed role of the sexes.

Dendrocopos represents an advanced development of the behavior pattern in other ways. This genus has the short nesting period of 34 days from the time the eggs are laid until the young fly. The incubation period is only 12 days and is correlated with short attentive periods. The genus has some of the most rapid feeding rates in the entire order. In general, the behavior pattern approaches that of the next and highest order, the Passeriformes. It should be noted, however, not only in this genus but also in the Picidae and Ramphastidae, in general, that short incubation periods are joined with long periods for the young to stay in the nest.

Order: Passeriformes

This is the largest order of birds and the most highly advanced and specialized. Four suborders are recognized. There are no data available on the suborder, Eurylaimi, with its single family of broadbills. In the

TABLE 43. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Proportion by sexes: Male	Nest building: Proportion by sexes: Female	Nest building: Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Order: PICIFORMES; Family: GALBULIDAE								
1. Black-chinned jacamar	*Galbula ruficauda (melanogenia)*	Skutch, 1937a	...	+	+++	...	4	...
Family: BUCCONIDAE								
2. Black-breasted puffbird	*Notharchus pectoralis*	Skutch, 1948c	17	++	++	10	3	...
Family: CAPITONIDAE								
3. Prong-billed barbet	*Semnornis (Dicrorhynchus) frantzii*	Skutch, 1944b	8	++	++	...	4–5	...
Family: RAMPHASTIDAE								
4. Toucan	*Ramphastos sulfuratus (brevicarinatus)*	Van Tyne, 1929	...	...	...	...	1–4	1–4
5. Blue-throated toucanet	*Aulacorhynchus prasinus (caeruleogularis)*	Skutch, 1944a	...	...	...	...	3–4	2
Family: PICIDAE								
6. Wryneck	*Jynx torquilla*	Bussmann, 1941	...	...	...	...	7–10	...
7. Wryneck	*Jynx torquilla*	Steinfatt, 1941b	0	0	0	0	8	7–8
8. Olivaceous piculet	*Picumnus borbae (olivaceus)*	Skutch, 1948b	...	++	++	...	2–3	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 43 *(cont.)*. Summary of attentive data by species.

			Nest building				Egg-laying	
Common name	*Scientific name*	*Reference*	Duration (days)	Proportion by sexes: Male	Proportion by sexes: Female	Time from completion to first egg (days)	Number of eggs	Time incubation begins, egg
9. Yellow-shafted flicker	*Colaptes auratus*	See pp. 99-101	7–21	++	++	...	5–8	4–5
10. Golden-naped woodpecker	*Melanerpes (Tripsurus) chrysauchen*	Skutch, 1948d	...	++	++	...	3	...
11. Black woodpecker	*Dryocopus martius*	Pynnönen, 1939	14	++	++	...	5	4
12. Great spotted woodpecker	*Dendrocopos (Dryobates) major*	Steinfatt, 1937c	...	...	...	...	6	4
13. Great spotted woodpecker	*Dendrocopos (Dryobates) major*	Pynnönen, 1939	12	+++	+	...	6	4
14. Ivory-billed woodpecker	*Campephilus principalis*	Allen & Kellogg 1937, Tanner, 1942	8–14	++	++	...	...	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 43 (*cont.*). Summary of attentive data by species.

Common Name	*Incubation*: Duration (days)	*Incubation*: Proportion by sexes: Male	*Incubation*: Proportion by sexes: Female	*Incubation*: Male feeds female	*Incubation*: Attentive periods (min.)	*Incubation*: Inattentive periods (min.)	*Feeding young in nest*: Duration (days)	*Feeding young in nest*: Number of young	*Feeding young in nest*: Age of young (days)	*Feeding young in nest*: Trips per hour: Male	*Feeding young in nest*: Trips per hour: Female	*Feeding young in nest*: Trips per hour: Total
1	19–20	++	++	+	145	160	20	4	. . .	++	++	. . .
2	. . .	++	++	0	58	83	. . .	. . .	. . .	. . .	. . .	. . .
3	13	++	++	+	36.6	45.2	. . .	. . .	. . .	++	++	. . .
4	. . .	++	++	0	20–60	. . .	45	4	23	1.6	1.2	2.8
5	16	++	++	0	37.9	49.7	43	2	42	++	++	4.0
6	13	++	++	0	132.3	132.3	21	. . .	4–23	++	++	8.8
7	13	++	++	0	94.0	131.3	22–23	8	10–18	+++	+	9.0
8	14	++	++	0	58	58	24	. . .	. . .	++	++	. . .
9	11	++	++	0	147.0	160.0	26	. . .	1, 14, 18, 20	++	++	3.2
10	. . .	++	++	0	23.8	28.6	33–34	3	14	++	++	20.0
11	12	+++	+	0	122.1	122.8	27	. . .	4–23	++	++	1.4
12	12	+++	+	0	15	7	21–23	5	3–22	+++	+	9.9
13	12	+++	+	0	22.5	32.3	22	. . .	2–19	+++	+	12.6
14	. . .	++	++	0	87.4	88.8	35	1	19	++	++	2.2

Key: . . . No information is available. 0 No time or activity is nvolved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

suborder, Tyranni, there are two superfamilies. Information is not available on seven of the thirteen families. There are data on one of the two families of the suborder, Menurae. In the large suborder of songbirds, Passeres, there is no breakdown into superfamilies, and this group is represented by data on 34 families. Fifteen families are not included. Some families have been divided into subfamilies, but these are indicated only in the Fringillidae where there are enough data available to permit some reliable estimation of their significance in the analysis of behavior patterns.

Suborder: TYRANNI; *Superfamily:* FURNARIOIDEA; *Family:* DENDROCOLAPTIDAE. Skutch's (1945a) observations on the nesting behavior of the allied woodhewer (Table 44) show that both adults participate in nest building, incubation, brooding, and feeding the young. For a time after hatching, brooding is nearly continuous, but as the young mature, it decreases in amount during the day but continues at night until the young are 12 days old. In the wedge-billed woodhewer, *Glyphorhynchus cuneatus,* both sexes also alternate at incubation, but in the Carriker dendrocincla, *Dendrocincla anabatina,* no more than one bird has been seen participating in any phase of nest life.

Family: FURNARIIDAE. Alexander F. Skutch has kindly supplied me with unpublished data on the attentive behavior of this family. Much of this material is summarized in Table 44. Apparently both sexes participate in nest building. This was also observed in *Furnarius leucopus* and *Cranioleuca erythrops.*

Both sexes commonly share incubation, brooding, and feeding the young, although at one nest of *P. boissonneautii* only the female was observed to do so. Eighteen hours observation were taken during the incubation period of *A. ochrolaemus.* The six attentive periods ranged from 62 to over 138 minutes in duration. Five attentive periods were measured during six hours observation of *P. boissonneautii,* and these varied from 3 to 93 minutes. During ten hours with *S. brachyura* the male had nine attentive periods ranging from 4 to 44 minutes, and the female had eight periods ranging from 18 to 44 minutes. During five hours spent with *S. erythrothorax,* the three attentive periods of the male ranged from 14 to 18 minutes and the six periods of the female ranged from 6 to 40 minutes. Nine hours were spent with *X. minutus* where the nine attentive periods varied from 12 to 118 minutes. Finally, in *S. quatemalensis* four attentive periods during six hours ranged from 54 to 74 minutes in length.

Skutch states that the nestling period in this family commonly ranges from 13 to 29 days. In addition to the species listed in Table 44, he found two feathered nestlings of *Rhopoctitis rufo-brunneus* to be fed 11 times in four hours or at the rate of 2.8 times per hour. The rates of feeding given in Table 44 are based on only three or four hours observation in each case.

Family: FORMICARIIDAE. Skutch (1945b) writes: "Antbirds as a rule take long sessions on the eggs, male and female replacing each other infrequently. Even the smaller species often sit for two or three hours without interruption; and once I watched an antpitta *(Grallaria perspicillata)* incubate for five hours without a break. At least in those species in which the sexes can be distinguished, the male usually takes somewhat longer sessions on the eggs by day than the female; but the female sits through the night."

Gross (1927) recorded that in the spotted antbird, *Hylophylax naevioides,* and spotted-crowned ant-vireo, *Dysithamnus puncticeps,* the two sexes alternate at incubation duties and in the latter species the attentive periods likewise are long, being two or three hours throughout the day.

In 90 hours observation at nine nests of nine different species, each with two young between 1 and 9 days of age, Skutch (1949a) found the rate of feeding by the two parents to be 1.3 to 5.3 times per hour. He (1945d) records incubation periods for various species between 14 and 17 days and nestling periods between 9 and 13 days. It is unusual to have nestling periods so much shorter than incubation periods. Data for four species are compiled in Table 44.

Superfamily: TYRANNOIDEA; *Family:* COTINGIDAE. The few observations on *Platypsaris aglaiae* and *Tityra semifasciata,* mostly made by Skutch (Table 44), indicate that the male sometimes aids the female in nest building and regularly feeds the young, but only the female incubates the eggs and broods the young. He (1945) gives an incubation period of 18 to 19 days for *Pachyramphus polychopterus* and in three other species indicates that the nestling period is at least 19 days long. In a personal communication he indicates that the nestling period may extend to 25 days in this family.

Family: PIPRIDAE. Skutch (1949c) has the only study of attentiveness in this family (Table 44). An interval of 3 or more days occurs between the laying of the two eggs. This slow reproductive rate is further shown by the long incubation period, the long attentive and inattentive periods, and the very low feeding rate. In a personal communication he gives the incubation period as 19 to 21 days for this family and the nestling period, 13 to 15 days.

Family: TYRANNIDAE. Bent (1942) has summarized the data for North American flycatchers and some detailed data are presented in Table 44. From 3 to 10 days are used in nest building. The female does most of this work (see also Tinkham 1949), but the male occasionally aids in some species. All recent studies indicate that the female is solely responsible for incubation of the eggs, yet in the earlier literature there is frequent reference to the male sharing these duties in several species. Further attention should be directed to this point. The male has been observed feeding the female in *Sayornis saya, Empidonax wrighti,* and *Contopus cinereus,* in addition to those listed in Table 44. The incubation period varies rather widely between the various genera of this family from 18-19 days in the tropical *Megarhynchus* to 12-13 days in *Contopus* and *Tyrannus.*

Normally only the female broods the young after hatching, but both sexes feed the young in many species. Skutch writes me that the male apparently takes no part in nesting in *Myiobius, Pipromorpha, Rhynchocyclus, Oncostoma, Onychorhynchus,* and *Terenotriccus,* except that in *Onychorhynchus* he guards the nest. The male may occasionally stand on the nest rim and shade the young from the sun in *T. tyrannus* and *E. minimus.* This family is remarkable in the fast rates at which the young are fed. In addition to those listed, Saunders (1938) recorded a rate of 24 feedings per hour of two young in *E. minimus* and Lawrence (1948a) found the same rate at another nest; Bent (1942) gives 24 feedings per hour for *E. difficilis,* 30 feedings per hour in *E. traillii,* and 14 feedings per hour in *Myiarchus cinerascens.* Fitch (1950), however, found three to four young *Muscivora forficata* fed only 1.7 times per hour by the male and 5.1 times per hour by the female. Since all these species are flycatchers in habit as well as in name, probably the amount of food they bring to the young on each visit is small, hence the large number of trips they usually need to take. Lawrence (1948) observed the adults bringing only one fly per trip during the first four days, but later four to five flies per trip.

Megarhynchus has a very slow rhythm for the entire nesting cycle, including a 2- or 3-day interval between laying of successive eggs. In writing about the black-tailed myiobius, *Myiobius atricaudus,* Gross (1927) states:

> As is the case with many birds in the Tropics, this flycatcher frequently left the eggs for long periods of time during the warmer hours of the day, but she always faithfully brooded them at night. So far as I could determine only one bird, probably the female, did the work concerned in rearing the brood . . . the incubation period of eggs was 21 days, whereas the flycatchers in the temperate regions hatch in much less time. . . . Further the time spent by the young of this species in the nest was three weeks. . . .

Suborder: MENURAE; *Family:* MENURIDAE. Tregellas (1931) states that only the female lyrebird, *Menura* sp., is concerned with nest building, incubation, and raising of young. This is verified by Ward (1939). About a month is required to build the nest and the one egg is not laid for another week or two. Incubation begins after still another week. Ward (1940) found that 28 days were required to hatch a fresh egg under

Table 44. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Nest building: Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Order: PASSERIFORMES; Family: DENDROCOLAPTIDAE								
1. Allied woodhewer	*Lepidocolaptes affinis*	Skutch, 1945a	...	++	++	...	2	...
Family: FURNARIIDAE								
2. Chiriqui automolus	*Automolus ochrolaemus*	Skutch, letter	...	...	...	...	3	...
3. Pseudocolaptes	*Pseudocolaptes boissonneautii*	Skutch, letter	...	...	...	...	...	...
4. Sooty spine-tail	*Synallaxis brachyura*	Skutch, letter	...	++	++	...	2	...
5. Rufous-breasted spine-tail	*Synallaxis erythrothorax*	Skutch, letter	...	++	++	...	4	...
6. Xenops	*Xenops minutus*	Skutch, letter	...	++	++	...	2	...
7.	*Sclerurus guatemalensis*	Skutch, letter	...	++	++	...	...	...
Family: FORMICARIIDAE								
8. Slaty ant-shrike	*Thamnophilus punctatus*	Skutch, 1934	...	...	...	...	2	...
9. Ant-thrush	*Formicarius analis*	Skutch, 1945b	...	...	...	...	2	...
10. Spotted antbird	*Hylophylax naevioides*	Skutch, 1946b	...	9.5	6.5	...	2	...
11. Black ant-wren	*Myrmotherula axillaris*	Skutch, 1946b	...	++	++	...	2	...
Family: COTINGIDAE								
12. Xanthus becard	*Platypsaris aglaiae*	Bent, 1942	14+	10.4	19.2	...	4–6	...
13. Costa Rica tityra	*Tityra semifasciata*	Skutch, 1946a	...	+	+++	...	2	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 44 (*cont.*). Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Family: PIPRIDAE								
14. Yellow-thighed manakin	*Pipra mentalis*	Skutch, 1949c	...	0	7.2	...	2	...
Family: TYRANNIDAE								
15. Kingbird	*Tyrannus tyrannus*	Springer (MS)	...	...	...	...	...	...
16. Kingbird	*Tyrannus tyrannus*	Goodell (MS)	...	...	...	...	...	...
17. Kingbird	*Tyrannus tyrannus*	Herrick, 1905	...	...	...	...	...	...
18. Sulphur-bellied flycatcher	*Myiodynastes luteiventris*	Bent, 1942	...	...	...	...	...	...
19. Streaked flycatcher	*Myiodynastes maculatus*	A. O. Gross, 1950	8	0	++++	1	3	3
20. Crested flycatcher	*Myiarchus crinitus*	See pp. 101-02	10	+	+++	...	4	3
21. Phoebe	*Sayornis phoebe*	See pp. 102-09	3–10	0	++++	...	4–6	3–5
22. Least flycatcher	*Empidonax minimus*	Muirhead (MS)	...	...	...	...	...	...
23. Gray flycatcher	*Empidonax wrighti*	Russell & Woodbury, 1941	3	...	6	1	3	3
24. Wood pewee	*Contopus (Myiochanes) virens*	See pp. 109-11	...	...	14	3	3	...
25. Boat-billed flycatcher	*Megarhynchus pitangua*	Skutch, 1951	6–14	0	9	9	2–3	2–3

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

Table 44 (*cont.*). Summary of attentive data by species.

Common Name	*Incubation* Duration (days)	Number periods per hour: Male	Number periods per hour: Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	*Feeding young in nest* Duration (days)	Number of young	Age of young (days)	Trips per hour: Male	Trips per hour: Female	Trips per hour: Total
1	15(?)	1.8	1.8	0	26.7	32.5	19	2	1–8	++	++	4.8–14.6
2	18–20	++	++	0	96.8	...	18	3	2, 12–13	++	++	3, 4.2
3	...	0	++++	0	44.0	...	...	...	...	0	++++	...
4	18	++	++	0	29.3	...	14–15	...	...	++	++	...
5	17	++	++	0	21.6	...	14–15	...	...	++	++	...
6	15–17	++	++	0	49.8	...	13–14	2	5–6	++	++	2
7	...	++	++	0	59.3	...	...	2	2–3, 14	++	++	2.5, 5
8	...	++	++	0	34–131	...	...	2	5.6	1.5	1.0	2.5
9	...	++	++	0	109–180	...	...	...	...	...	...	...
10	15(?)	0.3	0.3	0	111	126	11	2	...	++	++	...
11	16	0.3	0.3	0	79	99	8	2	4	1.8	1.5	3.2
12	...	0	2.9	0	12.0	8.5	...	...	...	++	++	...
13	...	0	1.1	0	37.1	19.6	21+	...	...	++	++	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 44 *(cont.)*. Summary of attentive data by species.

Common Name	*Incubation* Duration (days)	Number periods per hour Male	Number periods per hour Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	*Feeding young in nest* Duration (days)	Number of young	Age of young (days)	Trips per hour Male	Trips per hour Female	Trips per hour Total
14	19(?)	0	0.5	0	110.6	22.0	...	2	8–9	0	1.2	1.2
15	...	0	1.8	0	23.1	10.5	16	2	0–15	2.7	5.9	8.6
16	...	...	...	...	...	...	17	4	2–14	5.3	7.1	12.4
17	12–13	...	...	...	...	...	18	...	10	9.2	12.5	21.7
18	15–16	0	2.4	0	17.0	8.5	...	...	...	...	...	...
19	15	0	...	0	49.0	60.3	18+	...	...	++	++	...
20	14	0	1.7	+	21.3	13.0	15–18	3(?)	3–18(?)	1.4	3.9	5.3
21	16	0	3.9	0	8.8	6.4	17	4	0–17	++	++	35.0
22	...	0	2.6	0	15.5	7.2	12–14	3	2–13	22.4	11.4	33.8
23	14	0	++++	0	14.3	...	16	3	7	++	++	7.5
24	12–13	0	2.3	+	19.6	6.8	15–18	3	0–12	0.4	4.1	4.5
25	18–19	0	0.9	0	56.8	11.6	24	1	5–19	++	++	3.7

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

a domestic hen. Feathers are added to form a nest lining during incubation. The young leave the nest at six weeks of age.

Suborder: PASSERES; *Family:* ALAUDIDAE. There has been a neglect of detailed studies of attentive behavior in this family. According to Forbush (1927), three days are required for nest building in *Eremophila (Otocoris) alpestris.* Sutton (1932) states that only the female builds. This is true also in *Alauda arvensis* (Lebeurier and Rapine 1935). Usually three to five eggs make up the set, and the incubation period averages 11 or 12 days in most genera of the family. Criddle (1917) reports in horned larks that the male shared the incubation duties with the female, but this is questionable as other observers record it as exclusively the duty of the female, not only in horned larks but also in some other genera (Pickwell 1931, Lebeurier and Rapine 1935, DuBois 1936, Lovell 1944, Witherby *et al.* 1938). Sutton found that the female horned lark had regular periods on and off the eggs, although the male occasionally brought her food. Niethammer (1937) records that in *Lullula arborea* also the male feeds the incubating female. Both parents share in feeding the young which remain in the nest 11 or 12 days, sometimes less. Steinfatt (1939b) found the average feeding rate for four young, 4 to 9 days old, to be 5.9 per hour. Hartley (1946) found in the Asiatic race of *Galerida cristata* that four attentive and inattentive periods of the incubating female averaged 11.4 minutes and that both adults fed five young, 7 to 10 days old, eight times per hour. He found the young leaving the nest at 8 to 11 days of age. Bourke (1947) found the average feeding rate of two young between 3 and 9 days old to be 7.1 times per hour. He also mentions that the male, as well as the female, incubates.

Family: HIRUNDINIDAE. Considerable study has been made of attentive behavior of the swallows, especially by Moreau in Tanganyika, Africa. His data are presented in a manner not easily transposed into the tables here used. Some of the averages given here were calculated from his figures. It should be noted that in *Psalidoprocne holomelaena* the sexes are indistinguishable, and while Moreau does not state which sex is the one that carries on the nesting duties, it is given in Table 45 as the female.

In a detailed study of *H. rustica,* Purchon (1948) estimates that a thousand trips are required to build the nest. The male helps in the early stages of nest building, but the female is responsible for the nest lining. Nest building is more energetic in early morning, decreasing from 26.5 trips per hour to the nest between 0600 and 0800 hours to 4.5 trips per hour between 1600 and 2000 hours.

Observational data, not only in the species indicated in the table but also in *Hirundo abyssinica* and *Ptyonoprogne rufigula* (Moreau 1939a), and in *Hirundo javanica* (Ali 1949), show both male and female sharing incubation. Reports of others indicate that the same is true of our North American barn swallow as well as the European race (Table 45). However, our own data obtained with a thermocouple in the nest showed only one bird, presumably the female, incubating both in *Hirundo rustica* and *Progne subis.* The male occasionally came and stood over the eggs in the nest but did not apply heat to them. Purchon (1948) made similar observations on the male. E. M. Davis (1937) observed that the male *H. rustica* did not have a well-developed brood patch. In *H. smithii,* the male may occasionally perch on the side of the nest during incubation. Moreau writes me, however, that he has one unpublished record of a nest where the male sat on the eggs an appreciable proportion of the time. Only the female incubates in *Progne chalybea* (Skutch). One gets the impression that in this family the behavior pattern for incubation is in a state of flux. It may well be that the original pattern for the family was for the male and female to share about equally in all phases of nesting duties. From this there has been an evolutionary trend to a behavior pattern in which the female alone does all of the actual incubating although some males may still attend the nest on occasion while the female is inattentive. If this conjecture is accepted, then the incubating behavior of *Hirundo, Progne,* and *Psalidoprocne* is the most advanced in the family from the evolutionary point of view. According to Niethammer (1937), the male *H. rustica* and *D. urbica* may occasionally feed the incubating female. In *P. holomelaena,* a further development of the behavior pattern is suggested in the lack of evidence of the male participating not only in incubating and brooding but also in feeding the young. This phylogeny is not in harmony with that proposed by Mayr and Bond (1943). They consider genera nesting in natural hollows or cavities the most primitive, such as *Progne, Iridoprocne,* and probably *P. holomelaena;* while those that excavate their own nest burrows in the ground are more advanced, such as *Riparia,* as are also those that use mud in building their nests, as *Hirundo* and *Delichon.*

According to data compiled by Allen and Nice, north temperate species commonly lay from four to six eggs per set, tropical species two or three. These authors also show that in two north temperate species where the female alone incubated, she spent an average of 70 per cent of the daytime on the eggs, while in three tropical species the average was only 56 per cent. In four species where both sexes shared incubation, 87 per cent of the daytime was spent on the eggs.

The nestling period in swallows in general is relatively long. This may be correlated with the need to develop good flying ability before leaving the nest.

Moreau writes me that the long nestling period of *P. holomelaena* may be correlated with the probability that the young get no care from the parents after leaving the nest. The slow rhythm in the species is also evident in the slow rate of feeding and the long incubation period, but perhaps this is not unusual for a tropical species. If the behavior pattern has evolved in this family to prolong the period of time that the parents are required to be in attendance at the nest and to shorten the period of care after the young become fully fledged, this is contrary to the general trend over the class of Aves as a whole.

Purchon observed an increase in the rate of feeding as the young became older, but in cold rainy weather the rate decreased even to the extent of bringing death to the nestlings at two nests that he had under observation. A few additional observations on rate of feeding the young may be cited. Beyer (1938) found in one full day of observation of two young *Riparia riparia,* 13 days old, that the average feeding rate was only 7.7 times per hour. In similar observations by R. O. Wagner (1941) on three young 2 weeks old, the rate was 9.5 times per hour. However, these slow rates are not substantiated by the other records given in the table. Edson (1943) found in the violet-green swallow, *Tachycineta thalassina,* a high rate of feeding of about 30 times per hour during the morning hours but with a decline in rate during the middle of the day, and states that the nestling period is rather long, 23 or 24 days. Shirling (1927) recorded only 17.3 feedings per hour in one all-day observation of this species.

R. H. Brown (1940b) found that a brood of four young *H. rustica,* 15 days old, were fed at the rate of 27 times per hour, which agrees well with our other data. However, the rate of 46.5 per hour for a nestfull of 11-day-old young, reported by Emmet (1944), is high. Bent (1942) quotes an all-day record of feeding of four young *D. urbica* which averages 21.6 per hour. Witherby *et al.* (1938) record the nestling period for *H. rustica* at 21 days and for *Delichon urbica* at 19 to 22 days.

Family: ORIOLIDAE. Only a few pertinent observations are available for the Old World orioles. Niethammer (1937) and Witherby *et al.* (1938) state that both sexes in *Oriolus oriolus* share in nest building. Three or four eggs are laid and incubation lasts 14 to 15 days. During incubation the male relieves the female during the middle of the day. Both adults participate in feeding the young, and the nestling period is apparently only 14 to 15 days.

Family: CORVIDAE. There seem to have been considerable casual observations on the attentive behavior of species in this family with very few comprehensive studies (Table 45).

One study of *Perisoreus canadensis* presented a very unusual development of attentive behavior with two birds not only participating in the incubation duties but doing so simultaneously with one bird sitting on the eggs and the other bird sitting on it. Either bird was on top or underneath and attentive periods averaged 38 minutes (Lawrence 1947). However, this behavior is probably not typical, as Warren (1899) recorded incubation and brooding only by one female. Warren found the incubation period at one nest to be 17 to 18 days. Four half-grown young were timed as being fed by both parents at four times per hour.

The observations of D. J. Nicholson (1936) that in *Cyanocitta cristata* both male and female participate in nest building, incubating, and care of the young, and that the male will feed the female are supported by data given by Bent (1946). One may doubt, however, if the part of the male in incubation is extensive. The incubation period is 17 to 18 days, and the nestling period is 17 to 21 days. Murray (1947) believes that incubation begins with the first egg in *C. cristata*. In *Aphelocoma (Cyanocitta) coerulescens*, Amadon (1944b) reports only the female incubating. A. O. Gross (1949) observed two birds participating in incubating duties in the Mexican jay, *A. ultramarina* but was not sure of their sexes. In this species incubation begins with the first egg and lasts 18 days. The nestling period is 25 days.

In species of magpies, *Pica pica* and *P. nuttalli*, the male aids in nest building, but the female does most, if not all, of the incubation. The male feeds the incubating female in *P. nuttalli* (Linsdale 1937 and in Bent 1946, Evenden 1947).

In the nutcrackers, *Nucifraga columbiana* (J. B. Dixon 1934) and *N. caryocatactes* (Witherby *et al.* 1938) only the female incubates, although Dixon believes the male shared equally with the female in brooding the young. Both sexes feed the young. Witherby *et al.* for *Garrulus glandarius* and Ali (1949) for *G. bispecularis* record that incubation may be by both female and male. In *Pyrrhocorax pyrrhocorax* incubation is by the female (Schifferli and Lang 1940). In this latter species the nestling period is 37 to 40 days. Hosking (1942) found incubation to begin with the last of a six-egg set in *G. glandarius* and to be 16 days long.

In the ravens and crows, only the female incubates in *C. frugilegus* (Yeates 1932), *C. corone* (Kuhk 1931), *C. cornix*, and *C. monedula* (Bent 1946, Witherby *et al.* 1938) and in *C. brachyrhynchos* and *C. corax* (Table 45), although the male is sometimes at the nest when the female is absent. Nethersole-Thompson and Musselwhite (1940) describe one incident where the male *C. frugilegus* appeared to take his turn at incubation. Both adults share in feeding the young. Yeates observed in *C. frugilegus* that the male brought all of the food until the young were 13 days old. The feeding rate averaged 2.4 per hour.

There are repeated observations in *Psilorhinus* (Skutch 1935), *Calocitta* (Skutch, personal communication), *Cyanocitta, Aphelocoma, Pica, Corvus, Nucifraga,* and *Pyrrhocorax* that the male feeds the female during incubation either on or off the nest whether or not he also shares in

TABLE 45. Summary of attentive data by species.

Common name	Scientific name	Reference	*Nest building* Duration (days)	Trips per hour Male	Trips per hour Female	Time from completion to first egg (days)	*Egg-laying* Number of eggs	Time incubation begins, egg
Family: HIRUNDINIDAE								
1. Tree swallow	*Iridoprocne bicolor*	Kuerzi, 1941	14	+	+++	...	...	...
2. Bank swallow	*Riparia riparia*	Stoner, 1936; Stoner & Stoner, 1941	...	++	++	...	...	...
3. Bank swallow	*Riparia riparia*	Moreau & Moreau, 1939b	...	...	...	...	...	...
4. Rock swallow	*Riparia rupestris*	Prenn, 1937	...	...	...	...	...	...
5. Barn swallow	*Hirundo rustica erythrogaster*	See pp. 111-17	6–9	+	+++	1–3	3–5	2–3
6. Barn swallow	*Hirundo rustica rustica*	Moreau & Moreau, 1939c	...	...	...	...	...	...
7. Barn swallow	*Hirundo rustica rustica*	DeBraey (see Nice 1947)	8	+	+++	...	...	...
8. Barn swallow	*Hirundo rustica rustica*	Purchon, 1948	6–10	+	+++	3	4	4
9. Wire-tailed swallow	*Hirundo smithii*	Moreau, 1939c	...	...	...	...	...	...
10. Purple martin	*Progne subis*	See pp. 117-19	...	+	+++	...	...	...
11. House martin	*Delichon urbica*	Moreau & Moreau, 1939c	...	...	...	...	...	...
12. Rough-wing bank martin	*Psalidoprocne holomelaena*	Moreau, 1940	...	...	...	...	...	...
Family: CORVIDAE								
13. Florida jay	*Aphelocoma (Cyanocitta) coerulescens*	Amadon, 1944b	5–6	++	++	2	2–4	1
14. Raven	*Corvus corax*	Harlow, 1922	14–18	+	+++	3–7	4–5	4–5
15. Crow	*Corvus bachyrhynchos*	C. T. Black (MS.)	7+	++	++	...	4.5	3

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 45 *(cont.)*. Summary of attentive data by species.

Common Name	*Incubation* Duration (days)	Number periods per hour: Male	Number periods per hour: Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	*Feeding young in nest* Duration (days)	Number of young	Age of young (days)	Trips per hour: Male	Trips per hour: Female	Trips per hour: Total
1	15	+	3.0	0	10.9	9.3	18–20	...	1–18	19.2	12.6	31.9
2	14–16	++	++	0	...	...	18–22	3–5	2–10	++	++	17.1
3	...	1.1	1.1	0	26.7	26.7	...	3.3	13+	++	++	33.7
4	14	+	3.6	0	11.6	5.2	25–26	4.0	4–10	++	++	30.0
5	14–15	0(?)	2.3	0	15.8	10.6	18–20	...	7–10	++	++	40.0
6	...	2.4	2.4	0	10.0	15.5	...	3.2	3–20	++	++	23.2
7	14	0	4.8	0	8.9	3.6	22	3–5	6, 11, 16	...	...	32.8
8	15	0	3.7	0	11.4	4.8	20	4	1–20	++	++	33.1
9	14	0	6.1	0	5.5	4.3	18–21	2.0	13–19	11.0	13.3	24.3
10	15–16	0	1.5	0	32.8	9.3	28–36	3.7	2–35	++	++	18.7
11	...	++	++	0	7–15	7–15	...	3	10–11	++	++	37.7
12	18–19	0	1.9	0	16.4	15.3	24–27	1.8	1–25	0(?)	++++	4.5
13	...	0	1.5	+++	34.7	4.7	...	...	0–15	++	++	4
14	20	0(?)	++++	+++	...	...	28	...	...	++	++	...
15	19	0	0.6	++	94.0	4.0	27	...	2–10	++	++	1.7

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

incubation. Apparently this male-feeding-female behavior is well established in this family. This results in very short inattentive periods in such species as *C. brachyrhynchos.* Harlow (1922) states that the female leaves the nest only two or three times daily in *C. corax.*

An unusual development in this family is that of communal nesting and incubation in the white-winged chough, *Cocorax melanorhamphus,* of Australia (Knowlton 1909). Some communal behavior is also developed in *Aphelocoma ultramarina* where seven or eight birds may work at building one nest (A. O. Gross 1949). It is uncertain whether the two birds observed alternating at incubation were the male and female or possibly two females. Skutch (1935) also reports communal behavior in *Psilorhinus mexicanus.*

According to Amadon (1944a) the jays are the most primitive group of Corvidae both in structure and in habits. There is some indication of this relationship in their attentive behavior, since the male may share in incubation in some species of jays, while in the crows the behavior pattern has become more specialized, with the female doing all of this work.

Family: PARADISEIDAE. Rand (1938, 1940) has made behavior studies of birds-of-paradise. In *Macgregoria pulchra* the female apparently did all of the nest building, although the male accompanied her back and forth on her trips to the nest, as he often did also during incubation and brooding. The female does all the incubation of the eggs; two attentive periods were 15 and 17 minutes in duration and two inattentive periods were 10 minutes each. The female brooded the young for four periods of 7 to 14 minutes each. Both adults participate in feeding the young in the nest. During one early period when the female was brooding part of the time the male fed the young 10.9 times per hour and the female 2.0 times. In another species, *Diphyllodes magnificus,* the male was not observed participating in the duties of reproduction after courtship had terminated. In a third species, *Manucodia ater,* only the female was observed to incubate but the male brooded the young, and it is believed that he would also have incubated had it not been for the disturbance of the observer's presence. Both sexes feed the young. The attentive periods of the incubating female varied between 21 and 51 minutes and her inattentive periods between 5 and 51 minutes. At one nest the incubation period was between 14 and 18 days.

Dharmakumarsinhji (1943) observed in *Paradisea apoda* in captivity that the female was solely responsible for building the nest, incubating the one egg during the 13- to 15-day period, and feeding the young. The nestling period was 31 days. The female was a close sitter on the egg, leaving for inattentive periods of 5 to 10 minutes only, two to four times per day. The female was observed to drive the male away from the vicinity of the nest.

In the satin bowerbird, *Ptilonorhynchus violaceus*, P. A. Gilbert (1939) and Chaffer (1945) found that the female alone builds the nest, incubates, and cares for the young. Chaffer remarks that "most male birds, which habitually use a definite area for display, do not attend the nest." Gilbert states that 18 to 19 days are required for the incubation of the two eggs and that the young remain in the nest for 17 to 19 days. The female incubates closely but leaves for a half-hour inattentiveness before 0700 and again after 1600 hours.

Family: PARIDAE. In 13 species of *Parus (Penthestes, Baeolophus)* of the subfamily Parinae, (Table 46, Bent 1946, Witherby *et al.* 1938), evidence is ample that both male and female share in nest building. These species mostly nest in holes that have to be excavated, so several days are usually required for this and for the construction of the actual nest with materials brought in from the outside. In *P. cristatus*, however, Ross (1935) found that the male did not participate. The female required 6 days for excavation and another 6 days to build the nest. One day elapsed before the first egg was laid. Witherby (1934) observed both sexes working at nest excavation in *P. atricapillus* with periods of attentiveness of less than 10 minutes to 50 minutes and periods of inattentiveness of 10 minutes to over an hour. Usually the female does all the incubation of the eggs, but observations indicate a possibility that the male may share this activity in *P. carolinensis* and *P. atricristatus* (Bent 1946). Without a thermocouple record, there is doubt about this. The male feeds the incubating female not only in *P. atricapillus*, *P. coeruleus*, and *P. major* (Delmée 1940), but also in *P. ater*, and *P. cristatus* (Witherby *et al.*). In all species, both male and female feed the young. In 13 days of continuous recording with the terragraph, Bussmann (1940b) found in *P. ater* that nine young were fed 7,743 times or at an average of about 33 times per hour. Gibb (1950) recorded in *P. major* an average rate of feeding 9.5 young throughout nest life of 430 per day or about 25 per hour. In *P. hudsonicus* Eleanor R. Pettingill (1937) found both sexes sharing equally in feeding seven young 3 days old at an average all-day rate of 24.3 times per hour. Butts (1931) reported for *Parus (Penthestes) atricapillus* a nearly equal share by male and female in feeding seven young, 8 to 11 days old, at an average rate of 25.6 per hour. Kendeigh observed six young *P. bicolor*, 1 to 5 days old, brooded in attentive periods of 23 minutes and fed by both parents 3.6 times per hour. The attentive pattern is much the same in *Aegithalos caudatus*, and in *Panurus biarmicus*, except that in the former species the male occasionally shares incubation duties, and in the latter species he supposedly does so regularly (Niethammer 1937).

In the verdin, *Auriparus flaviceps,* belonging to the subfamily Remizinae, the male builds several nests and the female lines the one of her choice. The female feeds the young by regurgitation for the first five days, after which both adults conduct feeding in the normal manner (Bent 1946). In *Remiz pendulinus* Merkel (1932) and Steinfatt (1934a) found also that the male did most of the nest building while the female did all the incubation and feeding of the young. When the young were 4 to 5 days old, Steinfatt observed them being fed 33 times per hour. Merkel reported the nestling period as 15 to 20 days.

The male bush-tit, *Psaltriparus minimus,* of the Psaltriparinae, appears to share all nesting duties about equally with the female. However, he does not develop a brood patch as does the female. This lends doubt as to whether he actually sits on the eggs or applies very much heat to them if he does. All nests in this family are enclosed, so that his behavior inside the nest has not been directly observed. In this bush-tit, both adults are in the nest cavity at night (Addicott 1938), and this is true also of *P. melanotis* (Skutch 1935).

Family: SITTIDAE. Both sexes participate in nest building (Venables 1938), only the female incubates and broods, the male feeds the female on the nest, and both sexes share in feeding the young (Table 46). Bent (1948) gives the incubation period as 12 days.

Family: CERTHIIDAE. There has been very little study of reproductive behavior of the Certhiidae. Brewster (1879) and Tyler (1914) found in *Certhia familiaris americana* that only the female is involved in nest building and incubation but that both adults are about equally concerned with feeding the young. However, in *C. f. zelotes,* Grinnell and Storer (1924) state that the male as well as the female aids in gathering nest material. Tyler, and also Niethammer (1937), report that the male feeds the female during nest building and incubation. In *C. f. britannica* both sexes are concerned in building the nest and the male may take some share in incubation. In *Tichodroma muraria,* the male brings nest material, but the female does most of the work. She also does the incubating, and as in *C. familiaris* both sexes feed the young (Witherby *et al.* 1938). The incubation period is about 15 days and the nestling period between two and three weeks. Williams (1949) has recently recorded 19 or 20 days for the nestling period.

Family: CHAMAEIDAE. The wren-tit, *Chamaea fasciata,* differs in behavior from many other passerine birds in that both sexes share nearly equally in all phases of nest life (Erickson 1938, Table 46).

Family: TIMALIIDAE. The babbling thrushes are sociable or gregarious birds in their activities. Small flocks in some species will combine activities and all concentrate on building the same nest until several are built. Likewise they will often share in feeding the young (Knowlton 1909,

TABLE 46. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Nest building: Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Family: PARIDAE								
1. Black-capped chickadee	*Parus (Penthestes) atricapillus*	Odum, 1941	6+	0	++++	2	7	6
2. Great tit	*Parus major*	Kluijver, 1950	...	...	...	0	7–10	7–13
3. Marsh-tit	*Parus palustris*	Steinfatt, 1938d	...	0	++++	...	...	...
4. Blue tit	*Parus coeruleus*	Pullen, 1946	25	+	+++	...	11	11
5. Plain titmouse	*Parus inornatus*	K. L. Dixon, 1949	...	+	+++	0	6.8	...
6. Bush-tit	*Psaltriparus minimus*	Addicott, 1938	33	++	++	0	...	...
Family: SITTIDAE								
7. White-breasted nuthatch	*Sitta carolinensis*	Butts, 1931	...	...	...	...	...	...
8. Red-breasted nuthatch	*Sitta canadensis*	Gunderson, 1939	...	++	++	...	...	...
9. European nuthatch	*Sitta europea*	Steinfatt, 1938e	17	++	++	...	...	...
10. European nuthatch	*Sitta europea*	Bussmann, 1943	...	...	...	...	...	...
Family: CHAMAEIDAE								
11. Wren-tit	*Chamaea fasciata*	Erickson, 1938	3–8	7.5+	7.1+	1–3	3–4	3
Family: CINCLIDAE								
12. Water ouzel	*Cinclus cinclus*	Eggebrecht, 1937	...	0	++++	1	4–5	...
Family: TROGLODYTIDAE								
13. House wren	*Troglodytes aedon*	See pp. 14-92	2–3+	2	8	0–1	5–7	4–6
14. European wren	*Troglodytes t. troglodytes*	Kluijver *et al.*, 1940	...	+++	+	...	5–7	5–7

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 46 (*cont.*). Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Egg-laying: Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
15. Bewick wren	*Thryomanes bewickii*	Laskey, 1946	...	...	...	3	6.6	6.6
16. Bewick wren	*Thryomanes bewickii*	E. Miller, 1941	10+	2.1	4.5	...	6	6
17. Carolina wren	*Thryothorus ludovicianus*	Nice and Thomas, 1948	5	52	34	...	5	5
18. Carolina wren	*Thryothorus ludovicianus*	Laskey, 1948	...	++	++	...	5	5
Family: MIMIDAE								
19. Catbird	*Dumetella carolinensis*	See pp. 120-25	7	+	+++	3	4	3
20. White-breasted blue mockingbird	*Melanotis hypoleucus*	Skutch, 1950	...	0	++++	...	2	...
21. Brown thrasher	*Toxostoma rufum*	Gabrielson, 1912	...	...	...	...	...	...
22. Brown thrasher	*Toxostoma rufum*	Erwin, 1935	3–5	11.0	14.6	...	...	...

Common Name	Incubation: Duration (days)	Number periods per hour: Male	Number periods per hour: Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	Feeding young in nest: Duration (days)	Number of young	Age of young (days)	Trips per hour: Male	Trips per hour: Female	Trips per hour: Total
1	13	0	1.9	++	23.3	7.8	16	...	1, 13	5.8	4.6	10.4
2	14	0	1.7	++	26.9	9.4	19–21	6–10	0–20	12.3	10.0	22.3
3	13–15	0	1.3	0	37.9	7.1	17–20	7	8–9	7.3	5.7	13.0
4	13.5	0	3.0	++	15.0	5.0	20–21	11	2, 7, 14, 16	++	++	34.5

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+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 46 (*cont.*). Summary of attentive data by species.

	Incubation						*Feeding young in nest*					
		Number periods per hour								Trips per hour		
Common Name	Duration (days)	Male	Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	Duration (days)	Number of young	Age of young (days)	Male	Female	Total
5	14–16	0	1.6	++	28.5	8.5	21	...	1, 6, 11, 17	++	++	14.2
6	12	++	++	0	10.0	10.0	14	...	...	...	...	...
7	...	0	++++	++	...	...	...	...	1.7	11.5	6.8	18.4
8	...	0	0.4	++	...	23.8	...	...	...	++	++	...
9	16	0	1.4	++	31.1	11.3	22	6	2, 15	...	...	11.9
10	...	...	...	...	...	...	24	6	4–22	...	...	17.5
11	15–16	0.6	0.6	0	47.2	47.2	15–16	3+	1–12	4.0	4.8	8.8
12	...	0	1.5	++	30.9	8.2	23	...	9, 23	8.3	17.6	25.9
13	14	0	2.9	0	12.1	8.5	15–16	3.8	0–16	++	++	14.0
14	14.5–17.5	0	++++	...	...	...	16–18	...	...	+	+++	...
15	...	0	++++	+	17.5	12–63	...	...	...	...	...	...
16	...	0	++++	...	...	...	...	...	...	...	...	...
17	14	0	0.5	++	86.1	31.2	13–14	5	0–14	4.5	4.5	9.0
18	14–15.5	0	0.7	0	57.5	33.5	12–15	2.6	1–13	++	++	5.6
19	13	0	2.0	0	22.7	7.0	10–12	3	1–11	++	++	8.1
20	...	0	2.2	...	20.8	7.1	14–15	...	...	++	++	3.6
21	...	...	...	...	...	...	12–13	4	6–11	5.6	8.5	14.2
22	12–13	+	+++	...	...	...	11	...	0–12	1.7	2.2	3.9

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

Armstrong 1947). This trait is not universal, however. McNamara (1935) states that in the spine-tailed log-runner, *Orthonyx temminckii,* the female does all the nest building, incubation, and care of the young in the nest. The male will feed the female during her inattentive periods away from the nest and will also help feed the young after they leave the nest. There are two eggs per set and incubation lasts about three weeks. According to Ali (1949), both sexes share in nest building and incubation in *Leiothrix lutea* and *Mesia argentauris.*

Family: CINCLIDAE. Eggebrecht (1937) observed only the female building the nest in *C. cinclus aquaticus,* but Witherby *et al.* (1938) report both sexes participating in *C. c. gularis.* Likewise in the latter subspecies the male rarely fed the incubating female, which occurred regularly in the former. Witherby *et al.* give the incubation period as 16 days and the nestling period, 19 to 24 days. Cordier (1927) records only the female brooding the four young which she fed at an average rate of 8 times per hour. The male fed the young 0.8 times per hour.

Family: TROGLODYTIDAE. In the wren family (Table 46), the male's nest-building drive is overdeveloped and supernumerary nests are made in at least the following species: *Troglodytes aedon* (Kendeigh 1941c), *T. t. troglodytes* (Kluijver *et al.* 1940), *Telmatodytes palustris* (Welter 1935), *Cistothorus platensis* (Bent 1948), *Campylorhynchus (Heleodytes) brunneicapillus* (Antevs 1947), and *Thryomanes bewickii* (Edwin V. Miller 1941). He takes no part in incubation but usually aids in feeding the young.

Stanwood (Bent 1948) did not observe the male winter wren *(T. troglodytes hiemalis)* taking part in nest building nor feeding the young while in the nest, but he apparently assisted in their care afterward. Likewise, in another race of the winter wren, *T. t. alascensis,* Heath (1920) did not find the male participating in nest building, but he did feed the young in the nest. It is doubtful if this lack of nest building on the part of the male holds true for *T. t. pacificus,* and it certainly is not the case in *T. t. troglodytes.* In this last subspecies, however, many males do not feed the brood either before or after they leave the nest. In *T. t. islandicus,* the male built the rough part of the nest and, at some nests at least, helped to feed the young (Armstrong 1950). More observations are needed on the various subspecies of this wren as to the parental role of the male.

The male occasionally feeds the incubating female in *Thryomanes bewickii* (Laskey 1946), in *Thryothorus ludovicianus* (Nice and Thomas 1948), in *Troglodytes rufociliatus* Skutch (1940), and in *Salpinctes obsoletus* and *T. troglodytes hiemalis* (Bent 1948). The incubation period is long in *T. t. troglodytes* (14.5 to 17.5 days, Kluijver *et al.* 1940) and in several tropical species (15 to 19 days, Skutch 1945). Heath (1920), in

T. t. alascensis, found the attentive period during incubation to be 18 to 21 minutes long and the inattentive period, 2 to 5 minutes.

The average rate of feeding in *Cistothorus platensis (stellaris)* has been determined over short periods as 12.1 times per hour by Walkinshaw (1935) and only 4.5 times per hour by Mousley (1934b); in *Thryomanes bewickii,* M. B. Skaggs (Bent 1948) measured it at 19.2 times per hour; and in *T. t. troglodytes,* Marples (1939) gives data for several days in the nestling life of two birds being fed entirely by the female parent an average 18 times per hour, while an editorial comment mentions observations of feeding nestlings by both adult parents at the rate of 15.3 times per hour.

Family: MIMIDAE. In *Dumetella, Mimus,* and in *Nesomimus* (Venables 1940), the male participates in nest building and in feeding the young in the nest (Table 46). In *Dumetella, Melanotis,* and *Nesomimus* only the female incubates, but in *Mimus* the male may occasionally share to some extent. In *Toxostoma* and in *Oreoscoptes* the male regularly shares in incubation and in brooding the young (Bent 1948).

Family: TURDIDAE. The female thrush is almost entirely responsible for nest building, incubating, and brooding, but both adults feed the young (Table 47). The bluebirds show a tendency away from the typical behavior of Turdidae in that the male feeds the incubating female on the nest and occasionally participates in nest building and incubation (Bent 1949). Feeding of the female has also been observed in *Oenanthe oenanthe* (Mildenberger 1943), *Turdus torquatus* (Wenner 1930), and *T. migratorius.* Haecker (1948) found in *Sialia currucoides* that incubation began with the last egg of the set, which is the rule also with *S. sialis.*

In the several European members of this family, the incubation period is commonly 13 or 14 days. In all species the female takes the preponderant part in incubation, but the male supposedly helps on occasion. In the redwing, *Turdus musicus,* he may do so more regularly (Niethammer 1937). Marples and Gurr (1943) give the average attentive period of the female *Turdus merula* as 30 minutes and the inattentive period as 8 minutes. Both sexes help to feed the young which commonly stay in the nest for 12 to 15 days (Witherby *et al.* 1938). The female *O. oenanthe* may have attentive periods of two hours and inattentive periods of 8 to 15 minutes (Mildenberger 1943), and *Phoenicurus phoenicurus* attentive periods of 12 to 45 minutes and inattentive periods of 6 to 16 minutes (J. Buxton 1950).

Shirling (1927) recorded in *Sialis mexicana* an average all-day feeding rate of 21.5 per hour. Observations by Bussmann (1940a) on *P. phoenicurus* show averages of about 130 feedings per day when the young were in their second day, 400 feedings on the ninth day, and 240 feedings on the fifteenth day. Buxton (1950) used an automatic recorder on a nest with five young and obtained an average of 19.3 per hour for five to 16 days, and quotes Salmen for a record of 25.4 feedings per hour for six young 13 days old. Ruiter (1941) found in this species that feeding began 39 minutes before sunrise and ended 15 minutes after sunset. A brood of seven young were fed by both parents 150 times on the first day and 248 times on the seventh day. C. B. Ashby (1942) found the average rate of feeding three young *P. ochrurus* throughout nest life by both parents to be 7.6 per hour. Lack and Silva (1949) found in *Erithacus rubecula* an average feeding rate of 13.8 times per hour for broods of three to seven young, 7 to 14 days old. Steinfatt (1937a) recorded a rate of 13.4 per hour for six young in this species 2 days before leaving the nest, and an average rate of 19.8 per hour for five young *Saxicola rubetra* during their last 3 days in the nest. E. M. Nicholson (1930) records the feeding rate of a nestful of young *Oenanthe oenanthe* at 28 per hour when 4 to 6 days old and 49 per hour when full grown. We have already noted (p. 138) an average feeding rate throughout the nestling period in *Hylocichla guttata* of 8.1 per hour. For the first 3 days after hatching, brooding periods averaged 7.7 minutes. Ali (1949) records the male sharing nest building, incubation, and care of young in Indian species of *Enicurus, Kittacincla, Geokichla, Monticola, Saxicola,* and *Myiophoneus.*

Family: SYLVIIDAE. This family is predominantly one of Europe and Asia (Table 47). According to Witherby *et al.* (1938), the female does most of the nest building, but the male may often take part. In a few species the male builds cock nests, one of which the female may line and use. The number of eggs per set varies commonly from four to six in different species. May (1947) found in *Phylloscopus trochilus* that only the female built the nest, although the male usually accompanied her, that the incubation period was commonly 13 to 14 days long, and that the nestling periods in three instances were 14, 15, and 16 days. In nearly all of the 25 species discussed by Witherby *et al.* the male is reported to share to some extent in the incubation duties. Niethammer (1937) records the female doing all or nearly all the incubating in *Phylloscopus,* and Yamashina (1938) reports only the female incubating in several species in eastern Asia. Rarely the male may feed the incubating female. In *Hippolais icterina,* Neumann (1940) recorded the male feeding the female every one-half to one hour. Her attentive periods were then 40 to 65 minutes and her inattentive periods 8 to 15 minutes. In *Sylvia atricapilla* attentive periods average 27.5 minutes (Steinfatt 1942). Howard (1914) recorded both sexes of *Acrocephalus scirpaceus* alternating on the eggs at an average interval of 18 minutes, and Hosking and Smith (1943) found the rhythm to be 15 minutes, but Brown (1946) found the female incubating much more than the male. The incubation period varies usually from 12 to 15 days, and the nestling period 9 to 14 days.

Both sexes may feed the young, but the female is usually the more energetic.

Steinfatt (1939a) found five young *Phylloscopus trochilus,* 5 and 8 days old, fed at an average rate of 11.0 times per hour, nearly equally by both sexes. In 1938 Treuenfels reported six nestling *P. collybita,* 1 to 6 days old, fed only by the female and only five times per hour, but in 1940 he found a nestful of young fed 21.6 times per hour by both adults. Bussmann (1932) recorded the feeding of five young "Drosselrohrsänger" *(Acrocephalus arundinaceus)* by both parents on four scattered days at 9.5 per hour. Schweppenburg (1941) gives a record of 28 feedings per hour for three young *A. palustris,* 9 and 10 days old. Steinfatt (1940d) reports the feeding rate of five young *Sylvia curruca,* 7 to 10 days old, participated in by both sexes, to average 15.8 per hour, five young *Sylvia nisoria,* 9 and 10 days old, to average 19 per hour (1938a), and four young S. *atricapella* 7 days old about 10 times per hour (1942). His report that the nestling period of S. *communis* was only 9 days (Table 47) is unusual, but he claims that the birds were undisturbed.

The subfamily, Polioptilinae, gnatcatchers, is represented by records on only one species in Table 47. The male in this species, and also in *Ramphocaenus* (Skutch), shares nearly equally with the female in nest building and incubation as well as feeding the young. Weston (Bent 1949) indicates an unusual situation in *Polioptila caerulea,* in that nest building regularly precedes egg-laying by the long interval of 10 to 14 days. Apparently this delay is not due to unfavorable weather as occasionally happens in other species. He finds the incubation period to be 13 days. Apparently the two sexes do not always share equally in incubation duties, as at some nests the female does it alone. There are some observations also of the male feeding the incubating female. The nestling period is 10 to 12 days. Weston reports one series of observations over seven hours of two adults which fed the young at an average rate of 33 times per hour. Myers (1907) found three young gnatcatchers being fed at rates on different days from 17 to 46 times per hour.

Although not usually noted, periods of attentiveness and inattentiveness occur in nest building and in the feeding of the young as well as in incubation. During attentiveness the birds bring nest material or food at short intervals while during inattentiveness there is a pause when the birds take food themselves and rest. H. E. Howard (1914:14-15) and Nice (1932:21-22) described such periodicities for the wood warbler and blue-gray gnatcatcher, respectively.

Family: REGULIDAE. There are no data available for North American kinglets, but in Europe Witherby *et al.* (1938) report that in *Regulus regulus* both sexes are involved in nest building, the female incubates the seven to ten eggs for 14 to 17 days, and both parents feed the young

TABLE 47. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Family: TURDIDAE								
1. American robin	*Turdus migratorius*	See pp. 125-34	2–6	+	+++	3.5	3–4	2
2. Fieldfare	*Turdus pilaris*	Steinfatt, 1941c	...	...	...	...	5–6	5–6
3. Wood thrush	*Hylocichla mustelina*	See pp. 134-37	5	...	...	...	3–4	2–3
4. Olive-backed thrush	*Hylocichla ustulata*	Stanwood, 1913	...	...	...	...	3–4	...
5. Gray-cheeked thrush	*Hylocichla minima*	Wallace, 1939	...	0	++++	...	...	...
6. Bluebird	*Sialia sialis*	See pp. 140-43	4–12	+	+++	1–8	3–6	3–6
7. Mountain bluebird	*Sialia currucoides*	Criddle, 1927	...	0	++++	...	6	...
8. Nightingale	*Luscinia luscinia*	Steinfatt, 1939c	...	0	++++	...	...	...
Family: SYLVIIDAE								
9. Chiff-chaff	*Phylloscopus collybita*	Steinfatt, 1938f	...	0	++++	...	...	...
10. Chiff-chaff	*Phylloscopus collybita*	Prenn, 1936	6–10	0	++++	1	6	6
11. Willow warbler	*Phylloscopus trochilus*	Kuusisto, 1941	5–6	+	+++	0	5–8	6
12. Wood warbler	*Phylloscopus sibilatrix*	Steinfatt, 1937d, 1939a	...	0	++++	...	...	...
13. Wood warbler	*Phylloscopus sibilatrix*	Treuenfels, 1937	2–3	0	++++	1–2	...	...
14. Mountain warbler	*Phylloscopus bonelli*	Prenn, 1932; Heilfurth, 1934	7	0	++++	1	5	5
15. Reed warbler	*Acrocephalus scirpaceus*	P. E. Brown, 1946; Brown & Davies, 1949	4.5	+	+++	0	4	3
16. Marsh warbler	*Acrocephalus palustris*	H. E. Howard, 1914	...	0	++++	...	...	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 47 *(cont.)*. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
17. Icterine warbler	*Hippolais icterina*	Steinfatt, 1940b	...	++	++	...	...	...
18. Whitethroat	*Sylvia communis*	Steinfatt, 1940d	...	...	...	...	6	5
19. Blue-gray gnatcatcher	*Polioptila caerulea*	Nice, 1932	...	13.5	19.2	....	...	...
Family: MUSCICAPIDAE								
20. Pied flycatcher	*Muscicapa hypoleuca*	Nöhring, 1943	4–8	+	+++	....	4–5	4–5
21. Restless flycatcher	*Sisura inquieta*	N. L. Roberts, 1942	6–7	++	++	...	...	...
22. Paradise flycatcher	*Tchitrea perspicillata*	Moreau, 1949a	...	++	++	...	...	...
Family: PRUNELLIDAE								
23. Hedge sparrow	*Prunella modularis*	Steinfatt, 1938b	...	...	...	...	3–4	2–3

Common Name	Incubation: Duration (days)	Number periods per hour: Male	Number periods per hour: Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	Feeding young in nest: Duration (days)	Number of young	Age of young (days)	Trips per hour: Male	Trips per hour: Female	Trips per hour: Total
1	12.4	0	1.9	+	24.1	7.4	13	...	0–13	++	++	6.4
2	...	0	1.1	0	49.6	5.7	12–14	...	7, 12	++	++	6.5
3	12	0	1.3	0	34.2	10.2	12–13	3	...	++	++	6.6

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TABLE 47 (*cont.*). Summary of attentive data by species.

	Incubation						Feeding young in nest					
Common Name	Duration (days)	Number periods per hour: Male	Number periods per hour: Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	Duration (days)	Number of young	Age of young (days)	Trips per hour: Male	Trips per hour: Female	Trips per hour: Total
4	12	0	++++	...	...	...	10–12	4	1–4	++	++	7.7
5	13–14	0	++++	0	10–15	10(–)	12–13	4	5	++	++	8.6
6	14	0	2.3	+	14	12	18	1	6–16	++	++	5.5
7	14	0	++++	++	...	...	...	...	...	10.4	5.7	16.1
8	...	...	...	...	...	...	9–10	5	3, 8	4.3	4.0	8.2
9	15	0	1.4	0	34.4	8.2	13–14	...	8–9	0	13.4	13.4
10	15–16	0	3.6	...	11.0	5.5	14–15	...	0–15	0	16.0	16.0
11	13–17	...	++++	...	...	...	13–14	...	0–14	++	++	15.0
12	12–14	0	++++	0	31	8	...	...	...	++	++	...
13	...	0	++++	0	45–80	...	12	6	0–11	12.2	13.2	25.4
14	14	0	0.9	0	55.2	12.5	12–13	...	7–10	++	++	21.5
15	11–12	+	+++	0	6–8	...	10–12	...	0–12	5.8	9.7	15.5
16	12	++	++	0	30	30	10–14	...	...	++	++	3–12
17	13	0	0.9	++	60.0	6.7	13–14	...	...	++	++	...
18	12	1.4	1.4	0	20.3	23.3	9	5	1, 9	5.4	4.8	10.2
19	...	1.1	1.1	0	25.8	28.9	...	...	...	10.0	7.2	17.2
20	11–15	0	0.7	++	86.7	4.8	...	5	0–10	++	++	8.0
21	...	3.5	3.5	...	17.2	17.2	...	4	...	++	++	25.0
22	12–13	1.7	1.7	0	30–40	30–40	11	2.7	2–11	++	++	6.2
23	11–12	0	1.4	+	29.7	14.6	13	3	1–12	2.4	2.7	5.1

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

for 18 to 20 days. S. Bergman (1937) found that about midway through the nestling period, the young at one nest were fed at an average all-day rate of 17.5 times per hour.

Family: MUSCICAPIDAE. Nest building may be shared by both sexes (Table 47), but the female is generally the more concerned (Witherby *et al.* 1938). In *Myiomoira toitoi,* she does it all and is fed by the male while she works (Wilkinson 1930). N. L. Roberts (1942) found both sexes of *Sisura inquieta* making 16.7 trips per hour during this process. There are three to seven eggs laid. Steinfatt (1937f) found that the incubating female *Muscicapa striata* had attentive periods of 46 to 59 minutes and inattentive periods of 5 to 8 minutes. R. H. Brown (1940a) found similar length of periods in this species and that the incubating female may be fed as often as four times per hour by the male. The male feeds the incubating female in *M. hypoleuca* at an increasing rate as incubation progresses up to 90 times per day on the eleventh day, but there is considerable variation between males (Nöhring 1943). Only the female incubates in *Muscicapa albicollis* (Witherby *et al.* 1938). Ecke (1938) found that the male *M. striata* may relieve the incubating female in periods of five to ten minutes in the hottest part of the day. Ryves (1943b) noticed the male regularly inspecting the eggs during the female's inattentiveness but not incubating them. In *Rhipidura leucophrys,* both sexes incubate in periods averaging 15.1 minutes (N. L. Roberts 1942). In *Terpsiphone viridis,* Hoesch (1938) found the male at one nest relieving the female on the nest from 0900 to 1200 and from 1600 to 1900 hours, but at other nests the attentive periods were shorter. Ali (1949) records both sexes sharing nest building, incubation, and care of young in *Eumyias thalassina, Niltava sundara,* and *Hypothymis azurea.* Jack (1949) claims that in *Pachycephala rufiventris,* the male shares in all phases of the nesting cycle except for nest building.

Jahn (1939) correlates the short nestling period of 10 days in *Terpsiphone atrocaudata* with the exceptionally small size of the nest. He found three young, 2 days old, fed 3.5 times per hour, and when they were 8 days old, 12 times per hour, mostly by the female. Both parents ordinarily feed the young in other species. Brown found the rate of feeding four young during the first 2 days after hatching to be 3.5 to 6.3 times per hour in *M. striata* and brooding periods to average about nine minutes. Steinfatt (1937f) found this rate increased to nearly 16 times per hour for four young during the last 3 days in the nest. In *M. parva,* both adults fed five young, 1 to 3 days before flight, at the rate of 10.4 times per hour (Steinfatt 1937b). N. L. Roberts (1942) reports a rate of 28.8 times per hour in *R. leucophrys* and S. Bergman (1934), a rate of 33.6 times per hour in *M. atricapilla* for five young on the day before leaving the nest. Nöhring found in *M. hypoleuca* the feeding rate for five young to increase from 50 times to 250 times per day from the first to the last day in the nest.

In *Miro australis* Richdale (1941c) credits nest building and incubation to the female, although the male brings food to her. Both parents feed the young. Both the incubation and nestling periods are unusually long, being 20 days in each case.

Family: PRUNELLIDAE. According to Witherby *et al.* (1938), only the female builds the nest in the hedge sparrow, *Prunella modularis.* Apparently the female does the incubation (Table 47). Niethammer (1937) gives the incubation period as 12 to 14 days and the nestling period as 13 to 14 days. In the alpine accentor, *P. collaris,* Witherby *et al.* state that the male participates in nest building and incubation as well as in feeding the young. This may also be true in *P. strophiata* (Ali 1949). The incubation period was 15 days for captive birds.

Family: MOTACILLIDAE. The attentive behavior pattern is different in the two genera representing this family. In wagtails, *Motacilla* sp., the female does most of the nest building, but the male may help. The male takes some turns at incubating in many species (Table 48, Witherby *et al.* 1938, Stuart Smith 1942), although Niethammer (1937) and Stuart Smith (1950) record that in *M. flava* and *M. alba* the female does most or all of it. Schuster (1941) gives the attentive period in *M. flava* as one-half hour and the inattentive period, five to ten minutes. In *M. cinerea* the average attentive period is 42.8 minutes (Eggebrecht 1939). Both adults feed the young. Incubation of the four to six eggs requires 12 to 14 days and the nestling period, 10 to 14 days. Ringleben (1935) observed for *M. flava* that six young were fed 15 times per hour when 5 days old, 37 per hour at 8 days, and only 21 per hour at 11 days, their last day in the nest.

In seven species of pipits, *Anthus* sp., the four to six eggs are incubated almost exclusively by the female for the required 13 to 14 days (Table 48). In *A. trivialis* the male may feed the incubating female, and this is apparently true also in *A. pratensis* and *A. cervinus* (Bent 1950). On two occasions, Harris (1933) observed the female *A. spragueii* to drive the male away from too close an approach to the nest when it contained young, and in *A. campestris* apparently only one adult feeds the young. This was also true of the three species of *Anthus* listed in Table 48. However, it is more usual for both adults to feed the young. H. S. Johnson (1933) found this true also in *A. spinoletta,* contrary to Table 48, with the six young fed 5.4 times per hour when one day old increasing to 11 to 12 times per hour when 5 and 6 days old, but at much slower rates during later nest life. In *A. spragueii* the male was observed with young after they had left the nest. The young spend 13 to 16 days in the nest.

Family: BOMBYCILLIDAE. Only one species, the cedar waxwing, *Bom-*

bycilla cedrorum, has sufficient data to be representative (Table 48). The male takes an active part in all the nesting activity. W. A. O. Gross (1929) and A. A. Allen (1930) state that the male shares incubation with the female, but according to other observers this is not usually the case. The male, however, feeds the female at or near the nest at frequent intervals so that her attentive periods are long and her inattentive periods are short. At times the female may sit so long without leaving that the usual attentive rhythm becomes lost (p. 144).

Family: PTILOGONATIDAE. In the single representative of this family for which information is available, *Phainopepla nitens,* both sexes share nesting duties, and the male may take the greater load in nest building, incubation, brooding, and feeding the young (Table 48). The female, however, sat on the nest at night in a single observation. Incubation begins with the first egg. According to information furnished by Gander (1927), the incubation period is 15 days and the young remain in the nest for 18 to 19 days. Myers (1908) recorded a feeding rate of 2.5 times per hour.

Family: ARTAMIDAE. The only observations found for this family are by D'Ombrain (1934) on the white-browed wood swallow, *Artamus superciliosus.* The male is chiefly responsible for building the nest and starts to incubate with the first of the two- or three-egg set. The two sexes exchange places on the eggs at frequent intervals, but it is the male who in most cases is on the nest at night. Both sexes feed the young.

Family: LANIIDAE. Although A. Miller (1931a, Bent 1950) gives no information on the male shrike, *Lanius ludovicianus,* participating in nest building, A. Johnson (1938) reports that at the nest construction he had under observation the male averaged about seven trips per hour, and that more than seven days were required to complete the nest. A two-day interval then occurred before the first egg was laid. In four species of European shrikes, Witherby *et al.* (1938) report both sexes participating in nest building, and in *L. collurio* the male apparently does most of it. Four to six days are required to build the nest in this species with only a one-day interval before the first egg (Schreurs 1941).

In *L. minor* and *L. excubitor,* both adults share the incubation duties with the female doing the major part; in *L. senator* and *L. collurio,* the male incubates only occasionally, but he feeds the female while she does this duty (Schreurs 1936). In *L. ludovicianus* the female apparently does all the incubation, and the male feeds her at frequent intervals. As a result her attentive periods may last up to 94 minutes, but average about 23 minutes (Johnson 1940). Schreurs (1941) says that the female may leave the nest for five- to ten-minute intervals. A. Miller (1931a) gives the incubation period as 16 days in this species. This one genus, therefore, shows in itself considerable evolution of the attentive behavior

TABLE 48. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Nest building: Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Family: MOTACILLIDAE								
1. African mountain wagtail	*Motacilla clara*	Moreau, 1949c	...	...	...	...	2–3	...
2. American pipit	*Anthus spinoletta*	Pickwell, 1947	...	...	...	1	...	...
3. Sprague pipit	*Anthus spragueii*	Harris, 1933	...	...	...	...	...	...
4. Tree pipit	*Anthus trivialis*	Steinfatt, 1941d	...	+	+++	...	4	4
Family: BOMBYCILLIDAE								
5. Cedar waxwing	*Bombycilla cedrorum*	See pp. 143-47	5–7	++	++	0–3	4–5	2–3
Family: PTILOGONATIDAE								
6. Phainopepla	*Phainopepla nitens*	Rand & Rand, 1943	...	20	2	1	3	1
Family: STURNIDAE								
7. Starling	*Sturnus vulgaris*	Kluijver, 1933	...	+	+++	0	...	...
8. Starling	*Sturnus vulgaris*	Marples, 1936	...	++	++	...	...	1–3

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 48 *(cont.)*. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Family: VIREONIDAE								
9. Bell's vireo	*Vireo bellii*	Nice, 1929	5	+	+++	0	4	3
10. Bell's vireo	*Vireo bellii*	Pitelka & Koestner, 1942	4–5	0	++++	0–1	3–4	1
11. Bell's vireo	*Vireo bellii*	Hensley, 1950	4–5	5.2	7.8	1	4	2
12. Yellow-green vireo	*Vireo flavoviridis*	Skutch, (Bent 1950)	. . .	0	++++	4	2–3	. . .
13. Red-eyed vireo	*Vireo olivaceus*	Katherine White, (MS)	. . .	. . .	. . .	. . .	. . .	. . .
14. Red-eyed vireo	*Vireo olivaceus*	L. de K. Lawrence, (MS)	. . .	. . .	. . .	. . .	. . .	. . .
15. Philadelphia vireo	*Vireo philadelphicus*	H. F. Lewis, 1921	. . .	. . .	. . .	. . .	4	1
16. Latimer vireo	*Vireo latimeri*	Spaulding, 1937	6	+	+++	. . .	. . .	. . .
Family: COEREBIDAE								
17. Flesh-legged honey creeper	*Cyanerpes cyaneus*	Skutch, letter	. . .	0	++++	. . .	2	. . .
18. Costa Rican diglossa	*Diglossa baritula*	Skutch, letter	. . .	0	++++	. . .	2	. . .

Key: . . . No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 48 *(cont.)*. Summary of attentive data by species.

Common Name	*Incubation* Duration (days)	Number periods per hour Male	Number periods per hour Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	*Feeding young in nest* Duration (days)	Number of young	Age of young (days)	Trips per hour Male	Trips per hour Female	Trips per hour Total
1	14	1.3	1.3	0	18.8	28	16	1.5	0–16	++	++	4.9
2	...	0	++++	...	...	...	...	4	...	0	12	12
3	...	...	...	...	...	...	10–11	...	4–11	0	11.4	11.4
4	14	0	0.8	+	48.0	26.5	...	4	2.7	0	3.6	3.6
5	12	+	1.4	+++	37.2	5.3	16	...	...	++	++	3.0
6	...	++	++	+	8.9	11.2	...	3	1.6	3.9	1.4	5.3
7	12	1.5	1.5	0	20	20	20–21	5.1	1+	+	+++	21.7
8	12	...	...	...	...	...	20–21	...	...	++	++	19
9	14	...	...	...	...	...	...	4	1–6	9.8	3.8	13.5
10	14	++	++	0	...	...	11	...	...	++	++	...
11	14	2.6	3.4	0	20.4	20.4	12	3	1, 3	5.6	4.4	10.0
12	14	0	...	0	26–38	9–16	12–14	...	...	++	++	...
13	...	0	1.1	0	37.6	14.9	10	3	0–10	2.2	1.7	3.9
14	...	...	3.0	...	14.5	5.2	...	...	...	...	...	...
15	14	++	++	0	10.5	10.5	12–14	4	4–7, 6–9	++	++	10.0
16	...	+	+++	0	...	...	...	...	...	+++	+	6.3
17	12	0	1.5	0	28.1	12.4	...	2	8–11	+	+++	13.2
18	14	0	2.0	0	19.1	10.5	...	2	2, 10	++	++	4.2, 5.2

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

pattern. In all species both sexes feed the nestling young, and their period in the nest is commonly 19 to 21 days, although in *L. collurio* Niethammer (1937) gives it as only 12 to 15 days.

Family: PRIONOPIDAE. Robinson (1947) states that both male and female magpie-lark, *Grallina picata,* work at nest building, incubation, and care of the young. While alternating at the incubation of the eggs, one set of observations gave an average of about 30 minutes for the length of the attentive period. N. L. Roberts (1942) gives the length of the attentive period on the eggs for *G. cyanoleuca* as 17.2 minutes and observed a brood of four young fed at the rate of 10.9 per hour. W. W. A. Phillips (1940) records both sexes alternating on the eggs in the pied-shrike, *Hemipus picatus,* and that both adults fed the young six to eight times per hour. In the grey shrike-thrush, *Colluricincla harmonica,* Gannon (1945), found that the male had attentive periods on the eggs up to 1.5 hours in length and the female up to 4 hours, although many periods were shorter. According to information compiled by Armstrong (1947), there is some communal nesting behavior in the helmet-shrikes, *Prionops poliocephala* and *P. pulmata.* In the white-crowned shrike, *Eurocephalus rüppellii* it is not unusual for two or more females to lay in the same nest (Moreau and Moreau 1939a).

Family: STURNIDAE. In the starling, *Sturnus vulgaris,* whose behavior pattern has been studied (Table 48, Allard 1940, Williamson 1947), both sexes share nearly equally in nest building, incubation, brooding, and feeding the young. Kluijver (1933) obtained continuous and complete records of feeding the young with his "aphisigraph," but there is scant information on the length of attentive and inattentive periods during incubation and brooding. Schüz (1943a) describes a case of bigamy where the male shared incubation at both nests but helped to feed the young at only one of the nests. Kluijver believed the young were brooded only by the female, but Allard (1940) and Freitag (1937) state that the male broods, which one would expect when he also incubates. Serebrennikov (1931) observed the male *Pastor roseus* helping in nest building and feeding the young, but only the female incubated.

Family: MELIPHAGIDAE. Milne (1938) reports that in the black honey eater, *Myzomela nigra,* the female builds the nest and incubates. She leaves the nest for short intervals to feed. There are only two eggs per set and both the incubation and the nestling periods last 18 days. In the bellbird of New Zealand, *Anthornis melanura,* Buddle (1941) states that both male and female incubate and feed the young.

Family: DICAEIDAE. Mayr and Amadon (1947) state that only the female builds the nest and incubates in flower-peckers of the species *Dicaeum vincens, D. hirundinaceum,* and apparently also, *Paramythia* sp. The male may accompany the female on her trips back and forth, and he helps in feeding the young. In *Pardalotus* sp., however, the male helps to dig the tunnel and probably aids in the construction of the nest itself. He also shares in the duties of incubation as well as in feeding the young. Ali (1949) states that the male *Arachnothera longirostra* shares in nest building and incubation.

Family: ZOSTEROPIDAE. In the white-eyes, *Zosterops palpebrosa* (Page 1911, Ali 1949), *Z. viridis* (Lovell-Keays 1915), *Z. madaraspatanus* (Someren 1947), and *Z. lateralis* (Fleming 1943) there is evidence that both sexes are involved in nest building, incubation, brooding, and feeding the young. Incubation of the two or three eggs requires 10 to 12 days and the nestlings leave the nest in 9 to 13 days. Fleming found that the feeding rate of nestling *Z. lateralis* varied from four to ten times per hour, the higher rate coming later in nest life, and that the young were cared for 16 to 21 days after they leave the nest.

Family: VIREONIDAE. In the Vireonidae, the female does the major part or all of nest building, but the males share in incubating, brooding, and in feeding the young (Table 48, Sutton 1949, Bent 1950). The male not infrequently sings while sitting on the nest, and his attentive periods for incubation and brooding average shorter than those of the female. On the other hand, he usually feeds the young at a faster rate than does the female. A divergent behavior pattern is expressed in *Vireo flavoviridis* and *V. olivaceus,* where the male seldom or never takes part in incubation and brooding, although he shares in feeding the young. There is considerable evidence that regular incubation begins unusually early, even with the first egg laid. This is verified from observation and from the fact that hatching extends over a long period with only one bird emerging each day. Petrides (1944) and Brackbill (1945) have shown this for the red-eyed vireo. Petrides reported the incubation period in this species to be only 13 days and states that the young remain in the nest 11 to 12 days.

Family: COEREBIDAE. The information on honey creepers is supplied by Alexander F. Skutch, mostly from unpublished data. The nest is built by both sexes only in *Coereba flaveola;* in *Dacnis cayana* and *Chlorophanes spiza,* in addition to the two species listed in Table 48, only the female performs this chore. Likewise, only the female incubates, which has also been observed in *Coereba.* Skutch's observations at the nest of *C. cyaneus* during incubation extended over 12.5 hours divided between two days. Attentive periods varied from 12 to 53 minutes and inattentive periods from 6 to 22 minutes. His observations of the incubation of *D. baritula* also extended over 12.5 hours. Attentive periods varied from 4 to 62 minutes and inattentive periods from 4 to 24 minutes. Twelve and one-half hours watch at a nest of *Coereba flaveola* found attentive periods ranging from 47 to 82 minutes and averaging 60.7

minutes, and inattentive periods ranging from 12 to 29 minutes and averaging 17 minutes.

Nestlings in this family stay 14 to 19 days before they leave. Only the female broods but both sexes share in feeding the young. Five and three-quarter hours were spent in measuring the feeding rate of *C. cyaneus* and eight hours in *D. baritula*.

Family: PARULIDAE. The male wood warbler occasionally helps in the building of the nest but never shares in the incubation duties (Table 49). He may at times bring food to the female on the nest, but this is not a regular trait except in the bay-breasted and yellow warblers. In fact, there is evidence that the female may force the male to keep away from the immediate vicinity of the nest in some species: black-throated green warbler (Nice and Nice 1932:157), oven-bird (Hann 1937:173), magnolia and blackburnian warblers (Kendeigh 1945:149, 154). Attentive periods during incubation are comparatively long but become shorter while brooding. Both sexes share about equally in feeding the young.

On the whole, the attentive behavior pattern in this family varies little between species. The attentiveness of the male for feeding the incubating female in two species has been mentioned. There are some exceptionally slow-feeding rates. The slow rate given for the yellow-breasted chat is in harmony with an all-day record, obtained by Copeland (1909), which averaged 1.8 per hour. Both sexes participated. Other slow rhythms, exposed by the studies of Skutch (1945c, d), are in the nonmigratory tropical warblers that have a long interval between completion of the nest and the laying of the first egg, a long incubation period (up to 17 days), and a long peroid for the care of the young in the nest (up to 14 days).

Family: PLOCEIDAE. Not a great deal is known concerning the nesting behavior of the English or house sparrow, *Passer domesticus*, one of our most abundant birds (Table 50). Most authorities maintain that the male shares almost equally with the female in the duties of incubation and brooding (Groebbels 1932, Daanje 1941), but Weaver (1939, 1943) stoutly maintains the contrary. Weaver did not find the male to possess a brood patch nor did he often observe the male at the nest. Even when the male enters the nest cavity, Weaver suggests that he may not effectively apply heat to the eggs. More observations are needed to settle this point. Both sexes are involved in nest building with the male sometimes doing the major part. Both adults feed the young. Marples and Gurr (1943) found the rate to be at least 20 times per hour with four young in the nest. The incubation period is 12 to 14 days and the nestling period 14 to 16 days. Attentive behavior is essentially similar in *Passer rutilans* (Ali 1949) and in *Passer montanus* and *Montifringilla nivalis* (Witherby *et al.* 1938). Boyd (1932) states that in *P. montanus* both sexes

TABLE 49. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Family: PARULIDAE								
1. Black and white warbler	*Mniotilta varia*	W. P. Smith, 1934	...	0	++++	1.5	5	4
2. Prothonotary warbler	*Protonotaria citrea*	Walkinshaw, 1938, 1939a, 1941	3.3	+	+++	2.1	5.0	4
3. Nashville warbler	*Vermivora ruficapilla*	Lawrence, 1948b	...	...	...	...	...	...
4. Parula warbler	*Parula (Compsothlypis) americana*	Mousley, 1924, 1926	3.5	0	13	...	...	...
5. Yellow warbler	*Dendroica petechia (aestiva)*	See pp. 146-51	...	0	10	2.5	4	3
6. Magnolia warbler	*Dendroica magnolia*	Mousley, 1924	...	...	...	...	...	...
7. Magnolia warbler	*Dendroica magnolia*	Nice, 1926	...	0	++++	...	...	...
8. Black-throated blue warbler	*Dendroica caerulescens*	Mousley, 1924	...	...	...	...	...	...
9. Black-throated blue warbler	*Dendroica caerulescens*	Nice, 1930	...	...	...	...	...	...
10. Black-throated blue warbler	*Dendroica caerulescens*	Harding, 1931	...	0.9	24.3	1	4	4
11. Black-throated blue warbler	*Dendroica caerulescens*	Kendeigh, 1945	...	0	35.0	1	...	...
12. Black-throated green warbler	*Dendroica virens*	Stanwood, 1910a, 1914	8	+	+++	1.9	4	4
13. Black-throated green warbler	*Dendroica virens*	Nice & Nice, 1932	...	...	...	...	...	...
14. Black-throated green warbler	*Dendroica virens*	Pitelka, 1940	4	+	+++	1	(?)	4
15. Chestnut-sided warbler	*Dendroica pennsylvanica*	Mousley, 1924	...	...	...	...	...	...
16. Chestnut-sided warbler	*Dendroica pennsylvanica*	Kendeigh, 1945	...	0	++++	...	...	...
17. Chestnut-sided warbler	*Dendroica pennsylvanica*	Sawyer, 1947	...	...	...	...	...	...
18. Chestnut-sided warbler	*Dendroica pennsylvanica*	Lawrence, 1948, (MS)	...	0	++++	4.5	...	...
19. Bay-breasted warbler	*Dendroica castanea*	Mendall, 1937	...	...	...	...	...	...
20. Oven-bird	*Seiurus aurocapillus*	Mousley, 1926	...	...	...	...	...	...
21. Oven-bird	*Seiurus aurocapillus*	Nice, 1931c	...	...	...	...	...	...
22. Oven-bird	*Seiurus aurocapillus*	Hann, 1937	4–5	0	26	1–3	3–5	4

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 49 (*cont.*). Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Nest building: Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
23. Yellow-throat	*Geothlypis trichas*	N. Shaver, 1918	...	...	...	...	...	...
24. Yellow-throat	*Geothlypis trichas*	Mousley, 1933	...	...	...	...	...	...
25. Yellow-breasted chat	*Icteria virens*	Petrides, 1938	...	...	...	...	...	...
26. Hooded warbler	*Wilsonia citrina*	Odum, 1931	...	...	...	...	...	...
27. Redstart	*Setophaga ruticilla*	Mousley, 1924	...	...	...	...	...	...
28. Redstart	*Setophaga ruticilla*	B. Baker, 1944	...	...	...	...	...	...
29. Redstart	*Setophaga ruticilla*	Sturm, 1945	3	0	19	0–1	2–4	3
30. Redstart	*Setophaga ruticilla*	Kendeigh, 1945	...	...	...	...	4	2–3
31. Redstart	*Setophaga ruticilla*	Victor Kehrer, Jr., (MS.)	4	0	8	0	4	2
32. Orange-bellied redstart	*Myioborus miniatus*	Skutch, 1945c	3–5	+	27	2–7	2–3	3
33. Collared redstart	*Myioborus torquatus*	Skutch, 1945c	...	0	20	6	3	3

Common Name	Incubation: Duration (days)	Incubation: Number periods per hour, Male	Incubation: Number periods per hour, Female	Incubation: Male feeds female	Incubation: Attentive period (min.)	Incubation: Inattentive period (min.)	Feeding young in nest: Duration (days)	Feeding young in nest: Number of young	Feeding young in nest: Age of young (days)	Feeding young in nest: Trips per hour, Male	Feeding young in nest: Trips per hour, Female	Feeding young in nest: Trips per hour, Total
1	13	0	++++	0	...	11.0	...	2	0–2	1.4	1.5	2.9
2	12.8	0	++++	+	...	...	11	4.5	0, 9	++	++	8.0
3	...	0	1.1	0	39.3	14.4	8	3.3	0–6	1.5	8.8	10.3
4	...	...	...	...	...	...	...	...	0–4	3.0	1.4	4.4
5	11	0	1.6(–)	+++	35.7(+)	3.0	10	2.5	0–10	++	++	14.9
6	...	...	...	...	...	...	...	3.5	0–7	3.4	3.4	6.7

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 49 (*cont.*). Summary of attentive data by species.

Common Name	*Incubation* Duration (days)	Number periods per hour Male	Number periods per hour Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	*Feeding young in nest* Duration (days)	Number of young	Age of young (days)	Trips per hour Male	Trips per hour Female	Trips per hour Total
7	12	...	...	...	...	...	9–10	3	1–9	4.2	3.3	7.5
8	...	...	...	...	...	...	...	3	0–4, 7	0.5	14.0	14.5
9	...	...	...	...	...	...	...	3	3–9	5.5	4.8	10.3
10	12–13	...	...	+	...	...	...	4	8	6.6	7.6	14.1
11	12	0	1.6	0	28.0	9.0	9–10	3.5	3, 6	2.6	2.1	4.7
12	12	...	...	...	...	...	10–11	4	7–8(?)	3.4	3.7	7.2
13	...	0	1.0	0	44	17	8–9	2.5	0–8	+	3.0	3.0
14	12	0	1.0	0	48.5	12.5	9–10	2.5	3, 5	1.0	1.4	2.4
15	...	...	...	...	...	...	8–9	3	0–8	3.1	2.1	5.2
16	11	0	2.5	0	17.0	7.0	...	3	0, 3	3.2	2.1	5.3
17	...	0	++++	+	...	...	...	4	1–8	4.6	5.6	10.2
18	12	0	1.5	0	34.6	6.6	9	3	1–8	2.7	4.0	6.7
19	12	0	++++	++	...	...	11	5	4–9	7.6	19.6	27.4
20	12	...	...	...	...	...	8	...	0–8	0.8	0.8	1.6
21	...	...	...	...	...	...	...	2.3	0–6	0.5	1.5	2.0
22	12.2	0	0.5	0	110.0	19.3	8	4	0–7	++	++	3.7
23	...	...	...	...	...	...	8	3	0–7	6.3	5.2	11.6
24	...	...	...	...	...	...	...	...	...	2.2	3.7	5.9
25	11	0	++++	...	...	...	...	3	4	++	++	1.5
26	...	0	++++	...	...	...	8	3	1–8	5.8	3.6	9.5
27	...	...	...	...	...	...	8	4	0–8	1.2	3.2	4.4
28	...	...	2.3	+	20.6	5.1	8–9	2	1, 6	0	9.0	9.0
29	11	0	2.2	+	24.0	3.5	8–9	...	0–8	7.6	4.4	12.0
30	12	0	3.2	0	13.5	5.0	10	...	3, 4–8	10.2	3.1	13.4
31	...	0	1.6	+	32.8	4.7	...	2	...	2.2	2.0	4.2
32	13–15	0	1.1	0	37.6	18.2	12–14	3	2–3	1.7	3.3	5.0
33	15	0	1.6	0	28.5	9.8	13	...	...	...	...	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

incubate. He gives the nestling period as only 12 to 13 days. Adlersparre (1931) states that both sexes share nest building in *Spermestes nigriceps,* incubation lasts 16 days and is performed chiefly by the male during the daytime, and the nestling period is 16 to 21 days. Stresemann (1928) mentions that in *Estrilda* both sexes may incubate simultaneously, not only at night but also during the day. Some related *Estrildinae* are parasitic in their nesting behavior. Likewise some members of the Viduinae are parasitic and polygynous (Hoesch 1939).

In *Ploceus philippinus,* Ali (1931) found that the male has a strong nest-building instinct and may prepare as many as three different and rather elaborate nests within the colony. The female is not concerned with nest building except to arrange the nest lining and to bring an occasional feather or mud pellet. She may, however, inspect several nests before deciding on one. The males are polygynous. The female lays two to four eggs, does all the incubation, and may do all the caring for the young. The male may sometimes aid in feeding the young late in the season after his nest-building proclivities have run their course. In a preliminary review of *Ploceus* sp. *(sensu lato)* Moreau and Moreau (1939a) give evidence that in the subgenus *Sitagra,* and perhaps in *Xanthophilus,* the males are polygynous, and all but the final stages of nest building are done by the male, and the female alone incubates and feeds the young. However, the subgenera, *Symplectes, Othyphantes, Hyphanturgus,* and possibly *Icteropsis,* are monogamous, and both sexes share nest building at all stages and also the care of the young.

The behavior of the bishop-bird, *Euplectes hordeacea* (Lack 1935), is similar to some other species above mentioned in that the male is polygynous, constructs several nests which his mates must finish, and takes no part in incubation or feeding the young. The female was observed feeding the young at the rate of three or four times per hour. Moreau and Moreau (1938) find *E. nigroventris* also to be polygynous and this condition in both species of *Euplectes* to be correlated with a sex ratio of four females to one male.

Family: ICTERIDAE. In the various species of this family, incubation and brooding are performed exclusively by the female, and in most species also nest building, although the male often accompanies the female at this time (Table 50). The male feeds the incubating female occasionally in *Xanthocephalus* (T. Roberts 1909), apparently as often as two times per hour in *Icterus,* although the actual process was not observed because of the deep nest, and frequently in *Euphagus carolinus* (Kennard 1920). Male *Dives dives* fed the incubating females once or twice in the morning, according to observations of Skutch.

After the young are hatched, the male aids in feeding them only irregularly or not at all in the highly polygynous *Xanthocephalus* and

Agelaius, in *Cassidix mexicanus* (McIlhenny 1937), in the colonial *Zarhynchus* (Chapman 1929), and in *Gymnostinops* and *Cacicus* (Skutch, personal communication), but in most other genera he aids to a smaller or larger extent. Gabrielson (1914) found that three young *Xanthocephalus* were fed 2.9 times per hour and two young *Agelaius,* 4.7 times per hour, entirely by the female. In the oropendola, *Zarhynchus wagleri,* the male apparently takes no part in nesting duties after courtship is completed (Chapman 1929). In the often polygynous *Dolichonyx oryzivorus,* the male bobolink helps care for the young at only one of his two or three nests (Kendeigh 1941a). Polygyny is certainly involved in the minimal development of the behavior pattern of attentiveness in the male. Skutch (1945d) records incubation periods as long as 14 days and nestling periods as long as 34 days in tropical species of icterids.

Social parasitism has developed in this family in the cowbirds which Friedmann (1929) has traced through various species showing intermediate tendencies to its full expression in *Molothrus ater.* In *Agelaioides badius,* whose behavior may approach the original condition, the birds will build their own nest, if they cannot get one already built. Both sexes participate, but the male does most of it. Five eggs per set are usually laid and incubation begins with the last egg. Occasionally two females will lay in the same nest. The incubation period is believed to be 13 days, as is the nestling period. The birds are monogamous. *M. ater,* on the other hand, does not build a nest, incubate, nor care for its own young. Its attentive behavior has been reduced to the ultimate minimum, involving only the process of egg-laying in the nests of other species. Friedmann describes a gradual loss of territorial behavior in this group and a loss of attunement and timing between the reproductive cycles and behavior of males and females, and this he believes may have led to the parasitic behavior pattern. Miller (1946) is in essential agreement with this theory. Nice (personal communication) calls attention to the fact that parasitism in *Molothrus* is a more recent development than in some of the cukoos, as *Cuculus conorus,* since there is very little adaptation in the cowbird to its various hosts in respect to size of egg, length of incubation, or behavior of the nestling.

Family: THRAUPIDAE. Surprisingly few studies are available on this group of conspicuous and common birds. The male scarlet tanager, *Piranga olivacea (erythromelas),* takes no part in nest building, apparently, which the female may complete in a day's time, working in periods of 15 minutes or more. Incubation of the three or four eggs lasts about 13 days and is carried on by the female. The male may feed the female on the nest and also helps in feeding the young after hatching (T. Roberts 1932, Todd 1940). Steinbacher (1938a) found that in captivity the male *Calospiza thoracica* brought nest material which the female built into the nest. Three or four days were required. Only the female incubated, beginning with the second of three eggs laid, and the incubation period lasted a little more than 12 days. The male fed the female during incubation and helped in feeding the young. Skutch (1945d and personal communication) states that in tropical species the incubation period varies between 12 and 16 days and the nestling period between 10 and 24 days. The male helps build in many species of *Thraupis, Tangara, Tanagra, Chlorophonia,* and *Eucometris;* the female alone builds in *Ramphocelus* and *Piranga.* In his experience with species in this family the male never incubates but regularly helps to feed the nestlings. In species of *Thraupis* and *Tangara* the male feeds the female.

Family: FRINGILLIDAE. In this family of grosbeaks, finches, buntings, and sparrows (Table 50), the female does practically all the work of nest building, incubation, and brooding, while both sexes share more or less equally in feeding the young. Incubation begins gradually as the eggs appear, so that the first eggs laid commonly have the equivalent of a full day's incubation before the last egg is laid.

The genus, *Pheucticus (Hedymeles),* is aberrant in both sexes alternating in the duties of incubation and brooding. Niethammer (1937) and Witherby *et al.* (1938) mention other genera or species in which the male is believed sometimes to take a part. The occasional finding of a male at the nest during incubation does not mean he is applying heat to the eggs or young, but when he regularly takes his turn, his behavior would indicate that he was playing an important part in their development. In *Emberiza calandra,* Walpole-Bond (1932) and Ryves (1934) found that the male, who is sometimes polygynous, took no part in incubation and also only a negligible part in feeding the young. Skutch writes me that in *Tiaris olivacea* the male is the chief nest builder. Bradley (1948) observed only the female *Passerina cyanea* building the nest, incubating, and feeding the young. In one all-day observation, three young, 8 days old, were fed 7.4 times per hour. Likewise in *Pyrrhula pyrrhula* Steinfatt (1944b) found only the female building the nest and incubating. Attentive periods on the nest averaged 111 minutes and inattentive periods only 12 minutes. Both adults fed the young at the rate of 1 to 2 times per hour. Linsdale (1950) reports in *Spinus lawrencei* that the female does all the nest building and incubation. As in other species of this genus, she sits on the eggs almost continuously, being fed by the male about once per hour. Both adults feed the young; during 11 days the rate of feeding averaged 1.3 times per hour. R. O. Malcomson (MS) found three young *Spiza americana,* 1 to 3 days old, fed 5.1 times per hour. Cartwright, Short, and Harris (1937) reported a feeding rate of 10 times per hour in *Ammodramus bairdii,* and Walkinshaw

(1937a) recorded only the female *Passerherbulus caudacutus* feeding the newly hatched young at a rate of 2.8 per hour.

The behavior pattern of the male feeding the incubating female on or close to the nest is well developed in certain genera. In addition to records given in Table 50, this has been observed in *Carduelis* (Windsor 1935, Timmerman 1938), *Pyrrhula* (Steinfatt 1944b), *Carpodacus* (Bergtold 1913), *Rhynchophanes* (Mickey 1943), *Plectrophenax* (Sutton 1932); and *Saltator* (two species), *Sporophila,* and *Spinus psaltria* (Skutch, letter), and in several European genera (Niethammer 1937, Witherby *et al.* 1938). The behavior is not associated with time of nesting, as *Spinus pinus* nests early in spring and *S. tristis* late in summer, while *Loxia* breeds at irregular times.

Three subfamilies are indicated in Table 50. In addition, in the subfamily, Fringillinae, J. H. Barrett (1947) found in *Frigilla coelebs* that the female built the nest, whose visits he timed at 6.5 per hour, incubated for 14 days, and fed the three young over 15 days at the rate of 4.2 times per hour. The male fed the young 2.5 times per hour. Steinfatt (1937) recorded five young, 9 days old, fed 4.3 times per hour. Lack (1945) reports for the *Geospizinae* on the Galapagos Islands that four eggs commonly compose the set. Incubation at one nest lasted for 12 days after the last egg was laid, and the young birds left the nest 14 days after the first one had hatched. The female alone incubated. During the heat of midday she commonly remained off the nest for several hours. The male brought food to the female, calling her off the nest to give it to her. Brooding lasted five days. Both adults fed the young, at the rate of four to five times per hour. No consistent variation in behavior associated with the classification to subfamilies appears warranted, except for the exceptional development in several species of Carduelinae of the male supplying the incubating female with nearly all her food.

Summary. The average behavior pattern for each family in this order is shown in Table 51. There is little doubt but that in *Passeriformes* the male typically aids the female, who ordinarily does most of the work, in construction of the nest. There is a strong suggestion, however, that in many families the male is in the process of losing this trait, but not in Ptilogonatidae, Artamidae, and Ploceidae, in which the reverse appears true.

A well-defined trend also exists in most families above the Dendrocolaptidae, Furnariidae, and Formicariidae for the male not to participate in incubation so that the female does it all, but again this appears not to be the case in Chamaeidae, Ptilogonatidae, Artamidae, Prionopidae, and Sturnidae. Repeatedly we have shown in discussing various species that the male may be recorded visiting the nest when the female is in-

TABLE 50. Summary of attentive data by species.

Common name	Scientific name	Reference	Nest building: Duration (days)	Nest building: Trips per hour, Male	Nest building: Trips per hour, Female	Time from completion to first egg (days)	Egg-laying: Number of eggs	Egg-laying: Time incubation begins, egg
Family: PLOCEIDAE								
1. English sparrow	*Passer domesticus*	Daanje, 1941	...	++	++	...	...	...
2. English sparrow	*Passer domesticus*	Bodecker, (MS)	...	+++	+	0	4	4
Family: ICTERIDAE								
3. Eastern meadowlark	*Sturnella magna*	Esten, 1924	...	...	...	...	...	...
4. Yellow-headed blackbird	*X. xanthocephalus*	Fautin, 1941a, b	...	...	...	1–4	2–5	1–3
5. Red-winged blackbird	*Agelaius phoeniceus*	A. A. Allen, 1914	6	0	++++	0–3	3–4	3
6. Baltimore oriole	*Icterus galbula*	Kendeigh, (MS)	...	...	...	...	...	...
Family: FRINGILLIDAE; Subfamily: RICHMONDENINAE								
7. Cardinal	*Richmondena cardinalis*	Laskey, 1944	5.3	+	+++	5.7	3	3
8. Rose-breasted grosbeak	*Pheucticus (Hedymeles) ludovicianus*	Esten, 1924	...	...	...	...	...	...
9. Rose-breasted grosbeak	*Pheucticus (Hedymeles) ludovicianus*	Ivor, 1944	...	...	...	...	...	...
10. Black-headed grosbeak	*Pheucticus melanocephalus*	Weston, 1947	3–4	...	...	3	3–4	2–3
11. Dickcissel	*Spiza americana*	A. O. Gross, 1921	4	0	++++	2	...	...
Subfamily: CARDUELINAE								
12. Scarlet finch	*Carpodacus e. erythrinus*	Steinfatt, 1937e	...	...	...	...	5	4
13. Rosy finch	*Leucosticte tephrocotis*	J. B. Dixon, 1936	...	0	++++	...	...	...
14. Continental goldfinch	*Carduelis carduelis*	J. B. Dixon, 1936	...	0	++++	...	...	...
15. Continental goldfinch	*Carduelis carduelis*	Conder, 1948	8	+	+++	1	4–5	4–5
16. Pine siskin	*Spinus pinus*	Weaver & West, 1943	5	0	++++	5	2	1
17. Goldfinch	*Spinus tristis*	See pp. 151-56	4–5	+	+++	2	4–6	2–3
18. Red crossbill	*Loxia curvirostra*	Lawrence, 1949a	...	...	...	...	...	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 50 (*cont.*). Summary of attentive data by species.

	Common name	*Scientific name*	*Reference*	*Nest building* Duration (days)	Trips per hour Male	Trips per hour Female	Time from completion to first egg (days)	*Egg-laying* Number of eggs	Time incubation begins, egg
	Subfamily: EMBERIZINAE								
19.	Towhee	*Pipilo erythrophthalmus*	Esten, 1924	...	...	...	...	...	...
20.	Grasshopper sparrow	*Ammodramus savannarum*	Walkinshaw, 1942	...	...	...	...	...	...
21.	Henslow sparrow	*Passerherbulus henslowii*	Hyde, 1939	...	0	15.7	2	...	...
22.	Slate-colored junco	*Junco hyemalis*	Greulach, 1934	...	...	...	...	...	...
23.	Tree sparrow	*Spizella arborea*	A. M. Baumgartner, 1937	7	0	++++	2–5	4–6	4–6
24.	Chipping sparrow	*Spizella passerina*	See pp. 156-59	3.4	0	++++	...	3–4	3
25.	Field sparrow	*Spizella pusilla*	Walkinshaw, 1936, 1939b	3.5	0	++++	1	3–4	2–3
26.	White-crowned sparrow	*Zonotrichia leucophrys*	Blanchard, 1941	7–9	0	35	3	3–4	2–3
27.	Song sparrow	*Melospiza melodia*	See pp. 159-67	4	0	++++	1	3–5	3–4
28.	Chestnut-collared longspur	*Calcarius ornatus*	Harris, 1944	...	...	...	...	4–5	...
29.	Yellow bunting	*Emberiza citrinella*	Steinfatt, 1940c	...	+	+++	...	3–6	2–5

Common Name	*Incubation* Duration (days)	Number periods per hour Male	Number periods per hour Female	Male feeds female	Attentive period (min.)	Inattentive period (min.)	*Feeding young in nest* Duration (days)	Number of young	Age of young (days)	Trips per hour Male	Trips per hour Female	Trips per hour Total
1	...	++	++	0	12	12	...	...	...	+	+++	...
2	12	0	++++	0	10–20	3	16	...	...	...	...	...
3	...	...	...	...	...	...	...	4	6–9	1.6	3.9	5.5
4	12–13	0	4.1	0	9.1	5.4	9–12	...	1–12	+	9.6	9.6

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 50 (*cont.*). Summary of attentive data by species.

Common Name	Incubation: Duration (days)	Incubation: Number periods per hour: Male	Incubation: Number periods per hour: Female	Incubation: Male feeds female	Incubation: Attentive period (min.)	Incubation: Inattentive period (min.)	Feeding young in nest: Duration (days)	Feeding young in nest: Number of young	Feeding young in nest: Age of young (days)	Feeding young in nest: Trips per hour: Male	Feeding young in nest: Trips per hour: Female	Feeding young in nest: Trips per hour: Total
5	11	0	++++	...	...	...	9–11	...	1–4	2.0	9.4	11.4
6	...	0	1.6	0	30.2	7.6	...	...	7–15	7.7	10.0	17.7
7	12–13	0	1.0	+	54	6	9–10	3	0–8	2.7	3.4	6.1
8	...	...	...	...	...	...	...	4	6–9	2.9	1.8	4.7
9	12–13	++	++	...	...	...	10	.3	4–5	4.5	4.5	9.1
10	12	1.3	1.1	0	25	25	12	2.8	1–12	2.2	2.9	5.1
11	...	0	++++	...	...	...	8–10	...	...	0	10	10
12	12	0	17	+	48.5	9.2	12	4	1, 9	0.3	1.4	1.7
13	...	...	...	...	47.5	15	10(–)	...	...	++	++	...
14	13	0	++++	++	12–305	15–38	13	6	12–13	++	++	3.1
15	12	0	++++	+++	30–80	1–4	15–16	...	0–16	++	++	1.0–2.8
16	13	0	++++	++++	continuous	+	15	2	1–15	2–4	1–5	...
17	13	0	++++	+++	132	8.7	13	6	1–13	++	++	1.5
18	...	0	++++	++++	continuous	+	17	...	1–16	++	++	1.3
19	...	...	...	+	...	...	...	4	6–9	5.0	3.8	8.8
20	...	0	++++	...	...	...	...	3.3	1–6	0.6	0.9	1.5
21	11	0	++++	...	...	...	9–10	...	0–9	++	++	4.9
22	11	...	...	...	...	...	12–13	4	0–12	4.1	3.4	7.5
23	12–13	0	3.2	0	14.6	9.6	9–10	...	1–9	6.5	7.2	13.8
24	11–12	+	2.5	+	15.2	8.5	9	3	0–7	++	++	11.4
25	11	0	++++	...	...	...	7.5	...	0–7	0.7	4.9	5.6
26	12	0	2.2	0	20	7	10	2	1	+	8.3	8.3
27	12–13	0	1.6	0	28.5	8.8	10	3.7	0–10	7.4	5.1	12.5
28	10–12	0	++++	...	...	...	9–11	5	1–3, 5–7	5.0	16.4	21.3
29	...	+	0.9	0	53.9	16.3	...	5	1	1.7	3.7	5.5

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
\+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

attentive but may not apply effective heat to the eggs. In several instances, the lack of a brood patch in these males has been demonstrated.

Associated with the loss of the incubating behavior is the development of a tendency in many families for the male to feed the female as she sits on the eggs, especially in Corvidae, Bombycillidae and Laniidae. In a few species of Parulidae and Fringillidae, this tendency has evolved so far that the female is seldom required to leave the nest and may be attentive for hours at a time.

Aside from the very long attentive and inattentive periods on the eggs in the tropical Furnariidae, Formicariidae, and Pipridae, there is no consistent difference in behavior between families at various points along the scale of increasingly more specialized morphological forms. However, more careful attention to trends within some of the families shows that the behavior pattern tends to evolve toward shorter and more frequent periods of the female alone, although this is often countered by the male feeding the female so that she is induced to stay for longer periods on the eggs without leaving.

In spite of an appreciable amount of variability and irregularity from family to family, the length of the incubation period appears to decrease from the low to the high groups.

It is the rule in nearly all families for the male to aid in feeding the young. Often his share is fully equal to the female; actually he may feed the young more frequently, as the female's time is partly consumed in brooding the young during the first few days after hatching.

Some very fast rates of feeding the young are found in scattered families. This does not mean that the young are fed a greater quantity of food, as the figures do not take into account the amount that is carried on each trip to the nest. The Bombycillidae, for instance, has one of the slowest rates of the entire order, which is easily explained as the adults carry a large amount of food in their throats on each trip, which is then regurgitated to the young. Kluijver (1950) found a correlation within a single species between size of food brought to the young and the number of trips made to the nest per day.

There is difficulty in discerning any general trend from family to family in the length of the nestling period. A short or long nestling period is compensated for by a corresponding difference in the length of time that the young are cared for after leaving the nest. Nice (1943) states that there is a tendency for birds to stay in the nest longer when the nest is safely located and this is true also of larger species. The majority of passerines become independent of parental care at about 28 days after hatching, in spite of nestling periods varying between 9 and 20 days. The long nestling period in the Hirundinidae permits the better development of the flight feathers before leaving. On the other hand, species that nest on the ground or in low bushes commonly have a very short nestling period.

Phylogeny and Dynamics of Evolution

The survey of parental behavior in the orders and families of birds, just completed, emphasizes the prevalence of joint responsibility of male and female on nearly equal terms in incubation as well as in other phases of nest life (Table 51). This is particularly evident in the orders, Sphenisciformes, Gaviiformes, Colymbiformes, Procellariiformes, Pelecaniformes, Ciconiiformes, some Gruiformes, Charadriiformes, Columbiformes, Cuculiformes, Apodiformes (Apodidae), Trogoniformes, Coraciiformes, Piciformes, and some Passeriformes. Even in the other orders, at least of the Neognathae, the male and female usually share in nest building and in the feeding and care of the young even though the male may only occasionally sit on the eggs. Where the sexes can be easily distinguished, the female is almost invariably the sex on the eggs at night, but in the Struthioniformes, some Gruiformes and Charadriiformes, Piciformes, and apparently also in the Artamidae of the Passeriformes and some Crotophaginae of the Cuculiformes, it is generally the male. Often the alternation of sexes on the eggs for incubation is accompanied by more or less elaborate display and ceremony. Armstrong (1947) has discussed and summarized these nest relief ceremonies in various species. Obviously, the widespread equal sharing of nesting duties is the basic primitive pattern of attentive behavior in the class Aves, even though some authorities have believed otherwise (Hutson 1947).

The possibility has been suggested, since in ratite birds the male takes the preponderant share of the nesting duties, that this may represent the basic pattern and that the development of an equal share by both sexes represents convergent evolution in the various orders brought about by the supposed greater efficiency of such a behavior pattern. This is highly improbable, however. Some authorities believe that the ratites are a very specialized group that has evolved from flying ancestors. Furthermore, the development of different behavior patterns within an order can often be traced from forms considered primitive within that order from the morphological point of view and where both sexes share equally in nesting duties. The wide occurrence of this latter behavior pattern in so many orders could have come about because of common ancestral origin. This would seem a more logical and probable explanation than to suppose independent convergent evolution in each order.

It is possible, of course, that in some scattered families, such as Chamaeidae, Ptilogonatidae, Prionopidae, Sturnidae, and Zosteropidae which are classified relatively high in the order, Passeriformes, this behavior pattern has been reacquired. On the other hand, the occurrence of the behavior pattern in the Dendrocolaptidae, Furnariidae, and Formicariidae may represent a persistence from the original ancestors of the order.

There are divergent trends in various orders in the evolution of behavior from the primitive pattern. In the Palaeognathae, only the Struthioniformes have the male and female sharing incubation and care of the young. In the Rheiformes, Casuariiformes, Apterygiformes, and Tinamiformes the male does all the incubation and takes full charge of the precocial young. An extreme type of behavior is reached in the Tinamiformes with the female possessing the brighter coloration and assuming the usual masculine role of aggressive courtship. This behavior pattern in the Tinamiformes is correlated with a sex ratio out of balance in favor of a higher proportion of males to females. One should not, however, consider evolution of behavior in this superorder to have followed a linear development from the Struthioniformes to the Tinamiformes. On the contrary, it has gone on independently over a long period of time after each order became separated from the ancestral stock. The Struthioniformes have retained a more primitive type of behavior in spite of considerable morphological specialization. The Tinamiformes probably conform more closely morphologically to the original generalized structural plan yet have advanced farther than the other groups in developing a specialized behavior pattern.

Definite evolutionary trends also occur in the Gruiformes and in the Charadriiformes for the male to assume increasing responsibility for nesting duties. In the Gruiformes this trend is shown in the suborders, Mesoenatides and Turnices. In both suborders there is a preponderance of males at least in some species, and in the latter group the females are more brightly colored and larger in size.

In the Charadriiformes the trend is exhibited by the Jacanidae, Rostratulidae, in several members of the Charadriidae and Scolopacidae, and especially in the Phalaropodidae. There is again a reversal of the usual sexual dimorphism in plumage and aggressiveness in courtship. There appears to be little information available on the sex ratio in the Phalaropodidae, and what there is, is contradictory (Tinbergen 1935, Mayr 1939), but one would expect agreement with other groups where the male takes over nesting duties in there being a general preponderance of males.

There is one species in the Cuculiformes, *Centropus bengalensis*, where the male has taken over full responsibility for the nesting duties. In the Picidae of the Piciformes and in the Artamidae of the Passeriformes the trend is also strongly in this direction.

The assumption by the male of the major role in nesting duties must have been independently acquired in most of these groups. There may be significance in the frequent occurrence among them of an unbalanced sex ratio of the adults in favor of the male. One can well see in such a case that it would increase reproduction and be to the advantage of the species for the female to become polyandrous and to lay the largest possible number of eggs. Obviously this would be most effectively accomplished if the males took care of the eggs once they were laid. If this be a reason for the development of this behavior pattern, then one wonders what brought about the unbalancing of the adult sex ratio. Apparently this unbalance has persisted for a very long time and is deep-rooted. A preponderance of males is not necessarily correlated, however, with the males taking over most of the nesting duties. Richdale (personal communication) states that there is always a surplus of males able to breed in *Megadyptes antipodes*, an unfavorable surplus of males in *Diomedea epomophora*, and probably also a surplus of males in *D. bulleri*, yet the sexes share parental duties about equally. Likewise in some species of ducks the high surplus of males does not prevent the females from assuming practically all the duties of raising the young. However, in this latter group the lopsided sex ratio may be a recent development due to human influences.

Trends in the opposite direction, i.e., for the female to take on an increasingly larger share in the nesting duties, are much more common and are manifest in nearly all orders. The trend may be first evident (1) in the female having longer attentive periods than the male during the day and invariably to be the sex on the eggs at night. In a more advanced stage (2) the female does practically all the incubation although the male continues to help to care for the young. Extreme behavior (3) occurs in a few groups when the male abandons the female soon after mating is consummated, and the female is alone responsible for incubation and the raising of the family.

Stage (1) in this evolution of behavior is evident in Gaviiformes, possibly in Colymbiformes, in Falconiformes, in some Charadriiformes, in some Passeriformes, and doubtless also in other groups less well known. Stage (2) is reached by a few Charadriiformes; some Anseriformes; and by most Psittaciformes, Strigiformes, Caprimulgiformes, and Passeriformes. Stage (3), the extreme development of female attentiveness, is found in many Anseriformes, Galliformes, Gruiformes (Otidae), Apodiformes (Trochilidae), and rarely in Passeriformes (Pipridae, Menuridae). Here again it is apparent that evolution of behavior patterns has been initiated independently and has reached different extremes in the various orders. Frequently it is possible to find a series of stages all within a single order showing progressive development of the pattern.

TABLE 51 . Summary of attentive behavior by families.

Order and family		Nest building: Male	Nest building: Female	Incubation: Duration (days)	Incubation: Male	Incubation: Female	Incubation: Attentive periods	Incubation: Male feeds female	Feeding and care of young: Nestling period (days)	Feeding and care of young: Male	Feeding and care of young: Female	Feeding and care of young: Trips per hour
Struthioniformes:	Struthionidae	++++	0	42	+++	+	9–15 hrs.	0	0	++	++	...
Rheiformes:	Rheidae	...	...	35–42	++++	0	...	0	0	++++	0	...
Casuariiformes:	Dromiceiidae	...	...	58–61	++++	0	continuous	0	0	++++	0	...
Apterygiformes:	Apterygidae	++	++	75	++++	0	up to 7 days	0	6	++++	0	...
Tinamiformes:	Tinamidae	...	...	21	++++	0	...	0	0	++++	0	...
Sphenisciformes:	Spheniscidae	++	++	38–56	++	++	1–5+ days	0	56–112	++	++	1–2/day
Gaviiformes:	Gaviidae	...	...	28–30	++	++	...	0	0	++	++	...
Colymbiformes:	Colymbidae	++	++	21–27	++	++	0.5 – 5 hrs.	0	0	++	++	...
Procellariiformes:	Diomedeidae	++	++	63–80	++	++	5.3–21.8 days	0	150–251	++	++	2–5/week
	Procellariidae	++	++	51–58	++	++	1–7 days	0	49–95	++	++	0.5–2/day
	Hydrobatidae	++	++	38–50	++	++	1–5 days	0	56	++	++	1/day
	Pelecanoididae	++	++	56	++	++	1 day	0	54	++	++	1–2/day
Pelecaniformes:	Pha"thontidae	...	...	28	++	++	...	+	62	++	++	2–3/day
	Pelecanidae	...	...	28–42	++	++	...	0	14–35	++	++	3+/day
	Sulidae	++	++	42–45	++	++	1 day	0	45+	++	++	1+/day
	Phalacrocoracidae	++	++	24–25	++	++	1–3 hrs.	0	35–42	++	++	1/hr.
	Anhingidae	...	...	...	++	++	...	...	...	++	++	...
	Fregatidae	++	++	...	++	++	...	...	...	++	++	...
Ciconiiformes:	Ardeidae	++	++	18–28	++	++	1–6 hrs.	0	10–52	++	++	0.5–3/hr.
	Scopidae	++	++	21	++	++	...	...	42	++	++	...

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+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 51 *(cont.)*. Summary of attentive behavior by families.

Order and family		*Nest building* Male	Female	*Incubation* Duration (days)	Male	Female	Attentive periods	Male feeds female	*Feeding and care of young* Nestling period (days)	Male	Female	Trips per hour
Ciconiiformes:	Ciconiidae	++	++	30–38	++	++	1–4.5 hrs	0	63	++	++	5–11/day
(continued)	Threskiornithidae	++	++	21–24	++	++	6–18 hrs.	0	42+	++	++	12–20/day
	Phoenicopteridae	...	...	30–32	++	++	12 hrs.	...	3–4	++	++	...
Anseriformes:	Anhimidae	++	++	42	++	++	7–17 hrs.	0	0	...	...	...
	Anatidae	+	+++	21–35	+	+++	4–23.7 hrs.	0	0	+	+++	...
Falconiformes:	Cathartidae	...	...	39–56	++	++	...	0	56–70	++	++	...
	Accipitridae	+	+++	28–56	+	+++	1–20 hrs.	+++	28–133	++	++	0.1–4/hr.
	Falconidae	+	+++	28–29	+	+++	3 hrs.	+++	25–35	++	++	0.3–5.8/hr.
Galliformes:	Megapodiidae	++++	0	57–70	0	0	...	0	0	...	...	...
	Cracidae	++	++	22–24	0	++++	...	...	0	...	...	...
	Tetraonidae	0	++++	21–27	0	++++	6–11.5 hrs.	0	0	+	+++	...
	Phasianidae	++	++	21–28	+	+++	7–23+ hrs.	0	0	++	++	...
	Meleagrididae	0	++++	28	0	++++	23–24 hrs.	0	0	0	++++	...
	Opisthocomidae	++	++	...	...	...	...	...	...	...	...	...
Gruiformes:	Mesoenatidae	...	...	...	+++	+	...	0	...	+++	+	...
	Turnicidae	++	++	12–13	++++	0	...	0	0	++++	0	...
	Pedionomidae	...	...	...	++++	0	...	0	0	++++	0	...
	Gruidae	++	++	29–32	++	++	44–165 min.	0	0	++	++	...
	Rallidae	++	++	19–24	++	++	38 min.	++	0–2	++	++	...
	Rhynochetidae	++	++	36	++	++	...	...	...	...	...	...
	Eurypygidae	++	++	27	++	++	...	0	21	++	++	...
	Otidae	...	...	20–28	0	++++	...	...	0	0	++++	...

Key: ... No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

TABLE 51 *(cont.)*. Summary of attentive behavior by families.

Order and family		*Nest building* Male	Female	Duration (days)	*Incubation* Male	Female	Attentive periods	Male feeds female	*Feeding and care of young* Nestling period (days)	Male	Female	Trips per hour
Charadriiformes:	Jacanidae	...	...	23	++++	0	...	...	...	++++	0	...
	Rostratulidae	...	...	...	+++	(?)	...	...	...	...	...	...
	Haematopodidae	...	...	24–27	++	++	12 hrs.	0	0	++	++	...
	Charadriidae	++	++	23–28	++	++	0.5–2.3 hrs.	0	0	++	++	...
	Scolopacidae	...	...	18–29	++	++	11–15 hrs.	0	0	++	++	...
	Recurvirostridae	++	++	23	++	++	10–66 min.	0	0	...	...	...
	Phalaropodidae	++++	0	20–21	+++	+	...	0	0	+++	+	...
	Burhinidae	...	...	26–27	++	++	...	0	0	...	...	...
	Glareolidae	...	...	...	+	+++	...	...	...	...	...	...
	Stercorariidae	...	...	23–26	++	++	...	...	0	++	++	...
	Laridae	++	++	20–34	++	++	0.5–24 hrs.	+	0–several	++	++	0.2–7
	Rynchopidae	...	...	...	0	++++	...	0	0	++	++	...
	Alcidae	++	++	24–42	++	++	12 hrs.	+	2–49	++	++	...
Columbiformes:	Pteroclididae	...	...	22–28	++	++	12 hrs.	0	...	...	...	...
	Raphidae	...	...	49	++	++	...	...	...	...	...	...
	Columbidae	++	++	11–19	++	++	4–20 hrs.	0	10–35	++	++	0.2–1
Psittaciformes:	Psittacidae	+	+++	17–31	+	+++	continuous	++++	28–36	++	++	...
Cuculiformes:	Cuculidae	++	++	11–18	++	++	0.5–1.5 hrs.	0	6–22	++	++	2–12
Strigiformes:	Tytonidae	...	...	30–34	+	+++	...	+++	56–64+	++	++	1.4–2.0
	Strigidae	++	++	24–35	+	+++	23.5 hrs.	+++	21–35	++	++	1–8

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Table 51 (*cont.*). Summary of attentive behavior by families.

Order and family		*Nest building* Male	Female	*Incubation* Duration (days)	Male	Female	Attentive periods	Male feeds female	*Feeding and care of young* Nestling period (days)	Male	Female	Trips per hour
Caprimulgiformes:	Caprimulgidae	0	0	16–20	+	+++	1.4–14 hrs.	+	0	++	++	3.7
Apodiformes:	Apodidae	++	++	17–21	++	++	32–75 min.	+	20–42	++	++	0.7–2.5
	Trochilidae	0	++++	16–17	0	++++	5–99 min.	+	19–25	0	++++	1.1–3.3
Trogoniformes:	Trogonidae	++	++	18–19	++	++	2–16 hrs.	0	16–30	++	++	2.0–2.4
Coraciiformes:	Alcedinidae	++	++	21–23	++	++	1.7–24 hrs.	+	24–35	++	++	1.9–3.8
	Momotidae	+	+++	17–21	++	++	1–5 hrs.	0	28–30	++	++	4.0–4.8
	Meropidae	++	++	22	++	++	15–30 min.	...	30	++	++	...
	Coraciidae	...	...	18–19	++	++	...	...	26–28	++	++	...
	Upupidae	...	...	16	0	++++	11.5 hrs.	++++	29	++	++	1.9
	Phoeniculidae	...	...	...	...	...	...	...	...	++	++	3
	Bucerotidae	++	++	28–40	0	++++	continuous	++++	75	+++	+	1.6–2+
Piciformes:	Galbulidae	+	+++	19–22	++	++	145 min.	+	20–26	++	++	...
	Bucconidae	++	++	...	++	++	58 min.	0	...	...	...	...
	Capitonidae	++	++	13–15	++	++	37 min.	+	...	++	++	...
	Ramphastidae	...	...	16	++	++	38 min.	0	43–45	++	++	3.4
	Picidae	+++	+	11–18	+++	+	22–147 min.	0	19–35	+++	+	1–30
Passeriformes:	Dendrocolaptidae	++	++	15±	++	++	27 min.	0	19	++	++	9.7
	Furnariidae	++	++	15–20	++	++	22–97 min.	0	13–29	++	++	2–4
	Formicariidae	++	++	14–17	++	++	79–180 min.	0	9–13	++	++	1.3–5.3
	Cotingidae	+	+++	18–19	0	++++	12–37 min.	0	19–25	++	++	...
	Pipridae	0	++++	19–21	0	++++	111 min.	0	13–15	0	++++	1.2

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TABLE 51 *(cont.)*. Summary of attentive behavior by families.

Order and family		*Nest building*		*Incubation*					*Feeding and care of young*			
		Male	Fe-male	Dura-tion (days)	Male	Fe-male	Attentive periods	Male feeds female	Nestling period (days)	Male	Fe-male	Trips per hour
Passeriformes: *(continued)*	Tyrannidae	+	+++	12–21	0	++++	9–57 min.	+	12–24	+	+++	3.7–35.0
	Menuridae	0	++++	28	0	++++	...	...	42	0	++++	...
	Alaudidae	0	++++	11–12	+	+++	...	+	9–12	++	++	5.9–8
	Hirundinidae	++	++	14–18	+	+++	6–33 min.	+	18–28	++	++	4–40
	Oriolidae	+	+++	14–15	+	+++	...	...	14–15	++	++	...
	Corvidae	++	++	16–20	+	+++	35–94 min.	+++	15–38	+	+++	1.7–4
	Paradisaeidae	0	++++	14–18	+	+++	16–36+ min.	0	18–31	+	+++	12.9
	Paridae	++	++	12–15	+	+++	10–38 min.	++	14–21	++	++	3.6–34.5
	Sittidae	++	++	12–16	0	++++	31 min.	++	22–24	++	++	11.9–18.4
	Certhiidae	+	+++	15	+	+++	...	+	15–20	++	++	...
	Chamaeidae	++	++	15–16	++	++	47 min.	0	15–16	++	++	8.8
	Timaliidae	+	+++	21±	+	+++	...	+	...	+	+++	...
	Cinclidae	+	+++	16	+	+++	31 min.	+	19–24	+	+++	8.8–25.9
	Troglodytidae	++	++	14–19	0	++++	12–86 min.	+	13–22	++	++	5.6–19.2
	Mimidae	+	+++	12–13	+	+++	20.8–22.7 min.	0	11–14	++	++	3.6–14.2
	Turdidae	+	+++	12–14	+	+++	12–120 min.	+	12–18	++	++	5.5–38.5
	Sylviidae	+	+++	12–15	+	+++	11–80 min.	+	9–14	++	++	10–33
	Regulidae	++	++	14–17	0	++++	...	0	18–20	++	++	17.5
	Muscicapidae	++	++	12–20	+	+++	15–87 min.	++	10–20	++	++	6.2–33.6
	Prunellidae	+	+++	12–15	+	+++	19–30 min.	+	13	++	++	5.1
	Motacillidae	+	+++	13–14	+	+++	19–48 min.	+	10–15	+	+++	3.6–25

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TABLE 51 (*cont.*). Summary of attentive behavior by families.

Order and family		*Nest building* Male	Female	*Incubation* Duration (days)	Male	Female	Attentive periods	*Feeding and care of young* Male feeds female	Nestling period (days)	Male	Female	Trips per hour
Passeriformes:	Bombycillidae	++	++	12	+	+++	37 min.	+++	16	++	++	3.0
(*continued*)	Ptilogonatidae	+++	+	15	++	++	9 min.	+	18–19	+++	+	2.5–5.3
	Artamidae	+++	+	. . .	+++	+	. . .	0	. . .	++	++	. . .
	Laniidae	++	++	16	+	+++	23 min.	+++	15–21	++	++	. . .
	Prionopidae	++	++	. . .	++	++	17–30 min.	. . .	. . .	++	++	7–10.9
	Sturnidae	++	++	12	++	++	20 min.	0	20–21	++	++	19–22
	Melithreptidae	. . .	++++	18	+	+++	. . .	0	18	++	++	. . .
	Dicaeidae	+	+++	. . .	+	+++	. . .	. . .	. . .	++	++	. . .
	Zosteropidae	++	++	11–12	++	++	. . .	0	9–11	++	++	7
	Vireonidae	+	+++	13–14	+	+++	10–38 min.	0	11–13	++	++	3.9–13.5
	Coerebidae	+	+++	12–14	0	++++	19–61 min.	0	14–19	++	++	4.7–13.2
	Parulidae	+	+++	11–17	0	++++	23–110 min.	+	8–14	++	++	1.6–27.4
	Ploceidae	+++	+	12–16	+	+++	14 min.	0	13–19	+	+++	4–20
	Icteridae	0	++++	11–14	0	++++	9–30 min.	+	9–34	+	+++	6.2–17.7
	Thraupidae	+	+++	12–16	0	++++	. . .	++	10–24	++	++	. . .
	Fringillidae	+	+++	11–14	+	+++	14.6–continuous	++	8–17	++	++	1.3–21.3

Key: . . . No information is available. 0 No time or activity is involved. 0 ++++ or ++++ 0 One sex does all the work.
+ +++ or +++ + Both take part, but one sex does more work than the other. ++ ++ Each sex performs an equal share of the work.

It is difficult or impossible to find a single explanation for the evolution of parental care toward the female's responsibility that is equally satisfactory for all orders. A preponderance of females over males in the sex ratio could conceivably bring about such a behavior pattern, but there is no evidence on hand for the sex ratio in all these various orders being sufficiently unbalanced to bring about this effect. Polygyny does occur, as in some Galliformes and Passeriformes, when the sex ratio is unbalanced and this condition is associated with loss of attentiveness on the part of the males, but this condition is not extensive enough among birds to be the general explanation of this behavior pattern.

It is uncertain whether the evolution of sexual dimorphism in plumage and other body characteristics preceded or followed the evolution of this pattern of behavior. It is a common observation, however, that the duller colored sex is the one chiefly responsible for incubation and brooding; or when the sexes are alike, both may participate in nesting duties to a more or less equal extent (Burns 1924). The frequency of this correlation indicates a possible relation, although the number of exceptions is so great as to make any general correlation questionable. The duller colored mate is supposed more easily to escape detection by predators and hence have a greater chance of raising a brood successfully. However, the brightly colored male often aids in feeding the young after hatching and may even feed the incubating female, so there is considerable skepticism as to whether the sex difference in coloration arose solely because of the protective value of the duller plumage to the sitting bird.

Sexual dimorphism in plumage may well be a response to other factors in addition to or instead of the need for the incubating parent to be protectively colored. Bright display plumage often serves for sexual stimulation leading to pairing and mating. These displays may have developed in order to stimulate the female to earlier and fuller reproduction. If there is competition for mates or for a high position in a social hierarchy, the brighter colored males may be more successful. If these trends involving more aggressive sexual behavior on the part of the male were strong enough, they may have become of greater evolutionary importance to the species than for the male to continue aiding the female in incubation and care of the young. One may imagine this to be the situation in Anseriformes, Galliformes, Charadriiformes, Passeriformes, and Trochilidae, but it could hardly be true for the nocturnal Caprimulgiformes and Strigiformes, where sexual dimorphism in plumage is not much developed.

Bright coloration in the male may also serve for intimidation displays in defense of territory. This would be particularly important in many groups of Passeriformes where much of the male's time is fully occupied with establishing and protecting nesting territories. There is a useful division of labor here with the female doing the incubation and the male maintaining constant guard over the territory to protect his mate and offspring. This would surely have selective value in the evolution of behavior patterns in those forms that have nesting territories.

A similar idea is expressed by Armstrong (1947:244) in respect to arenas or courts used for display purposes by the male. "The maintenance of a court is incompatible with any considerable measure of attention to the domesticities, and thus we find that amongst court-keeping birds the males take little or no part in the building of the nest, brooding the eggs or tending the young. The nest-building impulses are diverted into the upkeep of the display area, and energy which in other birds is used up in family chores is devoted to posturing." Verheyen (1948) states that the aggressiveness of the male for defense of territory varies inversely with the development of parental care and that one way in which this is evident is the lesser concern of the male for territorial defense when he actively participates in feeding the young.

Territory is less highly developed in those orders where both sexes participate more or less equally in nesting duties. Many species are colonial in habit and what defense there may be is principally concerned with the nest itself and its contents. With so many birds in close proximity, there is need to have the eggs and young guarded continuously. Reproductive success may be higher and there may be a distinct advantage to the species in having the eggs protected by each parent alternately while the other is away getting food.

An additional factor involved is the feeding of the female by the male, thus relieving her of the necessity of leaving the nest or its vicinity. This trend in behavior has developed independently among miscellaneous species in several orders but especially in Falconiformes, Psittaciformes, Strigiformes, Coraciiformes, and Passeriformes. The behavior reaches extreme development in the Bucerotidae of the Coraciiformes where the female is physically confined to her nest-hole throughout the incubation period. In the Passeriformes the male commonly furnishes the incubating female with most of her food in the Corvidae, Paridae, Sittidae, Muscicapidae, Bombycillidae, Laniidae, and in certain members of the Parulidae *(Dendroica petechia, D. castanea)* and Fringillidae *(Carduelis carduelis, Spinus* sp., Geospizinae), besides others. The obvious advantage of this behavior trait is that it keeps the eggs covered, protected, and at a uniformly high temperature more continuously. In other species where the female must leave the eggs uncovered at intervals to get food, the eggs fluctuate appreciably in temperature (Kendeigh 1940). Although fluctuating temperatures sometimes may be stimulating, development is well known to proceed more rapidly at high than at low temperatures. There should thus be an advantage in evolving a behavior that keeps the eggs covered a greater percentage of the time.

Parasitism in nesting behavior has evolved in such widely variant groups as Anseriformes *(Heteronetta atricapilla)*, Cuculiformes (Cuculinae, also *Tapera naevia*), Piciformes *(Indicatoridae)*, and Passeriformes (Icteridae: *Molothrus ater* and related species; Ploceidae: Estrildinae, Viduinae). It has been suggested that parasitism arose as the result of breakdown in the timing of various phases of reproductive behavior and a consequent loss of effectiveness (pp. 212, 272). Just what might produce this loss of timing is uncertain, but it may lie internally in the endocrine or nervous-regulating mechanism. On the other hand, parasitism may have arisen for other reasons, proved advantageous so that it evolved into a definite behavior pattern, and the loss of timing and effectiveness in the species' own reproductive cycle followed subsequently. Doubtless the origin of this specialized behavior pattern will be the subject of speculation for some time to come (Makatsch 1934).

Communal nesting is another specialized behavior pattern. It is presumably found in the care of young in some species of Sphenisciformes, although the pertinent facts need more definite substantiation, and possibly in some Pelecaniformes. In the Piciformes the peculiar behavior of *Melanerpes formicivora* suggests communal nesting, and in the Passeriformes there may be communal nesting in certain species of Corvidae, Timaliidae, and Prionopidae. Scattered tendencies in this direction have been recorded for many kinds of birds (Skutch 1935, Nice 1943, Armstrong 1947). The extreme expression of this special behavior occurs, however, in the Crotophaginae, belonging to the order, Cuculiformes. Here again it has been suggested (pp. 212-14) that this behavior may be correlated with a loss of proper timing of the various phases in the nesting cycle. Communal behavior would seem most likely to develop in species that nest in colonies or where many individuals are obliged to be in close proximity with each other. However, this appears not to be a universal requirement for its development.

The family, Megapodiidae, in the order, Galliformes, has evolved the use of artificial incubation for their eggs. Various other birds make use of the sun's heat during the middle of the day to relieve them somewhat of attentive duty during these hours. In some Sterninae and Glareolidae there may actually be more concern in keeping the eggs cool during these hours than in keeping them warm. The Egyptian plover, *Pluvianus aegyptius,* is supposed to bury its eggs in the sand and depend largely on the sun's heat to hatch them. However, only in the Megapodiidae is artificial incubation generally developed to such a high degree as to constitute the sole means of reproduction. This behavior in the family is of such ancient origin as to have allowed time for evolving a more complete development of the embryo while still in the egg so that the chick is unusually precocious at hatching. There has been some speculation concerning the origin of this behavior, but the amount of true evidence available is so scant as to leave the question largely unsolved.

Aside from the various ways in which division of labor between the sexes occurs for incubation and other nesting duties, an evolutionary trend also exists that is progressive throughout the class, to shorten the average length of the attentive periods and to have them come more frequently during the day. The longest attentive periods are found in the Diomedeidae of the Procellariiformes, the shortest periods are found in the families of Apodiformes, Piciformes, and Passeriformes (Table 52). Possibly one factor affecting the length of the attentive period is the amount of food that can be ingested at one time and the rate at which digestion proceeds. Such birds as the Galliformes, Psittaciformes, and Columbiformes have well-developed permanent crops (Newton 1893-1896) which they can fill with food to digest at their leisure. In the domestic fowl the average retention of food in the crop is between 11 and 12 hours (Schwartz and Teller 1924). This would permit long periods of attentiveness without discomfort from hunger. Crops of various sizes or forms also occur in some Anseriformes, Falconiformes, and Tinamiformes. In some birds, although there may be no definite crop, the esophagus is distensible to various degrees and may hold a reserve supply of food. Furthermore the stomach of some species has a greater capacity than in others. Very little information is available on the rate of digestion in various kinds of birds. One could well expect that on a given amount of food those species with the slower rate of digestion would have the longer attentive periods. The rate of digestion is doubtless correlated with the general rate of metabolism and physiological activity of the species.

The shortening of periods and acceleration of the attentive rhythm is correlated with a decrease in the length of the incubation period (Table 52). The longest incubation periods occur in the Palaeognathae and in some of the Procellariiformes. The shortest incubation periods are found generally in the Picidae and in several families of Passeriformes. In discussing various factors controlling length of incubation, Skutch (1945d) calls attention to the possible importance of the amount of time that the eggs are kept covered by the adults, which varies during the daytime from 50 to 100 per cent in different species. This factor may be important between closely related species but appears unimportant in comparing different families and orders. Actually some of the longest incubation periods are found in groups where the eggs are kept constantly covered by one or the other adult. It is important to remember

TABLE 52. Relation between length of incubation period, length of attentive period, and rate of feeding the young in families segregated according to length of incubation period.[a]

Range of incubation periods	Attentive period Average	Attentive period Range	Rate of feeding Average	Rate of feeding Range	No. of familes involved
54-75 days	5.0 days	1–8 days	1.1 per day	0.5–1.5 per day	4
42–47 days	1.6 days	0.5–3 days	1.2 per day	1–1.5 per day	5
30–34 days	10.4 hrs.	1.7–23.5 hrs.	Mostly precocial		6
22–28 days	8.3 hrs.	22.5 min.–23.5 hrs.	Mostly precocial		18
14.5–20 days	2.4 hrs.	9 min.-12 hrs.	8.5 per hr.	0.5–22 per hr.	26
12–14 days	33.4 min.	14–66 min.	13.3 per hr.	8.7–22 per hr.	14

[a] The data used for each family are the media of the extreme values given in Table 51. Species are excluded where the female sits continually on the nest or is furnished most of her food by the male.

that the incubation period is also greatly influenced by physiological factors (Bergtold 1917, Kendeigh 1940).

Heinroth (1922) long ago stated his belief that a long incubation period is a primitive character. He associated a shortening of the incubation period with smaller egg size, less development of the young at hatching, greater exposure of the nest to external dangers, and repeated nestings during the year. All these factors may well be concerned in the evolving of a faster nesting tempo. Lack (1948) has worked out a correlation between length of incubation and nestling periods and number of eggs per set, the larger sets having the longer periods. Needham (1931) and Nice (1943) have given evidence that larger birds tend to have longer periods than closely related species of smaller size.

This correlation between short incubation and short attentive periods can sometimes also be detected in comparing different families in the same order or even different species in the same family, but the data are often contradictory, incomplete, or otherwise unsatisfactory to permit entire confidence that the correlation on a finer basis can be fully documented.

Long incubation periods may permit the young bird to hatch in a precocial state of development. Seth-Smith (1907) and Verheyen (1948) have suggested that the precocial and not the altricial condition is primitive in birds. A certain amount of brooding is required in precocial species at night and in bad weather, the young need to be taught what are proper food items, and they need to be taken care of for a considerable time, but their care requires less energy and is carried out more leisurely. In a few precocial species the young are actually fed by their parents for the first few days after hatching. This applies especially to the Otidae, Glareolidae, Gruidae, Rallidae, Colymbidae, Gaviidae; in a few gallinaceous birds, e.g., *Polyplectron;* and in a few shore birds, e.g., *Haematopus;* while in the Laridae the young, which are intermediate between precocial and altricial, are fed until fully fledged (Lack 1947). On the other hand, as the incubation period becomes shorter, the young are hatched in a more helpless or altricial state and require a great deal of attention from their parents simply for maintaining existence at all. More or less constant brooding is necessary to maintain their body temperature, food must be brought to them and put into their mouths, and they must be protected from enemies and predators. Attentive behavior becomes more highly developed with altricial than with precocial young. This usually involves a continuance of the fast attentive rhythm associated with the short incubation periods.

In the evolution of the altricial from the precocial condition there is a shift in the physiological use of energy resources by the adult birds, especially the female. The eggs of precocial species are larger and contain relatively more yolk and albumen than do the eggs of altricial species. Their caloric value is greater. These basic materials and this energy must be drawn from the female during the egg-laying period. Most precocial species, except for some shore birds, are larger than altricial species and can tolerate this rapid drain on their energy resources. The eggs of altricial species, on the other hand, do not contain sufficient energy and building materials to permit as great development of the embryo before hatching. Although the drain of energy from the female at the time of egg-laying is considerable, perhaps relatively more even than in precocial species, it is not as adequate because of the smaller size of the birds. The result is that adult altricial species must compensate for the smaller energy resources in the eggs by expending more energy in the care of the young after hatching. These changes in behavior and in the manner in which limited energy resources are expended have necessarily been advantageous in certain respects. The consequent reduction in body size, for instance, has permitted occupancy of new ecological niches that would not otherwise have been possible, and this in turn has resulted in the evolutionary differentiation of many new species and a general increase in bird population. Furthermore, the altricial condition allows small birds to raise more offspring than would be possible if their bodily energy resources were depleted to form a smaller number of larger precocial-type eggs.

Along with shortening of attentive periods there is a trend for increasing the rate at which the young are fed (Table 52). The highest rates are found in the Passeriformes (Table 51). A high rate of feeding does not necessarily mean that more food is given the young as this will depend also on the quantity brought on each trip to the nest. Skutch (1949a) has called attention to the fact that there may be an advantage in less chance of betraying the nest's location to predators by bringing large feedings at less rapid intervals than by frequent small feedings. The rate of feeding is affected also by the kind of food brought, whether it is partially predigested by the parent, and the number of young fed on each trip.

It is our impression, in confirmation of Heinroth (1922) and Lack (1948), that the shorter incubation periods are also correlated with shorter nestling periods among altricial species. A correlation probably also exists with time to reach adult size and independence, although exact information in this connection is difficult to obtain. Precocial young may leave the nest soon after hatching; yet they require several weeks to mature. The chief irregularities in the correlation between length of incubation and nestling periods among altricial species are in those families which nest in holes so that the young are well protected, in the Hirundinidae and Apodidae where they must mature flight feathers before venturing forth, in the Cuculidae where the young leave the nest early and then have a climbing stage, in the Formicariidae and Pipridae, and in several Parulidae and Fringillidae that nest on the ground or in exposed situations (Nice 1943, Lack 1948).

Certain advantages come to a species in shortening its nesting cycle. The time of juvenile helplessness is shortened, and one would suppose the mortality from predation thereby reduced. With short nesting cycles, two or more cycles may be completed in the same year, thereby increasing the reproductive potential of the species. Short nesting cycles permit reproduction in the far north, in arid regions, or in other areas with short seasons favorable for nesting. On the other hand, acceleration of the attentive and reproductive rhythm probably requires a higher rate for the expenditure of energy, greater activity, more food consumption, and a more intense physiological state in the adults in general. Lack (1948) has pointed out that in some situations a slower rate of development may have advantages, as when there is a scarce or erratic food supply (swifts, petrels) or, associated with safe nesting, the raising of a large brood slowly instead of a small brood quickly (hole-nesting passerines). The complete evaluation of these various factors requires further study.

Not all evolution has been in the direction of shortening attentive periods. Goodwin (1948) lists the following species in which the adult bird sits on the eggs without food almost continuously throughout incubation: emu, *Dromiceius* sp.; eider duck, *Somateria mollissima;* argus pheasant, *Argusianus argus;* golden pheasant, *Chrysolophus pictus*. Such behavior would seem possible only in species capable of storing considerable food energy in their bodies and to tolerate considerable depletion of this supply during the long incubation period. It does not seem an efficient type of behavior, and its scattered occurrence through the class would indicate its aberrant nature.

The time that steady incubation is initiated by the adult in relation to the completion of the egg set is quite variable between species. Some of the variability that is noted is due to difficulties of observation. A bird may sit on the eggs without applying full incubating heat to them if its brood patch has not completely formed. Birds are easily disturbed during the egg-laying process even to the extent of deserting the nest. The most certain evidence that incubation has really begun may be secured by measuring nest temperature. Full incubating behavior is indicated when attentive periods are longer than inattentive ones. One may judge with some confidence the time that incubation begins from the intervals between hatching of the young. In the owls incubation obviously begins with the first egg because of the very evident differences in the ages of newly hatched young. From our review of the literature, repeated observations indicate that incubation begins with the first egg of the set or at least well before the set is complete in at least some species of the following families: Gaviidae, Colymbidae, Phalacrocoracidae, Ardeidae, Ciconiidae, Accipitridae, Falconidae, Jacanidae, Chionididae, Laridae, Psittacidae, Cuculidae, Tytonidae, Strigidae, Upupidae, Bucerotidae, Corvidae, Ptilogonatidae, and Vireonidae.

Lack (1948) argues an advantage for asynchronous hatching in those species whose young spend a long time in the nest and which are dependent on a vicarious food supply. If food becomes short, the youngest and smallest bird receives proportionately less food and quickly dies. This leaves more food for the other young so that part of the brood may be raised to maturity. Had all the young been of the same age and size, a food shortage would likely weaken all of them, so that all would die. With most birds, however, especially in the higher orders, there is a strong tendency for incubation to begin gradually and not to reach full development until the set is nearly or quite complete. The result is that all young commonly hatch within one to two days. With an abundant food supply reproductive success is greater with the entire brood of the same age, since all young are then likely to survive to fledging. In passerine species, if the hatching of one young bird is delayed beyond the others, he will usually die in a few days since he is less successful in competition with his nest-mates for food from the parents.

One can discern but little relation between the attentive rhythm and conditions of the environment. Most species with precocial young nest on the ground. This permits the young to disperse with greater ease and safety than if they were arboreal (Pycraft 1907). As already stated, the nestling period of some species that nest in holes or cavities where they are well protected seems unusually long. In swallows and swifts the long nestling period is correlated with the need of obtaining good flying ability before leaving the nest. Attention has already been called to the fact that some, but not all, tropical birds seem to have longer incubation periods, longer periods of attentivity, and a generally slower reproductive rhythm than their closest relatives. This is evident in *Odontophorus* of the Galliformes; in the Trogoniformes; in Capitonidae and Ramphastidae of the Piciformes; in the Furnariidae, Formicariidae, Cotingidae, Pipridae, and in certain species of Tyrannidae, Hirundinidae, Troglodytidae, Parulidae, Icteridae, and Thraupidae among the Passeriformes. If such a relation to climate could be firmly established, it might indicate an ancient tropical ancestry for such forms as the Procellariiformes, Pelecaniformes, and others. The relation, however, can only be suggested as a possibility at the present time. The daily rhythm of activity may also be more pronounced in the tropics with the birds remaining a longer time away from the nest during the hot midday hours.

There has been increasing use of biological characters in recent years for understanding the phylogenetic relationship of birds. A. Miller stated in 1937 that "the significance of similarities in behavior pattern in distinct species of the same genus lies in the strong evidence they afford for common descent and for adaptation to similar modes of life. The characteristics of shrike behavior are as constant and as obvious as many structural features that relate the three species of *Lanius* under consideration. The inherited behavior is no less conservative in evolution than the structure . . . . In final analysis, the more prominent features of behavior ascertained through a study of natural history prove to be generic or even of family significance." In discussing various characteristics of value for classifying birds into categories higher than species, Mayr and Bond (1943) rank in order by increasing usefulness: size and shape of tail, bill, feet, nostrils, and wing; color patterns; behavior patterns. Delacour and Mayr (1945) pointed out that "habits and behavior are deeply rooted and are usually the product of very ancient evolution." In his study of Darwin's finches, Lack (1947) states that "there is much greater uniformity in courtship habits than there is, for instance, in the shape of the beak. This illustrates the fact that, in birds, breeding habits and display can be as valuable an indication of affinities as are structural characters." Armstrong (1947) presents additional evidence for the value to taxonomy of behavior patterns.

These quotations emphasize the concept that has come out of this study, that the behavior pattern of parental care is a conservative evolutionary characteristic of birds, in fact it is more conservative than many structural features of the body. It is surprising to see how the pattern of equal sharing by male and female in all phases of reproduction is found in nearly all orders from the lowest to the highest. This not only indicates the primitive nature of this behavior pattern but also the very early separation of the evolutionary lines from the ancestral stock that led to the modern orders of birds.[1] There has been both divergent and convergent or parallel evolution of behavior in the various orders. The extent of this evolution has progressed to various extremes. This is not correlated, however, with the degree of structural specialization, which is often taken to show lowness or highness in the evolutionary scale of development.

It is possible to describe a typical behavior pattern of parental care for most orders. This does not mean that there is no variation between families within these orders, but these variations are of secondary nature or are obviously divergent trends. For example, in the Coraciiformes, both sexes commonly alternate at incubation, but in the Upupidae and Bucerotidae there is the extreme development of the female doing it all with the male responsible for supplying her with food. There are a few orders, such as Charadriiformes, Cuculiformes, and Apodiformes, in which two or more diverging evolutionary trends are manifested. In these cases one can indicate what the basic pattern is from which each trend originated but can hardly describe a pattern that is now typical of the order as a whole.

There is greater uniformity of behavior within the family than within the order. In some large families, such as Charadriidae, Scolopacidae, Corvidae, Fringillidae, and in some others, there may be lack of consistency in behavior due to a more active evolution being in progress, but these cases are exceptional. Normally one can expect similar behavior among various species in the same genus, although here again there are exceptions and there is frequent variation in details, especially in the timing of attentive periods. Variations in behavior pattern are minimum between subspecies, although differences in behavior between the various subspecies of *Troglodytes troglodytes* are remarkable.

Group adherence to particular behavior patterns is not, therefore, rigid. There is a gradient of consistency in this adherence from the individual or species through the genus and family to the order and class. Such gradients also exist for structural characteristics, and the faithful-

[1] Six months after this statement was written, the paper by Hildegarde Howard (1950) came to the author's attention. She presents a phylogenetic tree showing the differentiation of most modern orders of birds all in the Cretaceous period and mostly from the same ancestral stock. She estimates this period to have lasted 60,000,000 years and the Cenozoic period that followed to have been of similar duration. It seems very probable that evolution of the different behavior patterns of parental care described in this paper developed independently in the various orders after they became differentiated and perhaps mostly during the 60,000,000 years of the Cenozoic period.

ness of behavior according to specific patterns is at least as consistent, if not more so, than is uniformity in details of structure. Behavior patterns are therefore very useful taxonomically in establishing phylogenetic relationships between various groups. They should be used more extensively. A word of caution must be added, however. Behavior patterns from forms obviously unrelated because of structural differences can be so arranged as to appear to present a phylogenetic series. Such pseudo-phylogenetic series must be guarded against. Obviously a bird evolves gradually in all of its characteristics, and true relationships can be demonstrated only when there is a consistent and logical development of all traits simultaneously. Pseudo-phylogenetic series can, of course, be constructed with the use of structural characteristics as well as those of behavior.

Behavior depends upon the organization of the nervous and endocrine systems. Behavior patterns are fundamentally dependent upon the arrangement and development of neurones, association cells, synapses, and other structural units in the nervous system and upon the release of hormones at the proper time and in the proper amount by the endocrine system. The sense organs are involved for the reception of external stimuli, and the brain is required for evaluating the nerve impulses that are received and for redirecting them to produce particular responses. Much of behavior is also conditioned by the physiological state of the organism. Physiological mechanisms vary in activity with environmental conditions, particularly temperature regulation, energy regulation, gonad development, thyroid, pituitary, and others. For a behavior pattern to be expressed, the organism must have first of all the basic nervous organization, after which it must receive the proper stimuli and be in the appropriate physiological state.

The nervous system is one of the least variable structural systems in the body, although it is subject to the same laws of inheritance, variation, and evolution as any other system. The conservative evolutionary status of behavior patterns is but an expression of the conservative evolutionary tendencies of the nervous system itself.

After this survey of parental care in the class, Aves, and the probable phylogenetic relations of the different behavior patterns to each other, one may well wonder what the phylogeny of parental care may be through the entire animal kingdom. We can do no more here than mention some of the more conspicuous steps involved in this phylogeny with the hope that specialists in different phyla and classes will analyze the problem in detail.

Verheyen (1948) has searched for the origin of the avian behavior pattern of parental care in the class Reptilla. Reptiles take care of their eggs by either (1) placing them in humus where they are incubated with possibly some benefit from the heat of decomposition, (2) surrounding or covering them with their own body which in the python, at least, keeps them at a temperature somewhat above that of the general surroundings, or (3) retaining them in the uterus until shortly before or after they hatch. The first procedure is found in some birds, notably the megapodes, although it has been independently acquired in this latter group. Verheyen believes intra-uterine development of eggs did not evolve in birds because of the handicap this extra weight would be in flight and because the abdomen could hold but one egg at a time. Bird behavior is more like that of the python with the notable advantage that birds are able to apply a much greater amount of heat to the eggs and to maintain them at a higher temperature. This became possible only with the evolution of homoiothermism. The evolution of the complicated patterns of parental care in birds was conditioned, therefore, by the evolution of warm-bloodedness.

The concept of parental care developed in the present study is one of behavior or psychology and involving the nervous and endocrine systems. Much of this behavior is doubtless automatic and instinctive but tempered extensively by experience, habit formation, other individuals, and the general environment. The ultimate objective of parental care is the protection and nursing of offspring until independence and self-sufficiency are attained. Protection of the offspring is accomplished in birds by the activities of the parents in building nests, setting up territories, and driving away enemies. Protection is also offered, although in an entirely different manner, in the formation of the egg, in which the embryo is enclosed within shell membranes and a hard shell, and supplied with food and a means for respiration. This aspect of parental care is physiological or morphological, rather than psychological, but is just as important. Both aspects need to be kept in mind in recognizing types of parental care in the lower and simpler types of animals.

Parental care is entirely lacking among several groups of animals. In the Protozoa, fission is a common method of reproduction and the parent entirely disappears as such when it divides to form offspring. Likewise parental care cannot be recognized in those Ctenophora, Echinodermata, Annelida, and Pisces where fertilization is external and no further attention is paid to the eggs after they leave the parent. All these forms live in an aquatic habitat.

Budding, such as is found in Porifera and Coelenterata, represents a special form of asexual reproduction wherein the offshoot may receive some nourishment and protection from the parent before it finally attains independent existence. The formation of cysts around the asexual spores of Protozoa, gemmules of Porifera, and statoblasts of Bryozoa give some protection to the offspring until they drift into favorable habitats where full development can occur.

Internal fertilization likewise makes possible the formation of cysts, envelopes, or shells around sexually formed zygotes or eggs so that when they leave the body of the parent they will survive until favorable conditions for development are reached. Such protection to eggs is given in a very large number of phyla from Protozoa even to Mammalia *(Ornithorhychus)*. Usually these eggs contain considerable food material or yolk so that early tender stages may be completed before liberation is effected.

The eggs, after fertilization, are often attached to the outside or retained within the body of the parent to permit a varying degree of development before they are released to an independent existence. Several Crustacea, as Copepoda and Decapoda, have the eggs attached to appendages or other external parts of the body. Even some frogs and toads, in the Amphibia, have the eggs undergo development while fastened to the legs of the adult, while held in the mouth or in the vocal sacs, or while embedded in small pockets in the back. Retention within the body may be between the two body layers as in Porifera and Coelenterata; or in a brood pouch, a uterus, or within the general body cavity as in some Platyhelminthes, Nemathelminthes, Trochelminthes, Bryozoa, Pelecypoda, Crustacea, Pisces, and Reptilia. There are many intermediate stages between ovipary and ovovivipary, but generally all nourishment is derived from the egg yolk and not from the parent. There is parental care, however, to the extent that the parent furnishes protection from the physical environment and from predators. The parent has no further concern for the offspring, once they have left the protection of her body.

Vivipary is truly developed only in Mammalia. Here there is not only morphological protection of the embryo but also internal nourishment of it through the placenta during a long period of early development. The high development of vivipary in this class may be correlated with the evolution of homoiothermism. By retaining the embryo within the body of the mother, it is maintained at a higher temperature than were it exposed to the environment, and consequently growth is faster. After birth, the young are further nourished from the mammary glands of the mother. Some mammals are born with functional temperature regulation. However, in those species where the young are cold-blooded and blind at birth, a warm nest is needed for their physical comfort. In all cases, the young must be trained in the traditions of the species so there is a period of early life during which parental care is required.

Evolution of parental care or protection of the offspring in the animal kingdom appears to have proceeded in two directions. One trend, already described, is to retain the embryo within the body of the parent during its early stages of development and to give it increasingly efficient protection and nourishment. This reaches its highest level in Mammalia. The other trend is to evolve increasing care of the egg and young outside and free from the body from very early stages until complete independence is attained.

An early stage in the development of parental care in this latter direction is the attention given to the places where the eggs are deposited. This increases their chances of survival and growth, but otherwise the adults give them no attention. The eggs may be laid singly or in masses in the ground, in humus, inside or attached to stems or leaves of plants, inside other animals, or in crannies or crevices of various sorts (Gastropoda, Insecta, Amphibia, Reptilia). Sometimes nests or artificial shelters are formed, as in some Diplopoda and Insecta; cocoons, as in the Oligochaeta; or egg sacs, as in the Arachnida.

The next higher stage in parental care is shown especially by many social Hymenoptera, a few Arachnida, and some Pisces, Amphibia, and Reptilia where eggs are not only deposited in nests or artificial structures but both eggs and young are guarded and cared for by one or both parents. Usually there is very little control over temperature or other factors that affect the rate of development of the embryo, although in some instances advantage is taken of special exposures to insolation, of heat generated by decaying vegetation, etc.

The most extensive evolution of parental care in this direction occurs in the birds, Aves. This is possible because the evolution of homoiothermism permits the transference of heat from the parent to the egg which in turn accelerates the rate of development of the embryo more or less independent of the environment. Thus, birds have attained an acceleration in the growth of offspring outside the body comparable to that produced by mammals by the retention of the embryo inside the body.

This has been accomplished, however, only by the evolution of more complex parental behavior patterns concerned with nesting than have evolved with the development of offspring within the body.

Oviparous animals care for both eggs and young; the behavior of viviparous animals is significantly modified only for the care of the young after birth when they are already far along toward an independent existence. The nesting behavior of the social hymenoptera, some fish, and practically all birds is much more intricate than those of most mammals. The high psychological evolution found in modern man is not motivated fundamentally by requirements for the care of young but by the complicated mores of social and economic life involved in modern civilization. Parental care in uncivilized primitive man was relatively simple. It is the recent new phenomenon of modern civilization and not physiological or morphological needs that has brought about the relatively long period for training and parental guidance of human offspring.

Parental care has doubtless evolved in the animal kingdom to insure a higher survival rate of the offspring. This has selective value in evolution as ordinarily those species which mature the largest number of offspring will exert the greatest influence in the biotic community, compete with other species most successfully, and occupy to capacity all available niches and regions of the world. Furthermore with higher survival rate of offspring, fewer need to be produced to maintain a stabilized population of the species in the balance of nature. An oyster, which shows no evidence of parental care, produces millions of eggs from which only one is required to reach maturity to take the place of the adult when it dies. On the other hand, a high degree of parental care allows the house wren to average only about 10 eggs in its lifetime, yet to maintain a highly successful and aggressive species. This greater reproductive efficiency conserves considerable energy, and this energy then becomes available for progressive evolution of other body systems and functions.

The phylogeny of parental care cannot be traced through the various described stages as a direct line of evolution from phylum to phylum. Various types of parental care often occur in a single phylum. It appears that the evolution of parental care has proceeded independently in each phylum as doubtless each phylum had its separate origin in the remote past and from relatively much simpler forms. Most phyla probably became distinguished morphologically from one another before the evolution of parental care had proceeded farther than its initial stages.

Even within many classes within the phylum there is considerable difficulty in describing general patterns for the protection and care of offspring. In some classes of lower rank in the evolutionary scale there is some similarity in morphological structures involved, but details vary. It is not until one gets down to the order and taxonomic categories of still lower rank that one can begin to define general behavior patterns with any consistency. The development of distinctive and adaptative behavior patterns concerned with care of offspring has come relatively late in the evolutionary time-scale, after the main taxonomic groups had already become distinct. Likewise, the evolving of complex behavior patterns had to wait for the nervous system and sense organs to become perfected and so is largely limited to the higher evolutionary types of animals. For various reasons, therefore, it appears that parental care has reached its highest and most elaborate development in birds.

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VII. Species Index

This index is limited to species. The reader is referred to "Contents" for locating information on particular orders or families. A subject index for this book was not feasible, especially for Chapters IV and V. Information on all topics listed in Chapter III has been compiled and summarized as far as it is available for all species, families, and orders and is best located through use of this Species Index and the Contents. These various topics are also included in the general discussions at the end of Chapters III, IV, and V.

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