THE LIFE HISTORY OF THE CEDAR WAXWING

LOREN S. PUTNAM

INTRODUCTION

THIS observational study of the Cedar Waxwing (*Bombycilla cedrorum*) began in 1939 and continued throughout 5 additional summers. The objective has been to determine the relationships between members of the pair, between the pair and other members of the population, and between the population and the environment, correlating these phases into the whole of the breeding behavior of the waxwing.

The Peach Point area, in which the major part of the study was carried on, is a small peninsula extending from the north central part of South Bass Island, which lies in Lake Erie, north of Sandusky, Ohio. The area is not on the main migration path, and waxwings are not common in this locality until the nesting population arrives. Peach Point is a park type area consisting mainly of closely spaced summer homes. At the base of the peninsula is an old orchard which slopes toward Terwilliger's pond to the south. West of the orchard is a dense second growth woods which was largely bypassed by the birds in their activities. The most abundant tree is cedar (*Juniperus virginiana*), although hackberry (*Celtis occidentalis*) and maple (*Acer* sp.), as well as domestic fruit trees and mulberries (*Morus alba*, *Morus rubra*), are common.

The collection of data for this paper has been largely a matter of field observation during 6 seasons from 1939 through 1946. No data were taken during 1943 or 1944. Several thousand hours have been utilized in an attempt to make the data quantitative with as many as 170 hours being devoted to 1 nest. In spite of this, weakness in certain data is apparent. Unless otherwise stated general descriptions of behavior have been supported by 25 or more observations. All hours are given in solar time.

The plan of work has been to survey the study area early in the season, determine the nesting population, and follow it and the individual pairs through the breeding season. Since the solution of many of the problems depended upon the identification of individual birds, much time and effort were spent in attempts to trap and band them. Feltes (1936) was able to trap numbers of waxwings from winter flocks in California, but lacking the favorable baiting conditions of his situation, other means had to be developed in the present study. Two methods have been used: the first using a nest trap and the second a drop trap.

The nest trap was cylindrical in shape, had a diameter of about 9 inches, and a height of about 10 inches. A trap door in 1 side was hinged at the top and closed downward. The trap was placed over the nest with the door facing

the normal path of the birds to the nest, and the bottom was closed with cloth netting. The most favorable trapping period was from 5 to 8 days after hatching, before the lag in attention by the female. It is desirable to place the trap on the nest at least a day before trapping. The birds were best trapped in the morning; both sexes should not be trapped on the same day. If the birds can be identified, trapping the female first is believed desirable. Before this method was refined, a successful trapping of the pair was accomplished in about 13% of attempts. Later, success was obtained in 67% of attempts.

The drop trap involved baiting with nesting materials. This method proved workable in 50% of attempts and is more simple to put into effect. Its difficulty lies in the fact that the pair must be located and trapped on the days, usually the second and third, during which the birds are most active in building. At best both methods leave much to be desired.

Since the work extended over several years, numbers which facilitated identification of nests were designed. The first figure indicates the year, the second the number of the nest, and the letter indicates the first or second nest of a pair known to raise 2 broods during the season, e. g., 46-09B; 1946, nest 9, second nest. To supplement field notes 9 young waxwings were taken from their nests during the summer of 1941 and confined until the fall of 1942. A comparative study of the caged young and of wild waxwings was made.

The production of this paper has been encouraged by Dr. T. H. Langlois. Dr. Charles F. Walker has contributed immeasurably by his stimulating guidance and thoughtful criticism. Plants were identified by Dr. R. B. Gordon. Statistical assistance was given by Dr. D. R. Whitney and Mr. R. S. Gardner of The Ohio State University Statistics Laboratory. The figures were drawn by Mr. Robert H. Albertin. Mrs. Mildred M. Putnam assisted in the field on many days, as well as in the preparation of the manuscript. This is a contribution from Franz Theodore Stone Laboratory, Ohio State University, Put-in-Bay, Ohio. Botanical names follow Core (1948).

Migration and Movements

The Cedar Waxwing is an erratic winter resident in northern Ohio. Jones (1910) noted occasional flocks in the lake area and described their winter occurrence in the larger Lake Erie Islands. Waxwings have been noted at Put-in-Bay many times throughout the non-breeding season. During the winter of 1941–42 small flocks, usually not exceeding 6 individuals, frequently perched near or on the cage of the captive young; however, the wintering population in this region is small and according to Charles F. Walker could account for only a fraction of the local nesting population. Banding efforts so far have failed to yield information regarding the wintering range of Put-in-Bay waxwings. Study of the recovery records (Lincoln, 1929, 1936, 1939; Cooke, 1937; Bryens, 1943) in addition to migration reports indicate that the

movement of waxwings is considerable both in area and numbers. Typical of such reports are those of Scott (1889) who observed large flocks in April and May along the Gulf Coast of Florida and Brown (1906) who saw on February 3, 1905, at Camden, South Carolina, migrations of robins and waxwings at an estimated rate of 14,000 per hour.

The nesting population usually arrives at Put-in-Bay during the latter half of May. In 1942 numbers of birds were noticeable on May 24, and 3 nesting attempts were observed by May 28. In 1946 the main migration was about May 30. The first fairly well built nest was found on June 6, and 2 were started on June 7. The season was retarded in 1947, and the waxwings did not arrive in numbers until June 6. The first nest building was seen on June 13. Only 2 of 54 banded adults returned, while none of 174 young ever has been reported again. The 2 adults were both males which returned in 1946 from a group of 10 adults banded in 1945. Eighteen adults were banded in 1946 and none of these was seen during the 1947 breeding season. The breeding population of this area varied somewhat during the time of study. The largest number of pairs nesting simultaneously was 15 in 1941 and the smallest was 8 in 1942

The birds are dependent upon the seasonal fruits and berries which abound, and their activities throughout the summer shift over the area in relation to the development of these food plants. The earliest birds, in late May and early June, feed principally in the laboratory region upon the cedar berries and such hackberries as may still be available from the preceding year. Soon thereafter feeding shifts to the sour cherries (*Prunus Cerasus*) in the Chandler yard, and when these cherries are exhausted, the concentration of feeding changes to the mulberry (*Morus alba*) at the laboratory. After this, flights are started to the red mulberry (*Morus rubra*) at Lescheid's, some distance away. Throughout the season waxwings also feed on Gibraltar Island, earlier on cedar berries and hackberries and then on shadbush berries (*Amelanchier sanguinea*) and choke cherries (*Prunus virginiana*). By the time these fail, the elderberries (*Sambucus canadensis*) along the lake shore and the black cherries (*Prunus serotina*) at Chandler's are ripening, and the birds feed on them. In late August flocks of 20 to 50 waxwings are often seen flycatching among the trees.

Formation of Pairs

The rapid formation of pairs after the first appearance of the birds and the early onset of nest building would indicate that pair formation may take place in the flock, or, at least, must originate in the flock and be completed soon after arrival, as appears to occur in some other species (Blanchard, 1941: 42; Odum, 1941; Davis, 1941; Thomas, 1946: 147).

Pairing behavior in waxwing flocks has been noted by several observers.

Warren (1890) mentioned "billing and pluming" between members of a spring flock, although Grinnell (1901) noted no attempts at pairing. Feltes (1936) reports courtship hopping and copulation in April in a migratng flock in California. Allen (1930) indicates that waxwings "get acquainted" with their mates in flocks. Shaw and Culbertson (1944) found both males and females in about equal numbers in a wintering flock in California, a condition which would facilitate pairing. On April 17, 1947, Mr. Douglas Stancombe reported seeing 2 pairs of waxwings from a flock of 30 at Columbus, Ohio, hopping back and forth and passing food. Two additional personal observations of this occurred in the same flock before May 1. Hopping and food passing were noted in the captive young in April 1942.

Although information regarding pairing behavior is not complete, observations of 7 pairs of waxwings which nested in the area (Fig. 1), supplemented by more than 30 other field notes, indicate that recognition involved in pairing is based on sexual differences in behavior. For example, on June 9, 1946 in a group of 6 waxwings 1 bird was observed to approach a second by the characteristic sidewise hopping, which is mentioned below under "Courtship". The second bird gave no response. The first waxwing then hopped toward a third bird which responded by hopping and a few minutes later they flew together. On another similar occasion 5 waxwings perched on the wires in the road area (Fig. 1) and performed as follows. Bird A approached B. B responded with a threat display, which involves forward tipping and lowering of the body, partial fluffing of feathers, and raising of the crest while the head is held close and the beak, which may be snapped quite vigorously, is opened. A then retreated and approached C. C retreated and flew about 2 feet away. Bird A finally approached D and was greeted by a strong threat followed by an attack, and A was driven off and left the area. D circled, returned, flew up to E and hopped. E responded by hopping. D and E then flew up to Nest 46-03 and B and C flew off together. In this same area (at a later date, July 2) the Nest 46-10 male was at his guarding perch and a second bird was below on the wires. This situation continued for about 5 minutes until the second bird gave several side hops. The guarding male at Nest 46-10 immediately attacked and drove the hopping waxwing from the neighborhood.

In the captive birds many observations of pairing tactics were made. On April 13, 1942, notes show that during the day Spike obtained food and hopped at various times to Chirp, Doc, and Butch. All 3 accepted the food and entered into the courtship dance. When Spike approached Dude on 2 occasions he encountered the threat display. Dude, however, was noted hopping with Butch in which case Dude was the instigator. Spike later proved to be a male and Butch a female, and although the sex of Dude never was known definitely, it probably was male. In these and other cases the bird instigating the court-

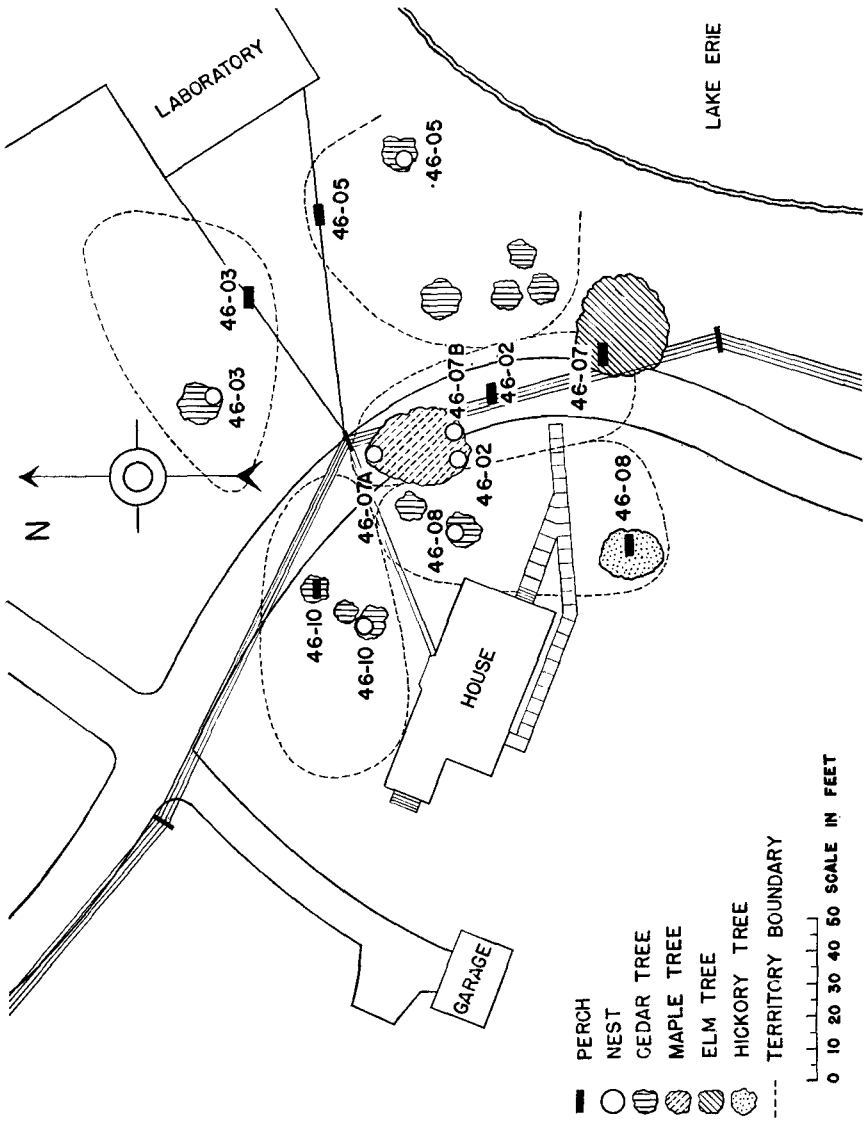

FIG. 1. Sites of nests near Laboratory, 1946

ship or pairing behavior was assumed to be a male. Females may respond by no movement, may retreat, or may return the hopping. In some cases, possibly when mated and on territory, females may give a threat display, since at least 3 notations describe females attacking strange males in a nest area and 1 describes an incubating female giving the threat display from the nest to a strange male. Breeding males probably respond by threat display or attack, and in either case the approaching male retreats. Additional evidence that the sexes behave as described might be drawn from the fact that in 7 cases of renesting (discussed later) where the pairs were banded, instigation of the courtship dance was seen only in males and completion of the dance occurred only when females responded by hopping. The precise point at which pairing may be said to be completed remains somewhat conjectural. Presumably pairing is complete when the female continues to reciprocate the hopping of the male and the birds remain in almost constant association. The soft vibrating "courtship note" is heard constantly and occasionally the sharper "location call" is given if the birds are separated. If the "location call" is not answered, it is repeated with greater intensity until the mate responds, whereupon the separated bird flies speedily to the mate. Such short separations, not over 2 or 3 minutes, frequently culminate in a burst of energy exhibited in fast circular flights about the nest area and often precede the courtship dance. Which of the sexes leads in the flight remains unknown. These flights may represent a critical point in the process of pair formation. In some early-season observations of hopping, the ceremony appeared to exhaust itself without resulting in such flights.

The retardation of breeding activities in 1947 gave opportunity for verification of pairing behavior. Flock behavior was noted in the mornings and evenings from June 9 to 12 when the birds gathered and fed on the staminate flowers of a mulberry tree. During the day, however, they broke into small groups of 2 to 6, and in these groups pairing behavior was noted frequently. By June 12 pairs were perched about in situations suggestive of nesting. Building was noted on June 13.

Pairs probably stay together through the breeding season. The pairs listed in Table 1 are known to have done so. In several cases in which pairs have been broken up during the nesting cycle, the females have completed caring for the young through fledging and for several days after. None of the separated members of these pairs was found renesting during the same season. That a rather strong bond exists between the pair is additionally indicated by the behavior of the birds when separated or during trapping. In at least 15 instances 1 bird has flown close and given the anger note when the mate was handled. The free bird perched near, gave the disturbance note, and flew rapidly to the banded bird when it was released. At Nests 45-10 and 46-11 when the males disappeared the females gave the disturbance note for the next 2 days.

The types of mating based on sex recognition described by Lorenz (1937) are reviewed by Tinbergen (1939: 52–55). Of these, the intermediate or cichlid fish type seems to best characterize the mating behavior of the Cedar Waxwing. Here dominance by 1 member is not essential and both members of the pair engage in pairing display which may or may not be identical in the sexes.

The formation of a pair is primarily a problem of discrimination of sex and of the individual. Nice (1943: 192) stresses this fact, pointing out that in birds the recognition process is probably visual or auditory. In a bird such as the waxwing in which sexual dimorphism is not present and in which functional song is absent, recognition must be based on behavior. For behavior to operate, the sexes must come into proximity. In many species (Nice, 1937;

TABLE 1
TIME INTERVALS OF NESTING CYCLE

NEST	BUILDING	1ST EGG	COMPLETE SET	HATCHED	FLEDGED	TIME FOR FLEDGING TWO BROODS
First nests						
45-08A	6/16	6/25	5–6/29	7/10	7/26	
46-07A	6/20	6/25	5–6/29	7/10	7/26	
46-15A	6/15	6/19	4–6/22	7/3	7/18	
46-16A	6/22	6/26	5–6/30	7/11	7/26	
41-10A	7/2	7/5	5–7/9	7/20	8/4	
42-12A	6/22	6/26	4–6/29	7/10	7/24	
46-18A					7/18	
Second nests						
45-08B	7/25	7/29	5–8/2	8/13	8/28	69 days
46-07B	7/17	7/25	4–7/28	8/8	8/23	65 "
46-15B		7/21	4–7/24	8/4	8/19	68 "
46-16B	7/23	7/27	4–7/30	8/10	8/25	64 "
41-10B		8/3	3–8/5	8/17	9/1	62 "
42-12B	7/21	7/24	3–7/26	8/6	8/21	60 "
46-18B		7/18	4–7/21	Deserted		

Average time for fledging first brood—34.8 days.
Average time for fledging two broods—64.7 days.

Lack, 1946) this is accomplished when the female enters the territory of the male. In the waxwing, proximity is maintained in the flock and the male originates pairing by "testing" the readiness of individuals to participate in the courtship dance or flight. The approach of the male probably is the same to either sex. From the data at hand, this approach in itself is a "signal" (Nice, 1943: 10) of maleness.

While some uncertainty regarding the response of another male or a nonreceptive female certainly exists, it seems fairly certain that the response from a sexually receptive female is active participation in the courtship dance. During this testing procedure the birds usually separate slightly from the group, and if sexual synchronization is obtained, the separation continues into

courtship. The entire behavior of a pair is one of mutual cooperation in the display, and no convincing evidence of sexual dominance by either member has been noted. While this description of pairing tends to oversimplify what is probably a complex behavior, the uniqueness of the courtship dance among behavior patterns of birds would certainly go a long way toward the prevention of false matings. This function of behavior is recognized by Nice (1943: 192) in the discussion of "isolating mechanisms", as well as by Tinbergen (1939: 57).

Territory

The social habits of the waxwing have been discussed more fully in the literature than have the territorial phases of its behavior. Crouch (1936) and Lea (1942) briefly mentioned territory but did not clarify its status. The territory is similar to *Type B* described by Nice (1941b) which includes mating and nesting but not feeding. Some mating behavior has been noted outside the territory, and it has been shown that the pairs are formed previous to the establishment of territories. As in the Kingbird (Davis, 1941), the territory is considerably influenced by the location of the nest site. Some question remains as to whether the territory or the nest site is selected primarily. In observations of Nests 46-02, 46-03, and 46-05, the pairs were found when scouting for nests, and building and territorial defenses were observed simultaneously. Pair 46-04, however, was found defending an area back of Stranahan Laboratory on June 7. On June 9 the birds made several trips to a fork in the limb of a cedar tree but did not carry nesting materials until the next day. Indication that territory may be the dominant factor is found in the fact that 5 out of the 7 pairs which raised 2 broods (Table 1) built their second nests in the same territories as the first ones. The other 2 second nests may have been in the territories since their boundaries were not as well determined.

The requirements of the territory are simple, consisting of a nest site, a guarding perch, and a small amount of space. The size of 3 territories was 270, 225, and 1100 square yards. The shortest distance between any of these nests was 38 feet. Several nests have been found closer; in 3 cases not over 25 feet separated 2 nests. However, in 1 case, a territory nearly an acre in size was defended. The guarding perch of this nest was on a tall elm tree (*Ulmus americana*) about 100 yards from the nest. Territorial defense of this area was observed from June 28 to 30 when the male and several times both of the pair attacked a new pair and drove it away. Both these new birds lacked the red secondary tips, and since, on July 3, a similar pair was found building in the west end of the orchard, it was thought to be the same. This nest was at least 300 yards away. Although there were numerous favorable nest sites, no other pairs nested in this area.

The male waxwing guards from a perch overlooking the territory, and his

frequent calls serve in communication to the female and may serve as warning for intruders as noted by Cameron (1908). There is little in the way of display. If an intruder comes within a distance of a yard or so the threat display may be given, and it is usually followed by direct attack. As the guarding bird is on the perch it is generally higher and thus dives on the adversary. Strange birds have always been noted to retreat and depart. Only once was actual contact observed: in a contest between 2 waxwings over a perch on the electric wires between the 2 territories. In this case one dived into the other while they were flying and both birds temporarily lost their equilibrium. The affair was settled by the establishment of opposing perches on adjacent wires.

Attacks on intruders may be made from any place in the territory. This is especially true during nest-building when both of the pair join in the pursuit. Of 55 records in which the sex and identity of the pairs have been quite definitely known, 71.0% of the attacks were made by the male while the female stayed at or near the nest, 12.7% by both members of the pair together, 9.0% by the female alone when the male was absent from the territory, and 7.3% by the male alone when the female was absent. These records indicate that the territory is recognized and defended by both members of the pair, and since attacks have been noted by either sex during the absence of the mate, the defense cannot be considered merely as defense of the sex partner. While the threat reaction is occasionally seen between birds coming close together in a feeding area, fighting or chasing does not occur as would be expected if strong sex-partner defense were present. A banded male was observed several times from June 11 to June 17 feeding with his mate in a cherry tree. During this time many waxwings fed in this tree and no fighting or attacking was observed. In 1 instance, on June 13, the pair alighted on an electric wire with 3 other birds, all within a span of 3 feet, and perched for several minutes in the sun. No aggressive behavior occurred.

A good example of the change in behavior from the feeding place to the territory was observed on June 9 by the corner of Stranahan Laboratory where a pair of waxwings was feeding on wild strawberries (*Fragaria virginiana*). Soon 8 birds were attracted to this locality and fed on the berries. When disturbed by the slamming of a door, the birds flew, perched together on a wire overhead, and after a short pause were back feeding. When the berries were consumed the birds scattered somewhat but 6 of them landed farther west on the same wire. Two of these, pair A, then began attack on the others, the B pair soon flew south to Nest 46-05, the third pair, C, subsequently chased by the A pair, circled into 46-05 territory and was immediately chased by the male of pair B which only a moment previously had fled from pair A. Pair number C continued hastily across the road into Nest 46-02 territory pursued by the pair B male. When the latter crossed into 46-02 territory, he suddenly checked his flight, circled rapidly, and returned to Nest 46-05 tree. Pair A,

the original attackers, in the meantime had circled, perched on the western part of the wire, and soon flown to Nest 46-03. These birds were evidently the pairs from Nests 46-02, 46-03, and 46-05 as indicated on Fig. 1. This instance not only exemplifies the change from gregarious feeding to territorial defense by waxwings but the sudden retreat of the 46-05 male presages recognition of the territory of a neighbor. Lack (1946: 36) described a similar behavior in the English Robin. Further evidence for the recognition of territorial boundaries was seen when pair 46-02 deserted on June 13 after the nest had been disturbed by trimming of the branches in which it was located. Although no attack could have been possible on June 14 and 15, it was noted that pairs 46-03 and 46-05 continued to detour this area in travelling to and from their own territories.

Aside from incubation and care of the young, scarcely any activity can be said to be strictly confined to the territory. A major share of nesting materials comes from the territory though trips outside have been noted. At one time the birds from Nests 46-07, 46-08, and 46-12 all were collecting wool yarn from an area at the edge of 46-12 territory. Pieces of this yarn were found later in all 3 nests. Much of the courtship takes place within the territory, chiefly near the nest site or the guarding perch of the male. Two pairs in 1945 were noted carrying on some courtship feeding in a feeding area adjacent to their nests, and the 46-03 pair was observed courting in a large tree not in its territory. Field observations of waxwings gave the impression that reduction in territorial disputes occurs as the nesting cycle proceeds. Of 46 ejections in which the nesting stage was known, the average per day was 4.2 during nest building (5 days), 1.8 egg laying (5 days), 1.0 incubation (12 days), and 0.25 nestling period (16 days). Two suggestions can be made in explanation of this behavior. First, the routine patterns of nest life are developed in such a way that trespassing is greatly reduced, and second, the aggressive tendency of the birds themselves is reduced. In the first instance pairs 46-07, 46-08, and 46-10 were building nests at the same time (June 10–24) and started incubation about June 27. During this period ejections occurred and were recorded at least some time on every day. Later during incubation and feeding of the young less friction was noted. The 46-07 pair always came and left the nest tree from the east while 46-08 pair travelled from the south and 46-10 from the west. A glance at Fig. 1 will reveal that under these conditions little chance for conflict would occur. On the other hand while observing Nest 46-15A during the middle of the nestling period, about July 10–12, no ejections or aggressive actions were seen but from July 18–21, the period during which Nest 46-15B, the second nest, was being built, there were several. Here it appears that changes in the behavior of the pair in relation to neighbors were responsible. Probably both of these factors have some influence though more data are needed to clarify their relation.

Both sexes ignore most other species of birds in the territory. The Yellow Warbler (*Dendroica petechia*), the Indigo Bunting (*Passerina cyanea*), and the Red-eyed Vireo (*Vireo olivaceus*) have all been observed within close range of nests with no apparent alarm on the part of the female waxwing. The smaller birds especially have been within a few inches of the nest without disturbance. The male at Nest 45-08B was noted attacking a Redstart (*Setophaga ruticilla*) and several times a House Wren (*Troglodytes aëdon*). The bird most consistently attacked was the Bronzed Grackle (*Quiscalus quiscula*) which was observed more than a dozen times being aggressively repelled by 1 or both members of a pair.

Courtship

The courtship of the Cedar Waxwing progresses through 2 phases: first, a display which strengthens the bond and culminates in copulation, and second, a display which maintains the bond throughout much of the nesting cycle. Behavior of the first phase is usually observed simultaneously with the arrival of the birds and is chiefly characterized by the courtship dance, or hop, which has been mentioned as a probable feature in the formation of the pair. This display is performed regularly from the earliest time that the pair can be recognized up to the onset of incubation. The dance itself may or may not be combined with actual feeding, but in a majority of the cases, food plays a part in the dance. The dance is seen more frequently in the morning and evening, usually 2–4 hours after sunrise and 1–3 hours before sunset, but may occur quite commonly at any hour of the day. A horizontal perch, ordinarily a small dead limb or electric wire, may be the scene of activity. The male flies away a short distance, procures an insect or berry (in many cases the food fragments are small and can be seen only with binoculars), and returns to the female. He approaches by hopping sidewise, usually facing the same direction as the female, thus bringing the bodies of the birds into parallel positions. The food is presented by a turn of the head. If the female is receptive she takes the food by a similar motion and hops away from the male then back to him and returns the food. He in turn hops away and back as the process repeats. Between hops the male frequently executes a bowing movement. The entire courtship dance is highly stereotyped and gives the impression of spring-wound mechanical toys in operation. Observations of banded birds or ones individually known showed that the female usually terminated the display by eating the food. Thus a dance of a dozen hops would be interrupted while the male made other short food forays. Courtship dancing may last for a period of 1–5 minutes then alternate with a fast circular flight in the nest area. The activity varies in duration from 3–15 minutes and usually is followed by a feeding trip or a session at nest building. Crouch (1936) gives a good description of this courtship display; however, he stated that, "At the end the male takes the berry

and either drops it or eats it". Other accounts of courtship hopping and feeding were given by Silloway (1904) and McCoy (1927).

Copulation takes place during a comparatively few days, and the behavior of the birds during copulation is quite subdued. Copulation records have been comparatively infrequent. During the 6 years' study only 25 observations of copulation have been made. In all cases except 1 these have taken place during courtship dances. After a few hops by both birds the female assumes a crouching position and the male mounts almost instantaneously. The female may vibrate the wings slightly but makes no audible sound. The male appears in an almost upright position with the crest somewhat elevated and has not been observed to use the beak in grasping the feathers of the female. The position is held only a few seconds after which the male hops down. Courtship may continue, the longest observed being 5 minutes interspersed by 3 copulations. The 1 exception in which no dancing accompanied copulation occurred after the pair had been feeding in a cherry tree. The female flew into a maple and the male followed and at once copulated with the female. Copulation was repeated 3 times in quick succession after which the birds flew away. Copulations were seen more frequently from 5:30 A.M. (Solar time) to 9:30 A.M. and after 2:30 P.M. in the latter part of the day. Only 1 was seen during the middle of the day. In 10 cases in which the identity of the pairs was reasonably certain the observed copulations took place between the third day before the first egg was laid and the day the third egg was laid. The distribution was: 2 on the third day before laying, 4 on the second day before, 2 on the day before, 1 on the day of the first egg, and 1 on the day of the second egg. Four of these copulations were near the nests and 6 close to though not in the feeding areas. None of the identifiable pairs was seen in copulation on more than 1 day, although it must certainly have been more frequent. The captive birds copulated on the 3 days preceding laying of the first egg, and the male attempted copulation on the day after the second egg was laid. (Only 2 eggs were laid.) The absence in the literature of comment concerning copulation indicates that it has not been seen frequently. Copulation probably takes place only during a restricted time when the pair is sexually synchronized and if successfully completed results in little subsidiary behavior. Copulation marks the climax of the first phase of courtship. Hereafter the courtship dance and the circular flights become less frequent and disappear as egg laying proceeds, while the character of the call notes and feeding behavior changes.

The second stage of courtship wherein the male feeds the female is characterized by 2 phases: an earlier one in which the male feeds the begging female, and a later one in which the male feeds the female previous to the feeding of the young. About the day of the first egg the male starts feeding the female at the nest and the female displays begging behavior. Herrick (1935: 61) mentioned and described this display as follows: "The perched bird, pre-

sumably the female, was shaking her wings and giving the sibilant call, when another waxwing appeared, passed something to her bill, and flew away". Nice (1941a) located a pair of nesting waxwings by means of the begging call of the female. The begging and feeding display takes place at either the nest or the "perch", although since the female actively pursues the male the pair may move about considerably. The attitudes, voice, and behavior of both birds are indistinguishable from those involved in the feeding of a young bird. Lack (1946: 61–62) in describing the begging by the English Robin might well be giving the behavior observed in the waxwing. The begging behavior of the female was at first believed to have some relation to sexual readiness. Later observations of banded birds showed that this display developed in association with egg laying and continued throughout incubation. So far as is known, begging is not involved in copulation behavior but only in the maintenance of the bond. This idea is ascribed by Lack (1946: 62) to the same display in the European Robin.

The second phase abruptly succeeds the begging reaction when the young hatch. The male comes to the nest, invariably feeds the female first, and then both adults feed the nestlings. Crouch (1936), Lea (1942), and others have described the feeding of the young, and their statement that the male presents food to the female first and then both parents feed the young together has been verified consistently during this study. Food presentation to the female continues throughout the brooding period, ceasing only when the young are well grown. Its relationship to the second production brood will be apparent later.

The importance of food as a factor in courtship should not be overlooked. It seems probable that much of the first stage (courtship dancing) is accompanied by the passing of food and that some reports of "symbolic" feeding may have been due to the small size of food particles; yet, there is little doubt that symbolic feeding does occur. Bagg and Eliot (1937: 470) quote Merriam's description of a courtship dance. "They had nothing in their bills and their bills were shut." Crouch (1936) described the birds "touching bills", and in several instances at Put-in-Bay the beaks of dancing birds were not opened when touching. Lack (1940: 173) notes symbolic feeding in the Cedar Waxwing. In either case the basic element of the behavior is food and the function of the act is the strengthening or intensifying of the bond between the pair. In the second stage of courtship food is presented to the female both during incubation and feeding of the young. The food presentation to the female during the nestling period is especially significant since it maintains the male with the female at a time when in many species association between members of the pair is weakened by the constant stimuli of the nestlings. This entire series of behavior patterns, which follows pairing and continues through the nesting cycle, promotes close contact between the members of the pair and in so doing maintains the bond. In this sense the series represents "true courtship" (Lack, 1946: 59).

Voice

The call notes of the Cedar Waxwing in the main are derived from a fundamental tone of high pitch, lacking, for the most part, in overtones and as a result having little of the resonance which gives quality to the song of many birds. This may result from the relatively poorly developed vocal organs, mentioned by Maynard (1928); however, the sound is transmitted for some distance, and under favorable conditions it may be heard at least a quarter of a mile. No exact tests were possible at Put-in-Bay, but it was thought that the pitch was somewhere near D_8 or slightly above 9,000 v.p.s. Brand (1938) found the pitch on 1 vocalization to vary from 7,675 v.p.s. to 8,950 v.p.s., with a mean of 8,400.

According to the definitions of Nice (1943: 144) and Tinbergen (1939: 74) song is not present in the Cedar Waxwing since of the call notes given by this species none is restricted to the male, none is definitely used as a warning, and none is particularly characteristic of the beginning of reproduction. The absence of song does not prevent a somewhat more extensive vocabulary than generally has been recognized. This vocabulary consists of 7 call notes which are divided into 2 groups.

Call types with constant vibration frequency: 1. Flock Call: A clear repeated note of unchanging vibration frequency used by members of a flock in flight and given as a signal in take offs or landings. Crouch (1936) and Nice (1941a) mention this note in connection with flight.

2. Distress Call: Similar to a location call but having a distinct drop in pitch as the note ends. The call is given by a bird separated for any length of time from its mate or is given as a signal when the nest area is entered, in which case either adults or young will go into "freezing" behavior (Allison, 1906; Nice, 1941a: 62). In 3 cases in which females were abandoned by their mates the females gave this note for a considerable part of the next 2 days. Cameron (1908: 406) described this note as given by the parent when a man attempted to capture a young bird.

Call types with variable vibration frequency: 1. Anger Call: The most intense call given by waxwings. It has a rapidly changing vibration frequency which gives the note a marked vibrato. This call may be given by the adults and accompanied by attack if the young are disturbed by banding operations, especially if the young themselves give the note when handled. Adults also frequently emit this note while being held in the hand. It is sometimes used in attack on intraspecific intruders but is commonly heard during interspecific attack on larger birds such as the Bronzed Grackle. Whittle (1928: 82) calls this "danger note", and Nice (1941a: 62) labels it "alarm seep".

2. Begging Note: The tone character is similar to anger call but has a medium intensity and is used exclusively by females or young in feeding behavior. This call occurs during begging behavior, as described by Herrick

(1935: 61), Nice (1941a), and Crouch (1936). It appears shortly before egg laying and continues throughout incubation.

3. Location Call: A modified flock call of less intensity than the begging note but more musical. It may be heard in flocks feeding or perching and is commonly used by a pair in the nest area or at a feeding station. During incubation a perching male quite frequently exchanges this note with a nesting female.

4. Courtship Note: A soft buzzing warble used by the pair during courtship and particularly during nest building. The begging note of young birds up to 5 or 6 days is very similar. Used as a field identification mark, this call has been useful in locating newly started nests.

5. Warbling Note: The most musical call given by the Cedar Waxwing and one not heard frequently because of its extremely low intensity. The captive young in 1941 and 1942 gave this note frequently while perching in the sun, and it is given in the wild under similar conditions. In 2 cases, where the nests were quite low, the females were heard warbling on the nests during incubation. Both Whittle (1928) and Crouch (1936) describe warbling given by their captive birds.

The various waxwing calls prove useful in the field as a gauge of the stage of the nest cycle. The courtship note usually indicates building, a begging female, a nest and, commonly, eggs. The location call given by a perching male ordinarily is an indication of later incubation or early feeding. During later feeding stages the young increase in begging while the adults become more silent, and at fledging the outburst of begging by the young is unmistakable. Call notes thus undergo certain cyclic tendencies during the breeding season.

Calling fluctuates also during the day. From 4:30 A.M. (Solar time) to about 9:30 A.M. in any area occupied by nesting waxwings, calling is heard frequently. A quiet period develops during the middle of the day and then another interval of calling occurs from 3:30 P.M. to about 7:00 P.M. The periods of vocalization are correlated directly with the periods of activity. There is evidence that physical activity of waxwings is reduced with high temperatures (90°F. or above), and since voice is almost synonymous with other physical activities it is much reduced on hot days.

Voice functions in species recognition and communication and probably in individual recognition. Evidence supporting this statement is largely circumstantial yet it merits some consideration. Numerous observations have been made in which 1 of a pair or both have answered and joined a small flock of waxwings en route to the feeding area. Several notations have been made of nestlings begging in response to the flight note of waxwings as they flew past. On July 23, 1946, 4 immatures and 2 adults "froze" when the Nest 46-15 male gave a disturbance call. At Nest 42-12 when the male was trapped the female flew down and gave the anger call. Two other Cedar Waxwings not

previously seen responded and flew to her. All 3 perched and gave the disturbance call for at least 5 minutes when the male was released.

Individual recognition of the calls of pair members at least must exist. In Webster's orchard, Nests 46-15, 46-16, and an unmarked nest were all within a 50 yard radius yet the females responded only to their respective males. In many of these instances there is reasonable certainty that the responses were not the result of visual stimuli. At Nest 41-10 call responses were noted although the "perch" was at least 75 yards away from the nest and

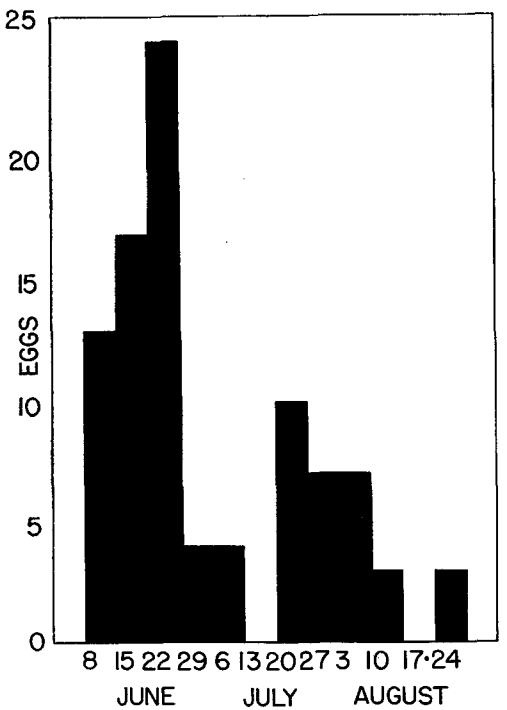

FIG. 2. Number of first eggs found per week

obscured from the nest by another tree. The male in this case was banded and could be identified through the telescope. The constant calling between pairs of waxwings is some evidence of recognition and communication.

NESTS AND EGGS

As mentioned previously nest building occurs soon after the main spring migration of waxwings. Usually some activity is noted the first week in June, but the height of nesting customarily falls in the latter half of the month (Fig. 2).

The early nesting attempts appear to lack much of the vigor which accompanies the later ones. Of 45 nests built before June 20 only 22% were successful. In contrast, of 51 nests built after June 20, 55% were successful. When interference was the probable cause of desertion, the nests were disregarded for these calculations. This failure of early nests and the late migration results in a delayed nesting season for the waxwing, a fact commented on by Herrick (1935: 60), Crouch (1936), Saunders (1911), and others. The loss of early nests seems in part due to inactivity on the part of the birds; however, storms are common at this season and hard rains and wind account for 10 out of 29 desertions in which causes could be ascertained.

The nest site is determined by the pair, although the female appears to be more active. At least 9 observations of the selection of nest sites have been made. A good example of this behavior is illustrated by pair 46-04. These birds were found on June 7 just north of the laboratory workshop. During the afternoon they were active in courtship feeding and hopping and in making circular flights. The birds flew from tree to tree in this area and the female frequently perched in favorable limb forks and went through body motions of nest shaping. It was noticed that after several trials the pair kept returning to a particular fork in a cedar tree and 2 days later the beginnings of the nest could be seen in this fork. This pair seemed slow in starting the nest as most of the pairs seen have started building on the day of nest location. Second nests built by the same pair usually are close to the first ones. In 5 cases both nests have been in the same tree.

In a record of 99 trees used as nest sites, the percentages were as follows: maple—28%, cedar—27%, apple (*Malus pumila*)—14%, pear (*Pyrus communis*)—10%, hackberry—6%, plum (*Prunus domestica*)—5%, sycamore (*Platanus occidentalis*)—4%, elm (*Ulmus americana*)—2%, and coffee nut (*Gymnocladus dioica*), yellow oak (*Quercus Muhlenbergii*), and cottonwood (*Populus deltoides*)—1% each. The nest height was generally 4 to 50 feet from the ground, though more usually from 5 to 20 feet, agreeing with Crouch (1936). The nests are built away from the trunks where the limbs become horizontal and usually where lateral forking occurs. Lea (1942) gave the average height of 11 nests as 3.63 meters and distance from trunk 2.06 meters.

Materials used in the waxwing nest vary considerably. Grass, small twigs, plant stems, rootlets, string, and many other fibrous materials have been found in nests. Nests are lined lightly with cobweb, fine grasses, or moss. One nest, 46-07A, was almost completely woven from wool yarn which had been scattered on the grass in the nest area. The writings of the major workers on waxwings are supplemented by many excellent notes on nests, i.e., Benson (1920) on the use of twine and rags, Burleigh (1923) on location and materials, Merrill (1898) on use of moss, and Smith (1915) on building. Cedar Waxwing nests are loosely woven and bulky. Good measurements of a typical nest were given by Crouch (1936).

The average time of nest construction as determined from 11 nests was 5.55 days (S. D. 1.6), with extremes of 3 days and 9 days. The time was counted from the start of nest building up to the day of the first egg. Lea (1942) found 2 nests built in 6 days and 1 nest in 5 days. The length of time for construction decreases as the season progresses. The 5 nests built between May 30 and June 10 averaged 6.8 days, while the 6 nests built between June 12 and 21 averaged 4.5 days. The nest building activity is not uniform but rises to a peak during the third or fourth day and then subsides. Some building, at least addition of lining, may continue through the second day of egg laying. During the height of nest building the birds may work a great part of the daylight hours, but activity during the morning is more intense. Building is not continuous and is alternated with periods of feeding, courting, and preening. A period of increased building also occurs in the late afternoon. Both sexes are active in construction and gathering materials. In some cases the female appears to be slightly more aggressive in building, but the general impression in most instances is that the work is quite equally divided. In dismantling an average-sized nest, 2,327 individual pieces could be recognized besides numerous fragments or lining such as cobweb or plant fiber which could not be counted. Taking the weight of a typical nest as 23.1 grams (average of 3 nests) and the weight of material carried on an average trip as 90 mg. (average of 20 straws from nests), a pair of waxwings would make 2,566 trips in building a nest, or 1,283 trips per bird. To accomplish this in 5 days working 10 hours per day, each bird would be required to make 1 trip every 2.35 minutes. While these are only estimates, they represent someting of the considerable effort expended by the birds. During the height of nest building 1 or 2 trips per minute for short periods of 10–15 minutes are not uncommon.

Egg laying commonly occurs as soon as the nest is completed. The eggs are laid in the morning usually between 5:00 A.M. and 8:00 A.M. (see Table 2), on consecutive days. Of 65 complete sets 41.6% had 5 eggs, 40% had 4 eggs, 10.7% had 3 eggs, and 7.7% had 2 eggs. A nest found by Sanborn and Goelitz (1915) contained 6 eggs. There is a definite tendency for birds to lay fewer eggs late in the season. In 36 cases of early nests in which incubation was in progress before July 5 the average number of eggs was 4.5 per nest. In 24 cases of late nests after July 15 the average of eggs per nest was 4.0. A statistical analysis of these data was conducted on the hypothesis that there is no relationship between the season and the number of eggs laid. This hypothesis was rejected since the value of χ^2 indicated a "significant difference" which would occur by chance less than 5 times in 100. Another indication that the greater reproductive activity falls early in the summer is that of 300 eggs laid during 5 years, 51.7% were laid between June 15 and June 30. These data are subject to some variation since field observations could not always be comparative.

INCUBATION

I. The Role of the Sexes

Throughout this study the only field method for the discrimination of sex has been the difference in behavior characteristics of the male and female. The confirmation of these characters has resulted from observations of 7 pairs of banded or marked birds. There were at least 10 other pairs in which the

TABLE 2
Time (Solar) of Egg Laying at Six Nests

NEST NUMBER	DATE	TIME OF LAST OBSERVATION BEFORE LAYING (A.M.)	TIME OF FIRST OBSERVATION AFTER LAYING (A.M.)	MIDPOINT A.M.
41-10A	7/5	5:29	7:19	6:24 ±55
	7/6	5:53	7:24	6:38 ±45
	7/7	5:52	7:54	6:53 ±61
	7/8	5:43	7:33	6:38 ±55
	7/9	5:58	7:36	6:47 ±49
41-14	7/23	5:53	7:53	6:53 ±60
	7/24	6:12	7:52	7:03 ±50
	7/25	5:55	7:38	6:46 ±52
	7/26	5:08	7:23	6:15 ±68
40-12	8/2	5:39	6:35	6:08 ±27
	8/3	4:58	6:21	5:40 ±41
	8/4	4:54	6:05	5:30 ±35
	8/5	4:53	6:03	5:28 ±35
41-10B	8/5	6:16	7:08	6:42 ±26
41-18	8/7	6:08	7:38	6:53 ±45
	8/8	5:53	7:53	6:53 ±60
40-13	8/7	4:43	6:53	5:48 ±65
	8/8	7:06	7:45	6:26 ±19
	8/9	6:28	7:53	7:10 ±43
	8/10	6:05	6:48	6:26 ±22
	8/11	6:39	6:02	6:51 ±12
Mean				6:29

sexes were determined positively by less obvious identification marks. The sex was determined at all nests by identifying the egg producing member of the pair. Such characters have been referred to by several writers. Littlefield and Lemkau (1928) wrote of the nesting female and her mate. Nice (1941a), Crouch (1936), Gross (1929), Herrick (1935:61), and Saunders (1911) differentiated male and female behavior while Post (1916) noted behavior differences but did not associate them with sex. The only structural character which proved valuable was the presence of a definite brood patch on the female during

the nesting season. With careful examination the male invariably shows down feathers scattered on the abdomen. In addition to behavior differences Crouch (1936: 4) described the female as having less black on the throat. While true in individual cases its reliability as a differentiating character has not been established. At Put-in-Bay during the observation of over 100 pairs of nesting waxwings all gradations of color have been seen in both males and females. Females either may be duller or brighter in color than their mates and may have more or less black on the throat. One of the most colorful of the captive birds, "Butch", reared in 1942 was the female which later nested in the cage. Mearns (1878), after examining a large series of specimens, commented on the variability of red wax-like appendages on the secondaries by saying, "In this series I can scarcely detect any sexual difference in that respect except that the particularly well developed specimens were all males."

Incubation probably is performed only by the female. During the summer of 1939 at the first nest observed during this study the adults were thought to have shared incubation, although at 10 nests in which 1 or both birds were color banded, the female alone incubated, and in more than 60 other instances there has been no clue of male incubation. Crouch (1936: 4) states that incubation is performed entirely by the female. Gross (1929: 181) observed 1 nest where both birds incubated and another where only the female was active. Saunders (1911) noted that only the female incubates. Lea (1942) stated, "The female waxwing did all the incubating and brooding".

Characteristic behavior of the female while on the nest includes frequent egg turning, changing directions, raising the crest to attention, "freezing" as described by Cameron (1908) and others, stretching, and feather preening. Notes for July 18, 1941, indicate that egg turning took place 12 times between 7:28 A.M. and 8:33 A.M. This frequency is not at all uncommon. In an hour's observation waxwings have been seen to face in all compass points, and on August 23, 1942, at 3:11 P.M. the female on Nest 40-15 was facing directly west into the sun. Crouch (1936) states that while on the nest the female faces away from the sun and changes as the day progresses.

Waxwings are more quiet during the period of incubation than at other times during the life cycle, although frequently females when coming to or leaving the nest give soft flock notes. The fact that females give the warbling note while incubating was discovered when the vibration of the throat of the female while sitting on the nest was noted. This movement was observed with the spotting telescope and when checked, the sound was found audible only to a distance of 15–20 feet from the nest. Nice (1941a) in describing notes of a captive bird under observation had not heard this note, but she mentions that Whittle (1928) described notes of similar character. Crouch (1936) mentions a "peeping call", probably the same and used under similar conditions as ob-

served here. This note was heard repeatedly among the group of 9 young captive waxwings.

While the male takes no part in incubation, he ordinarily is very active in feeding and nest attention. The male feeding behavior has been described well by Crouch (1936). The female may be fed by the male either at the nest or at a habitually frequented perch in a nearby tree. Herrick (1935: 61) never noticed this habit. This behavior, however, is recorded both by Crouch (1936) and Gross (1929) and has been seen frequently and consistently throughout observations at Put-in-Bay.

On the subject of feeding, there are 2 particulars worthy of mention: (1) the food carrying capacity of the male and (2) the visits by the male to the empty nest. Many nest feedings have been observed and the particles of food which were given to the female or young counted. The male may carry 5 large mulberries but usually only 3. The usual number of chokecherries was 7 and of elderberries 9–10, although once a male brought up 13, 1 after another. Several times males have been noted coming to the nests during incubation when the females were absent. On some of these visits the male takes his regular perch and regurgitates food. Then after peering into the nest, he finally swallows the food himself and may leave at once or may remain for several minutes exactly as though he had carried out the complete reaction.

As a criterion that incubation was in progress, a single perched waxwing seen frequently at a salient point such as an electric light wire, high, dead limb, or the top of a cedar tree has proved almost infallible. Numerous instances in the notes of observations on banded birds have shown this perching bird to be the male.

The correlation of changes in behavior of both sexes with variability in weather conditions has been mentioned by several writers. Herrick (1935) and Crouch (1936) mention the panting and crest raising displayed by the incubating female on warm days. This characteristic response has been recorded in the notes on almost every day in which the maximum temperature was 90°F. or above. A particularly marked response was observed on July 21 when the temperature was 90°F. The female spent from 2:10 P.M. until 4:30 P.M. alternating at about 3 minute intervals between covering the eggs and perching near the nest in the shade. This behavior occurred again on July 23 when the temperature was 91°F. Since the afternoon sun fell directly on the nest the actual temperature at the nest must have been considerable. Males are less active with increasing temperatures. Rain apparently retards activity in both sexes. Females stay close to their nests and males are less attentive. Feltes (1936) noticed that on rainy days the birds were more subdued and fed more frequently at his traps. The above statements are based on 15 to 20 observations, and further study of weather is contemplated before any comprehensive discussion is attempted.

II. Attentiveness

Rhythmic attention during incubation has been reported in a number of species. The existence of rhythm in the attention of the Cedar Waxwing cannot be established at present, although there is a tendency for the females to incubate more periods of a given length than other intervals.

The frequency of attention intervals (Table 3) of the female was prepared from the data on 11 nests involving 402 hours of observation. The mean time interval was 44.8 minutes (S.D. 31.1 min.). In the examination of these data on the hypothesis that uniform distribution of frequencies existed, a χ^2 test was carried out and a "highly significant" value of χ^2 was obtained. Thus the hypothesis can be rejected in favor of a definite grouping of the frequencies. This grouping of the frequencies is somewhat below the mean due to the influence of the few exceedingly long periods. On this point data are imperfect since the actual length of the longest periods is not always known. Many of

TABLE 3
Frequency of Attention Intervals at Eleven Nests

TIME INTERVAL (MINUTES)	FREQUENCY	TIME INTERVAL (MINUTES)	FREQUENCY
1– 7	12	85– 91	6
8–14	21	92– 98	6
15–21	23	99–105	1
22–28	26	106–112	5
29–35	26	113–119	3
36–42	30	120–126	1
43–49	14	127–133	0
50–56	18	134–140	2
57–63	14	141–147	1
64–70	8	148–154	0
71–77	11	155–161	1
78–84	6	162–168	1

the longer periods on the nest started before the observer arrived or ended after he left. The longest of these incompletely observed attentive periods exceeded 240 minutes. In interpreting the above, it appears that there is a significant tendency for the birds to incubate more periods of 20 to 40 minutes than other intervals. While this in itself is not proof of rhythmic attention it shows that if rhythm exists, the periods of the rhythms tend to have similar values. If hunger is the basis for incubation rhythms, as suggested by Nice (1937), the irregularity and the obscuring of possible rhythm in this species by extremely long attentive periods is understandable since the female is fed frequently and in considerable amounts by the male. Nice (1937) found that the Song Sparrow spent from 20 to 30 minutes on the nest and stayed off from 6 to 8 minutes. Fautin (1941), studying the Yellow-headed Blackbird, noted a fairly definite rhythm. Pitelka (1940) observing the Black-throated Green

Warbler described a rhythmic attention in which the periods lengthened during the middle of the day.

The lengths of the attentive periods during the morning and during the afternoon as well as at the beginning and toward the end of incubation are compared in Table 4. No significant differences in length were found between mornings and afternoons. The morning period for 3–7 days of incubation was significantly less than the (8–12) or (13–17) day morning period, and the (3–7) day afternoon period was significantly less than the (13–17) day period. Differences in inattentive periods were not significant. In the waxwing the instinct to incubate manifests itself before the eggs are laid, increases in intensity with their deposition, and continues to increase slightly until the young are hatched. At 2 nests observed during an average of 11 hours per day for 17 days during egg laying, incubation, and hatching, the percentages

TABLE 4
Attentiveness of Female at Eleven Nests

DAYS OF INCUBATION	MORNING			AFTERNOON		
	Periods	Mean Length	Standard Deviation	Periods	Mean Length	Standard Deviation
			Attentive			
3– 7	79	37.0	26.4	35	42.6	32.1
8–12	35	48.1	31.8	16	51.4	23.6
13–17	41	52.8	37.6	31	58.1	38.7
			Inattentive			
3– 7	91	7.2	—	52	9.1	—
8–12	40	3.2	—	21	2.8	—
13–17	44	5.8	—	35	5.3	—

of attention during observed periods were: 28% and 42% on the day of the first egg, 40% and 61% on the second, 65% and 70% the third, 77% and 78% the fourth, and 87% and 88% on the fifth when the clutches were complete. For the next 3 days the attentiveness increased gradually to 95%, and for the following 9 days varied only from 93% to 97%. The highest percentage of attention noted was 97.3, shortly before hatching. These figures are much above those of any of the 8 passerine species for which comparable data are summarized by Fautin (1941), but do not equal those given by Weston (1947) for the Black-headed Grosbeak in which both sexes incubate.

While male waxwings usually are quite active in bringing food to the nest during incubation, no definite feeding rhythm has been noted. In observations at 1 nest covering a 14 day period, attention intervals were highly variable, ranging from 0.38 feedings per hour to 1.4 per hour. A review of data from 7 nests based on average feedings by the male per hour is as follows: nests

visits decreased from 2.5 per hour on the day the first egg was laid to 0.75 per hour on the day the 5th egg was laid; the visits increased gradually to 1.9 per hour on the day before hatching; the visits were accelerated to 3.1 per hour on the day of hatching. At 1 nest, Gross (1929) reported male visits once every half hour during incubation and Saunders (1911) once every hour. From the standpoint of averages it can be seen readily that the statements of the writers mentioned could be true during some part of the incubation or feeding period, since there appears to be considerable variation in male attention. It is evident that there is a decline in male attention during laying and that after reaching a low ebb on the day after the last egg is deposited in the nest, there is a gradual increase in male nest attention until hatching, so that in a normal 5 egg nest, there is a decrease for the first 5 or 6 days and a gradual increase for about 11 days.

III. Incubation Period

Moreau and Moreau (1940) defined the incubation period as the time from laying to hatching of the last egg. At 2 closely watched nests this period was 12 days and 5 hours. At 6 other nests with less complete records the last egg is known to have hatched between 12 and 13 days. The incubation period has been given by various writers as follows: Crouch (1936) 12–14 days, Gross (1929) 14 days, Bergtold (1917) probably 14 days, Post (1916) 12 days, and Saunders (1911) 12 days. Lea (1942) gave the average incubation period for 18 marked waxwing eggs as 11.7 days, with a maximum of 13 days and a minimum of 11 days. Any of these might be accepted, depending upon the definition of the incubation period and the accuracy of observations.

During 1942, 1945, and 1946 the 12 day 5 hour incubation period in conjunction with the information below on the development of individual eggs in a nest has been used as a basis for the accurate prediction of more than 25 hatching dates of nests where dates of laying were known. Since in the waxwing some incubation occurs during laying, thus exhibiting Bergtold's (1917) "apparent period", an understanding of the incubation period would not be complete without a study of the complete set of eggs in a nest. To determine accurately the developmental period of the eggs, it was necessary to know (1) when each of the set was laid, (2) the time at which each of the eggs hatched, and (3) the amount of time spent by the incubating bird. To determine the time of egg laying, nests were examined early each morning before the eggs were laid and again as soon as feasible afterwards. Usually the observations were continuous and nests were inspected whenever the female left. The order of laying was recorded by marking each egg as laid with India ink.

Crouch (1936) reported that waxwing eggs were laid before 11:00 o'clock in the morning. While this has proved to be true, usually such statements are based on observations which extend from the previous day, and as pointed

out above may involve almost a 24 hour error in laying time. Error can be reduced greatly with more frequent observation. The hour of egg laying was taken as the midpoint (Table 2) between the time of last observation before laying and first observation after laying. The mean egg laying hour (6:29) is an average of the calculated egg laying times and might be considered as the most probable time for an egg to be laid.

The time of hatching was determined much in the same manner as egg laying. The pipping of eggs was often of assistance in determining the approximate time, and the female's habit of eating the shells was of great value in timing the completion. At 2 nests during manipulation of the eggs the India ink numbers which had been marked on them were plainly visible through the telescope, and the identity of the hatched young could be determined. The order of hatching in all cases in which it had been possible to mark the eggs was the same as the order of laying. Hatching is spread over a period of more than 2 days and is not a simultaneous hatching. Six other records were obtained in which hatching spread into the second day. Crouch (1936) and Gross (1929) state that the young hatch at the same time.

The incubation time of the female was determined by multiplying the percentage of observed time the female was incubating on the day by the number of daylight hours at that day of the year. As this would cover only the daylight period, an attempt was made to learn something of night incubation. It was possible to obtain 3 records of nests inspected nightly, following the laying of the first egg. In each case the bird was first found on the nest the night following the deposition of the third egg, and she continued to be present on the nest each night thereafter. With the above 3 factors of the data known it was possible to approximate rather closely the total incubation received by each egg before it was hatched. Table 5 summarizes the incubation of the individual eggs in Nest 41-10A

It will be noted that the lapse in time between the hatching of the first and last eggs is much less than that between laying of the eggs. Nice (1937:122) mentioned this in the relation to the Song Sparrow and related it to the irregularity in the starting of incubation by the female. If there were no incubation until all the eggs were laid, we would expect the eggs to hatch at the same time; however, since incubation increases progressively with laying of the eggs and hatching is spread over more than 1 day, there should be some relation between the two. That a relation does exist is apparent from the fact that the eggs have always been found to hatch in the same order as laid. A comparison of the figures (Table 5) of estimated incubation and intervals at hatching shows that there is a trend toward compensation which however remains incomplete. The earlier incubation, which consists of shorter periods more widely spaced, seems not to be as effective as the later, which is consistently at a higher level, since none of the first 4 eggs hatched quite as far in advance of

the fifth as would be expected from the amount of incubation received in the first few days. In relation to poultry, Jull (1938) states, "The longer that hatching eggs are stored at room temperature before being incubated the longer the time usually required for incubation". This might apply to the partial incubation of first eggs lying in the nest.

The facts as revealed by this study of incubation in the Cedar Waxwing show that it is impracticable to determine any one definite point at which incubation begins. For purposes of comparison with other species the incubation period as defined by Moreau and Moreau (1940) may be satisfactory. This leaves untouched a major problem of development, namely, the factors which control the rate of development of the embryo, upon which further field and laboratory study is needed before satisfactory conclusions can be reached.

TABLE 5
Incubation Data from Nest 41-10A

	EGG 1	EGG 2	EGG 3	EGG 4	EGG 5
Time laid	7/5 6:24 A.M.	7/6 6:38 A.M.	7/7 6:53 A.M.	7/8 6:38 A.M.	7/9 6:47 A.M.
Time hatched	7/19 11:24 A.M.	7/20 7:13 A.M.	7/20 6:56 P.M.	7/21 5:56 A.M.	7/21 11:57 A.M.
Hours in interval between laying and hatching	353.0	336.5	324.0	311.3	293.2
Per cent of incubation on day laid	43.2	63.8	71.6	79.2	90.6
Estimated hours of incubation during first day	6.5	9.6	10.7	11.8	13.6
Estimated hours of incubation at night	0	0	9	9	9
Total estimated hours of incubation before 5th egg	55.1	50.1	40.6	20.9	—
Hours hatched before 5th egg	36.5	28.7	17.2	6.2	—
Hours unaccounted for by difference in incubation	18.6	21.4	23.4	14.7	—

Care of Young

A striking change in male behavior at hatching apparently was set off by visual stimulation when the male saw the young in the nest. The female communicated the presence of the young by rising from the nest. Both spent a few minutes looking down into the nest, after which the male flew away, and the female settled back on the nest. Two developments followed: first, the male, previously having fed the female mulberries or wild cherries, produced on his next visit a white soft material which seemed to consist of a mass of small caterpillars; second, the average of nest visits was accelerated from 1 visit every 30 to 45 minutes to 1 every 15 or 20 minutes. It definitely was known that the male at Nest 41-10A did not see the young before 6:25 A.M., and the first appearance of the new type of food occurred at 7:12 A.M. Also

at Nest 41-10B the male first saw the young at 12:30 P.M., and at his next visit at 12:58 P.M. he brought insect food for the first time. The characteristic pattern of feeding has been described well by Lea (1942: 232).

Attempts to feed the young usually began within 2 hours after the first young hatched and often earlier. At Nest 41-10A, on August 17, only 20 minutes after the young was out of the shell, feeding was attempted. Gross (1929) saw feeding on the first day. Feeding progresses with considerable regularity after the first day. Post (1916) gave a good report of second-day feeding. From the third day on the food brought to the young is largely fruit. Lea (1942: 233–234) gives data on this somewhat unusual condition.

In regard to brooding all observations during this study indicate that the male did not brood. The female broods almost continuously for at least 3 days as 2 records for the third days after hatching showed the female to be on the nest for 89.6% of the observed time and 93.7% of the observed time (8–10 hours), respectively. From the third or fourth day after hatching a considerable decrease in the nest attention of the female was noted. The female does not desert the nest area as brooding wanes but perches in the nest area and guards the young. This guarding behavior is noticeable particularly after the eighth day. At Nest 45-08B on August 20, the eighth day, the female spent more time standing near the nest rim or perched in the tree than actually on the nest and on 1 occasion drove a grackle from the nest area. The fact that the young are becoming more active might play a part in reduction of brooding. Unusual stimuli may result in a recurrence of brooding as at Nest 46-07A when the female stayed on the nest continuously during the morning of the tenth nestling day in response to a heavy rain.

As brooding diminishes the female starts to make feeding trips. Feeding trips by females during the first 5 days usually are infrequent. At 2 nests feeding trips were not noted the first 2 days during 8 hour observation periods. One female captured a mayfly while brooding and attempted to feed it to the young on the third day but made no other feeding trips in a 3 hour observation. During a 4 hour observation no feeding trips by another female were observed on the third day.

Both sexes are active in nest sanitation. After feedings the adults probe the anal areas of the young and invariably eat the fecal sacs. During the first 10 days this behavior occurs as frequently as feeding (see Fig. 3) but then decreases when the young begin to defecate in or over the nest rim. The Figure 3 published by Lea (1942) is typical of the process as seen at Put-in-Bay. An excellent description of the nest sanitation behavior was given by Littlefield and Lemkau (1928).

The relationships between the brooding of the female and the feeding cycles of both males and females are shown in Figs. 3 and 4. The graphs of feeding are based on averages of several observations taken at 8 nests involving 90.5

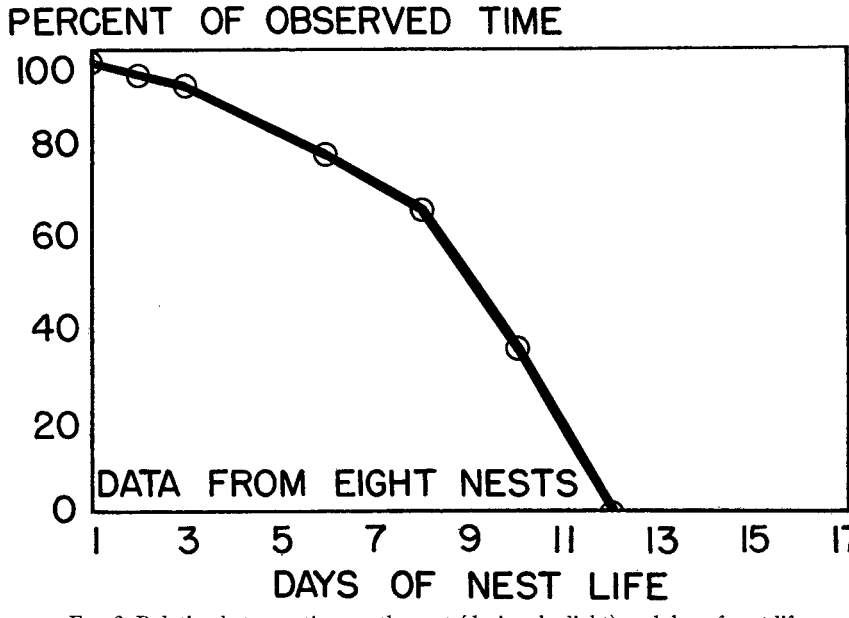

FIG. 3. Relation between time on the nest (during daylight) and day of nest life

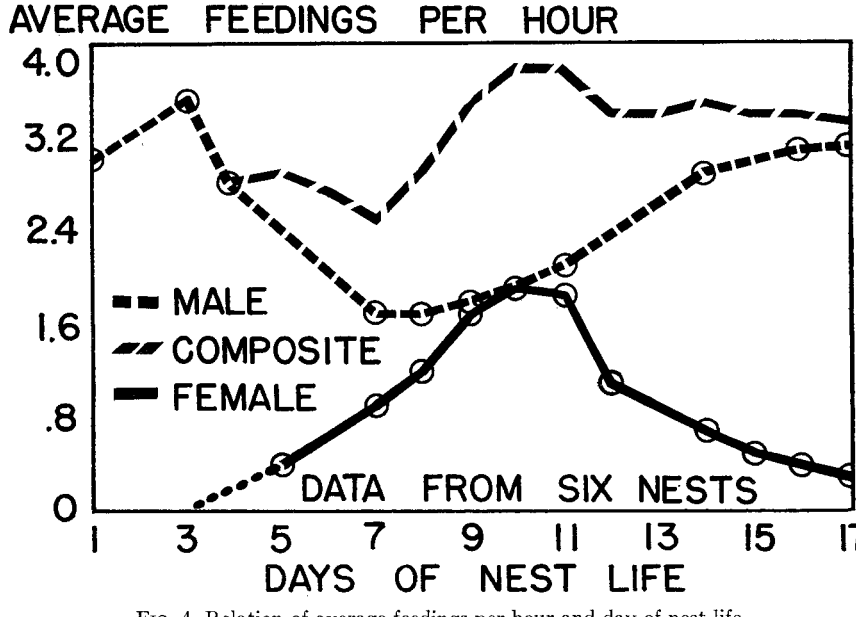

FIG. 4. Relation of average feedings per hour and day of nest life

hours of observations and are illustrative of the trends which have been noted in the field. During the first 5 days, when the female spends 75% or more of the daylight period in brooding, little time is available for feeding activity. As brooding decreases, feeding by the female increases until the latter part of the period, when the feeding activity is reduced or in some cases absent. This clarifies the behavior of the sexes as described by Littlefield and Lemkau (1928) who noted that both birds brought food to young on the ninth day but as late as the twelfth day found 1 bird perched in a tree while the other did most of the feeding. Post (1916) also did not specifically mention the presence of both birds at the nest after the tenth day.

The frequency of feeding by the male generally is inverse to that by the female. There is a sharp increase at hatching, followed by a decline in the early part of the nestling period, and then later by a gradual increase at the time of fledging. The composite graph line (Fig. 4) is the sum of feeding visits by the male and female. It should be pointed out that with the interaction of male and female feeding, the food delivered to the young is very probably proportional in amount to the requirements of the various growth levels of the young. Following the composite graph line it can be seen that during the period of rapid growth of young (days 4–10, Fig. 4), the total of food trips per hour increases. When the growth rate of the young diminishes, the rate of feeding also levels off but is maintained at a high level. The reduction of male feeding trips during the first 5 or 6 days may not involve a reduction in quantity of food since at the third day, as stated, there is a change from insect food, which probably is not regurgitated and thus carried only in small amounts, to fruit. Considerably more of the berry or fruit food can be carried per trip.

The young are fed by the parents for 6 to 10 days after fledging. In the 7 pairs, Table 1, which renested only the males fed the fledged young. Three cases were observed at Put-in-Bay in which females successfully reared young when males disappeared. At 2 nests where females were lost both males deserted the young.

Development of Young

The young of 1 nest were studied twice daily, at 5 A.M. and 5 P.M., from hatching until fledging. These data supplemented by other observations at 9 nests form the basis for a brief outline of development.

The newly hatched young were completely naked when examined under a binocular and the skin was soft and pink. The skin began to darken especially on the femoral, sacral, and primary regions when the young were half a day old. By the evening of the second day the rectrices had penetrated the skin slightly, and feather sheaths had ruptured the skin in all the principal feather tracts on the fifth day. The most noticeable change in plumage occurred on the ninth and tenth days when the feather sheaths rapidly disintegrated and the young

suddenly appeared in almost full feather (Herrick, Fig. 137). The plumage was quite complete by the fourteenth day although the rectrices were not full length.

During the first days of nest life the main activities were gaping and defecating. On the third day the young were able to maintain a sitting position (Herrick, Fig. 136) and also to produce a faint buzzing call note. On the sixth and seventh days wing movements were observed and the eyes were partially opened. By the ninth day the birds gaped at the hand and gave very audible begging calls. The legs were sufficiently developed that banding was feasible. During the eleventh day of nest life the young answered calls of their parents and "froze" in response to warning notes. They stood up, gaped, and begged when other waxwings gave calls in the vicinity. On the twelfth day and after

TABLE 6

Individual Weights of Young—Nest 46-22

DATE	"YELLOW" WEIGHT		"GREEN" WEIGHT		"BLACK" WEIGHT		"TAN" WEIGHT	
	A.M.	P.M.	A.M.	P.M.	A.M.	P.M.	A.M.	P.M.
Aug. 10		2.7g.		3.2g.		3.2g.		
11	3.5g.	5.4	3.6g.	5.2	4.0g.	6.2		3.2g.
12	5.5	7.9	5.3	8.1	6.7	8.7	3.7g.	5.4
13	7.4	11.1	8.2	11.9	8.1	12.9	5.4	8.3
14	10.9	14.9	10.7	15.6	11.8	16.3	8.5	12.6
15	14.1	17.8	14.2	19.1	15.1	20.4	11.1	17.0
16	16.3	22.5	18.8	22.2	18.3	23.5	14.5	20.2
17	20.9	26.9	21.3	25.5	22.4	27.3	18.4	24.3
18	23.6	28.3	24.5	29.6	25.0	30.6	22.6	28.5
19	26.4	30.8	28.5	30.7	28.7	31.6	27.1	31.7
20	29.1	30.1	30.1	31.6	29.9	31.7	29.1	31.4
21	29.8	32.0	31.0	33.5	31.0	33.2	30.3	34.5
22	32.4	35.0	31.6	33.0	31.0	35.2	33.4	36.2
23	33.5	32.2	32.6	34.0	33.3	33.9	33.7	35.6
24	31.2	32.8	30.4	34.3	32.6	33.8	34.4	35.8
25	Fledged		Fledged		Fledged		Fledged	

there was much activity demonstrated by stretching, wing movements, and preening. At this time the young may be flushed easily although until the fifteenth day are not able to maintain level flight. The general behavior and growth agreed favorably with descriptions by Post (1916) and Saunders (1911).

Table 6 summarizes the weight changes of young during nest life. Review of this table shows the rapid weight gain of the 46-16B nestlings during the first 10 days. Using the morning weights, which were subject to less fluctuation and thus give a more exact representation of the weight, it can be calculated that the average daily gain in weight for these days is 3.1 g. per day. This is a gain in weight per day approximately equal to the average hatching weight of 3.1 g. After the tenth day there was a leveling off of weight gain followed by a drop just before the young left the nest. The 4 fledglings gained weight with equal rapidity and individual weight curves drawn from the data in Table 6 show

similar sigmoid curves. Schrantz (1943) studying the Eastern Yellow Warbler shows graphs indicating a similar rapid growth period followed by decelerated growth as the young left the nest. He stated also that, "The last hatched of any nest may gain weight as rapidly as the first hatched". The overnight weight loss of the 46-16B nestlings was not excessive when compared with other species. Nice (1929) found that captive Mourning Doves lost between 8 and 9% of their early morning weight. Taber (1928) found an average of 7.7 per cent overnight weight loss for 15 species, and Kendeigh (1934) noted a 10 per cent loss in English Sparrows and a 14 per cent loss by House Wrens. The maximum relative weight loss of these young occurred during the sixth and seventh nights when the weight loss percentages were 9.08 and 10.23, respectively. For the first 3 days, overnight weight loss was minimal. Starting with the third night the weight loss increased rapidly, averaging 8 per cent for the third, fourth, and fifth nights. Weight loss continued about this level through the ninth night and then underwent a reduction to about 5 per cent during the following 4 nights. On the fourteenth night a sharp increase to 8.2 per cent weight loss was noted. Further study of these weight losses should reveal corresponding changes in the metabolism of the young.

Following the progress of the young after fledging was made possible by banding. For the first 3 days after leaving the nest the young are very dependent upon the parents, stay close to the nest during the day, and roost nearby at night. In 2 instances the young were not seen farther than 75 feet from the nests during the first 2 days, and in 6 cases the birds were 100 yards or less from the nests on the first 3–4 days. These young roosted in the area at night for the first 3 days, often perching close together. The movement away from the nest after this early period is probably related to the ability of young to feed. On the first day out of the nest the birds often pick at matter on leaves nearby. On the second day there is some improvement and one of the young (18 days old) was noted walking up and down a limb hunting and eating insects. This young was alert and fast in picking up food and on 1 occasion wiped its bill in adult fashion after eating. On the third day after leaving the nest the fledglings fed more by themselves. This feeding was particularly noted at 46-15A where 19 day old young were seen alternately eating currants and being fed by the male in Webster's orchard. The young are fed in part by the parents for 7–8 days after leaving the nest. During the first days out of nest the fledglings had some difficulty in landing, but by the fifth or sixth day they controlled themselves almost as well as the adults. Young at 46-15A fledged July 18 and were observed July 23 flying and handling themselves well. At this time their tail feathers were considerably developed, a structural factor probably important in this behavior change because landing precision of 3 adult birds noted with mutilated rectrices was also reduced. Nice (1941a) noted landing difficulty in her captive waxwing until it was almost 4 weeks old.

Independence probably is attained by the age of 25 days; almost certainly by

30 days. At least after this age the fledglings have not been observed being fed by the parents and have left the nest area. After independence is attained the young form small flocks which fly about feeding and catching flies. These flocks are seen in the latter part of July and early part of August. Instances of these juvenile flocks are cited under "Social Behavior". Toward the end of August these flocks may be composed of both adults and young. Crouch (1936) noted mixed flocks in late summer.

Renesting

At Put-in-Bay there is reason to believe that under favorable conditions most waxwings would rear 2 broods of young in a shorter span of time than might be expected since some of the activities at both nests may proceed concurrently. Of 8 pairs of waxwings which were together at the fledging of the first brood and in which 1 or both birds were banded and their identity definitely known, 7 were found rearing a second brood. These 7 pairs (Table 1) demonstrated a considerable overlap of activity at the 2 nests. During observation of first nests it appeared that the reduction of brooding during later nest life coincided with the resumption of courtship. Courtship behavior may appear after the seventh nestling day. Among 6 of the pairs listed courtship was seen once on the eighth day, twice on the ninth day, thrice on the the tenth day, and consistently in all by the thirteenth day. Building started within a day of courtship in the 4 cases where starting of the second nests was observed. Pair 46-07A was noted picking up building materials on the eighth nestling day, the same on which they resumed courtship. During this phase of the nest cycle the male is at the peak of activity. In addition to feeding the first young and courting the female he builds with early season vigor on the second nest. It was during this period that the male of 46-07A was trapped while obtaining nesting materials for the second nest. This bird was caught and banded at 12:52 P.M. July 21 and was seen at 7:22 A.M. July 22, feeding the young of the first nest. Observations during the day showed him to be building, courting the female and feeding the young about once every 20 minutes. During the afternoon from about 3:52 to 4:52 the male made either a feeding or building trip once every 7 minutes, which exceeded the female in building and feeding trips about 5 to 1. As mentioned under "Care of Young" the attention of the female to the first nest decreases at this time; however, as egg laying at the second nest approached the female became more active in building at the second nest. The resumption of begging behavior by the female occurred also.

The laying of the first egg in the second nest varies from the day before fledging at the first nest to 3 days after. The number of eggs in second nests tends to decrease slightly, there being an average of 4.57 eggs per nest in the first nests and 3.86 eggs per nest in the later ones . This corresponds with the data given previously on early season and late season nests.

With the exception of the male activity in feeding the first young the nesting behavior at the second nest is similar to that of the first. After 4–5 days when the young have moved away from the nest it is identical. In the later part of the second nesting the activity of the female in feeding the young is reduced as at the first nest but no further courtship behavior between the pair has been seen. How long the family remains together and what relationships exist are unanswered questions, requiring additional data. Theoretically, if the nesting cycle of a waxwing were to be repeated, 2 broods would be reared in about 75 days from beginning of construction of the first nest. The data from Table 1 show that Cedar Waxwings can nest and fledge 2 broods in from 60 to 69 days, or an average of 64.67 days. This rapidity of reproduction results from a definite overlapping of the 2 nesting cycles, in which building of the second nest may appear as much as 7 days before fledging of the first young. Frequently egg laying may take place in the second nest before the young of the first are fledged. At the nests shown in Table 1, attempts to trap and band the birds were made when second courtship should have recurred, a time probably critical to the beginning of the second nest, and the removal of this interference might further condense the production time of 2 broods. The data indicate that in a nesting population of waxwings, nesting overlap is certainly common, and with no interference it would occur regularly as part of the breeding cycle. Figure 2 supports this conclusion since the date of laying of first eggs in 104 nests reveals a peak from June 20 to 26 and a corresponding peak from July 20 to 28. The average time lapse between the known first and second nests was 29.84 days.

The overlapping of first and second nests is made possible by the tremendous activity and close cooperation of the pair. Two conditions notable in the behavior of waxwings which seem to be particularly involved in bringing about this relation are: the maintenance of the bond between the pair, and the assumption of the feeding of the young by the male during the latter part of the nestling period. Certainly the first factor is obvious since continued contact between the pair would facilitate courtship. In many species, i.e., Song Sparrow (Nice, 1937), English Robin (Lack, 1946), and House Wren (Kendeigh, 1941), territorial behavior tends to hold the pair together. In the waxwing where territory is not a completely isolating mechanism, the extended courtship behavior probably is the binding factor.

In regard to the second factor, Kendeigh (1941: 118) pointed out that male attention at the first nest aided remating for a second brood since the physiological condition and behavior patterns could be maintained in adjustment. This seems to apply in waxwings especially because of the relation between feeding and courtship. Fig. 4 is a graphic summary of the attention of the pair. Here the reduction of brooding by the female can be compared with her increased feeding activity during the early part of nest life. After the tenth day

the high feeding activity of the male concurs with a reduction of activity of the female thus permitting physiological readjustments involved in egg production. The fact that such adjustments are in progress is evident in the changes in behavior at this time. The material fact that eggs are found in the second nest before or at the time of fledging is proof that the changes are complete and the second nest is well under way.

Social Behavior

Social behavior perhaps is not as well developed in birds as in some groups of animals, but it is definitely apparent in the activities of birds when groups, under given conditions, act as a behavior unit rather than as several individuals. Cedar Waxwings demonstrate social characters throughout the year, except as stated above, not in the breeding territories.

Large flocks of waxwings are often seen during the fall, winter, and early spring. The compactness of the flock while in flight, perching, bathing, or feeding, and the unending communication by means of the "flock call" are evidences of gregarious behavior. Typical of many similar observations in the literature are those of Staebler and Case (1940) and Feltes (1936). An excellent example of flock unity was observed by Dr. Charles F. Walker at Put-in-Bay when 1 of a group of waxwings was struck and killed by a Sharp-shinned Hawk (*Accipiter striatus*). The birds "froze" as a group and shortly flewaw ay with extreme speed in a compact body.

During the breeding season large flocks are unusual but small social units composed of birds nesting in the same area are common. Due to the shape of the island, 2 definite groups could be identified at Put-in-Bay, one from Peach Point and the other from Webster's orchard. These groups often fed together in a large mulberry tree but behaved as separate units, arriving and departing at different times. The groups were identifiable by certain members which were color banded. In the vicinity of the nests known individuals and pairs have been seen joining or separating from the group as they passed by on the way to or from the feeding ground. Evidence of social behavior is found also in the change of feeding areas noted during the season. Under the discussion of territorial behavior an example of 6 waxwings feeding on wild strawberries was cited. These birds appeared in this spot, not more than 2 square yards in area, in not over 3 minutes time while the observer was standing only about 75 feet distant. Obviously something in the behavior and calls of the first birds present brought forth an aggregatory response on the part of the others. On a larger scale, observations during 5 summers have shown that the feeding areas of Peach Point birds shift in a regular predictable pattern throughout the season. It is understandable that birds should respond more strongly to certain foods, but it is not probable that acting in complete independence the majority of the Peach Point nesting birds would locate these food areas so rapidly as some of them were

over 0.75 mile apart. The mere gathering of food seems inadequate to account for the presence of the color banded female 46-11 feeding with the flock almost a mile distant from the place where she normally gathered food for her young. Saunders (1911) and Nice (1941a) commented on the group behavior of waxwings during the nesting season.

Social behavior is apparent rather early in the life of a waxwing. There seems to be a definite tendency of fledglings to remain together after leaving the nest and to join with the young of other nests in the area into local groups. In 2 instances the banded young from neighboring nests formed a small flock on the 3–4 day after fledging. Small groups of young are commonly seen flying about or feeding after the middle of July. The largest group of juveniles observed in a definite flock was noted on the east point of South Bass Island August 9, 1945, about 6:30 P.M. There were about 30 well-developed young flycatching from a tree and from light wires along the road. Flocks of young are common until the end of August when mixed groups may be seen. Crouch (1936) noted mixed age groups in late summer. The social nature of waxwings was demonstrated by the captive young which at regular intervals fed, bathed, sunned, and flew consistently in the cage as a group.

The Cedar Waxwing is an example of a social species during the non-breeding season but which in summer exhibits both social and territorial activity. The integration of these phases of behavior is an important feature in the life history of this bird since it is intimately related to reproduction and food habits and should be considered further.

The following elements in territorial behavior have been pointed out. First, the pairs are formed when the selection of the territory is made, and both birds are active in its selection. Second, much of the courtship takes place within the territory. Third, the male is more vigorous in defense of the territory but the female is also active against either male or female intruders. Fourth, while the territories are small they are strongly defended and do exist since away from them no intra-specific fighting is observed. These conditions of behavior apparently function in limiting interference with reproduction, as suggested by Nice (1941b). That crowding or interference does limit nesting behavior was demonstrated in 1942 with the captive waxwings. These birds, though kept in a cage 8 ft. by 4 ft. by 4 ft., seemed to be normal in their activity and gave indications of reproductive behavior fairly early in the season. Two nests were started in the cage but so much fighting and confusion resulted that little progress resulted. Attempts at courtship were frustrated continually by direct interference of other birds. When 5 of the birds were removed the remaining 2 finished a nest, the female laid 2 fertile eggs, and 1 young was raised. The activity of the pair and the young in all respects noted was identical with non-captive birds.

The function of social behavior in the waxwing seems to be related to the

highly seasonal food. The social responses of fear, sunning, tolerance in the group, and apparent recognition of group members culminate in units which enhance the opportunities of the individuals in obtaining food. Some attempt has been made to determine the factors which control the interaction of these 2 types of behavior. The territorial behavior of birds has been related generally to 2 major factors: seasonal physiological changes and the psychological effect of familiarity with a given area. Blanchard (1941: 12) associated the change from a social level of winter behavior to the more territorial activity which accompanied seasonal physiological changes. Nice (1943: 83) mentions a similar condition, the flocking of birds in cold weather. Physiological change is certainly in part responsible for territorial behavior in waxwings and may account for seasonal variation in a waxwing's aggressiveness, but it could scarcely account for the variation between behavior of a waxwing in the territory and at the feeding place. The factor of nearness to some central part of the territory, usually the nest (Davis, 1941), as increasing the defensive response seems more adequately to explain this change. The behavior of the female is illustrative in this regard since cases were mentioned in which sometimes a mere infringement of territory was disregarded, but intruders approaching the nest were driven off Since the territory is small the basic gregarious behavior could function away from the territory and the stimulus of area familiarity could bring into play the territorial level. An additional factor making possible the interaction of territorial and social behavior is the apparent absence of fighting in defense of mates. Such a condition permits close contact in flight and at feeding areas. On the other hand this might have led to reproductive confusion had not a particularly binding relationship developed between the pairs. When we consider the rather low mortality and the high nesting success of the waxwing it would seem that this integration of the territorial advantage of little nest interference with the normal advantages of social existence make for a rather high degree of efficiency. This efficiency in reproduction as well as in time has been stressed in various parts of this article. Late starting of nesting, cooperation of pair members in nesting activities, contraction of time in brood production, and the integration of territorial and social behavior are conditions remarkably adapted to the food habits of the species. The ceremonies of pairing, courtship, and bond maintaining are associated with food. It cannot be overlooked that the behavior of the waxwing centers in the problem of food. Fruit, which is the major item of diet, is highly seasonal in its availability and in addition is extremely variable in quantity from year to year. The entire sequence of waxwing behavior during the reproductive cycle seems to be admirably adapted to the efficient utilization of this food supply.

Nest Success

Over 200 nesting attempts have been observed throughout the 5 years; however, only 60 are considered here. Fifty-six nests were lost at various stages

as the result of observational interference and the remainder never contained eggs. Of this remainder, losses during nest building were: 54.8% caused by storms, 33.3% by desertion of unknown origin, and 12.0% by incompleteness of data. Sturm (1945) found weather to be a major cause of early nest loss over this same area.

Of the 245 eggs laid, 22.9% did not hatch, but only 4.6% had no observable development. Of the 60 nests in which eggs were laid, 76.7% fledged at least 1 young. The greatest cause of nest loss after the eggs were laid was predation. Eggs either were punctured or stolen from 4 nests, and young were taken from 3. Storms accounted for 4 nests. Mites probably caused desertion of 2 nests,

TABLE 7

Frequency of Eggs, Young Hatched, and Young Fledged

EGGS PER NEST	NESTS	YOUNG HATCHED	NESTS	YOUNG FLEDGED	NESTS
1	1	0	12	0	15
2	4	1	0	1	0
3	9	2	4	2	6
4	21	3	10	3	9
5	25	4	19	4	20
6	0	5	15	5	10
Totals	60		60		60
Mean...4.08		3.15		2.82	

TABLE 8

Annual Nesting Success

	YEAR					TOTAL
	1940	1941	1942	1945	1946	
Number eggs laid	53	50	43	36	63	245
Per cent young hatched from eggs	62.3	62.0	83.7	100	84.1	77.1
Per cent young fledged from eggs	56.3	48.0	81.4	88.9	82.5	69.8

which were the only ones ever found with mites. At both of these nests the birds had been observed obtaining nesting materials from old nests of grackles which were thought to be the source of the infestation. The cause of loss in the 1 remaining nest was unknown. Cowbird (*Molothrus ater*) eggs were not found in any of the Put-in-Bay waxwing nests. The considerable decrease of loss due to storms during this period can be attributed to the presence of the female in the nest. In the 60 nests, there was an average of 4.08 eggs laid per nest, 3.15 young hatched per nest, and 2.82 young fledged per nest (Table 7). Table 8 summarizes the data by years and as a whole.

The success of these nests is somewhat higher than that reported by Nice

(1937) for 11 studies of open nesting passerine species, and it is well above that of Lea (1942) in his study of waxwings at Douglas Lake, Michigan. His figure, 47.7% success, was based on nests producing fledglings rather than on a comparison of eggs laid to numbers of young fledged. From his Table 1, 25 young were fledged from 44 eggs laid, or 56.82%, a figure more comparable to the data presented here.

In reviewing the nesting cycle of these birds it should be recalled that once egg laying starts the nest is very infrequently left unattended by the birds. With the close incubation by the female and the attention of the male throughout incubation and feeding of young, there is good reason to believe that a high percentage of success should result. Since practically all nests known in this area were observed or checked in some manner there is a possibility that certain nests discarded because of interference would have been lost through normal desertion. This would tend to result in an increase in the percentage of nest successes. On the other hand failure to appreciate interference with nests could have been responsible for figures of lower percentages. To be valid, nesting success measures probably should be based on even larger samples with the factor of interference reduced to a minimum.

Summary

A study of the Cedar Waxwing was conducted at Put-in-Bay, Ohio, during 1939 and 5 additional summers. The Put-in-Bay area consists mainly of summer residences, old orchards, gardens, and vineyards. The objective was to determine the relationships between individuals or groups and their environment. Birds were trapped and color banded for identification.

An erratic winter population is present in this region in most years but never in sufficient numbers to account for the nesting population which arrives during the latter part of May. Nesting attempts are noted immediately but many of these early nests are not successful, and the height of the reproductive season is delayed until the middle of June. The movements of the birds throughout the summer are related to the seasonal fruits which compose a major part of the diet of both adults and young.

Pairing probably occurs in the flock or soon after arrival of the birds. Sex recognition involved in pairing is based on behavior probably instigated by the male. When the female responds a highly stereotyped "courtship dance" occurs which often is followed by fast circular flights. Following pair formation the members of a pair associate almost constantly and may stay together throughout the breeding season. The cichlid fish type of pairing behavior (Lorenz, 1937) seems to best characterize the waxwing, and no sexual dominance is apparent.

Small territories are established in which mating and nesting occur. Both sexes defend the territory although the male is more aggressive. Defense of the territory diminishes during feeding of the young. The same territories may be

maintained throughout the breeding season, although occasionally shifting does take place when second nests are built.

Courtship follows pairing and progresses through 2 phases: (1) a bond-strengthening display which culminates in copulation, and (2) a bond-maintaining display which continues throughout much of the nesting cycle. The focal point of both phases of the courtship display is the presentation of food, either actual or symbolic.

A distinct advertising song is not present in the Cedar Waxwing although several call notes are given by both sexes. Voice functions in individual and species recognition and is important in pair relationships, as well as in group activities.

The nest site is determined by the pair; the female, however, seems to be more active in its selection. Nests are constructed of various plant fibers and small twigs. They are somewhat bulky in appearance but usually are supported securely in a horizontal limb fork. Both sexes build and nests are completed in an average of 5.55 days. Egg laying takes place between 5:00 A.M. and 8:00 A.M. Early season nests have more eggs, averaging 4.5 per nest, while later clutches average 4.0.

Incubation is performed entirely by the female. During incubation attentiveness for the day is heightened as the incubation period progresses. The tendency to incubate manifests itself before egg laying and gradually increases as the eggs are laid. After the last egg is laid, attention rarely falls below 90% of observed daylight time. Periods of attention by the female are of unusual length, often extending more than 2 hours. While incubating, the female is fed frequently by the male either at the nest or on a perch near by. Females make some food forays alone. The eggs hatch over a period of 2 days, in the same order as laid, and the incubation period is 12 days, 5 hours (293 hours), using the last egg as a standard. The first eggs laid seem to receive more incubation before hatching than do the later ones.

At hatching there is a change in the type of food presented by the male at the nest. The fruit which the male has brought previously to the female is replaced by insect food, which both parents feed to the young. This feeding of insect food continues for approximately 3 days, after which fruit is again brought to the nest. Both sexes remove the fecal sacs ejected by the nestlings. Females brood closely for the first 3 or 4 days, after which brooding diminishes, ceasing entirely by the twelfth day.

As brooding diminishes the female gradually increases feeding of the young until the tenth day, when a rapid decline is noticeable. An increase in male attention at hatching is continued for the first 3 days, and then is followed by a decline until the seventh day. During the latter part of the nestling period the male assumes the major role in caring for the young.

Newly hatched young are devoid of natal down. Their skin color at first is

pink, but areas in which feather development takes place become darker on the first day. By the tenth day the plumage of the nestlings is fairly well developed, although it probably is not complete until a week after the young have left the nest. The nestlings gain weight rapidly for the first 10 days, less rapidly for the next 3 days, and decrease in weight shortly before fledging. The length of the nestling period averages 15.9 days, and young which remain in the nest for the full term are able to fly well upon leaving the nest. The young tend to stay together and are fed by the parents for at least a week after fledging. The fledglings from several nests form small flocks which often feed in the nesting area.

About the ninth day of nest life the first phase of courtship may recur and a second nest be built, in which eggs are laid before or soon after the first young fledge. The average fledgling time for 2 broods is 64.67 days from the beginning of building of the first nest. First broods fledge on the average in 34.83 days; the second follow in 29.84 days. Overlapping of broods results from the tremendous activity and close cooperation of the pair.

Cedar Waxwings are gregarious and even during the breeding season display social characteristics when away from their territories. Groups of the birds, seemingly local units, fly from the nesting regions to the feeding areas where they associate without discord. Social behavior is apparent early in the life of the waxwing when young birds tend to form small flocks. The integration of social behavior with territorialism is an important factor in the ecology of waxwings since nest life is free from interference, yet group activity enhances the procurement of food. Many of the distinctive features in the reproductive behavior of these birds seem to be related to the seasonal character of the food upon which they exist and upon its very local distribution.

As compared with other passerine species which nest in open situations, waxwings are fairly successful in the production of young. Of 60 nests which contained eggs, 76.7% fledged 1 or more young. Of 245 eggs laid, 77.1% hatched and 69.8% young fledged. The eggs are 95.4% fertile. The relatively high rate of success is due in part to the large amount of time which the adults spend near the nest after the eggs are laid. No parasitism by the Cowbird (*Molothrus ater*) has been noted.

REFERENCES

ALLEN, A. A. 1930. Cherry bird—the Cedar Waxwing. *Bird-Lore*, **32:** 298–307.

ALLISON, A. 1906. Notes on the winter birds of Hancock County, Mississippi. *Auk*, **23:** 46.

BAGG, A. C., AND S. A. ELIOT, JR. 1937. Birds of the Connecticut Valley in Massachusetts. Northampton, Mass.: The Hampshire Bookshop, 813 pp.

BENSON, M. B. 1920. The Waxwings' rag bag. *Bird-Lore*, **22:** 286–287.

BERGTOLD, W. H. 1917. A study of the incubation periods of birds. Denver, Colo.: Kendrick-Bellamy Co., 109 pp.

BLANCHARD, B. D. 1941. The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. California Pub. Zool.*, **46** (1): 1–178.

BRAND, A. R. 1938. Vibration frequencies of passerine bird song. *Auk*, **55:** 263–268.
BROWN, N. C. 1906. A great flight of Robins and Cedar-birds. *Auk*, **23:** 342–343.
BRYENS, O. M. 1943. A Cedar Waxwing recovery. *Bird-Banding*, **14:** 46.
BURLEIGH, T. D. 1923. Notes on the breeding birds of Clark's Fork, Bonner County, Idaho. *Auk*, **40:** 653–665.
CAMERON, E. S. 1908. The birds of Custer and Dawson Counties, Montana. *Auk*, **25:** 39–56.
COOKE, M. T. 1937. Some returns of banded birds. *Bird-Banding*, **8:** 53.
CORE, EARL L. 1948. The flora of the Erie Islands. F. T. Stone Lab. Contr. **9:** 1–106.
CROUCH, J. E. 1936. Nesting habits of the Cedar Waxwing (*Bombycilla cedrorum*). *Auk*, **53:** 1–8.
DAVIS, D. E. 1941. The belligerency of the Kingbird. *Wilson Bull.*, **53:** 157–168.
FAUTIN, R. W. 1941. Incubation studies of the Yellow-headed Blackbird. *Wilson Bull.*, **53:** 107–122.
FELTES, C. H. 1936. Trapping Cedar Waxwings in the San Joaquin Valley, California. *Condor*, **38:** 18–23.
GRINNELL, J. 1901. The status of the Cedar Waxwing in California. *Condor*, **3:** 146–147.
GROSS, W. A. 1929. A Cedar Waxwing study in northern Michigan. *Bird-Lore*, **31:** 178–182.
HERRICK, F. H. 1935. Wild birds at home. New York: D. Appleton-Century Co., 345 pp.
JONES, L. 1910. The birds of Cedar Point and vicinity. *Wilson Bull.*, **17:** 97–115.
JULL, M. A. 1938. Poultry Husbandry. New York: McGraw-Hill, 548 pp.
KENDEIGH, S. C. 1934. The role of environment in the life of birds. *Ecol. Mon.*, **4:** 299–417.
1941. Territorial and mating behavior of the House Wren. *Illinois Biol. Mon.*, **18** (3): 1–120.
LACK, D. 1940. Courtship feeding in birds. *Auk*, **57:** 169–178.
1946. The life of the Robin. London: H. F. & G. Witherby, Ltd., 224 pp.
LEA, R. B. 1942. A study of the nesting habits of the Cedar Waxwing. *Wilson Bull.*, **54:** 225–237
LINCOLN, F. C. 1929. An interesting Cedar Waxwing return. *Bull. Northeastern Bird-Banding Assoc.*, **5:** 155.
1936. Returns of banded birds. *Bird-Banding*, **7:** 126.
1939. The migration of American birds. New York: Doubleday, 189 pp.
LITTLEFIELD, M. J. AND F. LEMKAU. 1928. History of a Cedar Waxwing family. *Bull. Northeastern Bird-Banding Assoc.*, **4:** 85–89.
LORENZ, K. Z. 1937. The companion in the bird's world. *Auk*, **54:** 245–273.
MAYNARD, C. J. 1928. Notes on the Cedar Waxwing. *Bull. Northeastern Bird-Banding Assoc.*, **4:** 73–76.
MCCOY, H. 1927. A Waxwing ceremony. *Bird-Lore*, **29:** 188–189.
MEARNS, E. A. 1878. A description of unusually developed individuals of three species, and remarks on uncommon plumages in several others, taken near West Point, N. Y. *Bull. Nuttall Ornith. Club*, **3:** 69–72.
MERRILL, J. C. 1898. Notes on the birds of Fort Sherman, Idaho. *Auk*, **15:** 14–22.
MOREAU, R. E. AND W. M. MOREAU. 1940. Incubation and fledging periods of African birds. *Auk*, **57:** 313–325.
NICE, M. M. 1929. Some weights of Mourning Doves in captivity. *Auk*, **46:** 233–234.
1937. Studies in the life history of the Song Sparrow, I. *Trans. Linnaean Soc. N. Y.*, **4:** 1–247.
1941a. Observations on the behavior of a young Cedar Waxwing. *Condor*, **43:** 58–64.
1941b. The role of territory in bird life. *Amer. Midl. Nat.*, **26:** 441–487.
1943. Studies in the life history of the Song Sparrow, II. *Trans. Linnaean Soc. N. Y.*, **6:** 1–328.
ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee. *Auk*, **58:** 314–333.
PITELKA, F. A. 1940. Breeding behavior of the Black-throated Green Warbler. *Wilson Bull.*, **52:** 3–18.

POST, K. C. 1916. The Cedar Waxwing (*Bombycilla cedrorum*) during July and August 1916. *Wilson Bull.*, **23:** 175–193.

SANBORN, C. C. AND W. A. GOELITZ. 1915. A two-year nesting record in Lake County, Illinois. *Wilson Bull.*, **22:** 434–448.

SAUNDERS, A. A. 1911. A study of the nesting of the Cedar Waxwing. *Auk*, **28:** 323–329.

SCHRANTZ, F. G. 1943. Nest life of the Eastern Yellow Warbler. *Auk*, **60:** 367–387.

SCOTT, W. E. D. 1889. A summary of observations on the birds of the Gulf Coast of Florida. *Auk*, **6:** 318–326.

SHAW, W. T. AND A. E. CULBERTSON. 1944. A flock of Cedar Waxwings meets tragedy. *Condor*, **46:** 205–206.

SILLOWAY, P. M. 1904. Afield at Flathead. *Condor*, **6:** 12–14.

SMITH, A. P. 1915. Birds of the Boston Mountains, Arkansas. *Condor*, **17:** 41–57.

STAEBLER, A. E. AND L. D. CASE. 1940. Community bathing of the Cedar Waxwing. *Wilson Bull.*, **52:** 281.

STURM, L. 1945. A study of the nesting activities of the American Redstart. *Auk*, **62:** 189–206.

TABER, W. B. 1928. A method to determine the weight of food digested daily by birds. *Auk*, **45:** 339.

THOMAS, R. H. 1946. A study of Eastern Bluebirds in Arkansas. *Wilson Bull.*, **58:** 143–183.

TINBERGEN, N. 1939. The behavior of the Snow Bunting in spring. *Trans. Linnaean Soc. N. Y.*, **5:** 1–95.

WARREN, B. H. 1890. Report on the birds of Pennsylvania. Harrisburg, Penn.: Meyers, 433 pp.

WESTON, H. G., JR. 1947. Breeding behavior of the Black-headed Grosbeak. *Condor*, **49:** 54–73.

WHITTLE, H. G. 1928. The biography of a Cedar Waxwing. *Bull. Northeastern Bird-Banding Assoc.*, **4:** 77–85.

OHIO STATE UNIVERSITY, COLUMBUS, OHIO.