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AVIAN DAYBREAK AND EVENING SONG IN RELATION TO TIME AND LIGHT INTENSITY

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This paper reports an attempt to measure the variation in the time and the light intensity at the onset and at the end of daily bird song as recorded in southern Wisconsin, principally in the years 1944 through 1947. The first songs of birds at daybreak or their last songs at evening have been the subject of numerous papers in both American and European ornithological literature. The usual approach has been to construct an "ornithological clock" based on the order in which species join or leave the morning or evening chorus, respectively, or to relate such songs to some standard time-marker such as sunrise, sunset, or civil twilight. In America, at least, there has been a paucity of data on the light intensity at the time when these phenomena occur. Such data are reported here for 20 species of North American birds.

The field work on which this paper is based was done by the senior author whose death on April 21, 1948, brought to an end a study of bird song in which he had become increasingly absorbed during the last years of his life. The junior author's role has been to analyze Professor Leopold's abundant data as they were recorded in his charts and journals and to organize them for publication. Fortunately, there exists an unpublished manuscript by Leopold, written after the song season of 1944 and covering wider horizons, which expresses his thinking regarding much of the subject matter of this paper. This manuscript has been freely consulted and the discussion therein amplified or modified following an analysis of Leopold's field records for the years 1945 through 1947. The junior author has introduced certain ideas derived from his interpretation of the data, combined with a review of the expanding literature appearing after 1947.

The season of bird song *per se* will not be discussed because Leopold's data on that subject were published by Zimmerman (1951).

In this study, observations were made in a suburban habitat on the west side of Madison, Wisconsin (latitude 43° 4' N, longitude 89° 24' W), and on an abandoned farm 34 miles to the northwest in Fairfield Township, Sauk County. These study areas are referred to as town and farm, respectively, in this paper. They differ from one another by about one minute in their time of sunrise at the June solstice. Observations in the two study areas made possible the inclusion of more species than could be found at either area alone and at the same time allowed more or less daily observation of species common to both areas. The record for species not common to both is naturally discontinuous, but this is offset to some extent by the inclusion of data for several years.

The principal records were obtained between January 8, 1944, and April 20, 1948. Over these years observations were recorded on 804 mornings and 164 evenings (table 1). Of the 804 observations at daybreak, 445 fall in the period between January 8, 1944, and June 30, 1945. No attempt was made to obtain a daily record after the waning of the song season in 1945. The research emphasis then simply shifted to a sampling process in which many photometric data were accumulated.

For each species on a given day, "daybreak song" is the initial song of the day and occurs not later than one hour after the first song of the day by any of the species heard

at the study areas. The term daybreak song is preferred to "awakening song" as used by Wright (1912 and 1913), Allen (1913) and Nice (1943) because some birds are awake for a time before they sing. Armstrong (1955) found that the interval between awakening and the first song of the European Wren (*Troglodytes troglodytes*) seldom exceeded a minute, but Scheer (1951) found that it averaged 3 minutes in the European Robin (*Erithacus rubecula*), 5 to 6 minutes in the European Blackbird (*Turdus merula*), and 15 to 20 minutes in the Chaffinch (*Fringilla coelebs*). We agree with Allard (1930) and

TABLE 1

DISTRIBUTION OF MORNING AND EVENING OBSERVATION PERIODS

Month	Morning	Evening	Month	Morning	Evening
January	83	July	57	33
February	72	August	52	20
March	119	12	September	42	11
April	85	35	October	54	2
May	68	29	November	52
June	62	22	December	58

Davis (1958) that the term "awakening song" is inadequate, but we imply synonymy with those authors who have also been concerned with the first song of the day.

Similarly, "evening song" is the last song of the day and it occurs within the hour preceding the last song at evening by any of the species present. "Daytime song" is one falling between the two previously defined observation periods and will not be considered to any extent in this paper. True "night song" is that falling between the end of astronomical twilight in the evening and its beginning in the morning (Allard, 1930), and it was not recorded for any diurnal species during this study. However, birds sang occasionally as much as an hour before the beginning of civil twilight in the morning.

ACKNOWLEDGMENTS

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METHODS

Prior to 1944, Leopold recorded the times of evening song and daybreak song for a number of common birds in which he was interested. His systematic timing of all species at both town and farm study areas began in 1944.

After early 1945, a General Electric foot-candle meter was used in most daybreak or evening observation periods. This instrument is calibrated on a primary scale of from 1.2 foot-candles to 50 foot-candles; however, this scale may be increased by means of a rheostat to read twice these values, or the values may be decreased by factors of 10 and 100. The range of possible values thus runs from 0.012 foot-candle to 100 foot-candles. Leopold read the meter in a standard manner, holding it horizontally on his lap, against open sky.

The record for each daybreak or evening observation period consists of the time and light intensity of the first or last song of each species, as well as remarks on relative cloudiness, wind, temperature, and moonlight if present. In February and most of March, when only the Cardinal (*Richmondna cardinalis*) and Ring-necked Pheasant (*Phasi-*

anus colchicus) are singing in southern Wisconsin, observations are possible from an open window, provided an active territory is near. All later observations require the observer to be outdoors in order to record distant or faint songs.

In May and June the babel of voices, especially at daybreak, makes only the earliest and loudest songs audible at any distance. Hence, a standard observation post was used at this season. In July and August the bedlam has ceased, the number of species singing has greatly declined, and distant recordings again become feasible. A circuit of several hundred yards was then used in order to cover several habitats.

No special problem attended the recording of daybreak song; time and light intensity were entered as each successive species began to sing. For cessation in the evening, a list of singing species was written in advance, and the values for each were then recorded every 5 minutes until all song had ceased. Terminal dates in phenology are usually cruder than beginning dates (Leopold and Jones, 1947). Since one never knows which song may be the last one of the day, we can only say that this yardstick applies equally well to evening song, especially when several species are being studied simultaneously.

In lumping days that Leopold entered on the original data sheets as clear with those entered as partly cloudy, we are supported by Scheer (1952), who found that a cloud cover of from $\frac{1}{10}$ to $\frac{3}{10}$ gave higher light-intensity values than a clear sky. Indeed, he found little difference in his curves of total illumination up to $\frac{7}{10}$ cloud cover, but cloudiness beyond this produced lower values.

GENERAL PATTERN OF DAYBREAK SONG

Stability of daybreak song.—In 1944 and 1945, Leopold obtained a close approach to a daily record of the time of first daybreak song for five breeding species: Mourning Dove (*Zenaidura macroura*), House Wren (*Troglodytes aedon*), Catbird (*Dumetella carolinensis*), American Robin (*Turdus migratorius*), and Cardinal. This record includes data from both study areas. Leopold's notes indicate that his estimate of the number of territories on which males were audible in 1944 (table 2) was largely unchanged in 1945 except for the Robin, when the small lawn and garden at the farm did not attract their usual single pair, and only song by very distant Robins was audible there. There is an annual "tuning-up" period in each of these species during which song occurs, but not daily, and often not at daybreak. The full-song period begins when song becomes regular at daybreak and remains so until daybreak song becomes irregular again in July or August at our latitude.

TABLE 2

NUMBER OF TERRITORIAL MALES AUDIBLE AT THE STUDY AREAS IN 1944

Species	Town	Farm
Mourning Dove	5	5
House Wren	3	4
Catbird	2	2
Robin	10	1
Cardinal	2	2

Careful studies of marked birds have shown that the song season is subject to interruptions and fluctuations. For many passerines, temporary cessation of song by individual males at the initial stage of pair formation has been reported by numerous authors. In the Song Sparrow (*Melospiza melodia*), song is irregular while adults are feeding young (Nice, 1943), and cessation occurs between broods in some double-brooded species (R. A. McCabe, *in litt.*). All but sporadic song ceases in most passerines while they are

molting. The composite record of daybreak song in a species population therefore will differ from that of an individual, depending on the number of territories and the degree of synchrony in the nesting cycle. A nonsynchronized population of many territorial males would probably show longer duration and fewer mornings without daybreak song than would an individual male. Stoddard (1931) and Davis (1958) found that the unmated males in a population are the most persistent singers in the Bobwhite (*Colinus virginianus*) and Rufous-sided Towhee (*Pipilo erythrophthalmus*), and such persistence is probably common in other species as well. The isolated mated male Robin at the farm in 1944 sang hardly at all.

The five species differed in the proportion of daybreaks in which song failed to be recorded. In table 3, only the full-song period and the daybreaks when song failure was positively recorded are considered. To determine which failures are traceable to weather,

TABLE 3
COMPARISON OF FAILURE OF DAYBREAK SONG IN 1944 AND 1945

Species	Year	Full song period	No. days	Days not recording	Days of failure	Failure traceable to weather	Per cent not due to weather
Cardinal	1944	Feb. 26 to June 22	118	22	10	4	6
	1945	Feb. 28 to July 5	128	23	25	2	22
Robin	1944	Mar. 25 to Aug. 3	132	15	8	2	5
	1945	Mar. 13 to July 17	127	25	4	3	1
Mourning Dove	1944	Apr. 1 to Aug. 21	142	12	4	1	2
	1945	Mar. 27 to Aug. 23	150	42	15	11	4
House Wren	1944	May 2 to Aug. 7	98	3	2	1	1
	1945	Apr. 25 to Aug. 13	111	30	2	1	1
Catbird	1944	May 12 to July 24	74	6	2	2	0
	1945	May 13 to July 13	62	21	2	1	2

we considered only heavy rain or strong wind to be sufficient grounds except that, in the Cardinal, we evaluated heavy snowfall at daybreak in February and early March. It is a matter of common observation that heavy rain inhibits bird song at any time of day. Many authors have stressed the importance of wind strength in delaying or inhibiting daybreak song, and Scheer (1952) found that it was the only weather factor which yielded a significant correlation in his analysis of the early morning song of the European Blackbird.

If we consider the Mourning Dove, Robin, and Cardinal during the periods of the 2 years in which all three species were in full song, there was not a single morning on which at least one failed to sing. Of the 40 dawns on which one of these three species failed to sing, two of the others sang on 33 mornings. The Robin sang at every daybreak on which the Mourning Dove failed to sing, and only once did the failure of the Robin to sing coincide with the failure of the Cardinal. There were five mutual failures by the Mourning Dove and the Cardinal in 1945, but only one in 1944.

Before the other two species began to sing regularly, however, the Cardinal failed to sing on 12 mornings in March, 1945. There were no Cardinal failures in March, 1944, despite the fact that it was colder and there was more snow than in 1945. A peculiar failure occurred on May 9, 1944. One bird sang at 3 a.m. in darkness, but no Cardinal song occurred at daybreak an hour later. There was no change in the weather.

Occasionally, failures were grouped in a suggestive manner. Robin song failed on successive days, May 21 and 22, 1944, in cloudy but calm weather, and first broods were

seen to fledge on these days. To impute a causal relationship, however, implies an improbable degree of nesting synchrony among at least 10 pairs.

Our data for evening song are insufficient to warrant any conclusions regarding its stability.

Fluctuations.—The time of daybreak song is a response to the stimulus of a certain light intensity which, within narrow limits, is characteristic of the species, although subject to individual variation. Among early European investigators to recognize this, according to Scheer (1952), were Haecker (1916) and Schwan (1921–22). In America the early emphasis was on the time at which birds first sang in the morning (Wright, 1912, 1913; Allen, 1913) with little regard for some standard measure of equal light intensity and less regard for different latitudes and changing seasons. Craig (1926) was

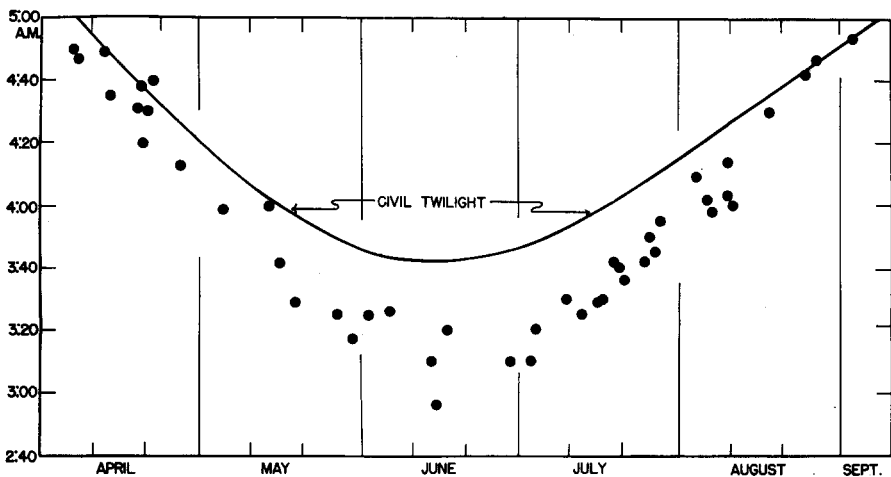


Fig. 1. Earliest daybreak song of the Field Sparrow (*Spizella pusilla*) on clear to partly cloudy mornings in relation to the beginning of civil twilight at the farm, 1944 to 1947.

the first to use the curve of the beginning of civil twilight in relation to the song of the Eastern Wood Pewee (*Contopus virens*), and Allard (1930) published a series of such curves. The latter were combined in a figure that clearly showed the limitations of the "ornithological clock," but he smoothed his curves mathematically by the method of least squares. This method seems to us to have a basic defect: it depicts the weather as well as the bird. To depict the bird alone, it seems preferable to plot the daybreak songs for clear or partly cloudy mornings and to note the fluctuations in relation to the beginning of civil twilight (figs. 1, 2).

The Field Sparrow (*Spizella pusilla*) had a daybreak song that showed a minimum amount of irregularity (fig. 1). We mean by this that, if a curve of best fit were to be drawn through the dots which indicate the earliest songs, it would be relatively close to all of them and would form a symmetrical arc with the greatest departure from the civil twilight curve corresponding very well to the earliest occurrence of that standard measure. The very early record for this species fell on June 15, 1944, at 2:56 a.m. with a clear moon at last quarter.

The Catbird, on the other hand, exhibited a maximum amount of irregularity (fig. 2). The song began very close to civil twilight in the second week of May, but then a wide scatter of readings followed, with the earliest songs occurring well before the solstice.

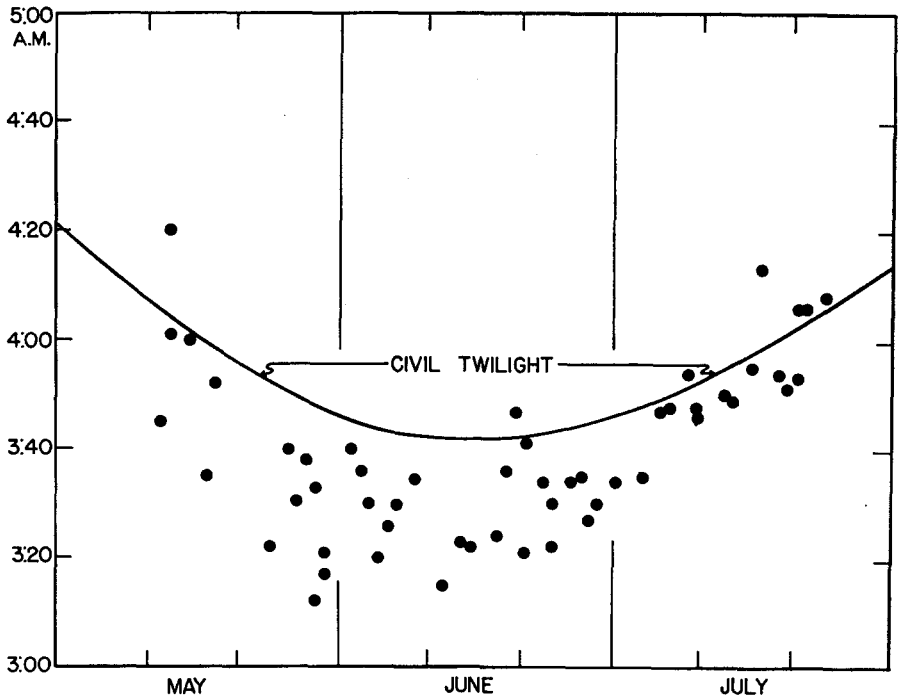


Fig. 2. Earliest daybreak song of the Catbird (*Dumetella carolinensis*) in relation to the beginning of civil twilight on clear or partly cloudy mornings only, 1944 to 1947. Data from both study areas are included.

After early June, daybreak song of the Catbird became later and displayed a gradual angle to the civil twilight curve, which it crossed in the third week in July. Curves for Catbirds for the individual years 1944 and 1945 on file in the Department of Forestry and Wildlife Management, University of Wisconsin, reveal that this irregularity is not an artifact of composite data.

Leopold's data are most complete for the Cardinal. These are presented in a somewhat different form (fig. 3) because the records are so numerous, and because this bird may sing at any time throughout the year. Song is rare, however, between the end of August and late December. Despite this annual hiatus, the time of daybreak song was recorded on 345 days during this study. Means for 3-day periods have been indicated when at least three records for such intervals are available and include daybreak song heard under all weather conditions. These means, we feel, are good indicators of when the daybreak song of Cardinals may usually be heard throughout the year. Some of the means are computed for as many as 12 observations. The earliest songs heard under clear skies have been added to indicate the normal song curve when conditions are ideal. These clear-sky records compare to the curves given previously for the Field Sparrow and the Catbird.

The Cardinal, if unhampered by weather, sang after the beginning of civil twilight from late December until about mid-March. By April 1, the daybreak song came well ahead of civil twilight, but the interval did not increase for a month. Two periods of irregularity are evident in the means and in the earliest records in early May and at the solstice. These periods are evident on the single-year curves as well, so that what is

shown here in composite form is a fair representation of what happened each year of the study.

The House Wren appeared to have as little or less irregularity than the Field Sparrow, but when the audible males at town and farm are analyzed as separate groups (fig. 4), the two populations are seen to begin singing at consistently different times. At the farm, these wrens gave the daybreak song ahead of civil twilight on all occasions except the initial song and during tapering-off periods at the end of the song season. However, daybreak song in town was rarely heard before civil twilight began. The reason for exclusion of the year 1947 from the curve for the House Wren is simple: there were no audible males at the town observation post.

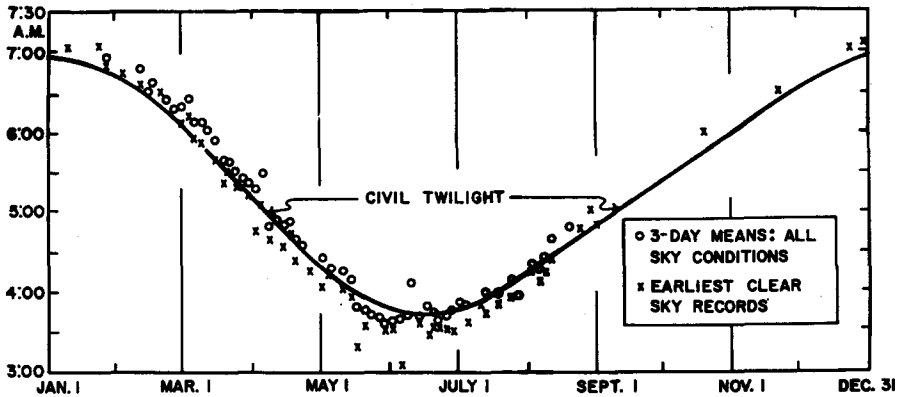


Fig. 3. Daybreak song of the Cardinal (*Richmondia cardinalis*), February 26, 1944, through April 20, 1948, in relation to the beginning of civil twilight; curve is based on 345 daybreak songs and includes both study areas. (See text for additional details.)

Allard (1930), who was able to observe two House Wrens with known roosting places, found one consistently singing earlier than the other. Armstrong (1955) found a similar difference between two European Wrens which amounted to about 10 minutes. Both of these observations involved birds at a single locality, and the variation could be attributed to a difference in exposure of the roosting site to the dawn light, to the individual bird's singing light intensity, or both. When localities as far removed from one another as our two study areas show a consistent difference, however, an examination of the comparative daybreak performance of other species seems warranted.

Difference between localities.—By using data from 1944, which are the most abundant, we see that the daybreak song of five other species occurred later in town (table 4). To make this comparison, each record at the farm was matched with a chronologically equivalent record from town. The Robin was eliminated from consideration because the single male at the farm had no rivals, sang very little, and ended his territorial song for the season on July 5; his average daybreak song was 33 minutes later than the average time for 10 territorial males in town.

Sunrise occurs one minute later in town than at the farm during the June solstice, but this could hardly account for the difference. The possibility of smog in town reducing light was rejected because the second half of the season, when little or no smoke is produced in town, shows the same tendency as the first half. The terrain is slightly more rolling in town, and there are houses casting shadows in which roosting sites occurred. However, some equally attractive sites were not so affected. Some 15 years apart the

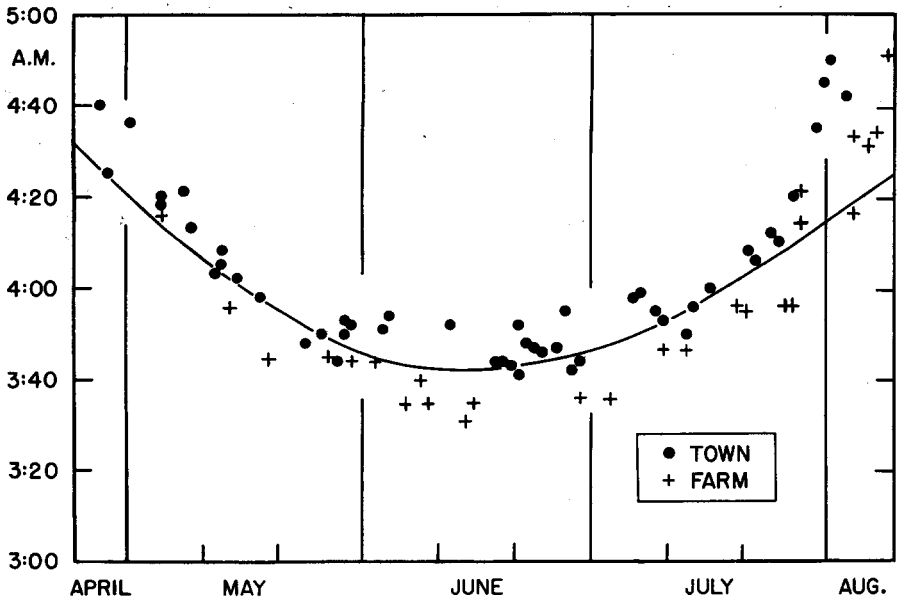


Fig. 4. Earliest daybreak song of the House Wren (*Troglodytes aedon*) at the two study areas on clear mornings only, 1944 to 1946, in relation to the beginning of civil twilight.

authors independently considered the question of why the difference should exist, and neither has been able to explain it.

Types of song curves.—There are at least three, possibly four, types of daybreak song curves in Leopold's data. First, a curve of the type represented by the Field Sparrow (fig. 1) departs from and then returns to the civil twilight curve at about the same angle on both sides of the solstice. Second, the daybreak song of the Cardinal (fig. 3) departs from the civil twilight curve at a medium angle until about the time of the solstice, after which the return to civil twilight curve is at a sharper angle. Third, the daybreak song curve of the House Wren follows the civil twilight curve so closely that it is virtually represented by it (fig. 4). A fourth possible type, obscured by much irregularity, is the song of the Catbird (fig. 2), which becomes earlier in a short time and then occurs later at a more gradual rate.

The Mourning Dove appears to be of the first type (Allard, 1930; Leopold, MS). The Song Sparrow (Nice, 1943), Rufous-sided Towhee (Davis, 1958), and perhaps the majority of song birds are of the second type. Armstrong (1955) found that the European Wren arose at about the same light intensity throughout the year so that it would appear to fall in the third category. However, we cannot find a published parallel for the Catbird.

A curve of different shape could be plotted in the Arctic where, according to Palmgren (1935) and Tinbergen (1939), birds begin to sing relatively later in relation to sunrise as the summer solstice approaches and the hours of darkness fall below the number required for sleeping.

Influence of moonlight.—Since the weak light intensity preceding the beginning of civil twilight is sufficient to stimulate daybreak song in the Field Sparrow, Catbird, and Cardinal (figs. 1, 2, 3), the question arises whether moonlight, with or without supplementary twilight, affects song curves.

TABLE 4

DIFFERENCE IN THE TIME OF DAYBREAK SONG BETWEEN THE TWO STUDY AREAS IN 1944

Species	Period	No. days	Mean time		Minutes earlier at farm
			Farm	Town	
Mourning Dove	April-June	16	4:12	4:16	4
	July-Sept.	12	4:02	4:07	5
	April-Sept.	28	4:08	4:12	4
Cardinal	April-June	8	4:08	4:13	5
	July-Aug.	9	4:02	4:13	11
	April-Aug.	17	4:05	4:13	8
Catbird	May-June	8	3:33	3:48	15
	July	7	3:42	3:48	6
	May-July	15	3:37	3:48	11
House Wren	May-June	10	3:47	3:59	12
	July-Aug.	11	4:05	4:16	11
	May-Aug.	21	3:56	4:08	12
Brown Thrasher ¹	May-June	5	3:53	4:07	14
Baltimore Oriole ²	May-June	9	3:50	4:20	30
All species		95	3:58	4:08	10

¹ *Toxostoma rufum*; ² *Icterus galbula*.

A zenithal full moon can produce up to 0.02 foot-candle (Humphreys, 1929), but since this condition does not occur north of Florida, the light intensity at full moon in Wisconsin is considerably less. Leopold in 1945 and Eynon in 1959 found the intensity to be less than the minimum capability of our meter, or less than 0.012 foot-candle under Wisconsin conditions.

Wright (1912) believed that moonlight was without influence, but in his second paper (1913), he reported that it had apparently affected a few of the species at his study area on the morning following a full moon in June. Haecker (1916) and Zimmer (1919) stated that the moon had no influence. Allard (1930) considered the effect of moonlight, but found his data insufficient to enable him to draw any conclusion. Nice (1943) stated that the moon is important just before and after it is full for crepuscular birds and diurnal birds that start singing very early, but she gives no data to support this conclusion for diurnal species.

Leopold suspected that moonlight affected daybreak song in the Robin on five mornings and in the Catbird and Field Sparrow each on single but separate mornings in 1944. Morning moonlight was frequently obscured by cloudiness in 1944, and Leopold tentatively felt that early singers might respond sporadically to moonlight.

When Eynon worked up the data on the Robin for 1945, however, the influence of the moon in March, April, and May was obvious (fig. 5). It is apparent that three, possibly four, daybreak songs were affected in March, four in April, and five in May. For those who might question the records as much as 2 and 3 days ahead of full moon, we point out that Leopold was often up and about more than an hour and a half before sunrise, or before the moon set.

Moonlight in June apparently was ineffective and did not arrest the more or less steady trend of the Robin to sing later and later after the solstice until daybreak song crossed the curve of the beginning of civil twilight in mid-July. This postsolstice trend is of annual occurrence in the Robin; it is apparent in all 4 years of the Leopold data and was verified by Eynon for 1959 and 1960. Armstrong (1955) found that of 119

observations on the arising of the European Wren 9 of the 13 earliest were on moonlit mornings; he concluded that it was probable that moonlight accelerates the arising time.

Moonlight also exerts an influence on species that are active in the dark. The well-known papers by Wynne-Edwards (1930) and Ashmore (1935) on the Nightjar (*Caprimulgus europaeus*) agree on the influence of moonlight on the *churring* time of this species. The first evening songs are delayed by moonlight, and singing starts earlier in

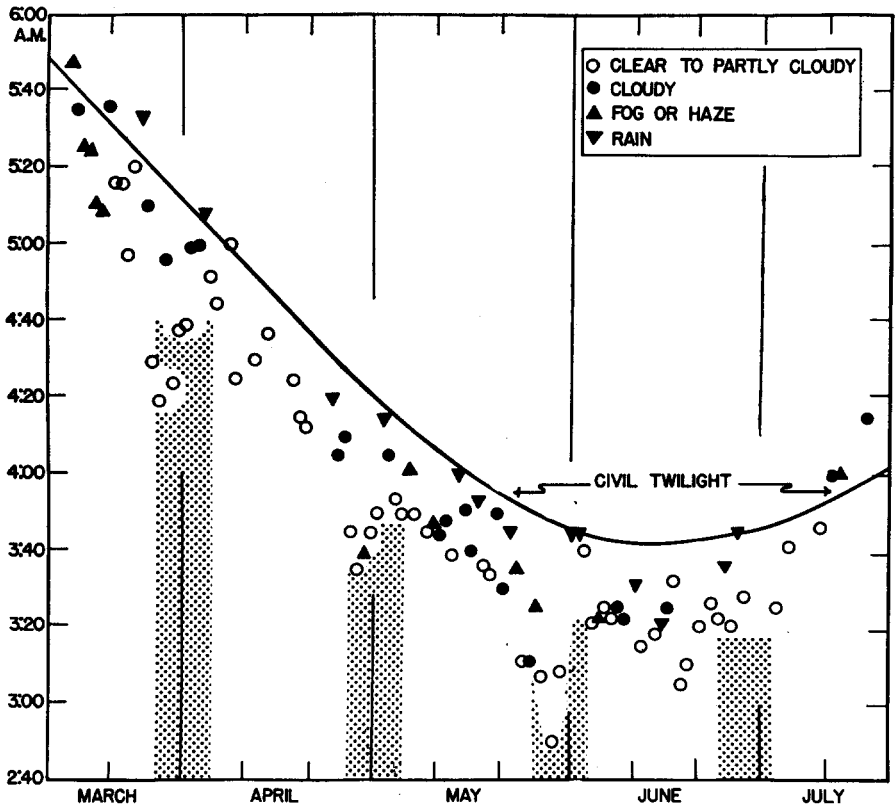


Fig. 5. First daybreak song of the Robin (*Turdus migratorius*) at the town study area in 1945 in relation to the beginning of civil twilight, weather, and moonlight. Stippling indicates periods from one day before full moon to last quarter.

the morning. Wynne-Edwards postulated a frequently quoted lunar periodicity in copulation and ovulation, but his admission that any such connection could be fortuitous (p. 244) seems to have been overlooked.

The Common Nighthawk (*Chordeiles minor*) showed a similar reaction to moonlight in the morning. Eynon recorded through the early morning hours of July 9, 1960, a clear night with full moon, and the first call of this species was heard at 2:38 a.m. with the bird "booming" shortly thereafter. In striking contrast, the bird was first heard at 3:26 on the following morning in completely overcast weather. The average time for the first call by the nighthawk on six clear mornings in July, 1959, was 3:10 a.m. Inasmuch as the Common Nighthawk starts hawking for insects in the evening and stops in the morning at higher intensities of light than the Nightjar, the only data that would be influenced by moonlight would be the first calling and the first booming in the morning.

From his manuscript and journals, it is obvious that Leopold suspected that the American Woodcock (*Philohela minor*), to be discussed later in another connection, stopped *peenting* earlier on moonlit mornings, possibly because it had *peented* and sky-danced all or most of the night. Visits to the farm coinciding with clear, moonlit nights were too infrequent to permit any firm conclusion on this point.

Role of hormones.—Allard (1930) thought it possible that the hormonal changes associated with activities of the testes were responsible for the increased sensitivity to low light intensities before the solstice, and Wynne-Edwards (1931) stated that the maturity of the gonads influenced the time at which Starlings (*Sturnus vulgaris*) awakened in the morning. Davis (1958) showed a close correlation between singing behavior and the gonad cycle in the Rufous-sided Towhee. The song season in this towhee began with the initial increase in the number of Leydig cells in the interstitial tissue, and the daybreak song became decidedly earlier when the males reached full breeding condition.

Leopold was convinced that the hormonal balance was more influential than temperature or other factors in determining song curves, but he did not have the opportunity to prove it. He was much interested in the daybreak crowing curve of the Ring-necked Pheasant, which shows the same general characteristics as the song curve of many passerines. Data have subsequently been collected by Greeley and Meyer (1953) that show the relationship between earlier crowing and stimulation of the testes in the region of our study. These investigators determined the mean gonadal weight and gonadotropin production of pheasant cocks at the game farm at Poynette, Columbia County, Wisconsin, which is just east of a line between our town and farm study areas. Their study was made between July, 1947, and June, 1948. Eynon believes that the crowing curve by Leopold and the data of Greeley and Meyer can be combined (fig. 6) because of the close proximity of Poynette, and because the periods of the two studies overlap. Leopold recorded daybreak pheasant crowing in 8 months of the year. Fall crowing began in September with the imperfect, juvenal crow which Leopold entered as "cackles" to separate such notes from the true, 2-note crowing with the accompanying wing-whir. By October, true crowing was heard, but it was not determined whether this represented the maturation of adult song in young cocks or the temporary resumption of territories by old ones. Greeley and Meyer (1953) found no increase in testis weight, but gonadotropin output by the pituitary increased from an August low until October. Testes that they examined in early October showed considerable histological advancement. Hiatt and Fisher (1947) reported that immature testes in the Ring-necked Pheasants that they studied in Montana developed in the fall and then involuted slightly.

The crowing curve of the Ring-necked Pheasant appears to be clearly correlated with gonadotropic activity of the pituitary, and presumably this is the case with passerines that sing earlier and earlier as the spring advances. However, in these species, fall song may or may not be related to hormonal activity. Blanchard (1941) and Miller (1948) reported fall singing in examples of *Zonotrichia* with inactive gonads. Marshall (1951) found that fall sexual display in male European Robins and Rooks (*Corvus frugilegus*), including frequent song in the former, occurred after regeneration of the Leydig cells in the gonads. Davis (1958) reported a limited amount of fall singing in the Rufous-sided Towhee as well as a slight increase in the number of Leydig cells in a few juvenal birds.

LIGHT INTENSITIES

Light intensities for civil twilight.—The beginning of civil twilight on clear mornings is a reliable and useful measure of equal light intensity because it is the time when the center of the sun is 6° below the horizon regardless of its declination on the par-

ticular day. Humphreys (1929) listed a value of 0.4 foot-candle for this position of the sun, but Nice (1943) found that 21 readings in Ohio averaged 0.217 foot-candle; her meter was not adapted to measure low intensities.

Of the hundreds of readings recorded by Leopold for daybreak song on clear mornings, there are 21 which happened to coincide with the minute at which civil twilight began, and these have a mean value of 0.029 foot-candle which matches the only read-

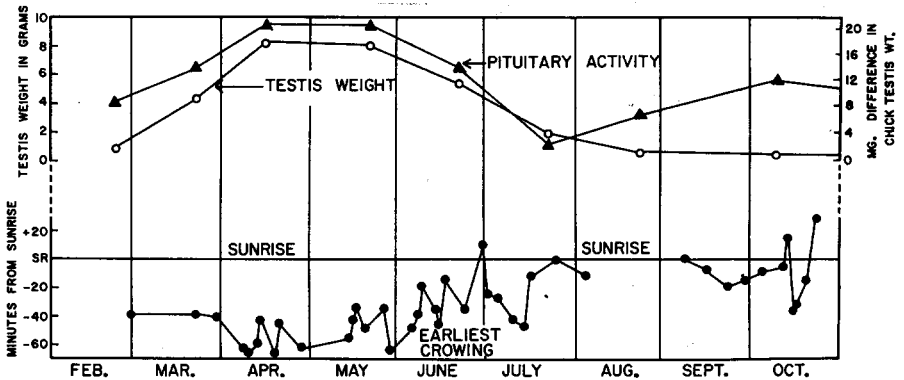


Fig. 6. Earliest daybreak crowning by the Ring-necked Pheasant (*Phasianus colchicus*) on clear mornings, 1944 to 1947, in relation to sunrise and to the annual cycle of testis and pituitary activity as determined by Greeley and Meyer (1953) for Poynette, Wisconsin.

ing (0.03) taken very soon after the instrument had been recalibrated. From its beginning until after the start of civil twilight, the light intensity at dawn increases in an exponential manner with respect to time. When one selects a clear morning with a sufficiently large and varied number of species in song, a curve of the increase in light can be drawn by plotting light intensities of daybreak songs on the ordinate against their time on the abscissa. The point at which such a curve is intercepted by a vertical line from the abscissa at the minute of the beginning of civil twilight yields a close approximation of the light intensity at that time. Eynon plotted five such clear dawns from Leopold's data at the height of the song season in May and June. A range of from 0.033 to 0.07 with a mean of 0.046 foot-candle resulted. After the foot-candle meter used in this study had been thoroughly checked and recalibrated in the fall of 1959, Eynon found that on 4 clear days at the start of civil twilight in the morning and 4 clear days at the end of civil twilight in the evening, the light ranged from 0.03 to 0.05 with a mean of 0.039 foot-candle at Madison, Wisconsin.

Scheer (1952) cites values recorded at sea by Rosenhagen (1949) that show civil twilight starting at 2 lucas (0.186 foot-candle). It would seem reasonable to expect measurements taken in terrestrial habitats to be somewhat lower than those from the open sea where illumination would be maximum. Leopold's data suggest the possibility that previously reported light intensities for the beginning of civil twilight in terrestrial habitats may be too high. Because daybreak singing begins within a few minutes of this position of the sun, the verification or refutation of this premise appears worthy of the attention of those workers who have suitable instruments available.

Light intensities at time of daybreak song.—The light intensity at which many birds begin their daybreak song is so low that most investigators have been hampered by the necessity of trying to estimate the readings on their photometers if daybreak song came at an intensity of less than one foot-candle. In a large measure, Leopold overcame this

TABLE 5

LIGHT-INTENSITY VALUES IN FOOT-CANDLES FOR FIRST DAYBREAK SONG, 1945 TO 1948

Species	March		April		May		June		July	
	N	Mean ± 2 S.E.	N	Mean ± 2 S.E.	N	Mean ± 2 S.E.	N	Mean ± 2 S.E.	N	Mean ± 2 S.E.
Ring-necked Pheasant ¹	6	.014	8	.013±.002	5	.031	4	.105	3	.417
	3	.021	4	.024	1	.030			3	.150
Mourning Dove	8	.028±.012	16	.045±.028	18	.023±.006	18	.037±.014	12	.040±.022
	2	.026	11	.051±.040	7	.029	4	.040	3	.150
Great Crested Flycatcher ²					6	.061	4	.166	3	.165
									1	.100
Eastern Wood Pewee					2	.014	2	.018	6	.014
									2	.019
House Wren					19	.039±.018	19	.055±.012	12	.053±.032
					8	.053±.022	4	.067	5	.037
Catbird					9	.013±.002	15	.018±.004	5	.060
					3	.026	4	.019	4	.035
Brown Thrasher			1	.050	8	.022±.008	3	.095		
			2	.046	2	.070			1	.020
Robin	15	.013±.001	24	.023±.008	19	.015±.002	17	.016±.004	8	.043±.044
	6	.041	12	.017±.004	7	.014	6	.016	3	.044
Eastern Bluebird ³	1	.050	10	.029±.016	8	.019±.004	5	.016	6	.047
	3	.024	4	.029	1	.020			3	.125
Warbling Vireo ⁴					3	2.400	2	.375	4	4.300
									2	.325
Yellowthroat					5	.012	1	.012	10	.020±.006
									3	.018
Eastern Meadowlark ⁵	1	.080	5	.110	4	.056	1	.050	1	.050
	2	.200	2	.020	1	.020			1	.300
Redwinged Blackbird	3	.043	7	.041	3	.800			1	5.000
	2	.250	2	.050					1	.050
Baltimore Oriole					7	.191	7	.161	1	6.000
					1	.040	1	.150	2	.350
Cardinal*	29	.032±.012	20	.022±.006	12	.033±.030	15	.034±.006	9	.036±.018
	20	.085±.072	7	.067	6	.352	3	.107	4	.026
Indigo Bunting ⁶					4	.014	4	.022	9	.074±.106
									2	.015
Rufous-sided Towhee			1	.020	7	.014	4	.022	7	1.437
			1	.040	1	.030			2	.014
Chipping Sparrow ⁷					7	.027	3	.019	2	.160
					1	.050				
Field Sparrow	1	.040	13	.022±.005	9	.012†	4	.015	10	.013±.002
	1	.050	4	.022	1	.020			4	.012
Song Sparrow	2	.025	11	.015±.005	8	.014±.002	4	.014	7	.060
	5	.052	6	.023					2	.033

¹Values on the upper line are for clear to partly cloudy skies, and those on the lower are for cloudy to overcast. Standard error of the mean computed only when readings per month total 8 or more.

²*Myiarchus crinitus*; ³*Sialia sialis*; ⁴*Vireo gilvus*; ⁵*Sturnella magna*; ⁶*Passerina cyanea*; ⁷*Spizella passerina*.

*Readings for the Cardinal before March are 0.018 ft.-c. for the clear dawn of January 7, 1948, and six readings for clear February dawns with a mean of 0.036 ft.-c.

†All values 0.012 for May.

difficulty through the use of the General Electric foot-candle meter described in the first part of this paper. However, it turned out that some daybreak songs were given at values lower than the minimum capability of the instrument. After a few attempts to estimate a fraction of 0.012, Leopold abandoned this for the notation “-0.012,” which occurs in his notes occasionally for the Ring-necked Pheasant, Mourning Dove, Catbird, Yellowthroat (*Geothlypis trichas*), Cardinal, Field Sparrow, and Song Sparrow at the farm, and frequently for the Robin in town. In order to handle the statistics, Eynon read all values so indicated as 0.012.

In table 5 the species have been arranged in phylogenetic order. To put them in order of increasing light intensity would require a separate table for each month. These data are for both study areas combined, but records for the Robin at the farm are excluded for reasons given earlier in this paper. The light intensities in this table are the lowest ever reported for daybreak song in North American birds. It therefore becomes necessary to consider their relative accuracy. Recently, values in the same range have been reported for European species by Scheer (1952) and Groebels (1956). Readings comparable to Leopold's “-0.012” converted to foot-candles from the lucas reported by these authors are 0.003 for the European Wren, 0.004 for the Great Reed Warbler (*Acrocephalus arundinaceus*), 0.007 for the European Blackbird and the Redstart (*Phoenicurus phoenicurus*), and 0.008 for the Reed Bunting (*Emberiza schoeniclus*). Peterle (1955) found that the first call of the Red Grouse (*Lagopus scoticus*) averaged 0.39 lux (0.036 foot-candle) for 10 mornings, but on four occasions it came at a light intensity of 0.1 lux (0.009 foot-candle). Thus our figures seem reasonable and may be presented with a fair degree of confidence.

Table 5 is self-explanatory, but at first glance the data suggest that some species appear to require more light for daybreak song on cloudy mornings early in the year. This may be seen in the values for Ring-necked Pheasants, House Wren, Catbird, Red-winged Blackbird (*Agelaius phoeniceus*), Cardinal, Rufous-sided Towhee, and Song Sparrow. The light intensity shifts to lower values for cloudy mornings as opposed to clear for these species in July. This is suggestive of a possible temperature relationship, since cloudy days in spring generally coincide with lower temperatures which might delay song, but lower temperatures in July are probably stimulating in the midst of heat, which Nice (1943) considered as having an inhibiting effect. However, in those species where the monthly data by Leopold are adequate for statistical testing, the difference in the light intensities between clear or partly cloudy mornings and cloudy or overcast mornings is not significant.

According to Scheer (1952), it was Haecker (1916) who first clearly stated that light intensity, modified by cloudiness, determined the time of daybreak song. Numerous authors have subsequently agreed on this point: Song is delayed on cloudy mornings until the illumination reaches the approximate intensity at which it would have started had the morning been clear. To demonstrate the delay, we have selected the two species that are the earliest singers at town and farm, respectively, the Robin and the Field Sparrow (table 6).

Light intensities at evening song.—Numerous investigators have found that daily cessation of bird song comes at light intensities higher than those at which it begins in the morning. Wright (1912, 1913) in America and Haecker (1924) in Europe were fully aware that the interval between sunset and the last song of the day was considerably shorter than that between daybreak song and sunrise. Allard (1937) commented upon the inconsistency of song and other activities near the close of the day as compared to dawn. Nice (1943) determined the ratio of the light intensity of evening song to that

of daybreak song in the Song Sparrow. More recently Grimm (1957) confirmed the earlier work by Heyder (1933) on the evening song of the European Blackbird by taking readings on 146 evenings. He then compared his mean values to the morning values reported by Scheer (1952) and found that the light intensity at the end of the evening song period was 10 to 30 times as high as that of daybreak song, depending on the phase of the annual cycle.

TABLE 6

DELAY OF DAYBREAK SONG ON CLOUDY MORNINGS, 1944 TO 1947

		April		May		June		July	
		No. days	Minutes before sunrise	No. days	Minutes before sunrise	No. days	Minutes before sunrise	No. days	Minutes before sunrise
Robin	Clear ¹	26	48	18	66	18	62	15	48
	Cloudy ²	12	41	13	50	11	52	3	27
	Mean delay		7		16		10		21
Field Sparrow	Clear	13	36	9	52	6	64	14	58
	Cloudy	6	32	2	41	1	47	4	55
	Mean delay		4		11		17		3

¹ Includes partly cloudy.² Includes complete overcast, but excludes days with rain, fog, or haze.

Leopold's data for evening light intensity are not as abundant as those for morning, and since the values are so much higher, they are not carried beyond two decimal places (table 7). The variance is high and inconsistencies are apparent. In some cases, the range of values from which the means were computed for clear or partly cloudy evenings is greater than that for cloudy or overcast evenings. This is due in part to fewer readings on evenings of the latter type. More important, however, is the tendency for evening song not to have the precise relationship to light as does daybreak song. With a few exceptions, the mean values for cloudy or overcast evenings are higher than for clear, the disparity being much greater than for daybreak song. The birds not only stop singing earlier on cloudy evenings in respect to sunset or the end of civil twilight, but they appear to do so at a higher absolute light intensity. This cloudiness effect on evening song has also been found in detailed studies of single species (Nice, 1943; Armstrong, 1955; Grimm, 1957).

The characteristic light intensity that governs daybreak song does not have a parallel in the evening cessation. Rather there seems to be a range of intensities in which the last song may occur, and the lower limit of such a range is generally higher than the light intensity for daybreak song. The recording of the last song of any diurnal species on our study areas never required a light, whereas it was impossible to read a watch at the intensities at which the earliest daybreak songs occurred for much of the season. There are exceptions to the general rule that diurnal birds stop singing in more light than that at which they begin. McCabe (1951) found that the Traill Flycatcher (*Empidonax traillii*) regularly sang until it was completely dark during its unique evening song period. Eynon (1951) found that the evening flight song of the Ovenbird (*Seiurus aurocapillus*) was given at light intensities too low to read a watch without the aid of a flashlight. Indeed, the exceptions may be confined to species with special flight songs or those which sing on the wing much of the time. Eynon has heard the Eastern Kingbird

TABLE 7
MEAN LIGHT INTENSITIES IN FOOT-CANDLES FOR EVENING SONG, 1945 TO 1947

Species	April		May		June		July	
	N	Mean	N	Mean	N	Mean	N	Mean
Ring-necked Pheasant ¹	7	2.13	6	3.26	0		0	
	0		0		0		0	
Mourning Dove	7	2.34	8	0.85	3	3.53	6	3.87
	0		0		2	10.15	3	5.00
Great Crested Flycatcher			6	0.12	2	0.12	5	6.28
			0		2	0.78	3	4.73
Eastern Wood Pewee			4	1.13	3	0.09	6	0.07
			0		3	0.23	2	0.55
House Wren			7	0.26	4	0.93	6	2.95
			0		2	4.80	3	3.33
Catbird			7	0.03	5	1.73	3	0.33
			0		4	0.24	3	0.55
Robin	6	0.54	5	2.86	6	0.50	0	
	0		0		0		0	
Yellowthroat			7	0.08	2	2.70	6	6.17
			0		3	0.14	0	
Eastern Meadowlark	7	0.85	7	5.38	3	3.93	0	
	0		0		0		0	
Redwinged Blackbird	5	4.92	6	0.75	0		2	13.25
	0		0		0		3	7.67
Baltimore Oriole			6	5.67	3	4.25	0	
			0		0		0	
Cardinal	6	0.59	3	1.00	2	0.50	6	1.19
	0		0		0		3	4.17
Indigo Bunting			4	0.51	2	1.00	6	8.92
			0		0		0	
Rufous-sided Towhee			3	2.47	3	0.60	5	6.74
			0		2	4.58	3	8.00
Chipping Sparrow			6	0.15	2	10.05	0	
			0		2	0.13	0	
Field Sparrow	6	0.24	9	0.21	4	1.34	7	2.07
	0		0		4	2.31	3	0.57
Song Sparrow	10	0.62	8	3.76	4	1.75	2	6.50
	0		0		3	5.17	0	

¹ Values on upper line are for clear to partly cloudy sky, and those on lower are for cloudy to overcast.

(*Tyrannus tyrannus*), Horned Lark (*Eremophila alpestris*), and Yellowthroat performing in the evening twilight when it was much too dark to see the birds.

COMPARISON OF DAYBREAK AND EVENING SONG

Diurnal species.—The ratio between light thresholds at daybreak and evening has been reported for only a few species in terms of actual incident light values. In the purest sense, each species should be compared for relatively short periods of the annual cycle (tables 5, 7). The Robin in July is not the same bird it was in April. If clear daybreaks are compared to clear evenings for each month, weather factors should average out over a 3- to 4-year period. However, it is probable that each species changes its hormonal balance and reproductive status at a different rate each year and that between species rates are rarely comparable. With these facts in mind, we present the composite data on light intensity at daybreak song and evening song (table 8). We have restricted this table to species for which the data by Leopold contain at least 15 evening readings for the 3 or 4 months involved. Once again the figures are influenced by more morning readings in five species, and the ratio is affected by the tendency of many species to stop

singing proportionately earlier in relation to evening civil twilight after the solstice. Evening song fails before daybreak song.

The species in table 8 have been arranged in ascending order of daybreak light values, but the evening intensities show no corresponding order. This is a reflection both of the lack of precision in the relationship of evening song to light and of a seasonal waning of the impulse to sing.

TABLE 8

RATIO OF FOOT-CANDLES AT DAYBREAK SONG TO EVENING SONG, 1945 TO 1947

Species	(a) Daybreak		(b) Evening		(c) Ratio (a):(b)
	No. days	Mean value	No. days	Mean value	
Field Sparrow	36	0.016	26	0.96	1:60
Robin ¹	68	0.021	17	1.20	1:57
Catbird	29	0.024	15	0.66	1:27
Song Sparrow	30	0.025	24	2.35	1:94
Cardinal	56	0.030	17	0.86	1:29
Mourning Dove	64	0.036	24	2.36	1:66
Yellowthroat	16	0.040	15	2.86	1:72
House Wren	50	0.048	17	1.37	1:29
Eastern Meadowlark	11	0.080	17	3.26	1:41

¹ Omits farm; no evening readings in July for town.

The fact that most diurnal birds stop evening song when there is more light than that for daybreak song raises the question of why this should be so. Provided the same day is calm and clear at both daybreak and evening, there are usually no other environmental changes except temperature and sometimes humidity, and the light increases and wanes at the same rate. Temperature correlation attempts have not been very successful (Shaver and Walker, 1931; Elliott, 1932). It appears that there is a factor operating at evening, either in the bird or in the environment, which is not present, or is different, at daybreak.

Crepuscular species.—The singing behavior of crepuscular species, which begin activity in the evening after a day's rest, should yield some insight into this question. To this end, Leopold used the American Woodcock as a test case. Several males performed annually at the farm, and a special effort was made to record this species. The times and light intensities of the first and last *peent* at evening and morning were used, respectively, as equivalents of the daybreak song and evening song of diurnal species. Some defense of this hypothesis seems justified.

We agree with Pitelka (1943) that *peenting* serves as a warning and advertisement for this species. While *peenting* usually precedes the first song flight of the evening and continues between flights, Leopold's records show that the song flight can occur without *peenting*. From this it would appear that *peenting* is equivalent to the territorial song in passerines. The *peent* note is rare after the end of the spring sky-dancing period in early June, but Leopold recorded it twice in 1944, once on July 4 and again on October 17.

At the farm the first *peent* of the evening usually came well before the end of civil twilight, occurring later on only three evenings out of 61 (fig. 7). The last *peent* at daybreak, however, occurred before civil twilight began on 22 mornings out of 45 (fig. 8). A tendency to delay *peenting* on clear evenings and to begin earlier on cloudy ones is evident, as is a trend toward earlier cessation on clear mornings. It seems apparent that the American Woodcock, at evening, is stimulated by a certain intensity of darkness and that at daybreak it is inhibited by a certain intensity of light. If light alone governed

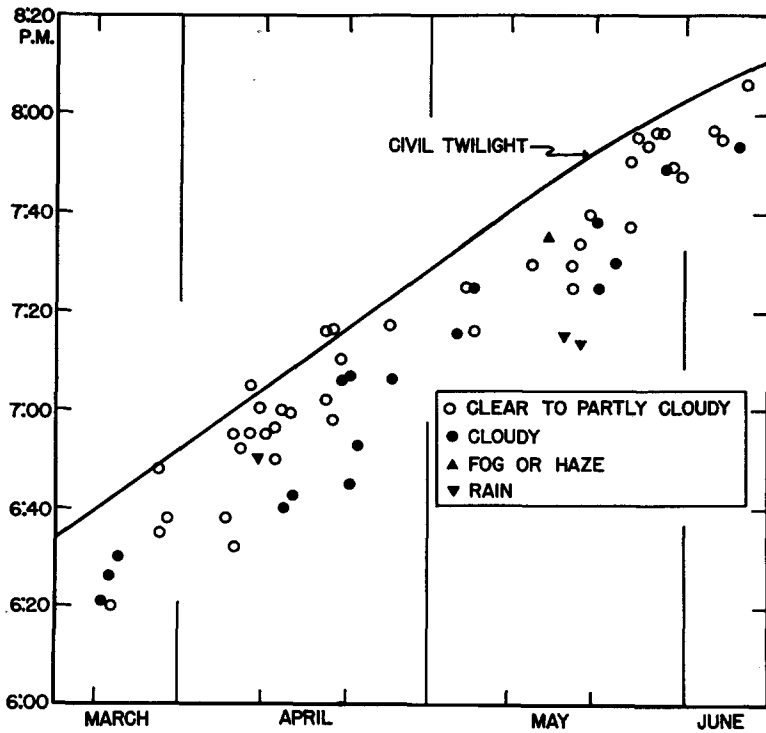


Fig. 7. First evening *peenting* by the American Woodcock (*Philohela minor*) in relation to the end of civil twilight and weather, 1944 to 1947.

the performance, the two sets of data points would yield a curve of best fit equidistant from the civil twilight curve. It takes less light to stop *peenting* at daybreak and more to start this activity in the evening.

Examination of the light measurements for clear and partly cloudy days confirm this disparity. Light-intensity values for the first evening *peent*, 1945 to 1947, ranged from 5.0 foot-candles down to 0.02 foot-candle for 24 readings. The evening mean intensity with standard error was 0.71 ± 0.26 foot-candle, but this was influenced by five high readings of 2, 2, 2.5, 3, and 5 foot-candles; the other 19 readings were not over 0.5 foot-candle. For the last *peent* at daybreak, there was an intensity range of from 0.012 to 0.06 foot-candle for 15 readings. The morning mean intensity of 0.028 ± 0.002 revealed just how precise cessation is in this species.

This disparity shows that our dark-active species, the American Woodcock, follows the same principle as that governing diurnal birds: Lesser intensities, of darkness in the former, and of brightness in the latter, stimulate song at the beginning of their respective active periods. Both kinds of birds seem to stop singing with larger quanta of light or darkness still present, in accordance with their habits, diurnal or crepuscular. The responsible factor, whatever it is, appears to be intrinsic and not due to the conditions of the environment at the time of day. In field studies of wild birds, this internal factor cannot, of course, be determined.

GENERAL REMARKS

In view of this response to light and the long-term modifying effect of hormones, two concepts should be examined. One is old yet recurrent in the literature on bird song;

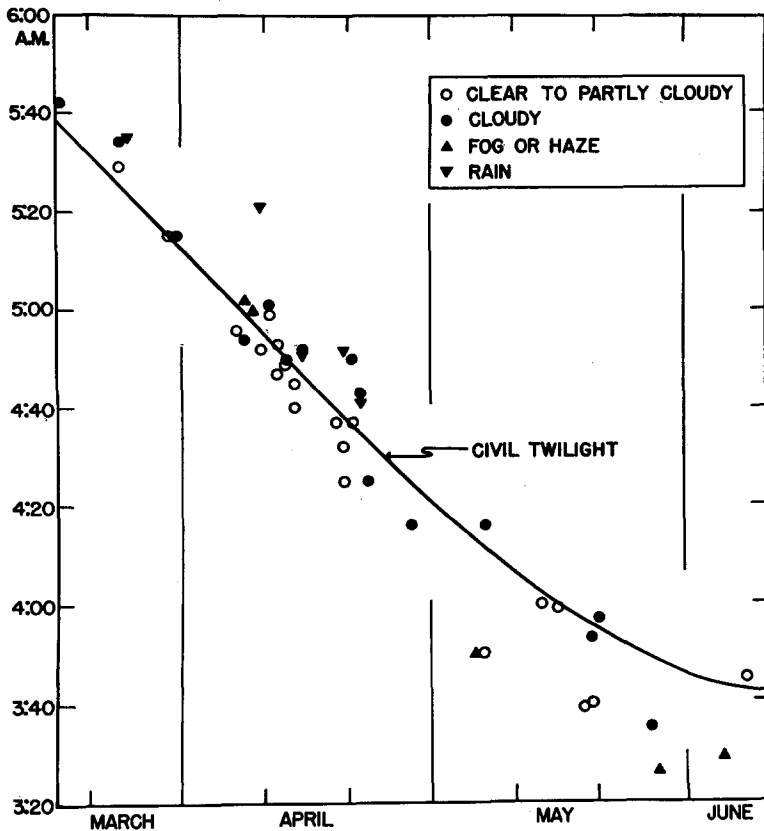


Fig. 8. Last peenting at daybreak by the American Woodcock in relation to the beginning of civil twilight and weather, 1944 to 1947.

the other is comparatively recent and embraces a wide variety of animals other than birds. These concepts, between them, probably account for the short-term factors regulating daybreak and evening song.

Activity rhythms.—The investigations of Kramer (1952), Matthews (1955), Sauer (1957), and other ornithologists working in the field of avian celestial navigation have demonstrated that birds have a precise sense of time. Rawson's (1954) demonstration of endogenous activity in the Starling suggests that this ability derives principally from a physiological "clock" which is reset continually by environmental clues. Aschoff (1958) called such clues "time-givers." Birds are not unique in having such "clocks," as their existence, but not their location, has been described for many classes of animals.

The study of biological periodicities, especially those of approximately 24-hour duration, has occupied the attention of a growing number of zoologists and botanists in the years since Leopold's field studies were made. Rhythms with a period of about one day, until recently called diurnal or daily, have now been designated as "circadian." Harker (1958) and Aschoff (*op. cit.*) have reviewed the literature on circadian rhythms in animals.

Among the more easily recorded circadian rhythms in birds are the times at which communal and hole-roosting species leave their roosts or return to them, the time of

arrival of lek species at their dancing grounds, and the time of daybreak and evening song. Of these, daybreak song offers the best opportunity to the investigator who wishes to study a number of species simultaneously.

Purely endogenous or free-running circadian rhythms can be determined with certainty only by isolating animals in a controlled environment. In most animals, 24-hour periodicities modified by daily environmental clues are entrained circadian rhythms with both exogenous and endogenous components.

The daybreak activity pattern of spontaneous awakening some time before daybreak song suggests such a combination in birds. Scheer (1951) reported a quiescent period for the European Robin, European Blackbird, and Chaffinch between the time they awoke and their subsequent daybreak song, and he thus confirmed Allard's (1930) premise that birds are "awaiting alert for the coming of the dawn." Presumably such spontaneous awakening is caused by an endogenous factor. Here it becomes necessary to introduce the concept of anticipation: the bird awakens in darkness without benefit of environmental clues. Once awake, the bird can sample the light, and daybreak song occurs when the proper intensity is reached.

This hypothesis of an anticipatory period during which the bird samples or tests the light intensity is supported by the behavior of other animals. Hodgson (1955) found that worker leaf-cutting ants (*Atta cephalotes*) appeared at the nest entrance about an hour before dawn but never left to forage until the light intensity on the forest floor reached 0.3 foot-candle. Departure time was advanced or delayed according to whether the investigator supplemented the normal light intensity with a lantern or retarded it with an awning. Twente (1955) reported that cavern-dwelling bats, principally *Myotis velifer*, appeared near the entrance in increasing numbers as the light diminished, and that the general emergence was preceded by short sorties by a few bats, out and back. The length of these sorties increased from a few feet up to 50 yards over a 15-minute period.

The only evidence against spontaneous, endogenous awakening is to be found in the influence of moonlight. The Nightjar and Common Nighthawk could easily have been awake most of the night, but the Robins, which in 1945 began to sing from 20 to 40 minutes earlier on moonlight mornings in May (fig. 5), presumably had been asleep. A possible explanation is that the Robin awakens normally at this season as much as 20 to 40 minutes before singing, and that it responds differently to the "clock" when there is more light.

Under controlled conditions, one of the criteria used by most workers in a test for a physiological "clock" is that the beginning of the active period should drift if no environmental synchronizers are available to the animal. The most potent of these synchronizers is light. De Coursey (1961) demonstrated control of the activity phase of 24-hour rhythm in the flying squirrel (*Glaucomys volans*) in an intensive study of both wild and laboratory animals. She found that light reset the "clock" by interacting with the endogenous rhythm but could not demonstrate such entrainment to either sound or temperature stimuli.

The comparative lack of precision in the evening song of most diurnal birds may indicate a reduced dependence on the endogenous rhythm at the close of the active period. Armstrong (1954) suggested that decreased light may have provided the principal cue for reducing activity in Arctic birds. It would appear that in the temperate zone, where the decrease of light is much faster, such a cue would be even more effective. Palmgren (1935) pointed out that most passerines in northern Lapland rested in the evening and resumed activity as much as 4 hours before midnight and that temperature

and humidity controlled the period of activity. He also stated (Palmgren, 1941) that the "autonomy of the internal rhythm" was involved at both awakening and roosting. An endogenous factor at cessation of song is difficult to document. The rather abrupt cessation of song by the Traill Flycatcher in darkness, reported by McCabe (1951), could be due to such a factor.

Fatigue theory.—Wright (1912) stated that fatigue caused the diurnal birds on his study area to stop singing in the evening with more light than that at which they had started in the morning. His idea was echoed by Haecker (1924), Allard (1930), and Nice (1943). Armstrong (1954) put the same hypothesis in more modern terms when he concluded that "apparently waning of the drives stimulating diurnal activity leaves the field open for the factors inducing sleep." The foregoing statement applied to birds in the continuous light of the Arctic, but Armstrong (1955) implied that, in the lower latitudes with a definite night, hunger was one of these drives. The European Wren, he found, varied its roosting time less in midwinter than in midsummer, and he suggests that in the former period, the bird does not roost until the light is so dim that foraging is "unprofitable." In summer, however, Armstrong suggests that this wren roosts at a higher light intensity because there is adequate food and "there is no pressure to stay up."

Craig (1926, 1943) attempted to demolish the fatigue theory. He raised the valid objection that in the evening not only the end, but also the beginning, of the song period in diurnal birds occurs at higher light intensities than those which govern the morning performance. He claimed, quite justly, that this earlier beginning is hardly consistent with fatigue. Since Leopold did not study the beginning of evening song nor the end of morning song in any diurnal species, we cannot debate the issue. Craig also suggested anticipation which, with regard to evening song, seems to have no more validity than fatigue. Armstrong (1955) also found Craig's use of the term inadequate. McCabe (1951) suggested that the beginning of the evening song of the Traill Flycatcher was probably controlled by light intensity, but that its cessation in the dark quite certainly was not. While not eliminating the possibility of fatigue, the last worker suggested a fading external stimulus, "irrespective of whether the bird is physically able to respond or not," as an alternative hypothesis. McCabe's suggestion appears to have much merit for species in which light is not a factor. The failure to respond may be due to the "monotony-threshold" of Hartshorne (1956). The song of the Traill Flycatcher would seem to come under Hartshorne's definition of the nonversatile, discontinuous singer.

Leopold, to the best of our knowledge, was the first to test the fatigue theory on a crepuscular or nocturnal bird. The papers on the Nightjar by Ashmore (1935) and Wynne-Edwards (1930), referred to earlier, reported only on the beginning of song during both twilight periods of the day. However, Hansen's (1952) data on the Tawny Owl (*Strix aluco*) showed that this species begins calling at a time closer to sunset than morning cessation comes in relation to sunrise. Leopold suggested the Whip-poor-will (*Caprimulgus vociferus*) as another test species, but birds of this species were generally too distant at the farm to provide reliable data. The caprimulgids vary so much among the different species that they may not be a happy choice. Brauner (1952), for instance, reported that the Poor-will (*Phalaenoptilus nuttallii*) both begins and ceases activity at about the same light intensity of less than one foot-candle. Except during migration, the Common Nighthawk is normally active around dusk and dawn, with a silent period during the middle of the night. Eynon heard this species begin to call on July 26, 1960, at 2:05 a.m., or over an hour ahead of the average time of its first call at this season. There had been a series of violent thunderstorms lasting throughout the normal active period on the previous evening. Eynon's premise is that the birds were unable to forage in the evening and that the earlier than usual foraging in the morning was due to a hunger drive.

Leopold's use of the American Woodcock as a test of the fatigue hypothesis does not prove its validity, however. We have shown that diurnal species begin to sing at daybreak at a rather precise light intensity, but the evening song intensity has a greater variance. By this criterion, the American Woodcock is the exact opposite, for it is the last song at daybreak that is precise. Allard (1937) studied the evening departure and the morning arrival of a pair of Screech Owls (*Otus asio*) at their roost in relation to sunset and sunrise. Using time rather than intensity, he also found a higher correlation in the morning. This led him to discard the fatigue theory to which he subscribed in his earlier (1930) paper and to account for the greater variation found in the evening in both diurnal and nocturnal birds as possibly "dependent upon differences in the sensitivity and adjustment of eyes that have become light-adapted and those that have not."

Grimm (1957) quantified pauses in the songs and calls of the European Blackbird for 37 evenings as a measure of disturbance susceptibility or fatigue. He combined the results of all evenings to suppress daily randomness and obtained an exponential curve showing the progressive pauses in evening vocalization up to cessation. However, this curve could measure a fading external stimulus or the waning of drives as readily as it measures fatigue. If there is any merit in the fatigue theory, Grimm's approach seems to be the most promising technique for use in the field, but laboratory studies are necessary to prove that the activities of an average day are sufficient to produce true fatigue in a song bird on its breeding territory.

Ehrström (1956) summarized reports by 107 observers during the solar eclipse of June 30, 1954. Totality occurred in the early afternoon, and the songbirds stopped singing for about 15 minutes. In general, they started to sing after the eclipse at a much higher light intensity than that at which they had stopped beforehand. This reversal of the usual relationship of song to waning or increasing light could be used to justify the fatigue theory of evening cessation of bird song as well as to demonstrate the rhythmic nature of daybreak song.

Absolute light intensity as a stimulus.—There appears to be an absolute light intensity, narrow in range and subject to individual variation within each species, which provides the stimulus for daybreak song. Seasonal shifts in the mean value of this light intensity seem to be due to the reproductive status and a changing hormonal balance. But when we measure the absolute light intensity are we necessarily determining the standard that acts as the minimum stimulus for the bird? Some birds may have a higher degree of retinal adaptation than others to increasing versus decreasing light. In the final analysis, it may be the relative brightness of various components of the habitat that is appraised by the newly awakened bird. The nucleus of this intriguing idea derives from a suggestion by J. P. Ditchman (personal communication). Further discussion of relative brightness is beyond the scope of this paper, but its evaluation by the use of modern photographic techniques is conceivably the next step in the study of stimuli for bird song at low light intensities.

SUMMARY AND CONCLUSIONS

The times and light intensities for the first daybreak or last evening songs of 20 species of birds were recorded over a four-year period at two study areas, town and farm, in southern Wisconsin. A daily record of daybreak song for five common species showed that simultaneous, interspecific failure to sing was rare. Failure to sing not due to weather ranged from zero in the Catbird to 22 per cent in the Cardinal, but an isolated Robin sang little and late. In 1944, daybreak song in six species averaged 10 minutes earlier at the farm than in town.

Daybreak song curves for the House Wren, Catbird, Cardinal, and Field Sparrow differed in their relation to civil twilight and in the tendency of each species to depart from its average time. The Robin sang much earlier on moonlit mornings in March, April, and May, 1945, but the June moon had no effect. Occasionally, the moon affected song in other species.

Close correlation existed between the earlier crowing of the Ring-necked Pheasant relative to sunrise and a curve of gonadotropic activity of pheasant pituitaries in spring; and daybreak crowing in the fall seems to be correlated with a more limited production of gonadotropin. It is suggested that a similar cycle is responsible for earlier song by passerines.

Tabulation of the light intensities disclosed that daybreak song came at lower, more precise values than evening song. The lower range came close to minimum values reported for European species. Song was delayed on cloudy mornings until light reached an intensity not significantly different from that of clear mornings. Mean light intensities at evening song ranged from 29 to 94 times higher than for daybreak song. The American Woodcocks stopped *peenting* at daybreak with more darkness than was necessary to start them in the evening, but it was cessation of song that was precise and not the beginning of song.

It seems probable that some birds, at least, awaken endogenously, test their environment during an anticipatory period, and sing when the light reaches a certain intensity. Such entrained circadian rhythms have been suggested for other animals. Cessation at evening may be due to fatigue, waning drives, or a fading stimulus, but none of these concepts nor the endogenous components in activity rhythms can be verified in the field.

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