BREEDING BIOLOGY AND BEHAVIOR OF THE BROWN THRASHER,

(Toxostoma rufum)

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of the Ohio State University

By

Howard Partin, B.S., M.A.

* * * * * *

The Ohio State University

1977

Reading Committee:

Dr. Loren S. Putnam
Dr. Maurice L. Giltz
Dr. Tom Grubb
Dr. Walter Rothenbuhler

Approved by

Loren S. Putnam

Advisor
Department of Zoology

ACKNOWLEDGMENTS

I wish to express my sincere appreciation to my advisor, Dr. Loren S. Putnam, for his encouragement, advice, thoughtfulness, and constant supervision during my graduate studies and dissertation research. Without his help this project would not have been brought to completion.

I am indebted to Dr. Tessa Unthank and Dr. Oline Carmical for offering constructive criticisms during the writing of the manuscript.

Special thanks are due Dr. Tom Grubb and Dr. Walter Rothenbuhler, members of my reading committee, for their helpful suggestions in arranging the material presented in this dissertation; to David Jordan for his advice and statistical assistance in analyzing much of the data presented in this paper; and to Mildred Chavous for her friendly advice and personal involvement in keeping my program of studies within the guidelines of the University.

I wish to thank my wife, Altha, for her patience, sacrifices, and understanding during the course of my studies and for her help in collecting the data for this dissertation.

VITA

July 7, 1923	Born, Bond, Kentucky
1943-1946	U.S. Armed Services
1960	B.S. Degree, Cumberland College, Williamsburg, Kentucky
1961-1963	Teacher, Hazel Green High School, Laurel County, Kentucky
1964	M.A. Degree, University of North Carolina, Chapel Hill
1965-1970	Teacher, Hazel Green High School, Laurel County, Kentucky
1970-1971	Assistant Professor, Biology Department, Cumberland College, Williamsburg, Kentucky
1971 (Summer)	Graduate Student, Franz Theodore Stone Lab. Put-in-Bay, Ohio
1971-1972	Teaching Assistant, Department of Zoology, The Ohio State University, Columbus
1972-1977	Associate Professor, Biology Department, Cumberland College, Williamsburg, Kentucky

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Although the Brown Thrasher, *Toxostoma rufum* (Linnaeus), is a rather common nesting species throughout the central and eastern United States, its breeding biology and behavior,like those of many other common birds, is relatively untouched. Most of the information provided in the literature is in anecdotal form and, if quantified, has not been statistically analyzed.

Previous studies of the nesting habits, geographical variations in behavior patterns, care of the young, and clutch size of this species include the works of Sherman (1912), Gabrielson (1913), Ekblaw (1918), Bent (1948), Thomas (1952), Mengel (1965) and Morgan (1968). Detailed information on the breeding biology and behavior of the Brown Thrasher comes from a single study, Erwin (1933). In none of the previous investigations are the data sufficiently quantified to permit statistical analyses.

An attempt has been made in this study to investigate those areas previously studied to detect changes, if any, in the breeding habits of the Brown Thrasher and to explore those areas formerly neglected by other workers. The avenues of approach to these problems were similar to those of Slack (1973). The primary objectives were as follows: (1) study by observation and electrical device the behavior of the incubating bird in relation to environmental temperature, time of day, and stage of incubation; (2) determine the influence on the incubating bird by its nonincubating mate; and (3) investigate certain aspects of the nesting cycle such as nest construction, eggs, age-specific mortality of eggs and nestlings, and foraging ecology and behavior of the parent birds.

Behavior of the Incubating Bird as Related to Temperature, Time of Day and Stage of Incubation

The diurnal pattern of incubation activity of passerine birds is of interest in discovering the nature of circadian rhythms and how they are influenced by environmental factors during the breeding season. Attempts have been made by investigators to determine the proportion of the day, or incubation period, during which heat is being applied to the eggs, and to determine also the proportion given to self-maintenance of the incubating bird. In this paper, session refers to behavior during which the bird is sitting on the nest, presumably applying heat to the eggs, and recess refers to the bird's absence from the nest (cf. Skutch 1962).

Information on incubation activity has been collected by personal observation and by automatic devices, usually electrical. While personal observation is, perhaps, the most accurate and informative method, the exhausting effect it has on the observer makes it difficult to obtain the needed volume of data from which meaningful conclusions may be drawn (compare Putnam 1949).

Various types of automatic devices providing continuous records of incubation behavior have been used with several species. Some of these instruments represented in the literature employ heat, some employ light, while still others employ pressure to record the sessions and recesses of the incubating bird.

The pressure or contact type device was used to record the movements of a wild partridge, *Perdix perdix*, on her nest during the egg laying and incubation periods by Fant (1953).

A recording device sensitive to light was used by Kessler (1962) to measure nest attentiveness in the Ring-necked Pheasant, *Phasianus colchicus*, and by Weeden (1966) to record the incubation patterns of sessions and recesses by the Tree Sparrow, *Spizella arborea*.

Devices that are sensitive to temperature changes within the nest have been used extensively to determine both nocturnal and diurnal patterns of incubation activity (Baldwin and Kendeigh, 1927, and Holcomb, 1974).

This present study employs the use of a thermistor-recording device with a sensing probe, which was first used by Slack (1973) in his extensive studies of the Catbird, *Dumetella carolinensis*. The sensing probe may be placed among the eggs to record temperature changes within the nest.

Factors Affecting Incubation

Incubation behavior of passerine birds may be affected by a number of factors. Some of those postulated are: ambient temperature, time of day, stage of incubation, rain, hunger, and behavior of the nonincubating mate.

Temperature

The application and maintenance of heat to the eggs is essential for the life and growth of the embryo. This is accomplished in nature in the majority of birds by warming the eggs with heat produced by the metabolic processes in the body. The heat is transferred from the bird to the eggs through the brood patch, an area on the ventral surface of the bird that becomes bare during the breeding season. Baerends (1959) has shown that prolonged interruption in the application of heat to the eggs, or the reduction in heat intensity below a critical level, results in the death or malformation of the embryo.

The question of the effect of environmental ambient temperature on nest attentiveness during incubation has received much attention by investigators. One finds statements indicating no relation between attentiveness and temperature (Kuusisto 1941, Davis 1960, Davis _et_ _al_. 1963, and Weeden 1966). Investigations by other workers reveal an inverse relationship, for example, that nest attentiveness decreases as the ambient temperature increases (Hann 1937, Kendeigh 1952, Lawrence 1953, Whitehouse and Armstrong 1953, Skutch 1962, Prescott 1964, and Maxwell and Putnam 1972). Such diversity of opinion among researchers might be due to faulty methods of measuring temperature and nest attentiveness, insufficient sample size, or innate individual characteristics among avian conspecifics (cf. Skutch 1957).

Time of Day

Another factor which might influence attentiveness during incubation is the time of day. That a relationship does exist between the amount of time spent on the nest and the period within the day has been suggested by Fautin (1941), Cox (1960), and Maxwell (1965). Skutch (1962) pointed out that many birds average more time on their eggs during the cool of the morning and evening than in the middle of the day when air temperature is usually higher. Kendeigh (1952) noted a decrease in attentiveness in mid-afternoon and an increase in the evening. Prescott (1964) suggested the differences in average incubation constancies during the course of a day are due in part to associated daily temperature changes and feeding behavior of the incubating bird. An attempt is made here to distinguish between the effect of temperature and the effect of time of day, as hourly temperatures were recorded throughout the study.

Stage of Incubation

A change in nest attentiveness as incubation progresses has been noted by several authors (Nice 1937, Fautin 1941, Kuusisto 1942, Putnam 1949, Baerends 1959, Cox 1960, Kessler 1962, Hardy 1963, and Drent 1970). Others, however, have suggested that such a progressive change was not apparent in their investigations (Sturm 1945, Kendeigh 1952, Lawrence 1953, Davis 1960, Weeden 1966, and McLaren 1975). Some researchers believe that the apparent irregularities regarding the relationship of nest attentiveness and stage of incubation might be explained on the basis of innate individual characteristics (Kendeigh 1952, Skutch 1962, and Prescott 1964). I suggest that some method must be used to distinguish those changes in nest attentiveness due to changes in environmental temperature from those produced by stage of incubation. The data for this paper should be of sufficient volume and are grouped in such a manner as to satisfy this requirement.

Influence on Attentive Behavior by the Nonincubating Bird

In *Toxostoma rufum* both sexes share the incubation chores but the female spends more time on the nest than the male (Erwin 1933 and Morgan 1968). Skutch (1962) suggests that two factors are at work when both sexes alternate on the nest. Extended periods off the nest foraging, particularly when the incubating bird is not fed on the nest by the mate, would permit the bird to strengthen itself in preparation for a long session upon returning to the nest. Also, the "eagerness" of the absent bird to return to the nest would tend to shorten the session of the mate, which, without this interruption, would remain longer on the eggs. Should each bird remain on the eggs until relieved by its mate, the absent bird, rather than the incubating partner, would determine the length of the sessions. Skutch (1962) suggested that the manner by which the incubating bird obtains food has a definite relationship to attentiveness. When only the female incubates and is fed on the nest by its mate, the sessions will tend to be longer than those terminated by foraging requirements. Prescott (1964) noted an increase in the length of sessions when the female was fed on the nest by the male Scarlet Tanager, _Piranga_ _olivacea_. A positive correlation between the frequency with which the male Pied Flycatcher, _Ficedula hypoleuca_ fed the incubating female, and the time she spent on the nest, was observed by von Haartman (1958). When the male was removed, both the sessions and recesses of its mate became longer.

Previous studies of the Brown Thrasher's reproductive cycle have provided little information regarding the effect of the nonincubating bird on nest attentiveness of its incubating mate. In some investigations, birds were not marked and others the extent of observation was negligible. Since this species shows little sexual dimorphism, sex identification of unmarked birds in the field is practically impossible. In this study individual birds were marked with dye in order to distinguish sex and to determine the role of the nonincubating partner in the breeding cycle.

In some passerines a characteristic termed "nest guarding" or "standing guard" is well developed and may or may not influence the mate's sessions and recesses (Skutch 1953). According to Skutch (1953) the habit of standing guard is best developed in birds strong enough to defend the nest against predators and in weak birds this activity may be an individual trait rather than a habit of the species. Among species in which the movements of the nonincubating bird are coordinated with those of its incubating mate, this coordination may take two patterns which are contrasting in nature: (1) standing guard over the nest during the mate's absence or, (2) accompanying the mate on its recesses. Some of the species in which nest guarding has been observed are as follows: Song Sparrow, *Melospiza melodia* (Nice 1937); Cedar Waxwing, *Bombycilla cedrorum* (Putnam 1949); Barn Swallow, *Hirundo rustica* (Kendeigh 1952); House Wren, *Troglodytes aedon* (Kendeigh 1952); Mockingbird, Mimus polyglottos (Laskey 1962);

and the Catbird, *Dumetella carolinensis* (Slack 1973). No significant instances of nest guarding by the Brown Thrasher have been reported. There are reports, however, of the incubating bird responding to vocalizations and/or sight of its mate (Thomas 1948). An attempt has been made in this research to determine the presence or absence of nest guarding by this species and to quantify the effects on nest attentiveness of vocalizations and sight of the nonincubating mate.

Study of the Nesting Cycle

Many studies of the life history and breeding biology of an avian species have been concerned with territoriality, pair formation, courtship, nest construction, incubation, and care of the young, but a relatively small amount of information is available on the population dynamics of passerine birds, especially those species with altricial young. Mortality studies have dealt primarily with the percent of eggs hatching and the number of young birds which are fledged from each nest (Young 1963). These data are useful but give little information on the early stages of avian life cycles and the approximate age at which losses occur. Only a few studies of age-specific mortality among altricial birds which have been reported give information about the early stages of eggs and nestlings (Young 1963, Holcomb

1972, and Slack 1973). Significant data on age-specific mortality of eggs and nestlings of the Brown Thrasher are absent from the literature. Losses of eggs and young of this species are mentioned by Erwin (1933) and Morgan (1968) but no information regarding the approximate age at which such losses occurred is given.

This study presents information for those early stages from oviposition to hatching and from hatching to fledging for the Brown Thrasher. Data were also collected regarding nest construction, weights and dimensions of eggs, egg weight loss during incubation, and the role of sex during incubation and care of the young.

Another important aspect of breeding biology and behavior studies, often neglected by investigators, is the amount and kind of food brought to the young and the manner in which it is obtained by the parent birds. Studies of this nature provide information which allows assessment of the economic importance of a single species and might allow predictions to be made regarding its survival or extinction. According to Lack, (1954, 1966), food is probably the most critical of all resources which might become short in supply. As a consequence of this food shortage, competition might exist between ecologically very similar species. During the peak of the Brown Thrasher's nesting cycle, when young birds are in the nest, food samples were collected and analyzed and some foraging activity patterns of the adult birds recorded.

There are at least two major reasons which suggest that studies of avian breeding biology and behavior are important today. First, much of the data available in the literature for a particular species was collected several years ago. The latest extensive study of the Brown Thrasher was conducted forty-three years ago by Erwin (1935). Since that time there have been major changes in habitat structure due to various encroachments by man and by geological processes of nature. Species which are reproductively successful today may have undergone adaptive changes in order to survive within the habitat presently available to them. Secondly, the complete reproductive cycles of many common breeding birds have not been thoroughly investigated.

STUDY SITE, METHODS AND MATERIALS

Study Site

This study was conducted in southwestern Laurel County, Kentucky, during the years 1973-1976. (See Fig. 1). Except for periodic searches for overwintering birds during the fall and winter months, the bulk of information was collected each year from April through August.

Based upon the physiographic subdivisions of Kentucky by Fenneman (1938), the study area was located in the northwestern section of the Cumberland Plateau which forms the southwestern flank of the Cumberland Mountains. Much of the area is underlain with Pennsylvanian rocks of the Pottsville series, predominantly sandstone alternating with shale. Along the western border of the Plateau there are occasional outcroppings of limestone which support the surface and often form strong scarps. The Cumberland Plateau is a narrow belt, never exceeding 120 kilometers in width, about 720 kilometers in length. It extends from southern Virginia through southeastern Kentucky and eastern Tennessee to Alabama. The headwaters of the Kentucky, Cumberland, and Tennessee rivers arise in the

Fig. 1. Aerial photograph of study area.

central portion of the plateau. Recent strip-mining operations have drastically affected otherwise slow geologic changes with unpredictable long-range results. Alterations immediately apparent are rock slides, streams completely destroyed or converted to acidic waters, loss of topsoil, and destruction of habitats for man and other life forms.

The specific study site in which this research was conducted consisted of approximately a 35 hectare tract of land, the center of which was located 84 degrees, 01 minutes west longitude and 37 degrees, 09 minutes and 30 seconds north latitude. The entire farm consisted of 162 hectares, but since this was too large an area for a single worker to encompass, the 35 hectare tract was designated and marked off from the original farm. The area offered a diversity of habitats including shrub, second growth deciduous forest, evergreen, open meadow, and pond margin. A small creek which formed nearly half the southern boundary bissected the farm near the center. The area was bounded on the eastern edge by State road 472 and on the western edge by State road 586. The average elevation above sea level was about 365 meters.

Selection of the study site was not arbitrary, but involved the following considerations: (1) a rather abundant bird population, particularly of the Mimidae (Passeriformes: Aves) was nesting in the area; (2) part of the study site was under cultivation; and, (3) the area was not restricted to the general public. I believe this kind of habitat is presently the most common breeding environment available to these birds. I desired to study the nesting habits of the Brown Thrasher under natural conditions. Morgan (1968), in contrast to my selection of a study site, preferred to study several species of birds on an old farm in northern Indiana which was not being cultivated and was restricted to the flow of human traffic. Due to agricultural, industrial, urban, and aesthetic encroachments upon avian breeding territories, few restricted areas are presently available to birds. Therefore, any valid study of breeding biology should be conducted within those disturbed areas which are becoming more prevalent. Survival of a species requires that its adult members be able to reproduce within and adapt to changing environmental conditions.

The predominant vegetation of the study area is listed in Table 1. Scientific names are after Britton and Brown (1952).

TABLE 1

PRINCIPAL VEGETATION OF STUDY AREA

virginia pine	(*Pinus virginiana*)
red cedar	(*Juniperus virginiana*)
black walnut	(*Juglans nigra*)
white oak	(*Quercus alba*)
yellow poplar	(*Liriodendron tulipifera*)
sassafras	(*Sassafras albidum*)
sycamore	(*Platanus occidentalis*)
sumac	(*Rubrus* spp.)
multiflora rose	(*Rosa multiflora*)
wild rose	(*Rosa carolina*)
american plum	(*Prunus americana*)
wild cherry	(*Prunus* spp.)
honey locust	(*Gleditsia triacanthos*)
hop clover	(*Trifolium* spp.)
sugar maple	(*Acer saccharum*)
red maple	(*Acer rubrum*)
riverside grape	(*Vitis riparia*)
dogwood	(*Cornus florida*)
black gum	(*Nyssa sylvatica*)
milkweed	(*Asclepias* spp.)
butterfly weed	(*Asclepias tuberosa*)
commom elder	(*Sambucus canadensis*)
honeysuckle	(*Lonicera japonica*)
giant ragweed	(*Ambrosia trifida*)
goldenrod	(*Solidago* spp.)

METHODS AND MATERIALS

Behavior of the Incubating Bird as Related to Temperature, Time of Day, and Stage of Incubation

Collection of data on attentive behavior during incubation was obtained by direct personal observation or recording instruments. A portable blind 122 cm square and 183 cm high constructed of 13 mm galvanized pipe and covered with waterproof canvas was used to conceal the observer while watching the incubating bird on the nest (see Fig. 2). The four legs could be unscrewed rapidly from the top crossbucks permitting the blind to be moved easily from one nest to another. The blind was placed 3-6 m from the nest and usually put in position the day before observations began. The incubating bird appeared generally undisturbed by the presence of the blind or the observer. Time intervals for sessions and recesses were recorded to the nearest minute and each period of observation lasted four and one-half hours. The length of the observation period was long enough to obtain sufficient information on the bird's activity for that period without creating excessive disturbance of the incubating bird. Following the method employed by

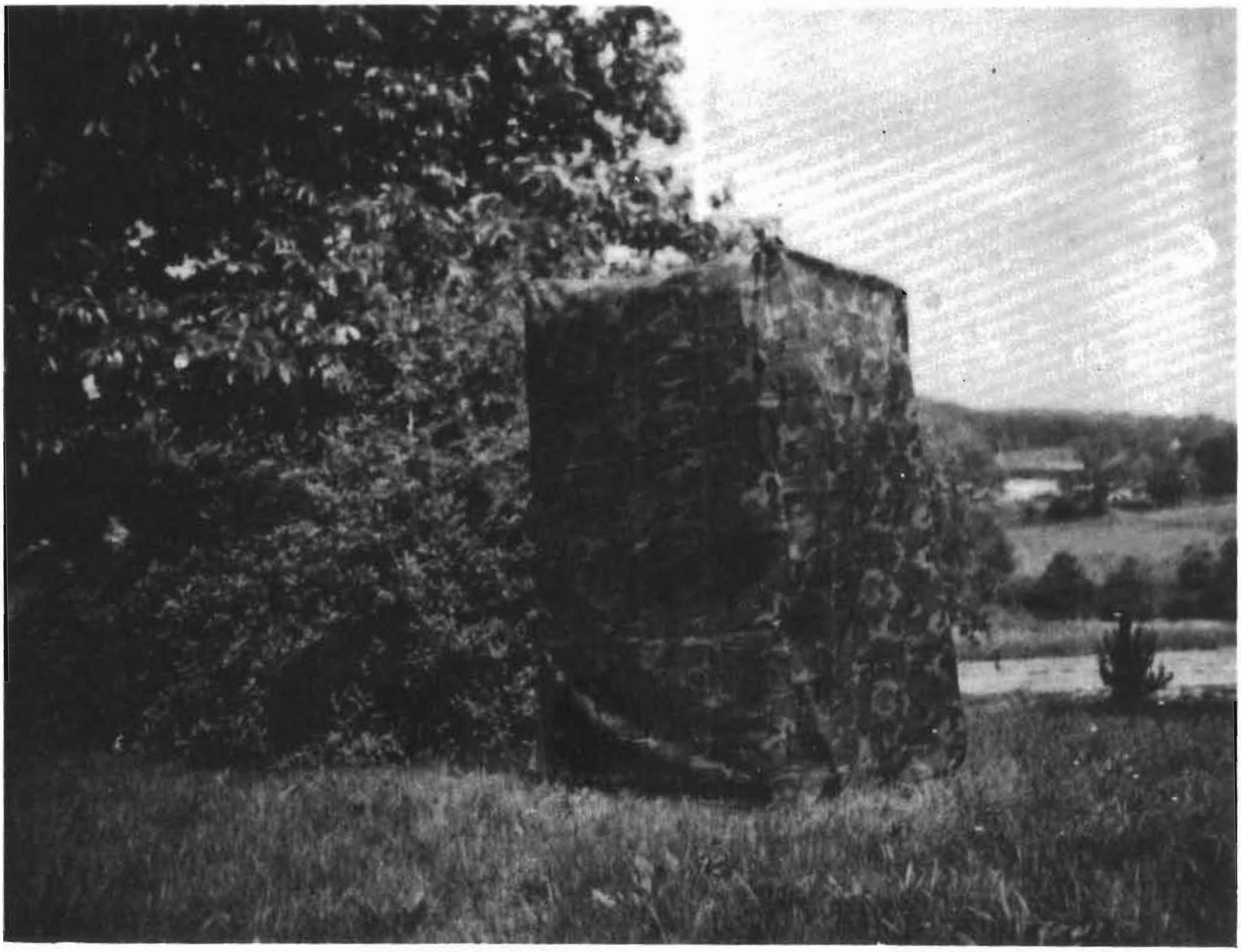

Fig. 2. Portable blind from which nests of Brown Thrasher were observed.

Slack (1973) the day was divided into three activity periods, 05:00-09:30 hours, 09:30-14:00 hours, and 14:00-18:30 hours. These periods which encompass the greater part of diurnal incubation activity for small passerines in this region were designated as activity periods 1, 2, and 3 respectively. When observations are made in a sizeable number of each of these periods, significant information will be gained regarding the proportion of the day the eggs are kept covered. Seven nests in 1973, five in 1974 and five in 1975 for a total of seventeen nests were available for this study. Observations were made in each of the activity periods approximately the same number of times during the nesting cycle. With the exception of a few instances, the same activity period was not used on consecutive days. Nests were kept relatively undisturbed in order to obtain more valid information on incubation activity. During each period, data were collected concerning the number and duration of sessions and recesses of the incubating bird, the location and behavior of its mate, and other associated behavior patterns of both parents.

The second method used to collect data on attentive behavior was by means of an electrical recording device. This device recorded temperature changes within the nest , thus providing information regarding the bird's presence on or absence from the nest. By using this instrument, a continuous record of incubation behavior was obtained. The device was a portable, thermistor probe chart recorder, Model 2133, manufactured by the Rustrak Instrument Company (see Fig. 3). The chart recorder, which rotated at the rate of 2.5 cm per hour, with a ± 5 percent factory-rated speed regulation, was powered by a 12-volt storage battery. The single channel type instrument with a temperature span from 0 to 100 degrees Celsius and an accuracy rating of ± 2 percent of the temperature span, was used in this study. A plastic, water-proof box sheltered the device and battery. A thermistor probe, Model 1331, with a flexible vinyl lead (0.5 cm diameter by 0.8 cm long) was attached to the recording instrument by a 3-m lead. The machine was placed a greater distance than 3 m from the nest to avoid disturbing the incubating bird with the clicking sound of the stylus. Several fruitless attempts were made to place the thermistor probe in the nest from beneath through a hole made with a pencil (cf. Slack 1973). The flexible vinyl lead tended to curl, preventing its insertion. To overcome this problem, a 25 cm length of copper tubing, 6 cm in diameter, was closed at one end, sharpened, and inserted through the nest from beneath. This permitted the probe to be passed through the tube into the nest and then the tube to be removed, leaving the probe inside the nest. Proper placement of the probe in the nest was critical in obtaining accurate readings on the chart recorder. It was positioned in the center of the nest with the sensing bead level with the top

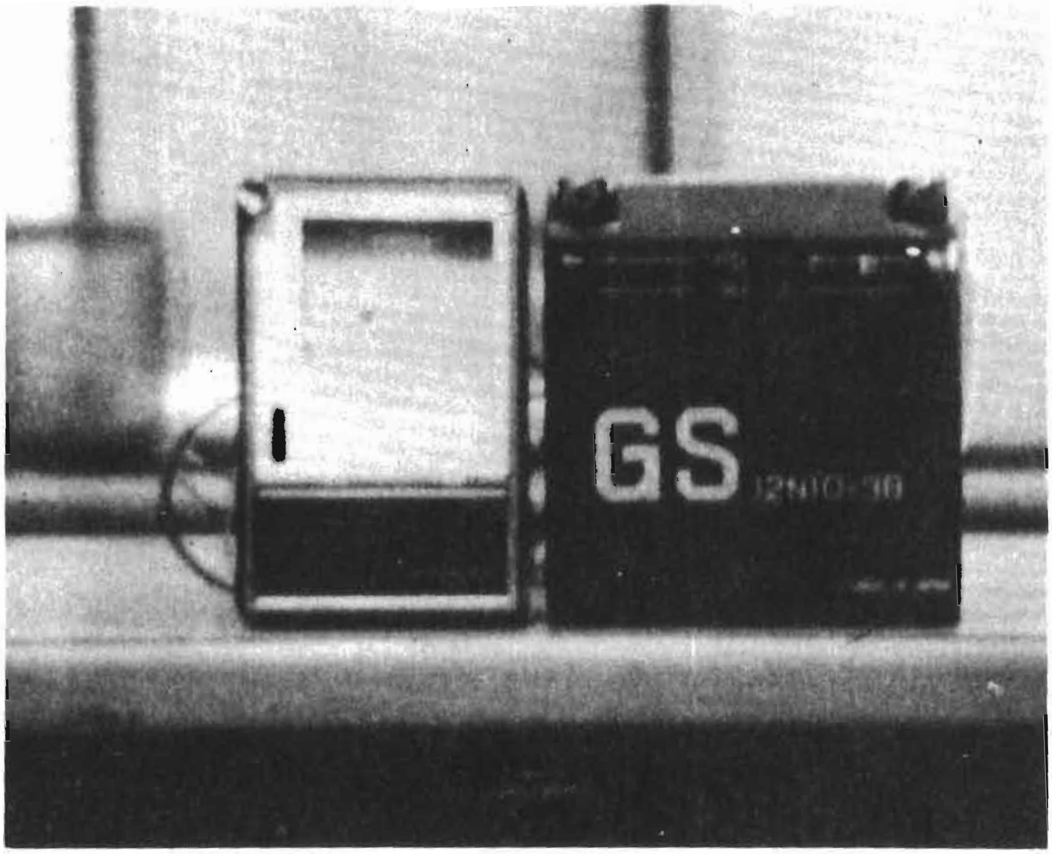

Fig. 3. Thermistor chart recorder and 12-volt storage battery

of the eggs (see Fig. 4). Correct positioning permitted the heat-sensing element to be in contact with the brood patch of the incubating bird. After the probe was correctly placed, it was secured by attaching it to vegetation beneath the nest with two small wires. Except on two occasions, the incubating birds appeared to be undisturbed by the probe in the nest. At one nest, the probe was prevented from being pushed back through the bottom by securing it in the nest with a small plastic washer and rubber band. The following day both washer and rubber band were missing, the insulation had been pecked off the heat-sensing element, and the nest deserted. On the other occasion, the probe had been placed too high above the eggs, resulting in the breakage of one egg and desertion of the nest.

Each electrical connection between the nest and chart recorder was made water-proof to prevent a short circuit during rainy weather and in the early morning hours when dew was heavy. This was accomplished by wrapping the connection with several layers of rubber tape and covering this with a few layers of plastic tape. Any interruption of the circuit pathway from probe to recorder resulted in irregular recordings. When the instrument was in operation, periodic checks for proper function were made. On several occasions, the recording device was placed inside the portable blind and while observing the activity of the incubating bird, calibration checks of the instrument were

Fig. 4. Properly placed thermistor probe in a Brown Thrasher nest.

performed. The incubation pattern registered on the chart recorder appeared to be the same as that observed directly. The amount of time the bird was on and off the nest could be determined because of the rapid response of the thermistor probe to heat changes within the nest and the constant speed of the recording drum. The heat-sensing element had a time constant of seven seconds. This means that a temperature change within the nest was detected and recorded within a period of not more than seven seconds. The speed of the chart recorder was such that one inch of recording paper represented one hour in time. The length of time to the nearest minute of each session and recess was recorded and averaged for each activity period. The recording chart was divided into "on" and "off" periods and the duration in time for each was determined by simple addition (see Fig. 5). A clear distinction between the "on" and "off" periods can be easily discerned. The line on the chart representing termination of a session is less vertical than the one indicating resumption of incubation. This difference is probably caused by residual heat of the eggs after the bird leaves the nest. The minor oscillations at the top of the chart were produced when the eggs were being turned or the bird was shifting positions on the nest. The right side of the chart represents retirement for the night and indicates little movement by the bird during this period.

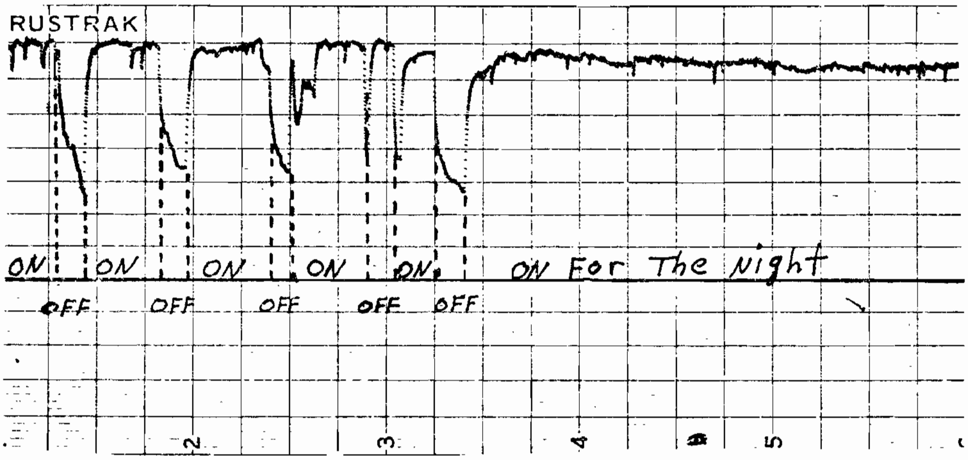

Fig. 5. Photograph of a chart recording of the type used to determine the amount of time the bird spent on and off the nest.

Influence on Attentive Behavior by the Nonincubating Bird

As mentioned earlier, in the Brown Thrasher incubation is performed by both members of the pair and begins only after the clutch is complete. An attentive period at the nest by either member was terminated by the bird leaving voluntarily or in response to the sight or vocalizations of the mate. In order to determine the manner by which a session was ended, notations were made of the nonincubating mate's proximity to the nest and of its songs and call notes. Since little sexual dimorphism is apparent in this species, attempts were made to mark one member of each of six pairs soon after egg-laying began. A 235 cc plastic bottle, equipped with a trigger-action spring-loaded pressure pump, was filled with water-resistant dye and sprayed on the birds. This procedure was possible because the Brown Thrasher is extremely belligerent in response to human intruders and attacks were made on the investigator by both members of the pair as the nest was being approached. Some evidence of the dye remained on the bird throughout the nesting cycle. Only one member of the pair was marked and the sex was determined by behavior and, at times, by identifying the bird which laid the eggs. Only one member of each pair, presumably the male, sang the territorial songs.

Study of the Nesting Cycle

An attempt was made to locate every nest of the Brown Thrasher within the boundaries of the study area throughout the four-year period. Only those nests which were located during construction or egg-laying periods were considered when the incubation period or age-specific mortality was calculated. As each nest was found, an identification number was fastened to nearby vegetation and a record of the contents of the nest was made. The nest was visited periodically until it was deserted, destroyed, or until the young had fledged. During the years 1973-1975, the nests were left relatively undisturbed in order to obtain accurate incubation and nestling information. After the young birds had fledged or the nest had failed, the following information was recorded: height of nest above ground level, outside distance from the bottom of the nest to the top rim, the inside depth, and the inside and outside diameters at rim level. Some of the nests were dismantled to determine the type of material used in construction. Egg weights and dimensions, and weights of young birds were obtained during 1976. An attempt was made to weigh the fresh egg before the onset of incubation and to weigh individually-marked eggs periodically until they hatched. This permitted calculation of the amount and percentage of egg-weight loss during incubation. Egg measurements noted in this paper were taken to the nearest millimeter with a sliding microcaliper.

The length of incubation was considered as the time from the laying of the last egg in the clutch until that egg hatched. The day the last egg was laid was considered as day one of incubation and the day the last egg hatched was excluded (cf. Nice 1954). For example, in a three-egg clutch, the day egg three was laid represented day one of incubation. Likewise, the nestling period was determined by counting the day the last egg hatched and every day thereafter the birds were in the nest.

Examination of nest contents, particularily of those nests positioned above eye level, was facilitated by attaching a small mirror to a 1.8 m length of 1.3 cm electrical conduit. Other sections of conduit were added as needed.

The instrument used to weigh the eggs and young birds was a Cent-O-Gram scale manufactured by the Ohaus Scale Corporation (see Fig. 6). The maximum capacity was three-hundred and eleven grams and measurements could be made to the nearest hundredth of a gram. Accuracy in weighing could not be obtained without making some modifications of the weighing scale. The instrument was secured by means of wood screws to the bottom of a wooden box which had a front panel of plexiglass. A carrying handle and leveling bubble were attached to the top of the box. Difficulty

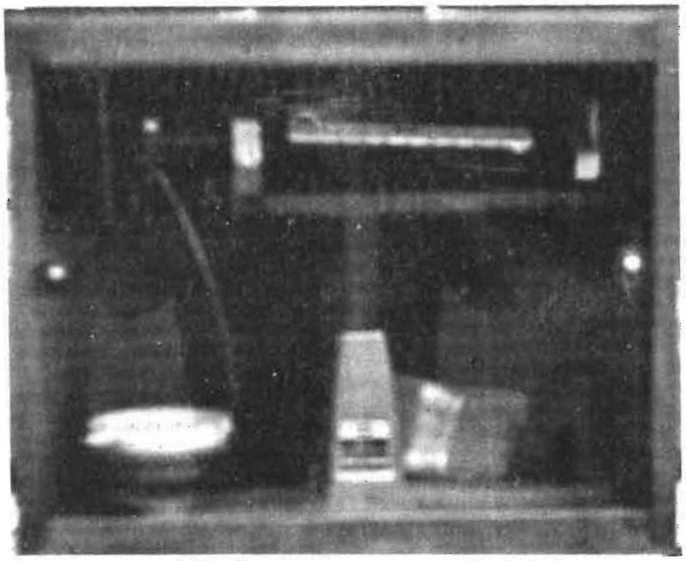

Fig. 6. Cent-O-Gram scale used to determine weights of eggs and young birds.

was experienced in getting the leveling bubble to remain within the designated circle, particularly in hard soil where the box could not be forced into the ground. To overcome this problem a small metallic base, to which four beveled iron rods were welded, was attached to the box.

A continuous record of environmental temperatures was obtained with a spring-driven Weather Measure Hygrothermograph, Model H-311 (see Fig. 7). This instrument had a temperature span of -20 to 40 degrees C. with an accuracy rating of ± 1%. The chart drum speed could be set to give one complete rotation in twenty-four hours or one rotation in seven days. The former speed permitted greater ease in reading the chart. The hygrothermograph was housed in a louvered box which gave shelter from sun and rain while allowing air to circulate freely around the heat-sensing element (see Figures 8 & 9). The legs of the shelter were of the proper length to allow the temperature sensing element to be approximately 1.2 m above ground level.

To determine the complex of prey items brought to the young by the parent birds, food samples were collected using a technique from Petrovic (1972). A short length of pipe cleaner was wrapped around the neck of each nestling under study. The constriction caused by the cleaner was such that swallowing was prohibited but respiratory functions were unimpaired. Immediately after food was given to young birds, samples were removed from their

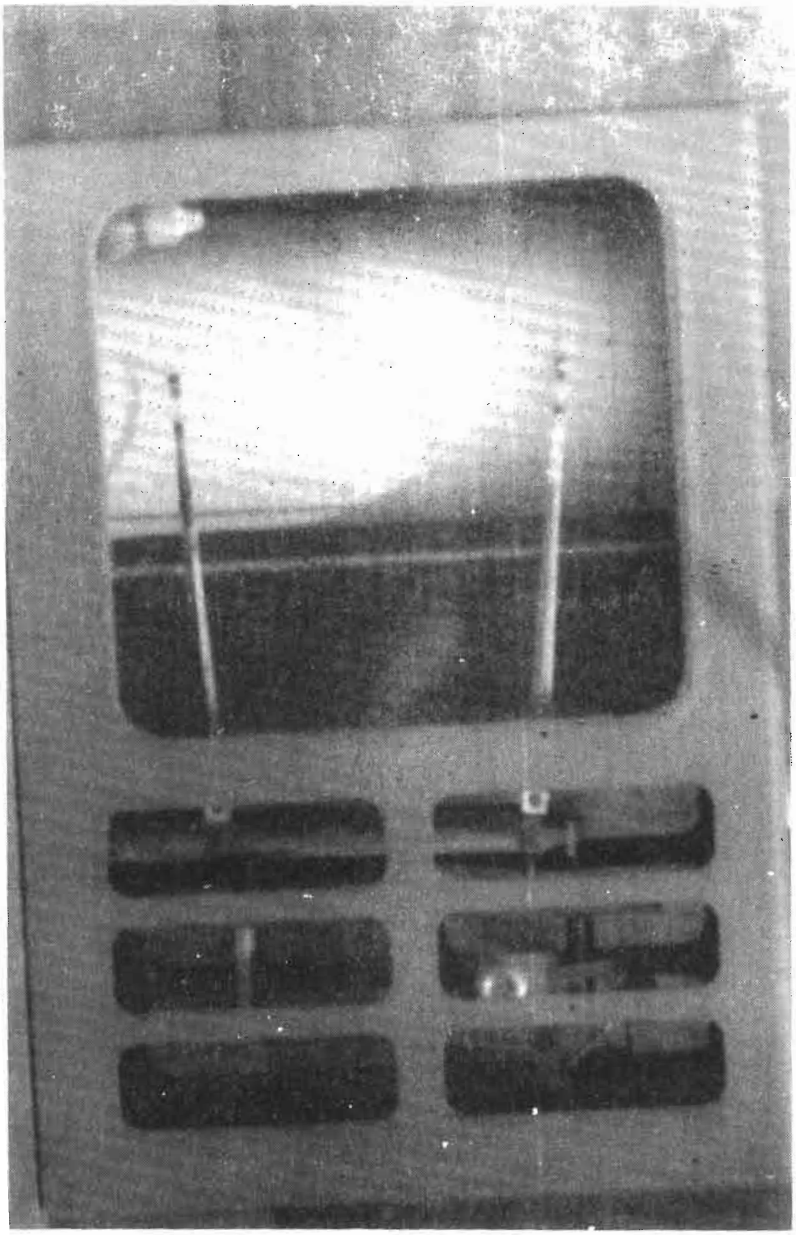

Fig. 7. Hygrothermograph used to record environmental temperatures.

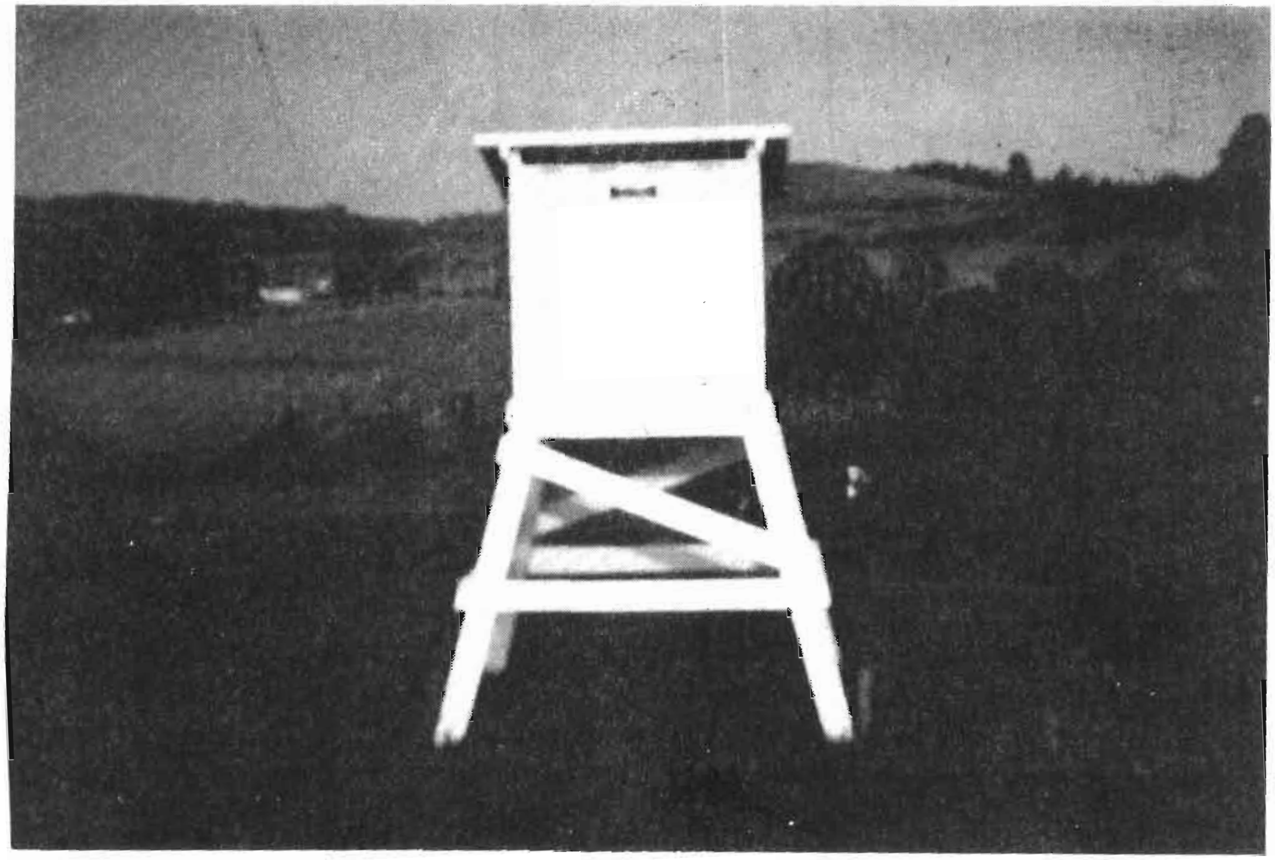

Fig. 8. Louvered shelter used to house the hygrothermograph.

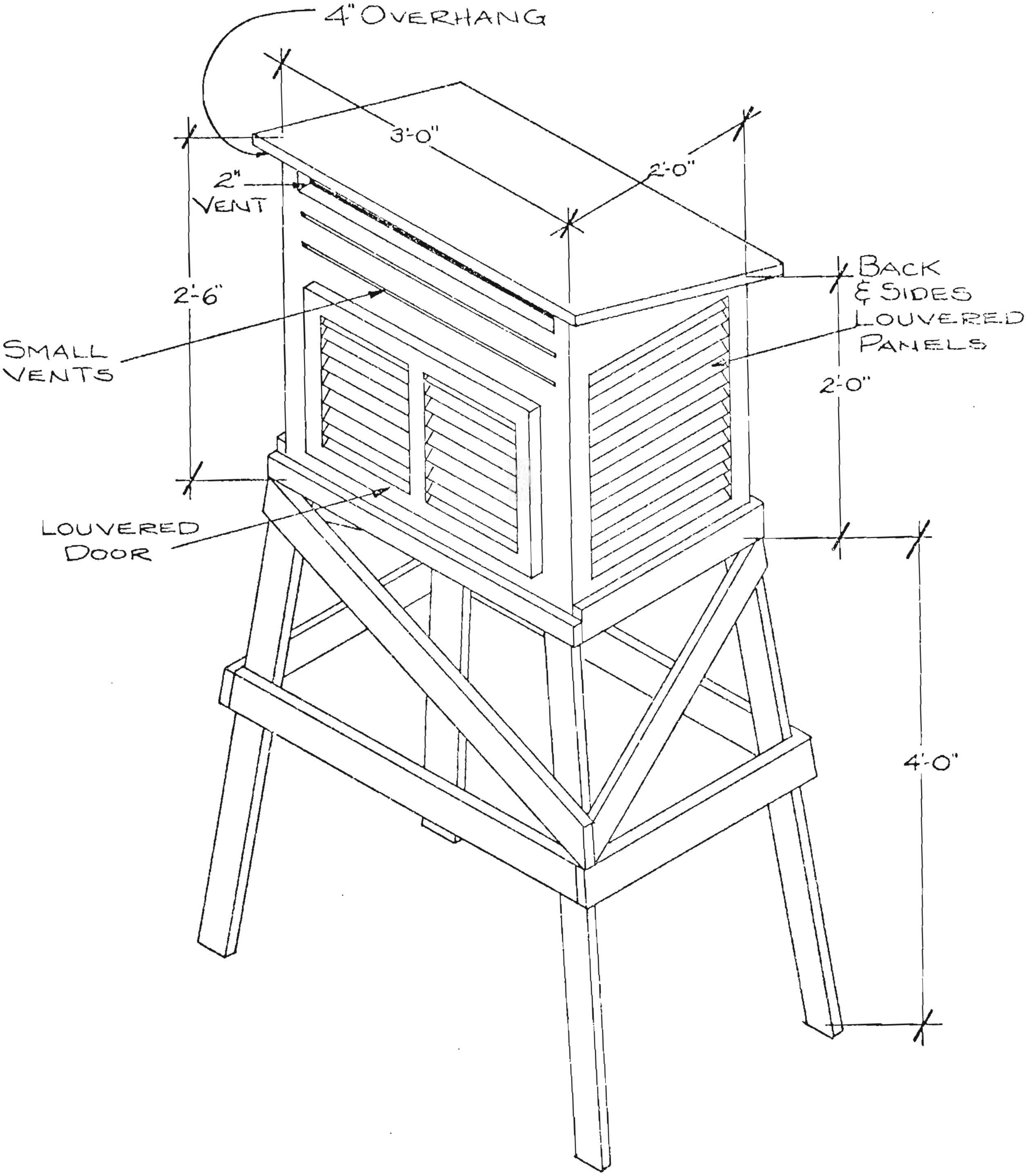

Fig. 9. Hygrothermograph shelter with dimensions

throats with tweezers and placed in a 10 percent formalin solution for later analysis. The primary intention was to classify the food as animal or vegetable, however, as the study progressed more precise identification was attained. A pipe cleaner was never allowed to remain on the bird longer than thirty minutes. One sampling period was conducted in the morning and one in the afternoon. Food samples were not collected from the adult birds and a measure of food abundance was not included in this study.

RESULTS AND ANALYSES

Behavior of the Incubating Bird as Related to Temperature, Time of Day, and Stage of Incubation

To obtain data of sufficient volume for statistical analysis regarding incubation activity of the Brown Thrasher, I studied several nests over a period of three years. In 1973, 65 activity periods from 7 nests were observed or monitored, 59 activity periods from 5 nests in 1974, and 53 activity periods from 5 nests in 1975. This resulted in a total of 177 activity periods from 17 nests and constituted 796.5 hours of observed or monitored incubation behavior. The number of activity periods recorded during the study is listed in Table 2. Data were collected for each day of incubation until hatching of the eggs. No data were collected beyond day 16 since eggs failed to hatch on or after this day. A complete listing of data by nest and year is given in Appendix A.

Data regarding the effect on incubation activity of ambient temperature, time of day, and stage in incubation were statistically analyzed using an analysis of covariance which incorporated analysis of variance and linear

TABLE 2

NUMBER OF ACTIVITY PERIODS OBSERVED AND RECORDED BY DAY OF INCUBATION

Day of Incubation	1973	Year 1974	1975	Total
1	3	5	4	12
2	3	5	4	12
3	7	5	3	15
4	5	6	6	17
5	3	8	6	17
6	7	7	2	16
7	2	5	1	13
8	8	5	2	15
9	5	5	7	17
10	6	4	4	14
11	5	2	6	13
12	3	1	4	8
13	2	0	0	2
14	1	0	1	2
15	1	0	0	1
16	1	0	0	1

regression. The basic model used in processing the data was a modification of that used by Scheffe (1959) and is as follows:

$$Y_{ijklmh} = \mu + \alpha_i + \delta_{j(i)} + P_K + D_e + \gamma_m + B + X_{ijklmh} + \varepsilon_{ijklmh}$$

The following interpretation is given for the model:

Y_{ijklmh} -A dependent variable representing the average length of sessions in minutes (average time on nest) for each activity period, or the average length of recesses (average time off) in minutes per activity period, or the percentage time on the nest per activity period.

μ - A population mean
α_i - Year effect
$\delta_{j(i)}$ - Between nests error component
P_K - Activity period
D_e - Day of incubation
γ_m - Method used to collect data
B - Unknown regression coefficient for temperature
X_{ijklmh} - Average temperature for activity period
ε_{ijklmh} - Within nests error component

An analysis of covariance was used to test the relationship between ambient temperature and the average length of sessions in minutes. A temperature regression coefficient of - 0.4567, which was statistically significant at the

.001 level, indicated an inverse relationship between the two. As the temperature increased, the average time on the nest decreased. For each degree increase in temperature, the bird tended to sit on the eggs about one-half minute less per session. For example, when the average length of sessions at 50 degrees was twenty minutes, at 60 degrees the average session length was fifteen minutes. A preliminary examination of the residuals, that is, the vector of observed responses minus the estimated responses led to some additional variables being added to the model. At very high temperatures (above 81 degrees) the tendency to sit was even less. To adjust the data for this effect, the following variable was added to the basic model:

$S^{(1)}_{ijklmh}$ = 1, when the temperature was greater than 81 degrees and, 0, when the temperature was 81 degrees or below. A regression coefficient of -3.814 for the higher temperatures indicated that the bird tended to sit on the average about four minutes less per session during these high temperatures than at temperatures below 81 degrees (see Fig. 10). The four-minute decrease in average session length was not cumulative but was observed at any temperature above 81 degrees. The one-half minute decrease in session length, as mentioned earlier, was on a per degree basis and was observed at all temperatures including those above 81 degrees. For example, when the average length of

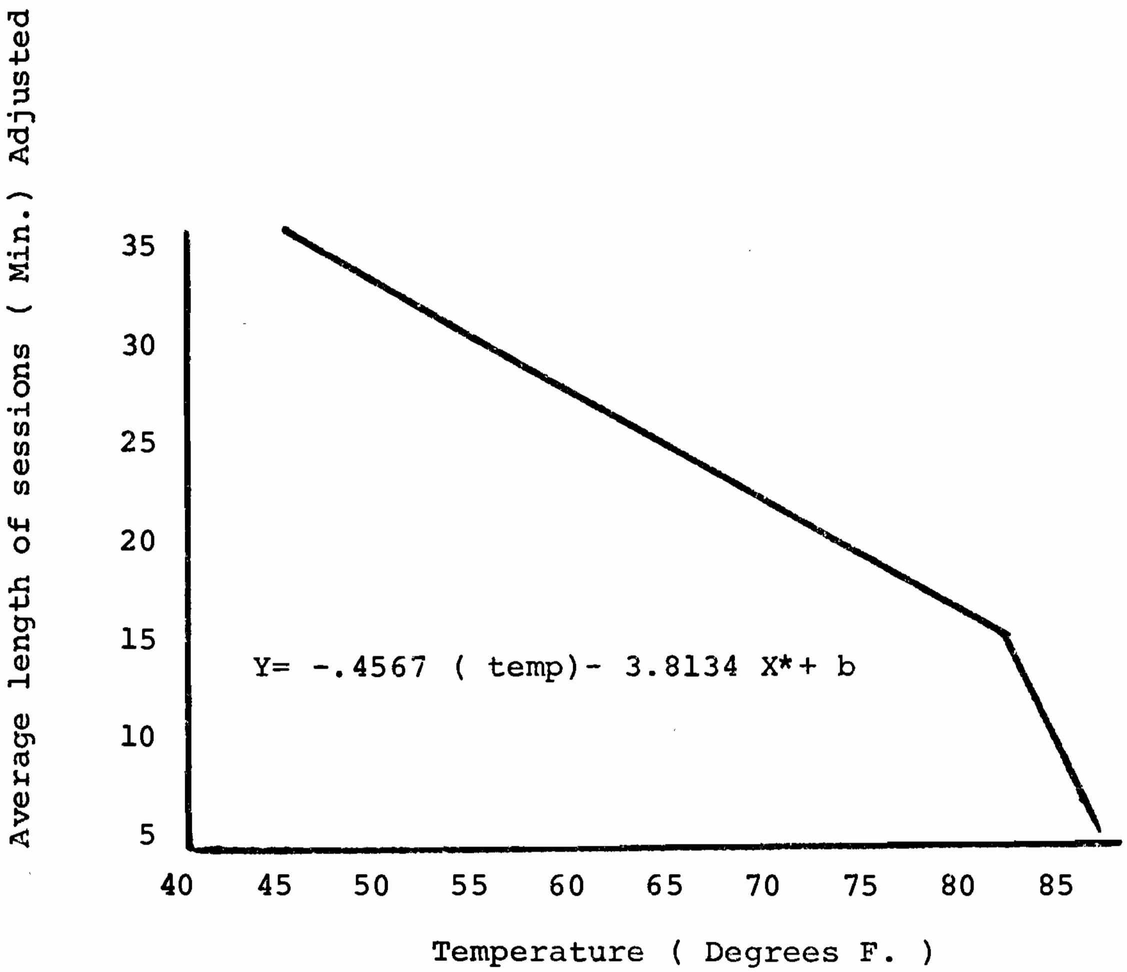

Fig. 10. Average length of sessions as related to temperature.

* X equals 1, when temperature is greater than 81 degrees and, 0, when temperature is 81 degrees or below.

sessions at 75 degrees was twenty-five minutes, at a temperature of eighty-five degrees, the average session length was approximately nine minutes less, or sixteen minutes.

An accumulate average session length was calculated from the total number of recorded sessions of each incubating bird. When the bird's sessions were longer than the accumulate average on a given day, they tended to be shorter the following day and vice versa. To determine the extent of this residual effect, another variable was added to the model.

$S^{(2)}_{ijklmh}$ = 1, when the previous day's sessions averaged more than 2.5 minutes above the accumulate average, -1, when the previous day's sessions averaged 2.5 minutes below this average and, 0, when the deviation from the accumulate average was less than 2.5 minutes. With other influencing factors, such as activity period, stage of incubation, etc, held constant, statistical analysis resulted in a regression coefficient of -2.551. This coefficient indicated that when the average length of sessions on a particular day was 2.5 minutes above the over-all average for that bird, the following day's sessions tended to average about 2.5 minutes less. Previous day residual effects were seen in about half of the total observations. Also, when the average length of sessions during the first activity period on a given day was longer than the accumulate average of all activity periods, the mean session length of the two activity periods immediately following tended to be shorter by about the same amount of time. To analyze the residual effect of the first activity period, a similar variable was added to the model. A regression coefficient of -1.8238, when other factors were held constant, indicated that when the average length of sessions the first activity period was extended by about two minutes, the mean session length of the nest two periods was shorter by about the same amount of time (see Fig. 11).

The F-statistics for the hypothesis of no difference between methods of collecting data and among activity periods were both less than one and were not significant at the 0.15 level. Thus the two hypotheses were accepted. The hypothesis of no difference among years was not rejected at the 0.15 level of significance.

Statistical analysis revealed no significant relationship between average time on the nest and day of incubation when incubation was considered on a day-to-day basis. However, there was a significant difference between the two factors when the days of incubation were grouped into days 1-6 and days 7+. The difference between the adjusted means per session for the last few days of incubation (days 7+) was higher than the difference between the adjusted means for the first few days (days 1-6). A regression coefficient of 2.641 at the 0.05 level indicated that the average length of sessions the last four or five days was about two and

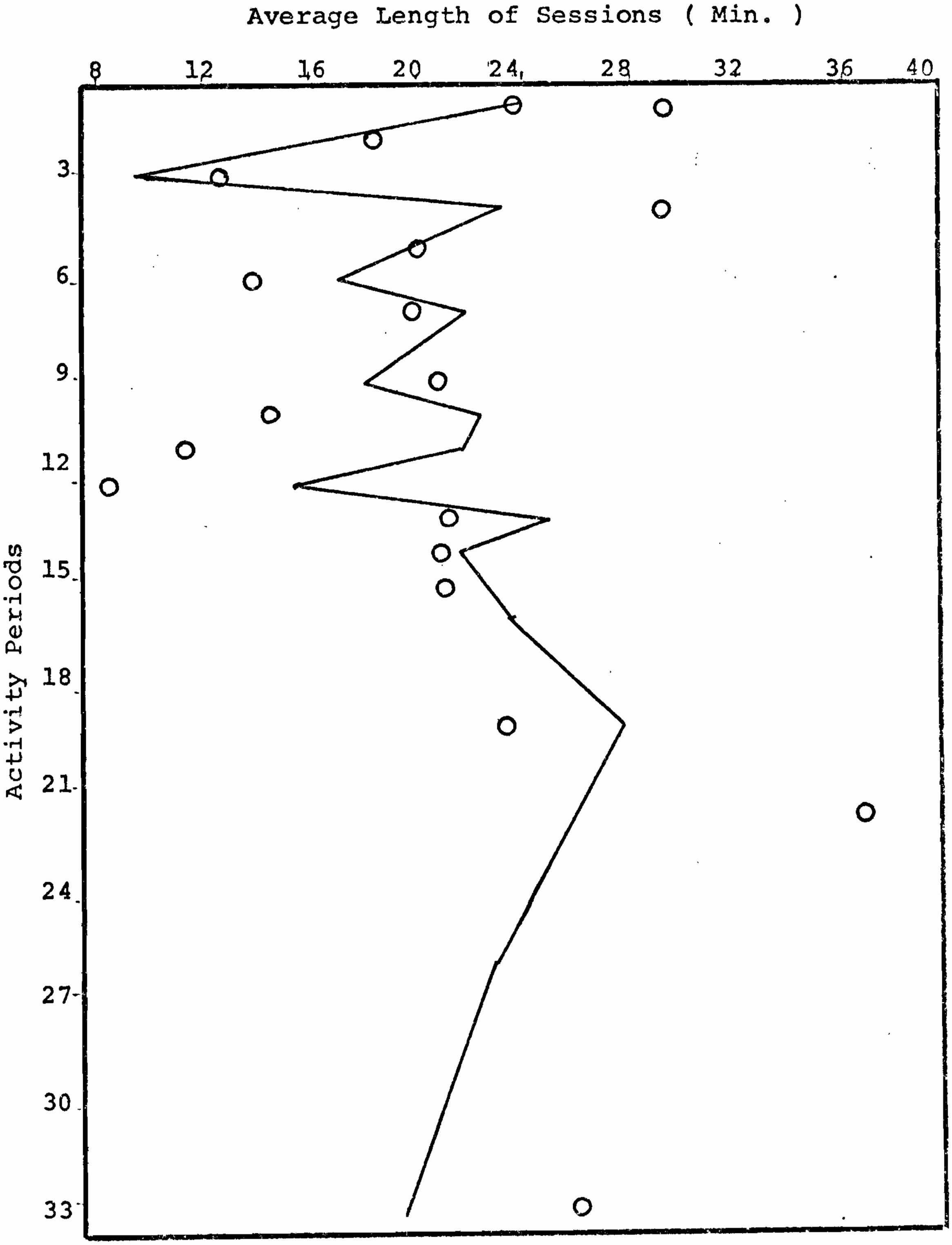

Fig. 11. Residual effect of first activity period. Circles represent observed responses; the line represents the computer estimate.

one-half minute longer than the first six days. Statistical analysis for average time on the nest as related to temperature and residual effects is given in Table 3. The residual effect of activity period one on the two periods immediately following is shown in Figure 11. For those activity periods which did not show the residual effect, temperature was the predominant influencing factor. Data and statistical analysis for average time on the nest as related to activity period, method of collecting data, and stage of incubation are given in Appendix A. The relations of nest and year to average time on the nest are listed in Tables 4-5.

An analysis of covariance was used to test the relationship between ambient temperature and the average length of recesses. A temperature regression coefficient of 0.104 indicated that the average length of time off the nest was directly related to temperature. As the temperature increased, the average length of recesses tended to increase. For each degree increase in temperature, the average length of recess tended to increase about one-tenth of a minute. With temperatures above 81 degrees, recesses were longer than for lower temperatures. With other influencing factors held constant, a regression coefficient for temperatures above 81 degrees of 2.4587 indicated that the average length of recesses for these higher temperatures increased by about two and one-half minutes (see Fig. 12).

TABLE 3

STATISTICAL ANALYSIS FOR AVERAGE TIME ON NEST AS RELATED TO TEMPERATURE AND RESIDUAL EFFECTS

	Regression Coefficient	S.E.	Significance Level	Degrees Freedom
Temperature	-0.457	± 0.082	.001	135
Temperature greater than 81 degrees F.	-3.813	± 1.817	.05	135
Residual effect of previous day	-2.551	± 1.105	.025	135
Residual effect of first activity period	-1.824	± 0.711	.025	135

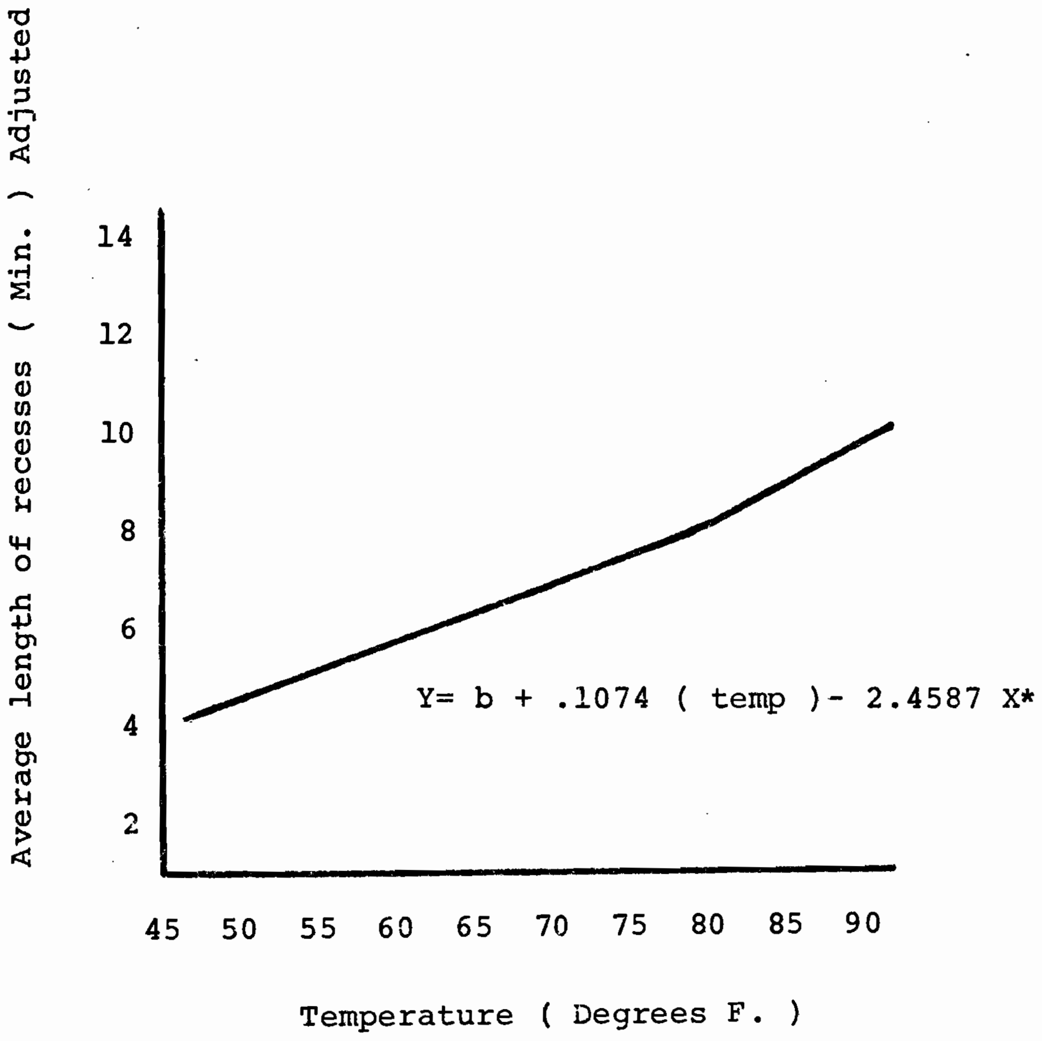

Fig.12. Average length of recesses as related to temperature.

* X equals 1, when temperature is greater than 81 degrees and,0, when temperature is 81 degrees or below.

TABLE 4

1973, 1974, AND 1975 DATA AND STATISTICAL ANALYSIS FOR AVERAGE TIME ON NEST (min.) ACCORDING TO NEST

Nest Number	Variable	Number	Mean	St. D.	Range	C.V.
1	Session	9	26.8	5.8	20.34-38.23	21.8
1	Temp.	9	64.8	9.5	43-76	14.7
2	Session	11	26.1	8.2	16.20-36.37	31.6
2	Temp.	11	58.6	8.4	46-70	14.4
3	Session	15	21.3	7.3	8.42-35.25	34.1
3	Temp.	15	71.5	7.3	60-85	10.2
4	Session	7	14.6	5.0	8.55-20.86	34.4
4	Temp.	7	79.7	6.6	70-86	8.2
5	Session	8	23.8	8.5	15.0-37.13	35.8
5	Temp.	8	76.6	5.2	70-83	6.8
6	Session	8	15.8	10.2	8.21-29.91	64.7
6	Temp.	4	79.8	8.7	70-90	10.9
8	Session	8	20.6	9.4	8.31-34.44	45.5
8	Temp.	8	76.3	6.1	67-85	8.0
9	Session	5	19.6	7.1	12.01-30.00	36.3
9	Temp.	5	76.2	6.7	68-84	8.8
10	Session	21	20.7	7.2	11.41-38.75	34.9
10	Temp.	21	75.2	4.4	67-82	5.8
11	Session	14	18.6	7.9	8.73-36.63	42.3
11	Temp.	14	78.7	5.2	71-88	6.6
12	Session	7	19.5	6.0	8.31-28.61	31.1
12	Temp.	7	66.9	10.4	58-85	15.5
13	Session	13	24.8	8.1	5.68-32.55	32.5
13	Temp.	13	68.5	9.3	52-81	13.6
14	Session	8	20.4	5.6	14.90-30.38	27.6
14	Temp.	8	71.6	6.5	62-80	9.0
15	Session	4	18.5	9.1	10.28-29.62	49.2
15	Temp.	4	70.3	9.9	60-81	14.1
16	Session	5	21.0	5.2	13.28-26.63	24.6
16	Temp.	5	69.4	8.7	55-77	12.6
17	Session	17	20.9	7.6	8.69-39.59	36.5
17	Temp.	17	72.2	7.0	60-82	9.8

TABLE 5

1973, 1974, AND 1975 DATA AND STATISTICAL ANALYSIS FOR TIME ON NEST (min.) ACCORDING TO YEAR

Year	Variable	Number	Mean	St. D.	Range	C.V.
1973	Session	54	22.3	8.3	8.21-38.23	37.1
1973	Temp.	54	70.2	10.6	43-90	15.1
1974	Session	55	19.9	7.4	8.31-38.75	37.0
1974	Temp.	55	75.3	6.8	58-88	9.0
1975	Session	47	21.7	7.3	5.68-39.59	33.8
1975	Temp.	47	70.6	7.9	52-82	11.1

When the bird's recesses were longer than the accumulate average of all recesses on a given day, they tended to be shorter the following day and vice versa. To test for the significance of this effect, the following covariant was added to the basic model:

$S^{(1)}_{ijklmh}$ = 1, when the previous day's recesses averaged more than 0.75 minutes above the accumulate average, -1, when the previous day's recesses averaged more than 0.75 minutes below the accumulate average, and 0, when the deviation from the accumulate average was less than 0.75 minutes. Statistical analysis indicated that when the average length of recesses on a given day was more than 2.25 minutes above average, a reverse effect was observed the following day (see Fig. 13). Statistical analysis of the average length of time off the nest during incubation as related to temperature and residual effect is given in Table 6. Though the residual effect was not as pronounced here as was observed for average time on the nest, it was significant at the 0.15 level.

The F-statistic for the hypothesis of no difference among years was less than 1.0 and the null hypothesis was accepted. The F-statistic for the hypothesis of no difference among activity periods was 1.21 which, with 2 & 140 degrees of freedom, was not significant at the 0.15 level. The F-statistic for the hypothesis of no difference between methods of collecting data was 7.48, which is significant

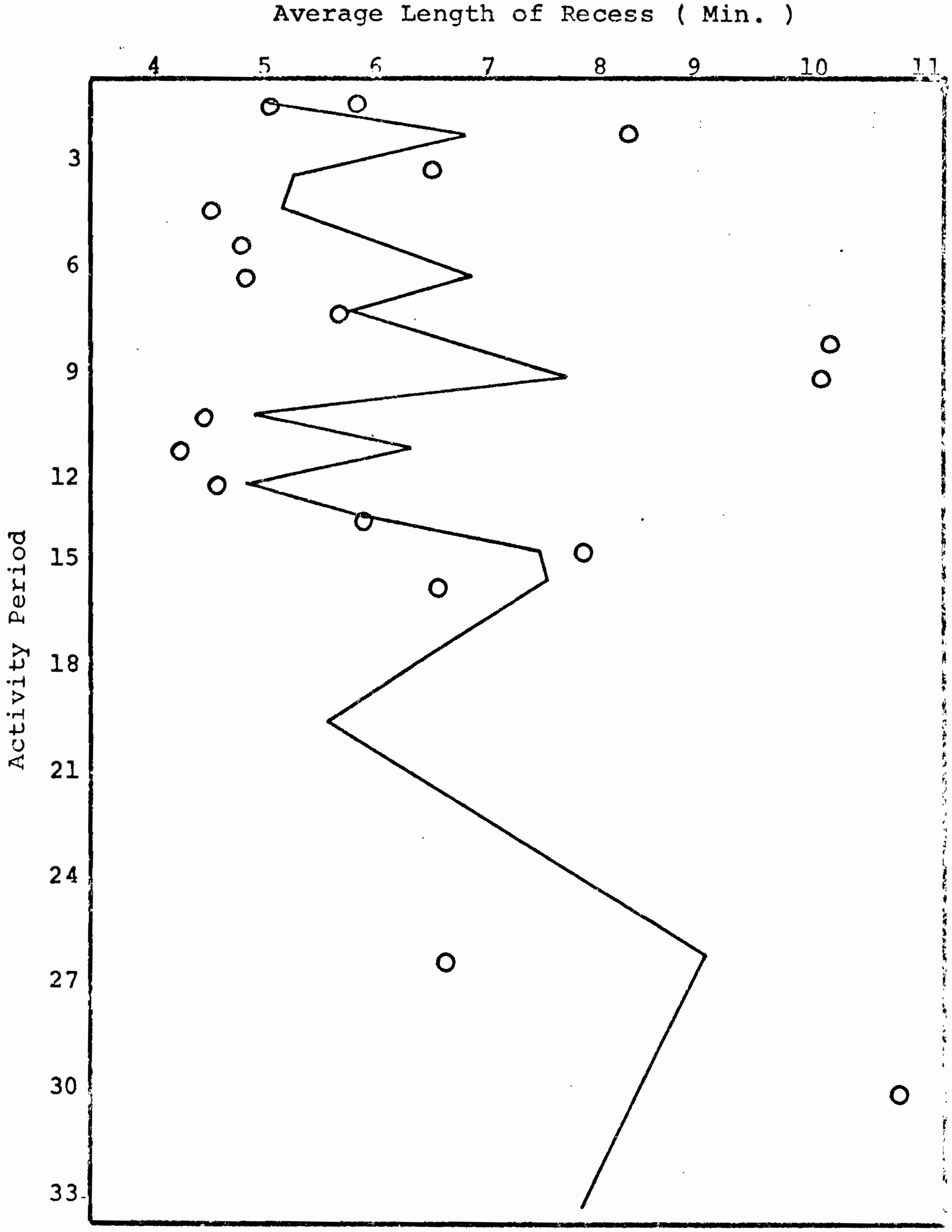

Fig. 13. Residual effects of average recess length. Circles represent observed responses; the line represents the computer estimate.

TABLE 6

STATISTICAL ANALYSIS OF TEMPERATURE AND RESIDUAL EFFECT AS RELATED TO LENGTH OF RECESS

	Regression Coefficient	S.E.	Significance Level	T Value
Temperature	0.1074	± 0.0306	.001	3.512
Temperature Above 81 Degrees	2.4587	± 0.4731	.001	5.20
Residual Effect of Previous Day	-0.2258	± 0.1579	.15	-1.43

at the 0.01 level. Therefore, the method of recording was related to the means of the dependent variable and the null hypothesis was rejected. A combined test of the hypothesis of no two or three factor interactions such as nest effect and day of incubation gave an F-value of 1.09 with 12 and 132 degrees of freedom and was not significant at the 0.15 level. Means and statistical analysis of average length of time off the nest as related to activity period, method, and stage of incubation are listed in Appendix A. The relation of nest and year to average time off the nest are listed in Tables 7-8.

The percentage of time on the nest per activity period was determined using the equation (Skutch, 1962),

$T = \frac{100S}{S+R}$, where T = percentage of time on the nest, S (session) = average length of time on the nest, and R (recess) = average time off the nest. The significance between percent time on the nest and ambient temperature was tested using an analysis of covariance. A temperature regression coefficient of -0.7645 indicated that for each degree increase in temperature, average percent time on was reduced by about three-fourths of one percent. Thus, the percentage of time the incubating bird spent on the nest was inversely related to temperature. Examination of the residuals indicated a nonlinear effect of percent time on for those observations with high and low temperatures. This suggested that a quadratic term for temperature was

TABLE 7

MEANS AND STATISTICAL ANALYSIS FOR AVERAGE TIME OFF NEST AS RELATED TO NEST

Nest	Variable	Number	Mean	St. D.	Range	C.V.
1	Recess	9	5.3	1.0	3.9-7.1	19.4
1	Temp.	9	64.7	9.5	43.0-76.0	14.7
2	Recess	11	4.8	0.8	3.5-5.8	16.9
2	Temp.	11	58.6	8.4	46.0-70.0	14.3
3	Recess	15	6.6	2.2	3.0-11.4	34.0
3	Temp.	15	71.5	7.3	60.0-85.0	10.2
4	Recess	7	5.8	1.1	4.5-7.1	18.0
4	Temp.	7	79.7	6.6	70.0-86.0	8.2
5	Recess	8	7.7	1.4	5.2-9.3	17.9
5	Temp.	8	76.6	5.2	70.0-83.0	6.8
6	Recess	4	6.6	1.8	4.1-8.2	27.3
6	Temp.	4	79.6	8.7	70.0-90.0	10.9
8	Recess	9	6.4	2.0	3.8-9.3	30.4
8	Temp.	9	74.9	7.0	64.0-85.0	9.4
9	Recess	5	5.9	0.7	5.2-6.8	11.1
9	Temp.	5	76.2	6.7	68.0-84.0	8.8
10	Recess	22	6.7	2.0	4.6-12.3	29.1
10	Temp.	22	75.2	4.3	67.0-82.0	5.7
11	Recess	15	6.9	2.4	4.6-12.3	34.6
11	Temp.	15	78.6	5.0	71.0-88.0	6.4
12	Recess	8	6.3	0.8	5.5-7.5	12.3
12	Temp.	8	66.0	9.9	58.0-85.0	15.0
13	Recess	14	6.1	1.6	4.0-8.7	26.0
13	Temp.	14	68.1	9.0	52.0-81.0	13.2
14	Recess	10	7.4	3.1	3.7-13.8	41.6
14	Temp.	10	70.1	7.3	57.0-80.0	10.4
15	Recess	4	5.1	1.6	4.0-7.5	31.6
15	Temp.	4	70.3	9.9	60.0-81.0	14.1
16	Recess	5	5.5	0.7	4.6-6.4	12.9
16	Temp.	5	69.4	8.7	55.0-77.0	12.6
17	Recess	18	6.4	2.2	3.7-11.0	34.4
17	Temp.	18	72.3	6.9	60.0-82.0	9.5

TABLE 8

MEANS AND STATISTICAL ANALYSIS FOR AVERAGE TIME OFF NEST AS RELATED TO YEAR

Year	Variable	Number	Mean	St. D.	Range	C.V.
73	Recess	54	6.1	1.8	3.0-11.4	28.9
73	Temp.	54	70.2	10.6	43.0-90.0	15.1
74	Recess	59	6.6	1.9	3.8-12.3	28.3
74	Temp.	59	74.9	7.0	58.0-88.0	9.4
75	Recess	51	6.3	2.1	3.7-13.8	34.0
75	Temp.	51	70.3	7.9	52.0-82.0	11.2

needed so the variable $(\text{temperature}-70)^2$ was added to the model. Since the quadratic effect was negligible near the center of the temperature scale, 70 degrees was appropriately selected for the variable. When the analysis of covariance model was adjusted for the two temperature covariables, and the resultant regression coefficient plotted against percent time on, a nonlinear effect was observed (see Fig. 14). Statistical analysis of the influence of temperature on the percentage of time the bird spent on the nest is given in Table 9.

A combined test of the hypothesis of no difference among the effects of activity periods and method of recording gave an F-value of 0.76 with 7 and 135 degrees of freedom. The null hypothesis was accepted at the 0.05 level. A test of the hypothesis of no differences due to years resulted in an F-value less than 1.0 and the hypothesis was accepted.

When the effects of incubation day on percent time on the nest were analyzed on a day-to-day basis, no significant relationship was observed. However, when the incubation days were grouped as day one until hatching and the day of hatching, a significant difference was detected. A regression coefficient for the differences in adjusted means of prehatching and hatching days of 3.7173 indicated the bird averaged about 3.7 percent more time on the nest on the day of hatching than during the prehatching days. For example, when the bird sat on the average of 81 percent during the

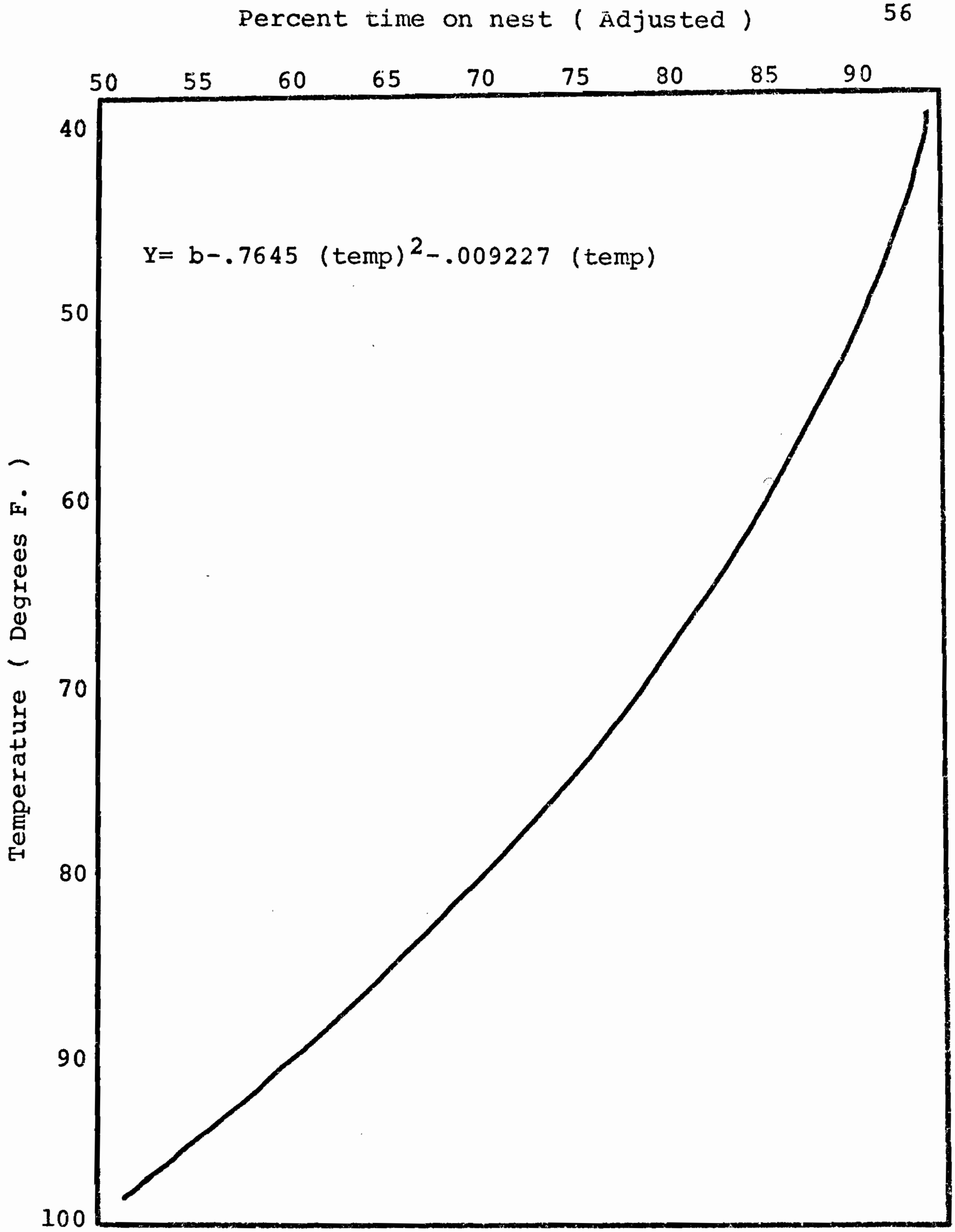

Fig. 14. Percent time on nest as related to temperature.

TABLE 9

STATISTICAL ANALYSIS OF PERCENT TIME ON NEST AS RELATED TO TEMPERATURE AND DAY OF INCUBATION

	Regression Coefficient	S.E.	Significance Level
Temperature	-0.7645	± 0.0600	0.001
(Temperature-70)^2	-0.0093	± 0.0042	0.05
Differences in Adjusted Means of:			
Hatch-Prehatch	3.7173	± 1.549	0.025
Observation Versus Monitor	1.4391	± 1.049	0.172

prehatching days, it tended to sit about 84.7 percent on the day of hatching (see Fig. 15).

Previous day residual effects which were influencing the average time on and average time off the nest had little effect on the percentage of time the bird spent on the nest.

Statistical analysis of percent time on nest as related to activity period, method of collecting data, and day of incubation are given in Appendix A. The relation of nest and year for percent time on nest are listed in Tables 10-11.

Influence of the Nonincubating Bird on Attentive Behavior

Based upon the interpretation of nest guarding as that behavior pattern in which the male spends a significantly greater amount of time near the nest when the incubating bird is absent than when it is present, such activity was not observed in the Brown Thrasher. In an attempt to determine the presence or absence of nest guarding in this species, a total of 42 observations were made from 6 different nests. During those occasions in which the incubating bird was absent from the nest, the mate averaged only 8.2 percent of time within a radius of 5m from the nest and 12.4 percent when the incubating bird was on the nest. Since nest guarding was obviously absent, statistical analysis

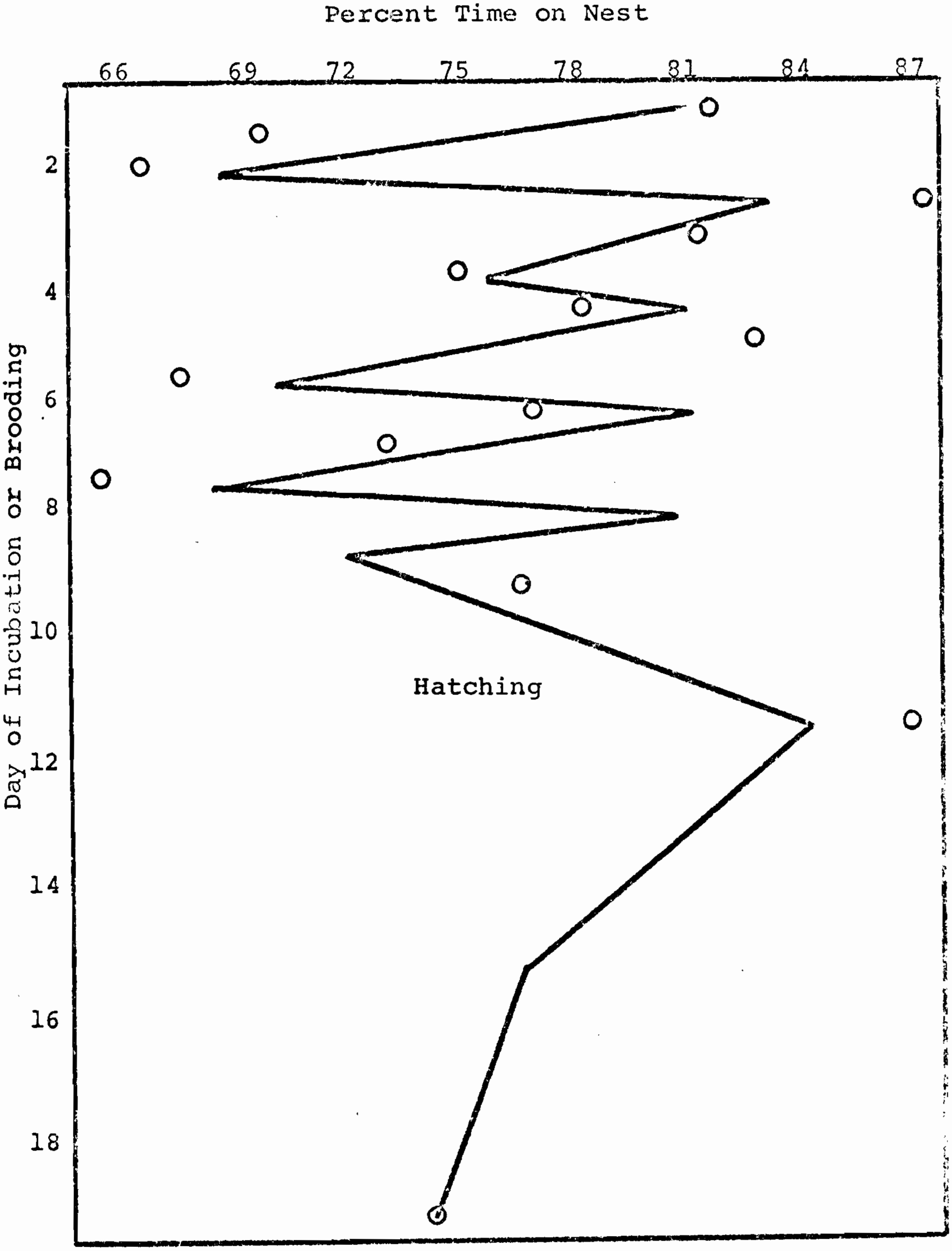

Fig. 15. Percent time on nest as related to day of incubation. Circles represent observed responses; the line represents computer estimate.

TABLE 10

MEANS AND STATISTICAL ANALYSIS FOR PERCENT TIME ON NEST AS RELATED TO NEST

Nest	Variable	Number	Mean	St. D.	Range	C.V.
1	Percent	9	82.9	4.0	79.9-90.8	4.8
1	Temp.	9	64.8	9.5	43.0-76.0	14.7
2	Percent	11	82.8	6.4	73.9-91.1	7.8
2	Temp.	11	58.6	8.4	46.0-70.0	14.4
3	Percent	15	74.4	8.9	55.2-87.3	11.9
3	Temp.	15	71.5	7.3	60.0-85.0	10.2
4	Percent	7	70.5	6.3	62.6-80.3	8.9
4	Temp.	7	79.7	6.6	70.0-86.0	8.2
5	Percent	8	73.9	6.4	67.2-84.3	8.6
5	Temp.	8	76.6	5.2	70.0-83.0	6.8
6	Temp.	4	79.8	8.7	70.0-90.0	10.9
8	Percent	9	76.3	8.8	60.1-89.5	11.6
8	Temp.	9	74.9	7.0	64.0-85.0	9.4
9	Percent	5	75.6	5.8	68.8-81.8	7.7
9	Temp.	5	76.2	6.7	68.0-84.0	8.8
10	Percent	22	75.1	5.1	66.9-82.9	6.8
10	Temp.	22	75.2	4.3	67.0-82.0	5.7
11	Percent	15	73.1	8.1	55.6-86.1	11.0
11	Temp.	15	78.7	5.0	71.0-88.0	6.4
12	Percent	8	76.5	7.8	60.1-85.4	10.2
12	Temp.	8	66.0	9.9	58.0-85.0	15.0
13	Percent	14	78.7	9.7	52.7-91.6	12.3
13	Temp.	14	68.1	9.0	52.0-81.0	13.3
14	Percent	10	76.6	10.1	60.6-88.9	13.2
14	Temp.	10	70.1	7.3	57.0-80.0	10.4
15	Percent	4	75.6	11.9	60.6-87.6	15.8
15	Temp.	4	70.3	9.9	60.0-81.0	14.1
16	Percent	5	78.6	5.7	69.9-85.2	7.3
16	Temp.	5	69.4	8.7	55.0-77.0	12.6
17	Percent	18	76.7	6.8	65.5-86.9	8.8
17	Temp.	18	72.3	6.9	60.0-82.0	9.5

TABLE 11

MEANS AND STATISTICAL ANALYSIS FOR PERCENT TIME ON NEST AS RELATED TO YEAR

Year	Variable	Number	Mean	St. D.	Range	C.V.
73	Percent	54	76.5	8.6	55.2-91.1	11.3
73	Temp.	54	70.2	10.6	43.0-90.0	15.1
74	Percent	59	75.0	6.9	55.6-90.0	9.1
74	Temp.	59	74.9	7.0	58.0-88.0	9.4
75	Percent	51	77.3	8.4	52.7-91.6	10.9
75	Temp.	51	70.3	7.9	52.0-82.0	11.2

was unnecessary.

Attentive periods were interrupted by the sight and/or vocalizations of the mate as well as for other, undetected reasons. Sessions were designated as mate-terminated when the nonincubating partner was seen or heard within 5 seconds before the bird left the nest. When the mate was not seen or heard just prior to departure from the nest, the interruption was classified as non-mate terminated. The influence on average session length by the nonincubating mate is shown in Table 12.

The hypothesis that there was no difference in the average length of sessions terminated by the nonincubating mate and the average length of sessions not terminated by the mate was tested using a T-test. A T-value of 2.577 was significant at the 0.05 level. Thus the average length of sessions terminated by the nonincubating partner was shorter than those not terminated by the mate and the null hypothesis was rejected.

Soft calls by the mate were the major causes of mate-terminated sessions. Seldom was the full song heard after incubation had begun. The incubating bird was called off the nest by its mate to be fed near the nest and on other occasions both birds flew off to forage together immediately after the call was heard. Often the incubating bird was observed lifting its head high above the nest, turning it in different directions, and appearing to be listening for

TABLE 12

LENGTH OF SESSIONS BY INCUBATING BROWN THRASHERS

Variable	Number	Mean	± S.D.	T Statistic With D.F. 5	Significance Level
Sessions terminated when not called by mate	79	13.83	11.45	2.577	0.05
Sessions terminated when called by mate	83	13.17	10.87		

the mate's call. Never during the study was feeding on the nest observed. Some sessions were momentarily interrupted when one member of the breeding pair relieved the other on the nest. Usually it was the female that kept the eggs and nestlings covered during rain. At nest number 8-75, the male was sitting on the eggs when a severe rain storm developed. The female immediately relieved the male and the exchange was rapid and well-timed; both birds passed each other in flight about 0.7m from the nest. The storm lasted about two hours, during which time the female never left the nest.

Thirty-six hours of observation, twelve hours at each of three nests in which one member of the pair was marked, were conducted to determine the amount of time each sex spent on the nest. During this period, the female covered the eggs twenty-five hours and thirty-three minutes, or 71 percent of the total time. The male was on the nest ten hours and twenty-seven minutes, or 29 percent of the total time. The number of sessions by females was 79 with a range of 16-29 minutes and averaged 22 minutes per session ±6.54. Male sessions totaled 39 with a range of 13-21 minutes and averaged 18.2 minutes ±5.24.

Numerous aggressive encounters, both interspecific and intraspecific, were observed during this study. The majority of these encounters occurred between the male member of a breeding pair and other male Brown Thrashers.

On a few occasions the female also engaged in aggressive behavior. Aggressive behavior tended to increase in intensity as the nesting cycle progressed. The investigator was more savagely attacked by both members of the pair when young birds were in the nest than during incubation. On one occasion, when I was weighing young birds, one parent struck me on the forehead producing blood. Aggressive encounters were observed to have occurred with twelve other avian species and two mammals; these are reported in Table 13.

Study of the Nesting Cycle

The earliest dates on which a Brown Thrasher was seen or heard within the study area were 11 April 1973, 26 February 1974, 11 April 1975, and 15 April 1976. The main spring migration of this species occurred the first week in May of each year.

Territory

The territory of the Brown Thrasher is the area it defends. Brown (1964) suggests that territory involves the defendability of the food supply, mate, nesting place, nest or other requisite for reproduction or survival and this behavior is attained through natural selection. The territorial song was heard a few days before a female was seen

TABLE 13

OBSERVED AGGRESSIVE ENCOUNTERS

Species	Male	Female	Total
Yellow-shafted Flicker (Colaptes auratus)	5	0	5
Eastern Phoebe (Sayornis phoebe)	1	0	1
Blue Jay (Cyanocitta cristata)	8	0	8
Carolina Wren (Thryothorus ludovicianus)	3	1	4
Catbird (Dumetella carolinensis)	12	1	13
Brown Thrasher (Toxostoma rufum)	24	5	29
Robin (Turdus migratorius)	6	0	6
Eastern Bluebird (Sialia sialis)	3	1	4
Starling (Sturnus vulgaris)	8	2	10
Cardinal (Cardinalis cardinalis)	4	0	4
Indigo Bunting (Passerina cyanea)	2	0	2
American Goldfinch (Carduelis tristus)	3	0	3
Song Sparrow (Melospiza melodia)	2	0	2
Domestic Cat (Felis domesticus)	7	6	13
Man (Homo sapiens)		numerous	
Totals	90	16	106

which indicated the males arrived from one week to ten days ahead of the females. In this study Catbirds usually arrived about two weeks before Brown Thrashers, and since both species build their nests in similar vegetation, competition for nesting sites often occurred. The exact size of territory was difficult to determine because it tended to vary with locality and male density. Near the banks of the small creek where sumac bushes entangled with honeysuckle were numerous, the territory was about 0.5 hectare. Two nests were no more than 15m apart. Along the edge of the forest, territory encompassed one or more hectares and nests were widely separated. The establishment of territory was evident when individual males were heard to sing in the same area on successive days.

Courtship

No elaborate courtship displays, as are seen in other passerines, were observed in this species. Based upon observations of 3 pairs of birds, the general courtship behavior consisted of the following: when a female was attracted to the territory of a given male, the male's primary song usually decreased in volume. On some occasions, the male flew from his perch to the ground near the female, picked up a twig in his bill and placed it on the ground before her. A gentle peck by the male on the head of the female was often observed. If the female flew away after this action, she was chased by the male, both birds flying in zig-zag fashion. Occasional fighting between the two was observed but this behavior could not be definitely linked to any stage in pair-formation. Since many courtship behavioral patterns were conducted beneath the cover of shrubs and under-growth, some were probably not observed. Eleven pairs of birds, one member of each having been marked, indicated that after the pair-bond had been formed, the general tendency was to remain constant to one mate throughout the nesting season. Only two changes of mate were detected.

Nest Construction

Both sexes of the Brown Thrasher engage in nest construction but the female appeared to play a slightly larger role than the male. Of 155 trips to the nest when nest 4-76 was being built, the female made 82 and the male made 73. The majority of nests, particularly those near the small creek, were built in sumac-honeysuckle. Others were built in multiflora rose, red cedar, wild cherry, wild plum, and wild rose. The number of nests by year and type of vegetation in which they were constructed is recorded in Table 14. Nests were started by placing small twigs on horizontal stems or on a fork between the main trunk and limb. After this foundation was completed, the next layer of material consisted mainly of dead

TABLE 14

VEGETATION SUBSTRATE OF NESTS BY MONTH AND YEAR

Vegetation Substrate	May 1973-1976	June 1973-1976	July 1973-1976	Total	% of Total
Sumac-Honeysuckle	11	7	8	26	50.00
Multiflora Rose	4	4	2	10	19.73
Red Cedar	2	1	0	3	5.77
Wild Rose	2	3	5	10	19.23
Wild Cherry	1	0	2	3	5.77
Total				52	100.00

<u>Average Height (in feet) of Nests by Month</u>

May--4.9

June--5.4

July--6.8

leaves. The last layer was composed largely of small rootlets which appeared to have been taken from live grasses. All nests were rather uniform in construction and architecture. The height range above ground for 48 nests was 0.4 to 2.8m with a mean of 1.3m. The measurements of the 48 nests are as follows: the outside distance from the bottom of the nest to the top rim--8.9cm, the inside depth--4.9cm, the inside diameter--8.4cm x 10.0cm, and the outside diameter--14.0cm x 15.7cm. Of the 6 nests which were discovered at the onset of construction, two required 3 days, one 2 days, one 8 days, one 4 days, and one 5 days to build for an average of 4.2 days.

Eggs

Egg-laying began 1 to 5 days after the nest had been completed but the predominant method was to lay the first egg the day immediately following nest completion. The first egg in the clutch was deposited on day one after nest completion at twelve nests, day three at two nests, and day five at one nest. The normal pattern of egg deposition was one egg per day until the full complement of the clutch had been reached. Observations at 14 nests indicated that eggs were laid early in the morning between 5:30 and 7:30. Of 48 nests, the clutch size ranged from one to four eggs with a mean of 2.8. Evidence from this study suggests that clutch size varies seasonally. The average clutch size for early nests (from mid to late May) was 3.1 eggs and that for late nests (from late June to early July) was 2.5 eggs. No nests were found which contained more than 4 eggs per clutch. The average dimensions of 124 eggs were 19.7 x 26.9mm. The mean weight of this number of fresh eggs was 5.94 grams and the average weight of eggs at the time of hatching was 5.12 grams. Egg weight-loss during incubation averaged 13.9 percent. There was no significant difference in weights and dimensions of eggs for early and late nests. Measurements of eggs and young birds for one early nest and one late nest are recorded in Tables 15-16. As mentioned earlier, eggs were marked with water-resistant dye to calculate the weight-loss of each egg. Figures 16-19 show the egg weight loss during incubation and the weights of young birds at the time of fledging.

The average length of the incubation period for 12 nests, for which complete records were kept from the time the first egg was laid until the young hatched, was 11.5 days. The shortest incubation period was 10 days and the longest 13 days.

Thirty-four nests were available for the study of nest success, parasitism, and mortality factors. During the entire four-year study, not a single Brown Thrasher nest was parasitized by the Brown-headed Cowbird (Molothrus ater) though Cowbirds were seen in the study

TABLE 15

WEIGHT IN GRAMS OF EGGS AND YOUNG BIRDS
NEST # 3-76

Weight of Eggs

Date	Red	Green	Blue
5-6-76	5.94	6.13	5.92
5-7-76	5.86	6.02	5.84
5-8-76	5.79	5.87	5.71
5-9-76	5.71	5.71	5.59
5-10-76	5.66	5.60	5.44
5-11-76	5.61	5.51	5.32
5-12-76	5.52	5.43	5.13
5-13-76	5.39	5.32	4.98
5-14-76	5.28	5.24	4.85
5-15-76	5.19	5.13	4.76
5-16-76	5.08	5.05	4.68

Weight of Young Birds

Date	Red	Green	Blue
5-17-76	5.46	7.10	6.93
5-19-76	17.79	19.47	19.13
5-21-76	29.47	30.39	33.56
5-22-76	41.08	42.00	42.81
5-23-76	43.24	45.15	45.00

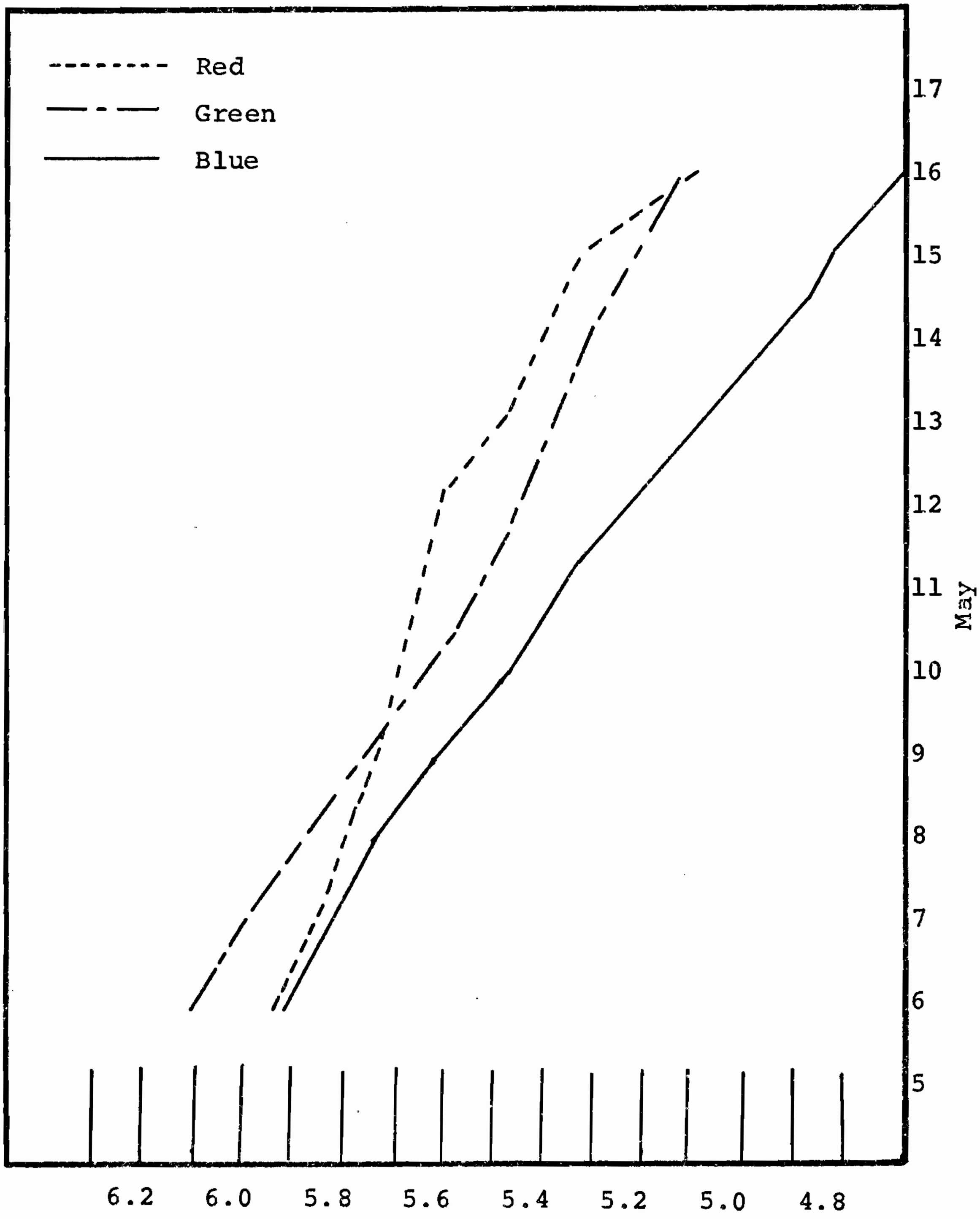

Fig. 16. Weight of Eggs in Grams---Nest # 3-76

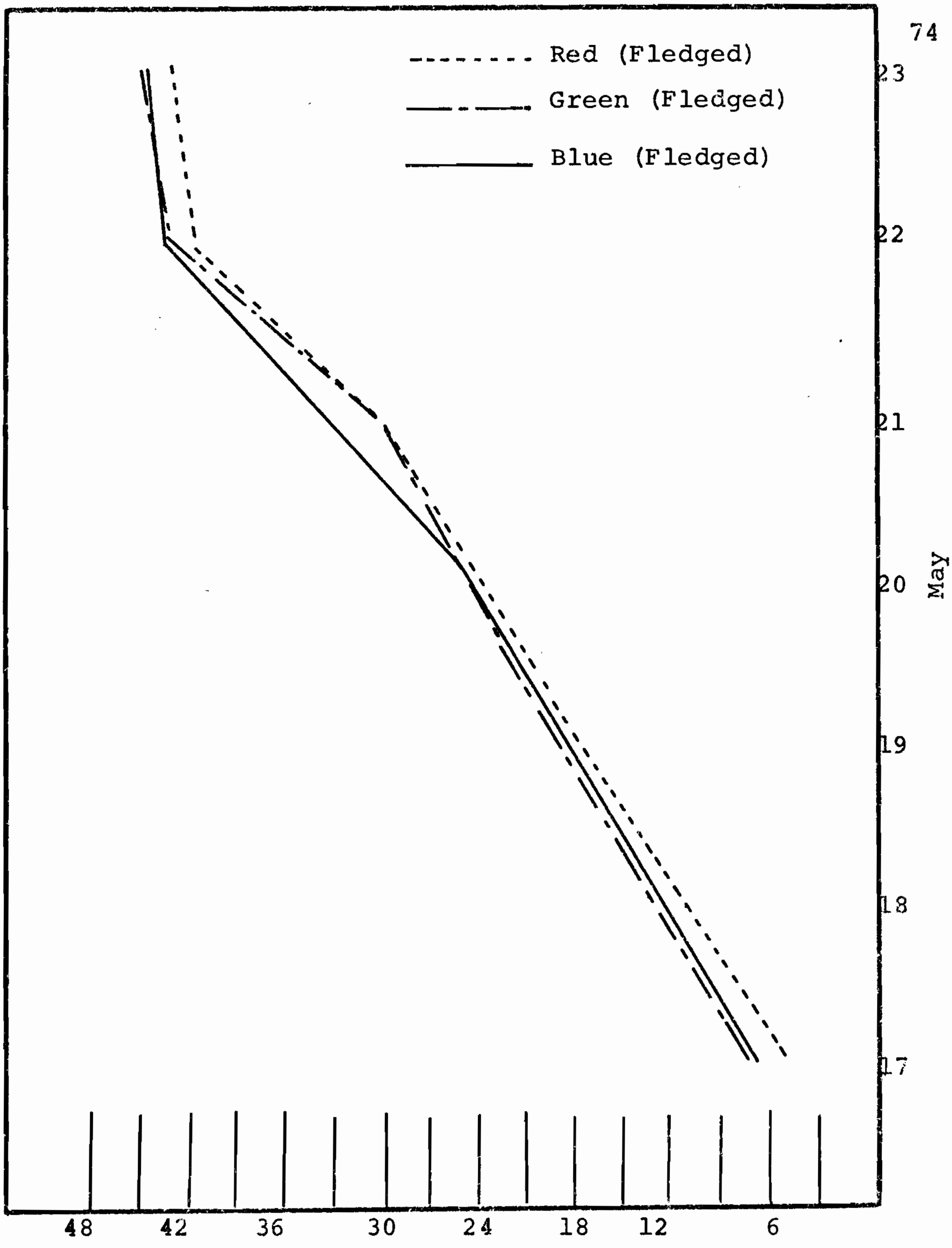

Fig.17. Weight of Young Birds in Grams---Nest # 3-76

TABLE 16

WEIGHT IN GRAMS OF EGGS AND YOUNG BIRDS
NEST # 10-76

Weight of Eggs

Date	Red	Green	Blue
7-9-76	5.62	5.92	6.15
7-10-76	5.58	5.87	6.06
7-11-76	5.51	5.81	5.97
7-12-76	5.47	5.77	5.88
7-13-76	5.40	5.72	5.81
7-14-76	5.36	5.65	5.76
7-15-76	5.31	5.58	5.68
7-16-76	5.26	5.51	5.59
7-17-76	5.19	5.45	5.52
7-18-76	5.17	5.38	5.46
7-19-76	5.13	5.26	5.37
7-20-76	5.13	5.18	5.33
7-21-76	5.09	5.12	5.29

Weight of Young Birds

Date	Red	Green	Blue
7-22-76	6.94	6.62	5.57
7-23-76	11.05	12.26	9.34
7-24-76	17.62	18.73	16.82
7-25-76	23.46	24.82	22.05
7-26-76	28.67	30.17	27.50
7-27-76	31.22	34.35	missing
7-28-76	34.48	37.00	
7-29-76	38.04	40.96	
7-30-76	41.37	42.33	
7-31-76	43.02	fledged	

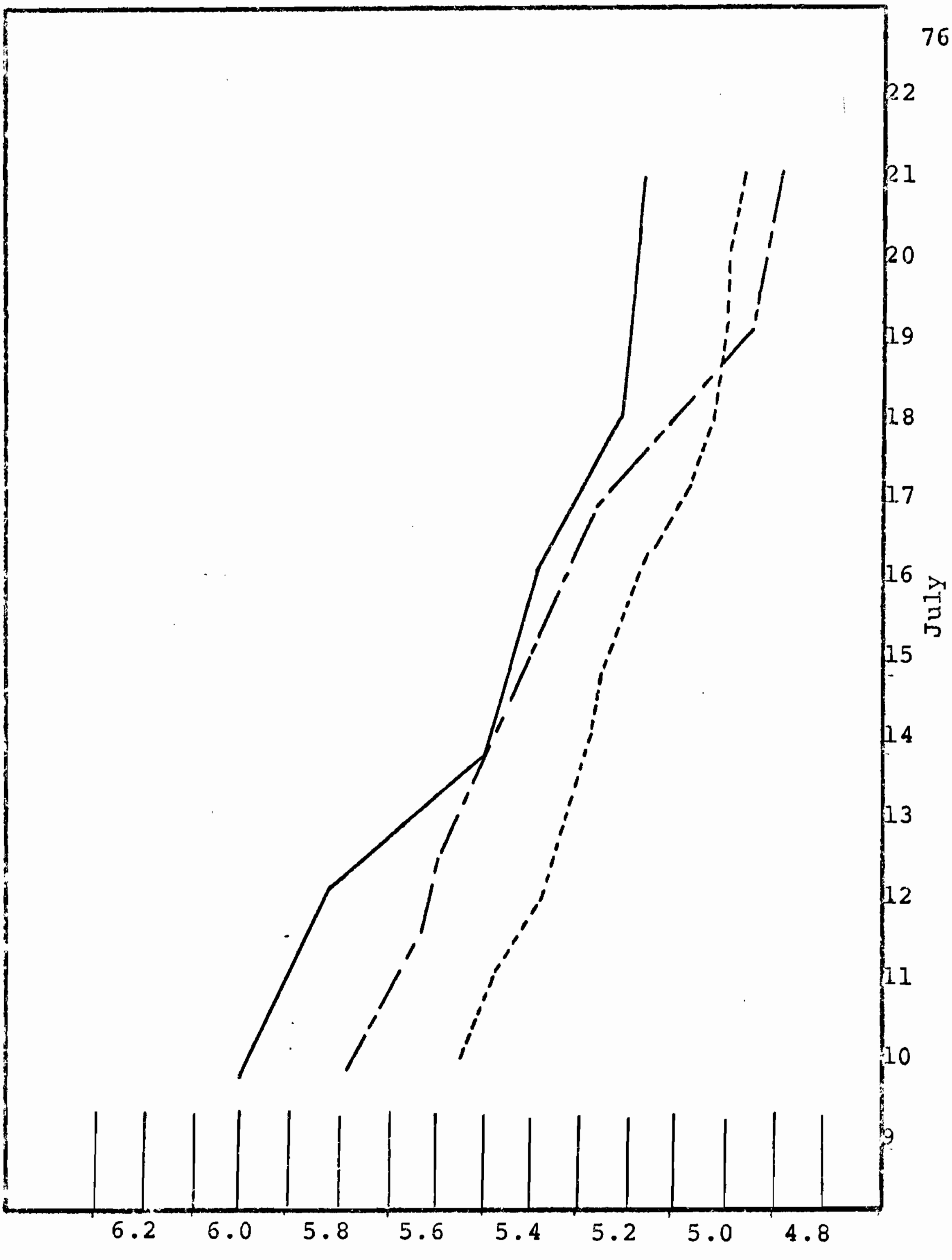

Fig.18. Weight of Eggs in Grams-- Nest # 10-76

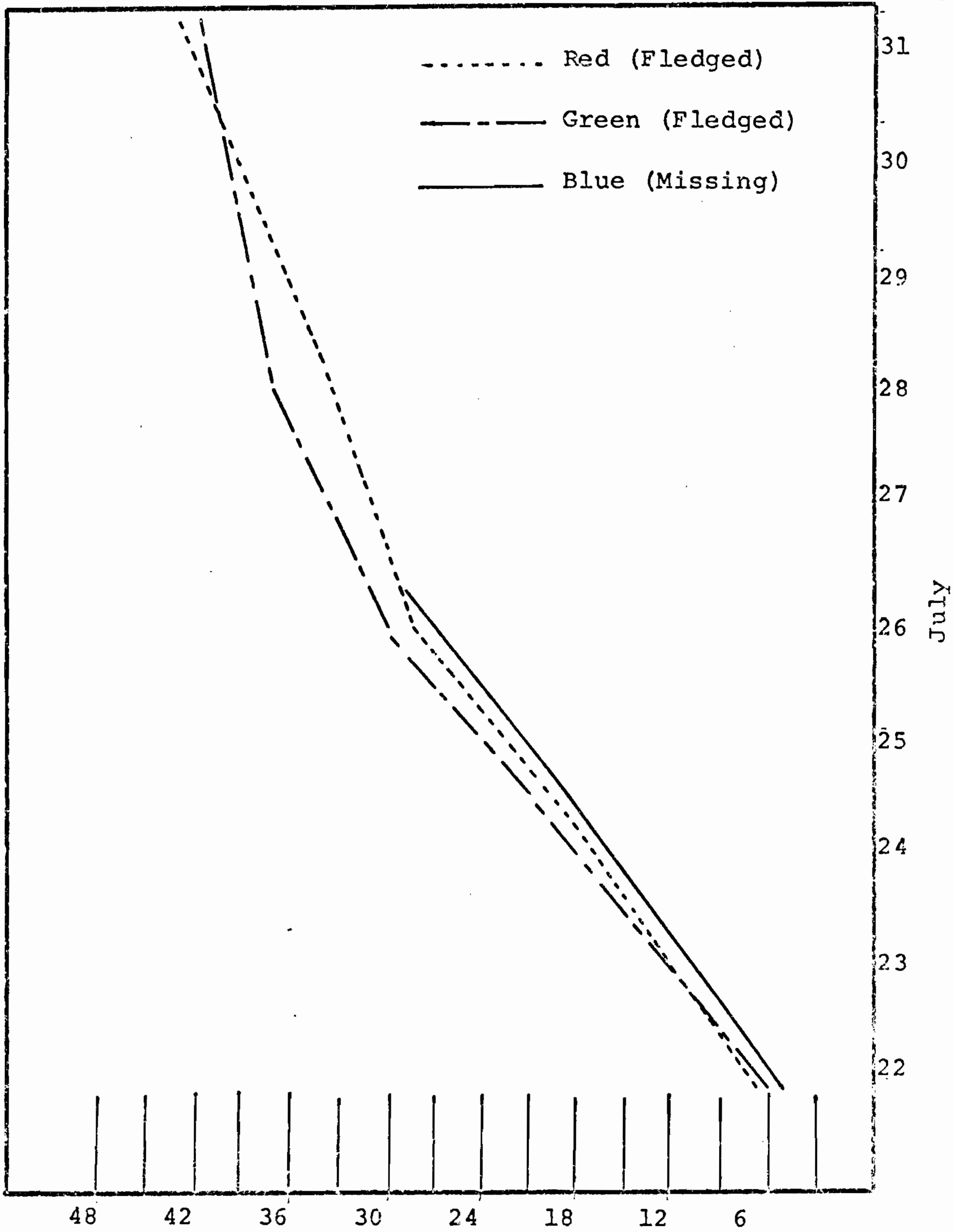

Fig.19. Weight of Young Birds in Grams-- Nest # 10-76

area. Those nests which failed as a result of the investigator's interference, such as those which were deserted due to improper placement of the thermistor probe, were not included in the study of nest success and mortality factors. The traditional method of counting a nest successful if at least one young bird fledged was used in this study. Nest success data for 1973-1975 are recorded in Table 17. During 1976, incubating and brooding birds were often disturbed by the investigator when eggs and young birds were being weighed. Such interference occasionally resulted in egg breakage and premature fledging of the young. The reasons for nest failures, other than human intrusion, were known for certain in 4 cases. The eggs of nest numbers 1-73 and 8-75 were observed being broken by avian predators. The former by a Yellow-shafted Flicker (*Colaptes auratus*) and the latter by a Blue Jay (*Cyanocitta cristata*). Young nestlings were killed by a domestic cat (*Felis domesticus*) at nest numbers 9-73 and 5-75.

Care of the Young

Both sexes of this species brooded, fed, and cared for the young. The exact percentage of time each partner spent in brooding was not determined, only that both members of the breeding pair engaged in this activity. Brooding constancy appeared to equal that of incubation constancy for the first three or four days after which time it began to

TABLE 17

NEST SUCCESS 1973, 1974, AND 1975

Year	Number of Nests	Number Successful	Number Failed	Percent Successful
1973	12	7	5	58.33
1974	10	5	5	50.00
1975	12	8	4	66.67
Total	34	20	14	58.82

subside. Diurnal brooding practically ceased on the sixth or seventh day but brooding at night continued until the young left the nest. Records of 12 nests indicate a nestling period from 9 to 12 days with an average of 10.5 days. These data were obtained from relatively undisturbed nests. Careful observations were made at five nests of marked birds to determine the role of sex in feeding the nestlings. Forty-six hours of observation suggested that the female was more engaged than the male in feeding the young. During this period, the different females made 280 trips to the nest and the males 211 for a total of 491 trips. The number of trips made by the female represented 57 percent of the total number of feedings. The kinds of food and the approximate number of each are recorded in Table 18. After the young birds left the nest, they were fed by both parents for an unknown period of time. One fledgling was observed being fed by a parent bird on day 13 of post nest life. Before young fledglings were able to forage alone, a new nest was built for another brood. This activity was observed in 3 pairs of birds.

Foraging Efficiency of Parent Birds

Foraging patterns of the parent birds could not be accurately determined. Attempts to record the direction of travel, number of deviations from a straight line, number of stops, and the number of pecks per unit of time were

TABLE 18

FOOD GIVEN TO NESTLINGS

Character		Number	Percent
Grasshopper	(Orthoptera)	62	19.56
Spider	(Arachnida)	12	3.79
Worms	(various kinds)	18	5.68
Beetles	(Coleoptera)	38	11.99
Mayfly	(Ephemerida)	17	5.36
Larvae	(Coleoptera) (Diptera)	76	23.97
Flies	(Diptera)	80+	25.24
Berries	(several species)	?	
Moth	(Lepidoptera)	8	2.52
Caterpillar	(Lepidoptera)	4	1.26
Butterflies	(Lepidoptera)	2	0.63
Unidentified		numerous	

unreliable. Often a single bird foraged alone while its mate brooded the young and at other times both birds foraged together. Since the amount of food brought to the young per unit of time reflected the results of parental foraging efficiency, it was used as a more reliable method of investigating foraging behavior. The 46 hour period of feeding observation mentioned earlier, which resulted in a total of 491 trips to the nest by both birds, reflected an average of 10.7 trips per hour. No attempt was made to quantify seasonal variation in foraging rates. However, the number of trips to the nest did increase with the age of the nestlings.

A survival curve for the eggs and nestlings from relatively undisturbed nests during the four-year study period is presented in Fig. 20. The curve is plotted on a semilogarithmic scale in which a uniform rate of mortality results in a straight line. Mortality data from 34 nests with 85 eggs are represented in Fig. 20. The rate of mortality is fairly uniform from oviposition through the first one-third of incubation with a pronounced decrease during the last third of incubation. The rate of mortality in the nestling period was rather uniform from hatching of the eggs to fledging of the young.

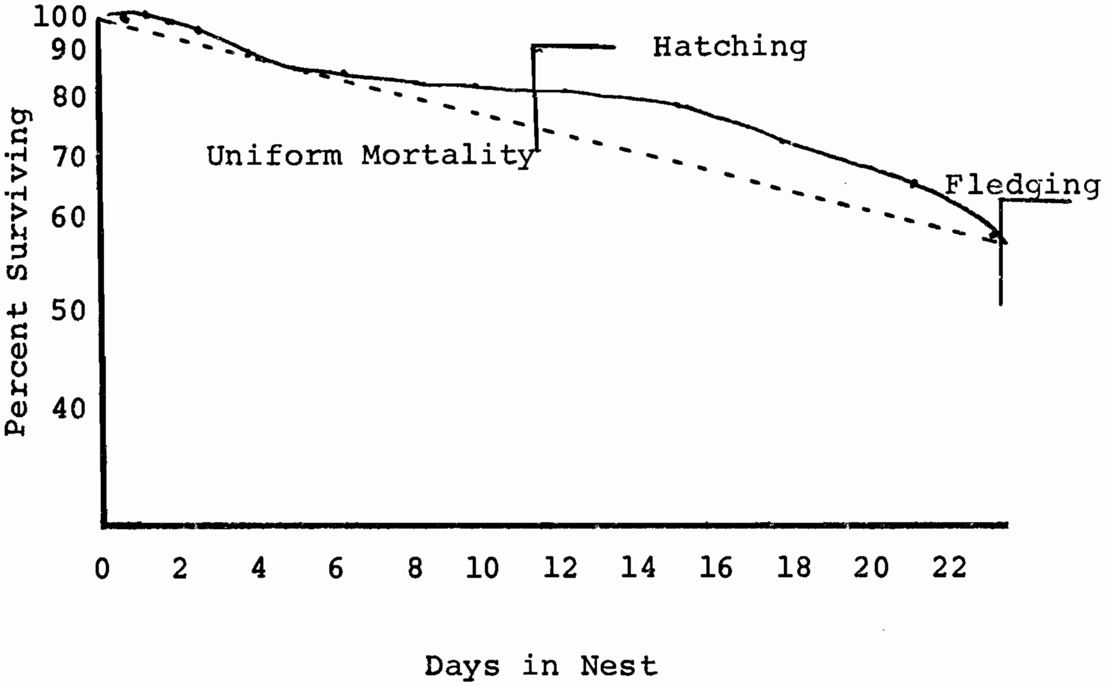

Fig. 20. Survival of eggs and nestlings during each day in nest.

DISCUSSION

Kendeigh (1963) suggests that energy requirements for embryonic development during incubation are derived from the oxidation of fats, carbohydrates and, perhaps, proteins in the yolk and albumin of the egg. In his experiments with the chicken egg (Gallus gallus) Sturkie (1965) indicates that carbohydrate is the main source of energy for the first week of embryonic development; during the second week protein is the major source; and during the last few days lipid oxidation takes precedence. Kendeigh has also shown that the amount of energy available for growth and maintenance is dependent on the amount of oxygen absorbed. The rate at which oxygen is absorbed is directly proportional to the temperature and the length of time the egg is maintained at that temperature.

Heat energy for the proper maintenance of temperature in the Brown Thrasher nest is generated by both male and female. Heat from the parent bird is transferred to the eggs in the nest by the incubation patch which, during the breeding season, shows increased dermal and subdermal vascularity. According to Bailey (1952) incubation patches are found in both males and females, depending on their role in incubating the eggs. When both parents share incubation, their eggs are covered from 60 to 80 percent of the daytime from the day the last, or even the first, is laid until they hatch (Skutch, 1962). In some species, however, both parents together may spend less time on the nest than other birds incubating alone. Skutch also suggests that in species in which the sexes share incubation, neither parent sits more than 80 percent of the day except in certain penguins, Procellariiformes, and a few others. Examination of the dependent and independent variables by nest as shown in Appendix A reveals that the eggs of the Brown Thrasher are covered 60 to 80 percent of the daylight hours as Skutch suggested. Since neither parent of this species incubated the eggs more than 71 percent of the daylight hours, it bears out Skutch's assertion. The upper limits of percent time on the nest are apparently set by the requirements of self-preservation of the incubating bird, and the lower limits are regulated by the heat requirements of the developing embryo (Skutch,1962). Birds are homeotherms and, as such, have incorporated into their anatomical and physiological make-up, feedback mechanisms which tend to regulate the rate of heat production and the amount of heat loss. Lustick (1975) suggests that a thermoneutral zone (optimal temperature range) exists in birds in which the amount of heat lost is compensated for by the amount of heat produced by chemical and physical processes.

During the process of incubation, heat is being transferred from the parent bird to the eggs and this heat is being lost to the environment. Extended periods of incubation, in the absence of food and physical activity, might imbalance the thermoneutral condition of the incubating bird. To balance the amount of heat lost and heat produced, the bird is required to leave the nest to obtain food for oxidation or to engage in some form of physical activity which will increase the rate of heat production. Finlay (1971) suggests that when an incubating bird departs to feed, the eggs become cool and embryo development is retarded. Throughout the entire range of percentage time on the nest, from the lower to the upper limits inclusive, incubation constancy is highly variable. The following discussion relates to those factors which were investigated with regard to their effect on attentive behavior of the Brown Thrasher in this study.

Factors Affecting Attentive Behavior

Temperature

Since the transfer of heat from the parent bird to the eggs is essential in maintaining the appropriate temperature for embryonic development which, according to Baerends (1959) is 40-41 degrees C., it seems logical to assume that attentive behavior is related to environmental temperature. This basic assumption has led previous workers to investigate the possible existence of such a relationship. Many workers have shown that attentive behavior and the constancy of incubation are related to ambient temperature, although contrasting opinions have been reported. Discrepancies in the results reported by investigators might be due to small sample size. Skutch (1962) and Verner (1965) suggest that temperature is one of several factors presumably influencing attentive behavior and to test accurately for this variable, a sufficient sample size is required. Weeden (1966) found no relationship between attentiveness and environmental temperature in the Tree Sparrow (_Spizella_ _arborea_). Since she reported only sixty nest recordings representing the egg-laying, incubation, and nestling stages, the number of recordings, from which incubation constancy was calculated, must have been rather small. Similarly, in studies of the Rufous-sided Towhee (_Pipilo_ _erythrophthalmus_) Davis (1960) observed no temperature effect although only three birds were investigated. The results of my study, involving seventeen nests and nearly five-hundred hours of observed or monitored incubation behavior, agree with those of the majority of workers regarding the effect of ambient temperature on incubation constancy. A regression coefficient of -0.4567 (see Fig. 10) clearly shows an inverse relationship between the average length of time on the nest and environmental temperature during incubation.

When calculating the total proportion of the day the eggs are incubated, both the average time on the nest (sessions and the average time off the nest (recesses) must be considered. The incubating bird may respond to changes in environmental temperatures by three types of adjustments: the bird may keep the average time on the nest constant and vary the recesses; secondly, the recesses may be held constant and the sessions varied; and thirdly, both sessions and recesses may vary together. Skutch also believes that the most common method of adjustment for passerines is to vary both the length of sessions and recesses. Studies by Nice and Thomas (1948), of the Carolina Wren (Thyrothorus ludovicianus) and by Kendeigh (1952) of the Barn Swallow (Hirundo rustica), support Skutch's contention. The records by Slack (1973) on the Catbird suggest that as the temperature rises the length of sessions decreases and the length of recesses increases. The data reported in this study on the Brown Thrasher agree with the records of Slack (see Fig. 10 and Fig. 12). Fautin (1941) and Whitehouse and Armstrong (1953) believe that a sufficient number of ambient temperature readings must be taken throughout the day to discern such adjustments by the bird in response to temperature changes. Many investigators obtain their ambient temperature data from the average of maximum and minimum daily temperatures, or from a temperature reading taken at one time during the day (Cox 1960, Davis 1960, Morgan 1968, and Maxwell and Putnam 1972). Unless a continuous record of hourly temperatures is kept throughout the study, the exact relationship between ambient temperature and the constancy of incubation cannot be derived. Attentive behavior data in this study indicated that an ambient temperature of 81 degrees F. may be the threshold to the upper limit of the thermoneutral zone for this species. At this temperature the average length of sessions decreased by about four minutes and the average length of recesses increased by about two and one-half minutes. One possible explanation for these shorter sessions and longer recesses is the incubating bird's need for larger amounts of water. Sturkie (1965) suggests that water consumption increases with increasing ambient temperatures.

Time of Day

Previous investigators of avian breeding biology have recorded changes in attentive behavior associated with the time of day. Fautin (1941), Cox (1960), Maxwell (1965), and Weeden (1966) feel that hourly variations in attentive behavior might be due primarily to fluctuations in temperature. Since the temperature during the early morning and evening hours is cooler than in the middle of the day, Skutch suggests that temperature may account for the hourly variations in attentiveness on the same day rather than the time of day. Obviously some method must be used to investigate the effect of time of day apart from other influencing factors.

The analysis of covariance model used in this study isolates the effect of temperature from an effect due solely to the time of day. Statistical analysis of the data presented in this paper indicated that the period within the day did not significantly affect the constancy of incubation. The question of whether temperature acts directly on the incubating bird, or indirectly through periodic fluctuations in insect activity, was not included in this study. Skutch (1962) suggests that as the sun rises higher insects become more active, enticing the incubating bird off the nest to secure food.

Stage of Incubation

Closely associated with the effect of temperature on incubation constancy are the apparent changes in attentive behavior patterns during the course of incubation. Whether birds begin at once to incubate with the same intensity they later display has been a subject of investigation by many workers. In her studies of the Song Sparrow (*Melospiza melodia*) Nice (1937) found that longer periods off the nest came during the first two days of incubation after which time the periods off consistently decreased in length and were shortest the last day before hatching. Putnam (1949) reported a gradual increase in the percentage of attentiveness by the Cedar Waxwing (*Bombycilla cedrorum*) the first three days of incubation with only a four percent increase during the remainder of the incubation period. He noted the highest percentage of constancy shortly before hatching. On the other hand, Kendeigh (1952), reporting on attentive behavior of many species, states that there is no evidence that the incubating birds consistently spend more time on the eggs during the later stages just before hatching. Skutch (1962) says that the majority of studies fail to demonstrate an increase in attentiveness as the eggs approach the point of hatching. Data obtained during the course of this study of the Brown Thrasher indicated that full incubation began after the laying of the last egg in a clutch. Further, the percentage of attentiveness was higher during the later stages of incubation with the highest percentage just before hatching (see Fig. 15).

Year

Most studies have failed to demonstrate any significant changes in attentive behavior from year to year. Weeden (1966) reported a difference in incubation constancy between years by the Tree Sparrow (*Spizella arborea*) but she suggested that this difference was due to changes in the environment during the two-year period. Pertinent data obtained in this study recorded in Tables 5, 8, and 11 indicated no difference in attentive behavior among years. The average length of time on the nest, average length of time off the nest, and percentage time on the nest were fairly constant throughout the three-year period.

Method of Collecting Data

The two methods most often used by investigators to obtain attentive behavior data are personal observation and with electrical monitoring devices. Both Drent (1970) and Slack (1973) statistically compared data obtained by these two methods. Slack suggests that the Rustrak thermistor-probe chart recorder, which he used, deserves evaluation because statistical comparison of the two sets of data was significantly different. There are at least two possible causes for variations in the data: one, the thermistor-probe, which is inserted in the nest, has a flexible vinyl head that might be moved to one side of the nest by the incubating bird; and, two, the probe might irritate the bird, resulting in abnormal behavior. The Rustrak instrument was used in this study and no significant difference in data was noted (see Tables 20 and 22). The thermistor-probe system of securing attentive behavior data is of value in relieving the worker of physical strain caused by long continuous periods of observation. Both the instrument and power supply are completely portable and are easily moved from one nest to another. Based upon a lack of significant difference between observed and monitored data in this present study, and the high percent of nest success, a properly placed thermistor-probe was accepted by the birds.

Behavior of the Nonincubating Bird

The great bulk of information in the literature on attentive behavior relates to those species in which only the female incubates the eggs. Previous workers have demonstrated an effect on incubation constancy by the frequent presence of the male near the nest when the female is both on and off the nest. When the female is incubating, the male's presence near the nest might shorten her sessions and when off the nest might lengthen her recesses. Zimmerman's (1963) study of the Catbird suggested that the female's recesses were longer when the male was near the nest than when he was not present. Hann (1937) noted that the male Ovenbird's presence tended to shorten the female's sessions. Slack (1973) reported that the male Catbird significantly affected the lengths of both the sessions and the recesses. Among species in which both members of the breeding pair incubate, little consideration is given by previous workers to the effect on attentive behavior by the nonincubating mate. Studies of the Brown Thrasher by Gabrielson (1912), Erwin (1935), Thomas (1952), and Morgan (1968) fail to report any effect on incubation constancy by the nonincubating partner. Results obtained from this study, (see Table 12), suggest that attentive periods terminated by the presence of the mate near the nest were shorter than those periods not terminated by the mate. These results were irrespective of sex since about equal numbers of observations of both members were considered. The female's sessions, when terminated by the male, were shorter than the session not terminated by the male; the male's sessions were shorter when terminated by the female than those not terminated by the female.

Kendeigh (1952) and Skutch (1955) assert that the primitive pattern of incubation among birds included the participation of both sexes with a tendency, in some groups, toward the attendance by a single parent. If this assertion is true, the Brown Thrasher has retained the primitive condition. Differences in the observed incubation roles among mimids might suggest that attentive behavior patterns of this group are in a period of transition. Studies of the Catbird by Slack (1973) and of the Mockingbird (_Mimus polyglottis_) by Laskey (1962) report no role in incubation by the male of either species. However, nest guarding has been observed in both. In the Brown Thrasher, in which the male regularly incubates, nest guarding has not been reported. Could it be that the male Catbird and Mockingbird have lost their primitive attentive behavioral patterns in the course of evolution and have compensated for this loss by engaging in guarding the nest? Many investigators of avian incubation patterns feel that nest predation is reduced when the eggs are almost constantly covered by the parents. Since the male Catbird and Mockingbird do not cover the eggs, nest guarding by these males might reduce predation. Whether the above hypothesis is true cannot be answered at this present time, but awaits further comparative studies in the Mimidae. Skutch (1962) implies that nest guarding in many species might be an individual peculiarity rather than a species characteristic. His assertion that standing guard is best developed only in those species strong enough to defend against predators requires reappraisal. I have weighed the eggs and young birds from many nests of Catbirds, Mockingbirds, and Brown Thrashers and the Brown Thrashers are far more belligerent in response to nest intrusions than either of the other two mimids. Yet, nest guarding has been demonstrated for both the Catbird and Mockingbird but has not been reported in the Brown Thrasher.

Study of the Nesting Cycle

Studies of the nesting cycles of birds provide many illustrations of both innate and acquired behavior patterns.

Many of these patterns are extremely rigid being genetically fixed within the species and are usually predictable. Other behavioral activities may be acquired by individual members of the species and are usually unpredictable. The discussion which follows relates to the various nesting activities of the Brown Thrasher such as their arrival in spring, location and construction of nests, clutch size, incubation period, and age-specific mortality of eggs and nestlings.

Early Arrival

Mengel (1965), reporting on observations of the Brown Thrasher conducted in the same general area as this present study, gives the arrival time for the major influx of birds at mid or late March. He indicates that clutches are completed from late March to early July with peaks evident at April 11-20 (first nestings) and June 1-10 (second nestings). Barbour, et al. (1973) concur with the observations of Mengel. In this study, the principal spring migration occurred in late April and early May. Clutch completion for first nestings was mid May; that for second nestings late June or early July. Morgan's (1968) study of this species in northern Indiana cites May 1 as the earliest date on which an egg was laid. This would place the arrival time about mid or late April corresponding to the observations of this investigator. Discrepancies in arrival times reported by workers may be explained, in part, on the basis of differences in environmental temperature. Miskimen (1951) reports that temperature is recognized as an important factor in bird migration. Warmer than average temperatures during the months of February and March for a particular year may result in earlier migration.

Nest Construction

As mentioned earlier in this paper, in the Brown Thrasher, both members of the breeding pair engage in nest construction with the female slightly more involved than the male. This bisexual arrangement is believed to represent the primitive condition which this species has retained (Skutch, 1955). Brushy situations in lowland thickets, including rosebushes, appear to be the choice nesting habitat for the Thrasher. Preston and Norris (1947), reporting on the heights of 741 nests, found that within a given species, some individuals consistently nested high and others low and that the individual bird does not change its nesting height over the entire range used by the species. Nice (1937) has shown that an individual Song Sparrow may vary its nesting height according to the season. Taylor (1965) averaged the heights of 127 nests of the Mockingbird and of 91 nests of the Brown Thrasher and found that nests of these species are placed at higher elevations as the season progresses. He calculated the heights of two nests of the Mockingbird, which were built in March, and reported a mean height of 4.5 ft (1.37m); the mean height of two nests of the Brown Thrasher, constructed in March, was 6.8 ft (2.1m); height of 19 July nests was 10.2 ft (3.1m). Barbour et al. (1973) give the nest height range of the Thrasher as 1.5 to 9 ft (0.5-2.7m) and report no variation in height according to season. Parkhurst and Lack (1948) reported that nests of the Yellowhammer (Emberiza citrinella) were placed at higher elevations late in the nesting season. Data obtained during the course of this study support the contention of Nice and Taylor that some species prefer higher elevations for nesting sites as the season progresses. I obtained a mean height of 4.9 ft (1.5m) for 20 nests built in May and a mean of 6.8 ft (2.1m) for 17 nests built in July (see Table 14). Whether there is survival value for the species in the seasonal change in nesting height has not been demonstrated. One area of speculation is that of a possible seasonal change in the foraging habits of potential predators. Another explanation is the leafing out of shrubs earlier than trees. Preston and Norris (1947) suggest that the remote ancestors of birds probably nested on the ground, or in the ground, as most reptiles do today. These men feel that birds prefer to nest on the ground but during the course of evolution have been driven upward owing to disturbance by humans and domestic animals.

Reports on the habits of Brown Thrashers in Iowa by Sherman (1912) and in Massachusetts by Bent (1948) indicate that geographical variations in the behavior and habits of this species may exist. These apparent variations pertain largely to the bird's choice of habitats and nesting sites. In Massachusetts, nests are often placed upon the ground or within three feet (0.9m) of ground level; but this species seldom nests upon the ground in the western and southern portions of its range. Taylor's (1965) study of 108 nests in Louisiana, the southern portion of the species' range, lists 30 nests positioned 10 ft (3m) or more above ground. Of 52 nests examined in my study, conducted in the central portion of the range, not one was placed upon the ground. The range in height was 0.4 to 2.8m with a mean of 1.3m ±0.3m. In Massachusetts, the Brown Thrasher is reported as being a nesting bird of the woodlands, seldom building near the homes of men; but in Iowa and Arkansas, it is eminently a house-yard bird, erecting nests in man-planted trees and shrubs not far from human homes (Sherman, 1912; Bent, 1948; and Thomas, 1952). Results of this study indicate that the Thrasher, in the central portion of its range, is both a house-yard and woodland bird. Of the 52 nests observed, 16 were built less than 200 ft (61m) from homes in which people were living and the remainder were built in woodlands and small thickets. Variations in the Thrasher's choice of nesting sites in Massachusetts, Kentucky, and Iowa may relate to the percent of woodland in these states. Of the total land area in these states, Massachusetts has about 60 percent forest, Kentucky 76 percent, and Iowa only 6 percent (Barrett, 1962). Since Kentucky is about intermediate in the amount of forestry, this could account for the Thrasher's choice of both yards and woodland for nesting sites here. The fact that all nests in this study were located in small shrubs and vines near homes or along the borders of forests, suggests that the Brown Thrasher is an "edge species".

Eggs and Incubation Period

Morgan (1968) gives the average clutch size for this species as 3.3 eggs with a range of 3 to 4. His study was conducted in northern Indiana at 41 degrees north latitude. No mention is made by him regarding seasonal variation in clutch size. Erwin (1935), reporting on observations at 30 nests of the Brown Thrasher in 1932, gives 6 (20.0%) with sets of 5 eggs, 19 (63.3%) with sets of 4, 3 (10.0%) with sets of 3, and 1 (3.3%) with 2 eggs. Erwin's study was done in Nashville, Tennessee at 36 degrees north latitude. The average clutch size for these 30 nests was 4.0 eggs. Of 21 nests he observed in 1933, 1 (4.8%) contained 5 eggs, 12 (57.1%) had 4, and 8 (38.1%) contained 3 eggs each. In 1932, 20 percent of the nests contained sets of 5 eggs, while in 1933, only 4.8 percent of the nests had this number. Erwin also reported that each of the nests having sets of 5 eggs was the first nest built by that particular pair during that season. Average clutch size grew consistently smaller during the course of the breeding season. Von Haartman (1971), and many other workers, have noted that there is a seasonal change in clutch size for both passerines and non-passerines. Slack (1973), whose study was conducted in northern Ohio at 40 degrees north latitude, reports a seasonal change in clutch size of the Catbird. He gives an average of 3.58 eggs per clutch for May nests, 3.00 for June nests, and 2.80 eggs for July nests. For 48 nests in this study, at 37 degrees north latitude, May nests averaged 3.1 eggs per clutch, and July nests 2.5 eggs. These data clearly indicate a diminution in the number of eggs per clutch as the season progresses and are in agreement with reports by numerous other workers. During the four-year period comprising this study, not a single nest was found containing more than four eggs. Of the 48 nests, 12 (25.0%) had sets of 4 eggs, 28 (58.3%) had sets of 3, and 8 (16.7%) contained 2 eggs. Evidence from this study indicates that the predominant clutch size consisted of 3 eggs.

The significance of clutch size in maintaining a rather uniform population in birds and its seasonal, annual, and geographical variations have been topics of investigations by many workers (cf. Lack, 1954; Wynne-Edwards, 1959; Brown, 1969; and Ricklefs, 1970). Contrasting opinions regarding the manner by which clutch size is regulated, particularly among wild birds, are apparent in the literature. Lack (1954) suggests that the average clutch size in nidicolous species has been evolved by natural selection to correspond with the size of the brood which will produce the greatest number of surviving progeny. According to this view, the reproductive rate (particularly the number of eggs in the clutch) of a species is regulated by density-dependent variations in mortality and in wild birds the most common density-dependent mortality factor is food shortage. This means that the upper limit of clutch size is set by the amount of food available to the young at that particular time and in that specific habitat. When the size of a clutch is above the upper limit, some of the young are undernourished and the parents tend to leave fewer descendants than those with broods of normal size. This relationship was demonstrated by Lack in his studies of the Alpine Swift (*Apus melba*) and the Common Swift (*Apus apus*) in which undernourished young died in the nest. In smaller passerines, such as the Starling and Robin, nesting mortality was not higher in broods of larger size. However, further studies revealed that most deaths of these small passerines occurred soon after the young left the nest. Lack attributed these deaths to malnutrition while the birds were in the nest. The survival of the young in relation to brood size needs to be re-examined since irregular variations are apparent which do not fit the view that clutch size has been selected to correspond with the highest number of surviving young. Lack suggests the possibility of adaptive phenotypic modifications in clutch size when the food supply is scarce or abundant; clutches tend to be larger when food is plentiful and smaller when food is scarce.

As mentioned earlier in this paper, many workers have reported a seasonal variation in clutch size with a tendency toward smaller clutches later in the nesting season. Lack (1966) suggests that this decline in clutch size is adaptive being correlated with the availability of food.

Another parameter of clutch size investigation, often neglected, is that of geographical variation. Lack (1954) reporting on the average clutch size of the Robin (Erithacus rubecula) cites an average clutch of 4.2 eggs at 35 degrees north latitude and 6.3 eggs at 58 degrees north latitude. He suggests that, in general, the average clutch size tends to increase from the tropics outward toward the poles. This variation may be accounted for on the basis of day-length. The length of a summer day in central Europe is about half as long again as in the tropics. Therefore, parent birds could collect more food per day in central Europe than in the tropics and should be able to raise a larger brood. When clutches show variations in size at the same latitude, the availability of food, rather than daylength, is, perhaps, the regulating factor (Lack, 1966).

Wynne-Edwards (1959, 1964, 1965) in contrast to the opinions of Lack, asserts that the richness or poverty of a habitat has nothing to do with average clutch size. While the populations of birds are ultimately limited by the availability of food, he says, this limit is not normally reached in nature because dispersion through behavior keeps the numbers near to the optimum. Wynne-Edwards asserts that reproductive rates of each species have been evolved to balance mortality and attributes such evolution to group selection. Birds, according to him, regulate their own numbers to prevent exhaustion of food supplies. This regulation is accomplished by "homeostatic" or self-balancing mechanisms which operate within the group rather than in the individual. The interests of the individual, he claims, are submerged or subordinated to those of the community. This view is in contrast to, or overrides, the Darwinian theory of natural selection of individuals. A population whose numbers are regulated in this manner would, of necessity, incorporate a social hierarchy or peck-order requiring that some individuals, probably those lowest in the order, refrain from eating, emigrate, or cease breeding, even though food is abundant, if eating would lead to overpopulation (cf. Lack, 1966).

Brown (1969) conducted a review and reevaluation of the effects of territorial behavior on population regulation in birds by examining the evidence from the best studied territorial species. Only those species which used the same territory for feeding, mating, and nesting were considered. To hypothesize the effect of territorial behavior or reproductive rate at different population densities, Brown postulated three critical levels of population density based upon the presumed effects of territoriality on patterns of dispersion. The density at level (1) was such that any individual would be allowed to breed in its preferred habitat without interruption by the territorial behavior of other individuals. Level (2) density inhibited some individuals from breeding in their preferred habitat but these birds usually bred in less desirable habitats. At level (3), the density was such that all breeding habitats were occupied by territorial individuals. This resulted in a "surplus" of potential breeders which were barred from engaging in reproductive processes and served as a non-breeding population reserve. In the event of death or emigration of territorial occupants, the reserve could move in and breed thus compensating for this reproductive loss. Whether the surplus failed to breed due to territorial conflicts or was permitted to breed when a vacancy occurred, it tended to regulate the growth of the population. Brown's views on population regulation reaffirm the hypothesis of the evolution of territoriality through individual selection and reject the hypothesis of group selection.

Ricklefs (1970) proposes a model to explain clutch size in birds as the outcome of interaction between predatory adaptations of birds to increase their feeding efficiency and adaptations of their food resources to avoid predation. He suggests that the efficiency with which environmental food resources, or prey, are converted to offspring of the predator depends on the balance between predator and prey adaptations. According to this model, clutch size in birds is not regulated by the availability of food resources, but by the ability of birds to catch prey and the ability of prey to escape capture. The decrease in clutch size toward the equator, he says, may be explained by an imbalance in predator and prey adaptations in favor of the prey.

This present study shows that the average clutch size of the Brown Thrasher diminished as the nesting season progressed. Whether food was a contributing factor will require further study since the amount of food available to the parent birds in the habitat was not determined. Variations in clutch size of this species throughout its breeding range are probably not the result of factors associated with latitude; from Nashville, Tennessee to northern Indiana the difference in latitude is only about five degrees. I suggest that clutch size of the Thrasher may have been selected during the course of evolution to correspond with a particular environment. Extensive banding of these birds should be conducted over a period of several years to determine their migratory patterns. That the same birds which produce an average clutch size of 4.0 eggs at Nashville, Tennessee would average the same in eastern Kentucky has not been demonstrated.

The incubation period is generally understood to be that period of time which elapses between the laying of the last egg in the clutch and the hatching of that egg. Erwin (1935) reports an average incubation period for the Brown Thrasher of 12.59 days, Morgan (1968) 13-14 days, and Bent (1948) gives the incubation period as 11-14 days according to temperature and other climatic conditions. The average period of incubation in this study was 11.5 ±0.24 days calculated from complete records of 12 nests. Kendeigh (1940) suggests that the length of the incubation period may be determined by the stage of development the embryo has attained at the time of hatching, by the total energy exchanges needed to reach this stage of development, and by the rate at which these energy changes are occurring.

Few investigators have obtained weights and dimensions of Brown Thrasher eggs. Morgan (1968) reported on the weights of six eggs obtained from two nests and listed a range of 5.36 to 6.02g with a mean of 5.65g. He cited the average loss of weight during incubation as 0.7g which represents 12.4 percent weight loss. Kendeigh (1940) weighed 29 eggs of the House Wren daily throughout their normal incubation period and the loss in weight before hatching compared with the weight when fresh amounted to 13.7 percent. Bent (1948) cites the average measurements of 50 eggs of the Brown Thrasher at 26.5 by 19.4mm. The average weight of 124 fresh eggs in this study was 5.94g and the average weight at the time of hatching was 5.12g. This represents a total weight loss of 13.9 percent which is 1.5 percent greater than the results obtained by Morgan. The average dimensions of the same number of eggs was 26.9 by 19.7mm which very closely approach the measurements reported by Bent.

Nest Success and Age-Specific Mortality

The nest success for 34 nests in the four years of this study was 58.8 percent. This is considerably higher than the 33 percent reported by Morgan (1968) and the 44.7 percent obtained by Erwin (1935). The extremely low success reported by Morgan is understandable since only two nests were considered. Kendeigh (1942) reports a nest success of 57 percent from seven nests of the Brown Thrasher. The relatively high nest success obtained in this study may be explained on the basis of nest site selection and the role of the parent birds in the nesting cycle. The great majority of nests were built in small sumac bushes entangled with dense honeysuckle vines. This arrangement provided excellent concealment from predators and protection from the elements of nature. Multiflora rose, in which many nests were constructed, would tend to discourage predators, especially large avian and mammalian, due to the density and/or thorns of the stems and leaves.

The second factor contributing to the high nest success of the Brown Thrasher is the role of the parent birds during the nesting cycle. Putnam (1949) suggests that the constant presence of an adult near the nest during the nesting cycle was a factor in the relatively high nest success of the Cedar Waxwing. Likewise, the high nest success of the Catbird, reported by Slack (1973), was attributed, in part, to nest guarding by the male. Though nest guarding by the male Thrasher was not observed in this study, his role in sharing the incubation chores with the female assured an almost constant attendance at the nest by at least one member of the breeding pair.

Of a total of 52 nests observed during the four-year study, not a single case of nest parasitism by the Brown-headed Cowbird was detected. Young (1963) reports 1 nest out of 19 as being parasitized by the Cowbird and Morgan (1968) reports none of two nests. Explanations regarding the lack of parasitism of this species to the same degree as other host species have not been reported. I suggest the belligerent response of this species toward nest intruders and the relatively high percent of nest attentiveness during incubation are deterrents to Cowbird parasitism. The color of the eggs apparently plays no role because this investigator placed a Robin's egg in a Thrasher nest containing three eggs, and it was incubated for a period of 5 days. Two days after the Thrasher's eggs hatched, the Robin's egg disappeared from the nest.

Survival curves for the eggs and nestlings of the Brown Thrasher are absent from the literature. Previous workers have reported losses but failed to note at what age these losses occurred (Gabrielson, 1912; Erwin, 1935; Thomas, 1952; and Morgan, 1968). Though reasons for losses were not always observed in this study, the approximate age at which eggs and young birds were lost from the nest was recorded. The percent of eggs and young surviving at the beginning of each age interval was plotted against the number of days in the nest and is presented in Fig. 20. This curve is plotted on a semilogarithmic scale in which a uniform rate of mortality produces a straight line extending from zero day to fledging day. Deviations to the left of such a line (positive skewing) represent significant losses during early nest days. Deviations to the right of the line (negative skewing) reflect losses later in life. Examination of the survival curve of the Brown Thrasher, Fig. 20, reveals a slight tendency toward negative skewing. Eggs were removed regularly through the egg-laying and first one-third of the incubation period. The percent survival remained fairly constant throughout the last two-thirds of incubation. An explanation for the early losses could be the behavior of the parent birds attracting more attention to the nest. Incubation constancy tended to be higher during the later stages which resulted in less trips to and from the nest. Nestling predation was fairly constant until fledging. Deevey (1947) suggests that life curves of most vertebrates are negatively skewed. Slack (1973) reports a negatively skewed curve for the Catbird. The universality of the survival curve for the Brown Thrasher obtained in this study requires further investigation of the early population dynamics of this species particularly in the eastern and western portions of its range.

Comparative Breeding Biology and Behavior of the Three Mimids: Brown Thrasher, Catbird and Mockingbird

A brief discussion of the breeding biology and behavior of the three mimids is contained in the following paragraphs for the sake of readers who may be unfamiliar with these species. My studies were concerned primarily with the nesting cycle of the Brown Thrasher, but some data were collected for the Catbird and Mockingbird. The species' characteristics mentioned here include my own observations in the field together with the works of several others (Erwin, 1935; Laskey, 1935, 1936, 1962; Nice, 1937; Kendeigh, 1942; Sutton, 1946; Preston, 1946; Bent, 1948; Thomas, 1952; Hunter, 1962; Skutch, 1962; Zimmerman, 1963; Nickell, 1965; Taylor, 1965; Adkisson, 1966; Morgan, 1968; and Slack, 1973).

Nest Sites and Nest Construction

The Brown Thrasher and Catbird prefer to nest in hedgerows, brushy fields, yards, forest undergrowth, and a variety of habitats provided "edge" is present and the density suitable. Mockingbirds may build their nests in brudhy fields, vines, and yards by have a preference for small evergreens such as cedar, spruce and pine. The males of all three species have been reported to assist the females in nest construction. Thrashers required an average of 4.2 days to build a nest, Catbirds 5.1, and Mockingbirds 4.2 days.

Egg-Laying

Eggs were laid in nests of the Thrasher and Catbird 1 to 5 days after completion with averages of 2.0 and 2.2 days respectively. Records on the chronology of nest completion and egg-laying in the Mockingbird are incomplete or lacking. All three mimids normally deposit their eggs in the early morning between 5:30 and 7:30. Egg-laying by the Mockingbird begins in late March or early April; the Thrasher and Catbird begin in late April or early May. Peaks in laying are evident in the Brown Thrasher during mid to late May and late June to early July, late May and late June to early July in the Catbird, and late March to mid April and late May to early June in the Mockingbird. The three species are normally double-brooded.

Role of Sex in Incubation

Of the three mimids, only the male of the Brown Thrasher assists the female in incubation. Males of Catbirds and Mockingbirds have been reported to share the incubation chores, only the female incubates. Male Catbirds and Mockingbirds guard the nest when the female is absent but this behavior has not been observed in the Thrasher.

Wing-Flashing

Wing-flashing is the jerky extension of both wings dorso-laterally in hitches and is very prominent in the Mockingbird. This behavior I observed on many occasions while a Mockingbird was pausing between runs on the ground. Laskey (1962) reports having observed this behavior in an adult Thrasher while it was investigating something in a dark area at the base of a plant. Such wing-flashing behavior has also been reported in the Catbird (Nickell, 1965). I did not observe this behavior in the Brown

Thrasher during the four-year study. The functional significance of wing-flashing has not been completely determined. Sutton (1946) suggests that it is a gesture associated with wariness, suspicion, and distrust. He further suggests that it may have accidentally become associated with the capture of food. Such descriptive terms as wariness, suspicion, and distrust should not be used in reference to avian behavior.

Comparative Breeding Biology Data

The averages of nest height above ground level, clutch size, incubation period, incubation constancy, nesting success, and nestling periods for the three mimids are recorded in Table 19. These data represent the averages of all records obtained by the numerous workers mintioned at the beginning of this section.

TABLE 19

COMPARATIVE BREEDING BIOLOGY OF THE BROWN THRASHER, CATBIRD, AND MOCKINGBIRD

	Brown Thrasher	Catbird	Mockingbird
Average height of nests (m)	1.83	1.78	2.22
Average clutch size (eggs)	3.22	3.21	4.44
Average incubation period (days)	12.5	13.1	12.7
Average incubation constancy (%)	84	74	73
Average nesting success (%)	57.9	59.3	56.0
Average nestling period (days)	10.5	11.3	12.0

SUMMARY

The breeding biology and behavior of the Brown Thrasher (Toxostoma rufum) were studied in 1973, 1974, 1975, and 1976 in southwestern Laurel County, Kentucky.

Data on incubation behavior, collected from 17 nests, were computer analyzed to determine the effects of temperature, time of day, stage of incubation, year, an behavior of the nonincubating mate. Statistical analysis revealed no significant difference in incubation attributable solely to year or to time of day. The data were adjusted in such a manner as to hold other factors constant when analyzing for a specific parameter. The average time on the nest and the percent time on the nest were inversely related to ambient temperature; average time off the nest was directly related to temperature. When the bird's incubating sessions were longer than the over-all average on a given day, they tended to be shorter the following day and vice versa. The average length of sessions the last 4 or 5 days of incubation was about 2.5 minutes longer than that of the first 6 days. When a bird's recesses were longer than the over-all average length of recesses of that bird on a given day, they tended to be shorter the following day and vice versa. The amount of time spent

on the nest during the day of hatching was about 3.7 percent longer than the average for all the prehatching days.

No evidence was found for nest guarding by either sex. There was no significant difference between the amount of time the male spent near the nest when the female was absent than when she was present.

There was a significant difference between the length of sessions terminated voluntarily by the incubating bird and those that were terminated by the behavior of its mate. Incubating sessions terminated by the mate were shorter than those which were not mate-terminated.

In the Brown Thrasher, both sexes share incubation. Thirty-six hours of observation revealed that the female covered the eggs 71 percent of the total time when they were incubated and the male 29 percent. The range of the incubation period for 12 nests was from 10 to 13 days with a mean of 11.5 days. Clutch size decreased as the nesting season progressed. The average clutch size for 48 nests was 2.8 eggs.

Aggressive behavior appeared to be correlated with the stage of the nesting cycle. Parental birds were much more belligerent in response to nest intruders when nestlings were in the nest than during incubation.

Parasitism of nests by the Brown-headed Cowbird was not observed. The average nest success was 58.8 percent.

A survival curve for the eggs and nestlings over the four-year study period indicates uniform mortality for the first one-third of incubation with a decrease the last third of incubation. Mortality rate was fairly constant during the nestling stage.

Small sumac bushes entangled with honeysuckle vines were the vegetation substrate most preferred for nest construction. The range in nest height was 0.4 to 2.8m with a mean of 1.3m; nests were not placed upon the ground. Evidence from this study suggests that the Brown Thrasher prefers higher elevations for nesting sites as the season progresses. The mean height of 20 nests built in May was 1.5m and a mean of 2.1m for 17 nests built in July.

APPENDIX

Attentive Behavior Data

TABLE 20

1973, 1974, AND 1975 DATA AND STATISTICAL ANALYSIS FOR AVERAGE TIME ON NEST (min.) IN RELATION TO ACTIVITY PERIOD, METHOD, AND STAGE OF INCUBATION

Period a	Method b	Incubation Day c	Variable	Number	Mean	St. D.	Range	C.V. d
1	1	1	Session	13	26.3	7.2	14.6-38.2	27.5
1	1	1	Temp.	13	63.2	9.2	43-76	14.6
1	1	2	Session	10	23.9	6.6	13.7-31.6	27.7
1	1	2	Temp.	10	66.1	6.4	55-74	9.7
1	2	1	Session	15	23.0	5.7	13.9-32.8	24.7
1	2	1	Temp.	15	68.4	4.6	59-75	6.7
1	2	2	Session	11	28.2	6.5	14.9-36.4	23.0
1	2	2	Temp.	11	60.5	9.2	46-73	15.2
2	1	1	Session	17	16.5	5.2	9.63-28.7	31.7
2	1	1	Temp.	17	76.2	6.5	62-85	8.5
2	1	2	Session	12	24.4	9.7	8.3-39.6	39.7
2	1	2	Temp.	12	77.0	5.2	69-84	6.8
2	2	1	Session	13	19.0	7.8	9.6-38.8	41.2
2	2	1	Temp.	13	76.5	5.6	65-83	7.3
2	2	2	Session	11	19.8	6.8	12.5-35.2	34.5
2	2	2	Temp.	11	70.2	7.3	55-78	10.4
3	1	1	Session	15	19.9	6.1	8.31-27.9	30.7
3	1	1	Temp.	15	75.5	7.5	61-86	9.9
3	1	2	Session	11	16.7	7.0	8.2-28.6	41.6
3	1	2	Temp.	11	79.0	7.5	66-90	9.5
3	2	1	Session	16	18.3	7.8	8.55-32.65	42.4
3	2	1	Temp.	16	76.3	6.9	62-83	9.0
3	2	2	Session	12	22.5	8.2	5.68-32.09	36.6
3	2	2	Temp.	12	72.5	8.2	56-81	11.3
1	1	0	Session	23	25.3	6.9	13.7-38.2	27.4
1	1	0	Temp.	23	64.4	8.1	43-76	12.6
1	2	0	Session	26	25.2	6.5	13.9-36.4	25.6
1	2	0	Temp.	26	65.0	7.9	46-75	12.1
2	1	0	Session	29	19.7	8.2	8.3-39.6	41.8
2	1	0	Temp.	29	76.6	5.9	62-85	7.7
2	2	0	Session	24	19.4	7.2	9.6-38.0	37.4
2	2	0	Temp.	24	73.6	7.1	55-83	9.6
3	1	0	Session	26	18.6	6.5	8.2-28.6	35.3
3	1	0	Temp.	26	76.9	7.5	61-90	9.8
3	2	0	Session	28	20.1	8.1	5.6-32.7	40.2
3	2	0	Temp.	28	74.6	7.6	56-83	10.1
1	0	0	Session	49	25.2	6.6	13.7-38.2	26.2
1	0	0	Temp.	49	64.8	7.9	43-76	12.2

TABLE 20 CONTINUED

Period	Method	Incubation Day	Variable	Number	Mean	St. D.	Range	C.V.
2	0	0	Session	53	19.6	7.7	8.32-39.6	39.5
2	0	0	Temp.	53	75.2	6.6	55-85	8.7
3	0	0	Session	54	19.4	7.4	5.7-32.7	38.0
3	0	0	Temp.	54	75.8	7.6	56-90	10.0
1	0	1	Session	28	24.6	6.6	13.9-38.2	26.7
1	0	1	Temp.	28	66.0	7.5	43-76	11.3
2	0	1	Session	30	17.6	6.5	9.63-38.75	36.9
2	0	1	Temp.	30	76.4	6.0	62-85	7.9
3	0	1	Session	31	19.1	6.9	8.31-32.65	36.4
3	0	1	Temp.	31	75.9	7.0	61-86	9.3
1	0	2	Session	21	26.1	6.7	13.71-36.37	25.8
1	0	2	Temp.	21	63.1	8.3	46-74	13.2
2	0	2	Session	23	22.2	8.6	8.32-39.59	38.6
2	0	2	Temp.	23	73.7	7.1	55-84	9.6
3	0	2	Session	23	19.7	8.0	5.68-32.09	40.7
3	0	2	Temp.	23	75.6	8.4	56-90	11.1
0	0	1	Session	89	20.3	7.2	8.31-38.75	35.6
0	0	1	Temp.	89	72.9	8.2	43-86	11.3
0	0	2	Session	67	22.6	8.2	5.68-39.59	36.2
0	0	2	Temp.	67	71.1	9.5	46-90	13.4
0	1	1	Session	45	20.5	7.3	8.31-38.23	35.4
0	1	1	Temp.	45	72.2	9.5	43-86	13.2
0	1	2	Session	33	21.7	8.5	8.21-39.59	39.2
0	1	2	Temp.	33	74.4	8.4	55-90	11.2
0	2	1	Session	44	20.1	7.3	8.55-38.75	36.3
0	2	1	Temp.	44	73.7	6.8	59-83	9.3
0	2	2	Session	34	23.5	7.9	5.68-36.37	33.5
0	2	2	Temp.	34	67.9	9.6	46-81	14.1
0	1	0	Session	78	21.0	7.8	8.21-39.59	37.1
0	1	0	Temp.	78	73.1	9.0	43-90	12.4
0	2	0	Session	78	21.6	7.7	5.68-38.75	35.6
0	2	0	Temp.	78	71.1	8.6	46-83	12.1

a -- Time of Activity Periods: 1 = 05:00-09:30, 2 = 09:30-14:00, 3 = 14:00-18:30

b -- Method of Collecting Data: 1 = Personal Observation, 2 = Electrical Monitoring Device

c -- Day of Incubation: 1 = Days One Through Six, 2 = Days Seven +

d -- Coefficient of Variation

TABLE 21

1973, 1974, AND 1975 DATA AND STATISTICAL ANALYSIS FOR AVERAGE TIME OFF NEST IN RELATION TO ACTIVITY PERIOD, METHOD, AND STAGE OF INCUBATION

Period a	Method b	Incubation c	Variable	Number	Mean	St. D.	Range	C.V. d
1	1	1	Recess	17	5.5	1.2	3.7-8.0	21.9
1	1	1	Temp.	17	63.0	8.5	43.0-76.0	13.5
1	1	2	Recess	3	6.7	2.3	4.2-8.6	34.2
1	1	2	Temp.	3	69.3	5.0	64.0-74.0	7.3
1	1	0	Recess	4	5.2	1.3	4.0-7.0	25.2
1	1	0	Temp.	4	66.8	5.9	59.0-73.0	8.9
1	2	1	Recess	19	5.7	1.2	3.8-8.6	21.1
1	2	1	Temp.	19	67.2	6.5	49.0-75.0	9.6
1	2	2	Recess	3	5.9	1.6	4.6-7.7	27.0
1	2	2	Temp.	3	58.3	9.6	48.0-67.0	16.5
1	2	0	Recess	6	4.6	1.2	3.5-6.7	26.1
1	2	0	Temp.	6	59.8	7.5	46.0-67.0	12.6
2	1	1	Recess	22	6.7	2.1	3.8-12.3	31.3
2	1	1	Temp.	22	75.3	7.0	60.0-85.0	9.2
2	1	2	Recess	1	6.7	2.6	6.7-6.7	34.2
2	1	2	Temp.	1	71.0	6.3	71.0-71.0	5.4
2	1	0	Recess	7	7.2	3.2	3.0-12.3	44.5
2	1	0	Temp.	7	78.9	4.7	71.0-84.0	5.9
2	2	1	Recess	18	6.4	1.9	3.7-10.1	29.2
2	2	1	Temp.	18	75.3	5.8	65.0-83.0	7.8
2	2	2	Recess	4	8.0	3.1	3.8-10.8	38.8
2	2	2	Temp.	4	69.5	9.7	55.0-75.0	14.0
2	2	0	Recess	5	5.9	1.3	4.3-7.9	21.8
2	2	0	Temp.	5	70.8	5.8	64.0-77.0	8.2
3	1	1	Recess	18	6.4	1.2	4.8-9.3	19.3
3	1	1	Temp.	18	75.8	7.2	61.0-86.0	9.5
3	1	2	Recess	2	11.3	0.1	11.3-11.4	0.7
3	1	2	Temp.	2	84.0	5.7	80.0-88.0	6.7
3	1	0	Recess	6	6.5	2.3	4.7-11.0	35.8
3	1	0	Temp.	6	78.2	8.5	66.0-90.0	10.9
3	2	1	Recess	20	6.2	1.3	4.5-10.1	21.4
3	2	1	Temp.	20	75.3	7.2	60.0-83.0	9.6
3	2	2	Recess	4	9.1	3.5	5.3-13.8	39.1
3	2	2	Temp.	4	72.3	11.0	56.0-80.0	15.3
3	2	0	Recess	5	6.8	1.5	5.1-8.4	22.4
3	2	0	Temp.	5	74.8	6.4	67.0-81.0	8.6
1	1	0	Recess	24	5.6	1.4	3.7-8.6	24.7
1	1	0	Temp.	24	64.4	7.9	43.0-76.0	12.3

TABLE 21 CONTINUED

Period a	Method b	Incubation c	Variable	Number	Mean	St. D.	Range	C.V. d
1	2	0	Recess	28	5.5	1.3	3.5-8.6	23.2
1	2	0	Temp.	28	64.7	7.7	46.0-75.0	11.9
2	1	0	Recess	30	6.8	2.3	3.0-12.3	33.9
2	1	0	Temp.	30	76.0	6.5	60.0-85.0	8.6
2	2	0	Recess	27	6.6	2.0	3.7-10.8	30.7
2	2	0	Temp.	27	73.6	6.7	55.0-83.0	9.1
3	1	0	Recess	26	6.8	2.0	4.7-11.4	28.9
3	1	0	Temp.	26	77.0	7.5	61.0-90.0	9.8
3	2	0	Recess	29	6.7	2.0	4.5-13.8	29.5
3	2	0	Temp.	29	74.8	7.4	56.0-83.0	10.0
1	0	0	Recess	52	5.5	1.3	3.5-8.6	23.7
1	0	0	Temp.	52	64.6	7.7	43.0-76.0	12.0
2	0	0	Recess	57	7.0	2.2	3.0-12.3	32.2
2	0	0	Temp.	57	74.9	6.6	55.0-85.0	8.9
3	0	0	Recess	55	6.7	2.0	4.5-13.8	29.0
3	0	0	Temp.	55	75.8	7.5	56.0-90.0	8.9
1	0	1	Recess	36	5.6	1.2	3.7-8.6	21.2
1	0	1	Temp.	36	65.2	7.7	43.0-76.0	11.8
2	0	1	Recess	40	6.6	2.0	3.7-12.3	30.1
2	0	1	Temp.	40	75.3	6.4	60.0-85.0	8.5
3	0	1	Recess	38	6.3	1.3	4.5-10.1	20.2
3	0	1	Temp.	38	75.5	7.1	60.0-86.0	9.5
1	0	2	Recess	6	6.3	1.8	4.2-8.6	29.1
1	0	2	Temp.	6	63.8	9.1	48.0-74.0	14.3
2	0	2	Recess	5	7.7	2.7	3.8-10.8	35.6
2	0	2	Temp.	5	69.8	8.4	55.0-75.0	12.1
3	0	2	Recess	6	9.8	3.0	5.3-12.8	30.3
3	0	2	Temp.	6	76.2	10.8	56.0-88.0	14.2
1	0	0	Recess	10	4.9	1.2	3.5-7.0	24.8
1	0	0	Temp.	10	62.6	7.5	46.0-73.0	11.9
2	0	0	Recess	12	6.7	2.6	3.0-12.3	38.4
2	0	0	Temp.	12	75.5	6.4	64.0-84.0	8.5
3	0	0	Recess	11	6.6	1.9	4.7-11.0	28.8
3	0	0	Temp.	11	76.6	7.5	66.0-90.0	9.8
0	0	1	Recess	114	6.2	1.6	3.7-12.3	25.6
0	0	1	Temp.	114	72.2	8.5	43.0-86.0	11.7
0	0	2	Recess	17	8.0	2.8	3.8-13.8	35.7
0	0	2	Temp.	17	69.9	10.4	48.0-88.0	14.9
0	0	0	Recess	33	7.1	2.1	3.0-12.3	34.8
0	0	0	Temp.	33	72.0	9.3	46.0-90.0	13.0
0	1	1	Recess	57	6.3	1.7	3.7-12.3	26.8
0	1	1	Temp.	57	71.8	9.4	43.0-86.0	13.1

TABLE 21 CONTINUED

Period[a]	Method[b]	Incubation[c]	Variable	Number	Mean	St. D.	Range	C.V.[d]
0	1	2	Recess	6	8.3	2.8	4.2-11.4	33.7
0	1	2	Temp.	6	74.5	8.4	64.0-88.0	11.3
0	1	0	Recess	17	6.5	2.5	3.0-12.3	39.4
0	1	0	Temp.	17	75.8	8.0	59.0-90.0	10.6
0	2	1	Recess	57	6.1	1.5	3.7-10.1	24.5
0	2	1	Temp.	57	72.6	7.5	49.0-83.0	10.3
0	2	2	Recess	11	7.8	3.0	3.8-13.8	38.3
0	2	2	Temp.	11	67.5	10.9	48.0-80.0	16.2
0	2	0	Recess	16	5.7	1.6	3.5-8.4	27.3
0	2	0	Temp.	16	67.9	9.1	46.0-81.0	13.5
0	1	0	Recess	80	6.4	2.0	3.0-12.3	31.3
0	1	0	Temp.	80	72.8	9.1	43.0-90.0	12.5
0	2	0	Recess	84	6.2	1.8	3.5-13.8	29.5
0	2	0	Temp.	84	71.0	8.5	46.0-83.0	12.0

[a] Time of Activity Periods : 1 = 05:00-09:30, 2 = 09:30-14:00, 3 = 14:00-18;30

[b] Method of Collecting Data : 1 = Personal Observation, 2 = Electrical Device

[c] Stage of Incubation : 1 = Days 1 Through 6, 2 = Days 7 +

[d] Coefficient of Variation

TABLE 22

1973, 1974, AND 1975 DATA AND STATISTICAL ANALYSIS FOR PERCENT TIME ON IN RELATION TO ACTIVITY PERIOD, METHOD, AND STAGE OF INCUBATION

Period a	Method b	Incubation c	Variable	Number	Mean	St. D.	Range	C.V. d
1	1	1	Percent	21	81.8	5.4	72.9-90.8	6.6
1	1	1	Temp.	21	64.1	8.1	43.0-76.0	12.7
1	1	2	Percent	3	79.8	6.6	72.2-84.3	8.3
1	1	2	Temp.	3	67.0	7.2	59.0-73.0	10.8
1	2	1	Percent	26	81.1	6.1	68.9-91.1	7.5
1	2	1	Temp.	26	65.0	7.9	46.0-75.0	12.1
1	2	2	Percent	2	89.7	2.7	87.7-91.6	3.0
1	2	2	Temp.	2	60.0	4.2	57.0-63.0	7.1
2	1	1	Percent	27	73.2	6.4	62.6-85.7	8.7
2	1	1	Temp.	27	75.4	6.6	60.0-85.0	8.7
2	1	2	Percent	3	74.3	5.2	69.6-79.9	7.0
2	1	2	Temp.	3	81.7	2.5	79.0-84.0	3.1
2	2	1	Percent	26	75.3	7.4	62.5-90.3	9.8
2	2	1	Temp.	26	73.9	6.6	55.0-83.0	9.0
2	2	2	Percent	1	78.8	7.8	78.8-78.8	8.8
2	2	2	Temp.	1	66.0	6.6	66.0-66.0	10.6
3	1	1	Percent	22	72.6	8.6	55.2-81.5	11.9
3	1	1	Temp.	22	76.0	7.4	61.0-88.0	9.8
3	1	2	Percent	4	67.6	11.4	56.0-79.8	16.8
3	1	2	Temp.	4	82.5	6.1	77.0-90.0	7.4
3	2	1	Percent	28	73.9	7.9	52.7-86.1	10.6
3	2	1	Temp.	28	74.6	7.5	56.0-83.0	10.1
3	2	2	Percent	1	79.3	7.9	79.3-79.3	9.3
3	2	2	Temp.	1	80.0	5.2	80.0-80.0	8.0
1	1	0	Percent	24	81.5	5.4	72.2-90.8	6.6
1	1	0	Temp.	24	64.4	7.9	43.0-76.0	12.3
1	2	0	Percent	28	81.7	6.3	68.9-91.6	7.7
1	2	0	Temp.	28	64.7	7.7	46.0-75.0	11.9
2	1	0	Percent	30	73.3	6.2	62.6-85.7	8.5
2	1	0	Temp.	30	76.0	6.5	60.0-85.0	8.6
2	2	0	Percent	27	75.4	7.3	62.5-90.3	9.7
2	2	0	Temp.	27	73.6	6.7	55.0-83.0	9.1
3	1	0	Percent	26	71.8	9.0	55.2-81.5	12.6
3	1	0	Temp.	26	77.0	7.5	61.0-90.0	9.8
3	2	0	Percent	29	74.1	7.8	52.7-86.1	10.5
3	2	0	Temp.	29	74.8	7.5	56.0-83.0	10.0
1	0	0	Percent	52	81.6	5.8	68.9-91.6	7.2
1	0	0	Temp.	52	64.6	7.7	43.0-76.0	12.0

TABLE 22 CONTINUED

Period a	Method b	Incubation c	Variable	Number	Mean	St. D.	Range	C.V. d
2	0	0	Percent	57	74.3	6.8	62.5-90.3	9.1
2	0	0	Temp.	57	74.9	6.7	55.0-85.0	8.9
3	0	0	Percent	55	73.0	8.4	53.7-86.1	11.5
3	0	0	Temp.	55	75.8	7.5	56.0-90.0	9.9
1	0	1	Percent	47	81.4	5.7	68.9-91.1	7.0
1	0	1	Temp.	47	64.6	7.9	43.0-76.0	12.2
2	0	1	Percent	53	74.2	6.9	62.5-90.3	9.3
2	0	1	Temp.	53	74.6	6.6	55.0-85.0	8.8
3	0	1	Percent	50	73.3	8.1	52.7-86.1	11.1
3	0	1	Temp.	50	75.2	7.4	56.0-88.0	9.9
1	0	2	Percent	5	83.7	7.3	72.2-91.6	8.7
1	0	2	Temp.	5	64.2	6.7	57.0-73.0	10.5
2	0	2	Percent	4	75.5	4.8	69.6-79.9	6.4
2	0	2	Temp.	4	77.8	8.1	66.0-84.0	10.4
3	0	2	Percent	5	70.0	11.1	56.0-79.8	15.9
3	0	2	Temp.	5	82.0	5.4	77.0-90.0	6.6
0	0	1	Percent	150	76.2	7.8	52.7-91.1	10.3
0	0	1	Temp.	150	71.7	8.7	43.0-88.0	12.1
0	0	2	Percent	14	76.5	9.8	56.0-91.6	12.9
0	0	2	Temp.	14	74.4	10.2	57.0-90.0	13.7
0	1	1	Percent	70	75.6	7.9	55.2-90.8	10.5
0	1	1	Temp.	70	72.2	9.0	43.0-88.0	12.4
0	1	2	Percent	10	73.3	9.3	56.0-84.3	12.7
0	1	2	Temp.	10	77.6	8.9	59.0-90.0	11.5
0	2	1	Percent	80	76.7	7.7	52.7-91.1	10.1
0	2	1	Temp.	80	71.3	8.5	46.0-83.0	11.9
0	2	2	Percent	4	84.4	6.3	78.2-91.6	7.5
0	2	2	Temp.	4	66.5	9.8	57.0-80.0	14.7
0	1	0	Percent	80	75.3	8.1	52.2-90.8	10.8
0	1	0	Temp.	80	72.8	9.1	43.0-90.0	12.5
0	2	0	Percent	84	77.1	7.8	52.7-91.6	10.1
0	2	0	Temp.	84	71.0	8.5	45.0-83.0	12.0

a -- Time of Activity Periods : 1 = 05:00-09:30, 2 = 09:30-14:00, 3 = 14:00-18:30

b -- Method of Collecting Data : 1 = Personal Observation, 2 = Electrical Device

c -- Stage of Incubation : 1 = Days 1 through 6, 2 = Days 7 +

d -- Coefficient of Variation

LITERATURE CITED

Adkisson, C.S. 1966. The nesting and behavior of Mockingbirds in northern lower Michigan. Jack-Pine Warbler, Vol. 44: 102-116.

Baerends, G.P. 1959. The ethological analysis of incubation behavior. Ibis 101: 358-368.

Bailey, R.E. 1952. The incubation patch of passerine birds. Condor 54: 121-136.

Baldwin, S.P., and S.C. Kendeigh. 1927. Attentiveness and inattentiveness in the nesting behavior of the House Wren. Auk 44: 206-216.

Barbour, Roger W., Clell T. Peterson, Delbert Rust, Herbert E. Shadowen and A.L. Whitt, Jr. 1973. Kentucky birds-A finding guide. The University Press of Kentucky.

Barrett, J.W. 1962. Regional silviculture of the United States. The Ronald Press Company. 610p.

Bent, A.C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Nat. Mus. Bull. 195.

Britton, N.L., and Addison Brown. 1952. Illustrated flora of the northeastern United States and adjacent Canada. New York Botanical Garden.

Brown, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160-169.

Brown, J.L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81: 293-329.

Cox, G.W. 1960. A life history of the Mourning Warbler. Wilson Bull. 72: 5-28.

Davis, J. 1960. Nesting behavior of the Rufous-sided Towhee in coastal California. Condor 62: 434-456.

Deevey, E.S. Jr. 1947. Life tables for natural populations of animals. Quarterly Review of Biology 22: 283-314.

Drent, R.H. 1970. Functional aspects of incubation in the Herring Gull, P. 1 to 132. In G.P. Baerends and R.H. Drent (ed). The Herring Gull and its egg. Behaviour Suppl. 17.

Erwin, W.G. 1935. Some nesting habits of the Brown Thrasher. Jour. Tenn. Academy of Science 10: 179-204.

Fant, R.J. 1953. A nest-recording device. Jour. Animal Ecol. 22: 323-327.

Fautin, R.W. 1941. Incubation studies of the Yellow-headed Blackbird. Wilson Bull. 53: 107-122.

Fenneman, N.M. 1938. Physiography of eastern United States. McGraw-Hill Book Company, New York. 714p.

Finlay, J.C. 1971. Breeding biology of Purple Martins at the northern limit of the range. Wilson Bull. 83: 255-269.

Gabrielson, I.N. 1912. A study of the home life of the Brown Thrasher, *Toxostoma rufum*, (Linn.). Wilson Bull. 24: 65-94.

Gabrielson, I.N. 1913. Nest life of the Catbird, *Dumetella carolinensis*, (Linn.). Wilson Bull. 25: 167-187.

Gander, F.F. 1959. The Mockingbirds of Kissing Rocks Garden. Audubon Magazine, Vol. 61: 169, 182-184.

Hann, H.W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bull. 44: 145-237.

Holcomb, L.C. 1974. Incubation constancy in the Red-winged Blackbird. Wilson Bull. 86: 450-460.

Horwich, R.H. 1969. Behavioral ontogeny of the Mockingbird. Wilson Bull. 81: 87-93.

Kendeigh, S.C., and S.P. Baldwin. 1930. The mechanical recording of the nesting activities of birds. Auk 47: 471-480.

Kendeigh, S.C. 1940. Factors affecting the length of incubation. Auk 57: 499-513.

Kendeigh, S.C. 1942. Analysis of losses in the nesting of birds. Jour. Wildlife Management, 6: 19-26.

Kendeigh, S.C. 1952. Parental care and its evolution in birds. Illinois Biol. Monogr. 22: 1-356.

Kendeigh, S.C. 1963. New ways of measuring the incubation period of birds. Auk 80: 456-462.

Kessler, F. 1962. Measurement of nest attentiveness in the Ring-necked Pheasant. Auk 79: 702-705.

Kuusisto, P. 1941. Studien uber die Okologie and Tagesrhytmit von Phylloscopus trochilus acredula (L.) mit besonderer Berucksichtigung der Brutbiologie. Acta Zool. Fenn. 31: 1-120.

Lack, D. 1948a. The significance of clutch size. Ibis 90: 25-45.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London. 343p.

Lack, D. 1966. Population studies of birds. Oxford Univ. Press, London. 341p.

Laskey, A.R. 1935. Mockingbird life history studies. Auk 52: 370-381.

Laskey, A.R. 1936. Fall and winter behavior of Mockingbirds, Wilson Bull. 48: 247-255.

Laskey, A.R. 1962. Breeding biology of Mockingbirds. Auk 79: 596-606.

Lawrence, L. De K. 1953. Nesting life and behavior of the Red-eyed Vireo. Can. Field Nat. 67: 47-77.

Lustick, S.I. 1975. The effects of wetting on Red-winged Blackbird energetics and survival. The Ohio State University Research Foundation.

Maxwell, G.R. II. 1965. Life history of the Common Grackel Quiscalus quiscula (Linnaeus). Unpublished Ph.D. dissertation. Ohio State University. 221p.

Maxwell, G.R. II., and L.S. Putnam. 1972. Incubation, care of young, and nest success of the Common Grackel Quiscalus quiscula in northern Ohio. Auk 89: 349-359.

Mengel, R.M. 1965. The birds of Kentucky. Ornithological Monographs #3. American Ornithologists Union. 581p.

Miskimen, A.M. 1951. The influence of social and physical factors on autumn bird migration. Unpublished Ph.D. dissertation. Ohio State University. 93p.

Morgan, F.D. 1968. A field study of the avifauna of an old farm in northern Indiana. Unpublished Ph.D. dissertation. Ohio State University. 339p.

Nice, M.M. 1937. Studies in the life history of the Song Sparrow. Vol. 1. Dover Publications, Inc. New York. 246p.

Nice, M.M., and R.H. Thomas. 1948. A nesting of the Carolina Wren. Wilson Bull. 60: 139-158.

Nice, M.M. 1957. Nesting success in altricial birds. Auk 74: 305-321.

Nickell, W.P. 1965. Habitats, territory, and nesting of the Catbird. Amer. Mid. Natur., 73: 433-478.

Petrovic, C.A. 1972. The foraging ecology of blackbirds on South Bass Island, Ohio. Unpublished M.S. thesis. Ohio State University. 90p.

Prescott, K.W. 1964. Constancy of incubation for the Scarlet Tanager. Wilson Bull. 76: 37-42.

Preston, F.W., and R.T. Norris. 1947. Nesting heights of breeding birds. Ecology, 28: 241-273.

Putnam, L.S. 1949. The life history of the Cedar Waxwing. Wilson Bull. 61: 141-182.

Ricklefs, R.E. 1970. Clutch-size in birds: Outcome of opposing predator and prey adaptations. Science, Vol. 10: 599-600.

Scheffe, H. 1959. The analysis of variance. John Wiley and Sons, Inc., New York. 477p.

Selander, R.K., and D.K. Hunter. 1960. On the functions of wing-flashing in Mockingbirds. Wilson Bull. 72: 340-345.

Sherman, A.R. 1912. The Brown Thrasher, Toxostoma rufum, east and west. Wilson Bull. 24: 187-193.

Skutch, A.F. 1955. The incubation patterns of birds. Ibis 99: 69-93.

Skutch, A.F. 1962. The constancy of incubation. Wilson Bull. 74: 115-152.

Slack, R.D. 1973. Breeding biology and behavior of the Catbird, Dumetella carolinensis. Unpublished Ph.D. dissertation. Ohio State University. 110p.

Sturkie, P.D. 1965. Avian Physiology. Cornell University Press, New York. 766p.

Sturm, L. 1945. A study of the nesting activities of the American Redstart. Auk 62: 189-206.

Sutton, G.M. 1946. Wing-flashing in the Mockingbird. Wilson Bull. 58: 206-209.

Taylor, W.K. 1965. Nesting heights of some Louisiana birds. Wilson Bull. 77: 146-150.

Thomas, R. 1952. Crip, come home. (the story of a Brown Thrasher, Toxostoma rufum, that lived for ten years in the author's garden in Arkansas). Harper and Brothers, New York.

Verner, J. 1965. Breeding biology of the Long-billed Marsh Wren. Condor 67: 6-30.

Von Haartman, L. 1971. Population dynamics, p. 391 to 459. In D.S. Farner and L.R. King (ed.) Avian Biology.

Wynne-Edwards, V.C. 1964. Population control in animals. Scientific American, August, 1964.

Wynne-Edwards, V.C. 1965. Self-regulating systems in populations of animals. Science 147: 1543-1548.