DIURNAL RHYTHM OF ATTENTIVENESS OF INCUBATING FEMALE TREE SPARROWS (*SPIZELLA ARBOREA*) AT A NORTHERN LATITUDE

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Diurnal activities of female passerine birds in arctic and subarctic environments have not been extensively studied, although the subject is of great theoretical interest in discovering the nature of circadian rhythms and how they are influenced by environmental factors during breeding periods. Much has been written describing the diurnal activity of male passerines in continous daylight (Armstrong, 1954; Brown, 1963; Cullen, 1954; Franz, 1948; Hoffman, 1959; Palmgren, 1949; Wagner, 1958). Some of these authors, namely Armstrong, Hoffman, and Wagner, were stimulated to collect information on feeding rhythms during the nestling stage by Karplus' (1952) and Baumgartner's (1937) theses that nestlings in the arctic mature more quickly than those of the same species in temperate regions. However, information on activity of incubating females is sparse. Kuusisto (1941) obtained some data on the diurnal rhythm of activity of incubating female Willow Warblers, *Phylloscopus trochilus acredula*, and of the effect of the temperature and continuous daylight on their activity.

The rhythm of incubation activity was studied in female Tree Sparrows (*Spizella arborea*) at Eagle Creek, 105 miles northeast of Fairbanks, Alaska (65°25′ N, 145°32′ E). In this species only the female builds the nest and incubates, although the male participates in feeding the young. Other pertinent information on the breeding biology of Tree Sparrows and a description of the habitat of the study area have been presented elsewhere (Weeden, 1965). From 15 May to 27 July there is continuous civil twilight between sunset and sunrise. On these dates the sun is below the horizon 5.28 hours, while at the June solstice it is below the horizon 2.00 hours. However, the study area is situated in a steep valley so that the light intensity is lower there than on the hilltops of the same locality.

The aspects of female activity most readily studied are nest attentiveness throughout the day, length of the night rest, and restlessness while the females are attentive at the nest. The environmental conditions most likely to have a bearing on these aspects of female activity are day length and temperature. Day length profoundly affects the activity pattern of males (Franz, 1948: 317). Franz also pointed out that males and females of a species respond slightly differently to the light factor in temperate regions. Is this difference in sexual response to light augmented or minimized under conditions of continuous daylight? Temperature influences incubation activity of some passerine species in temperate regions (Hann,

1937: 174; Kendeigh, 1952: 40; Lawrence, 1953: 60). Temperatures in the arctic and subarctic generally are lower during the nesting season and an evaluation of the effect of temperature on nest attentiveness at a northern latitude allowed comparison with similar studies in temperate regions.

The diurnal pattern of attentiveness of incubating females is not well understood for many passerine species, even outside of arctic and subarctic environments. Few studies are continuous for 24-hour periods. To obtain such records for a complete day, the use of mechanical recording devices, which give precise lengths for the periods on and off the nest, is imperative. A change in the nest attentiveness as incubation progressed has been noted by various authors (Fautin, 1941: 114; Hardy, 1963: 190; Kessler, 1962; Kuusisto, 1941: figure 9; Nice, 1937: 124; Putnam, 1949: 164). Other authors, however, have indicated that such a progressive change did not exist (Davis, 1960: 439; Lawrence, 1953: 61; Kendeigh, 1952: 169; Sturm, 1945: 194). All authors noted a great deal of individual variation in attentiveness. Changes in nest attentiveness due to individuality are difficult to distinguish from progressive changes when data are limited. A sufficient volume of records obtained mechanically on one species should provide a basis for distinguishing between individual variations and progressive changes.

It has been suggested that restlessness during attentiveness is an indicator of the strength of the brooding instinct. Again, quantitative data are completely lacking. The recording apparatus used in the study of incubation attentiveness also gave good information on the pattern of restlessness throughout the 24-hour day. The relation between restlessness and attentiveness is an important one and must be elucidated for a better understanding of the incubation pattern as a whole.

PROCEDURE

The mechanical device used to study activity of female Tree Sparrows at the nest was a small (three-quarter inch diameter) photo-resistor mounted in the floor of the nest. This photo-resistor was connected by an extension cord through the floor of the nest to an adjustable resistor and the recording element of an Esterline-Angus recorder, all in series.

The intensity of light falling on the photo-resistor determined the magnitude of the current passing through the system. When a female was on the nest, the photo-resistor was covered so that no light shone on it and no current passed through

the system. When the bird was off, however, light of varying intensity was recorded by the system. The photo-resistor was a particularly effective device under conditions of continuous daylight, since enough light was available even during the darkest part of the night to be registered by the photo-resistor. Further, the photo-resistors were about the size of the Tree Sparrow eggs and had smooth, rounded surfaces so they did not disturb the incubating bird.

The photo-resistors respond rapidly to light, so even very short intervals of light falling on the nest were recorded, such as when the bird stood up in the nest. Thus, it was possible to determine precisely the length of time the female was on and off the nest during incubation, and the number of times she turned the eggs or became restless.

The record obtained by the photo-resistor was relatively easy to interpret for the first two or three days after the eggs hatched. During this time the attentive periods included brooding (no light shining on the photo-resistor) and feeding young (rapidly alternating light and shadow due to activity of chicks), while the inattentive periods were characterized by a constant amount of light falling on the photo-resistor since the chicks slept and were too small to eclipse the photo-resistor completely. Later, however, the chicks may have been active even when the adults were absent, or when they slept they may have eclipsed the photo-resistor completely, thus making it impossible to distinguish between the presence or absence of the adults. The mechanical recordings continued to give the length of the night rest since the females spent the quiescent period on the nest throughout the nestling stage.

In the breeding seasons of 1961 and 1962, 60 nest recordings during egg-laying, incubation, and nestling stages were obtained from 16 female Tree Sparrows, as follows: in 1961, 4 recordings were obtained during egg-laying (4–7 June) by four females, 20 complete (24-hour) and 2 incomplete recordings during incubation (6–19 June) by ten females, and 8 recordings during the nestling stage (17–22 June) by four females; in 1962, 1 recording was obtained during egg-laying (6 June), 15 complete and 5 incomplete recordings during incubation (7–20 June) by ten females, and 3 recordings during the nestling stage (17–19 June) by three females.

From the recordings the duration in minutes of each attentive and inattentive period could be read. From these, means for both attentive and inattentive periods were calculated for various appropriate time intervals of the day. The means for the same time intervals for all the recordings were then calculated and compared to the means obtained for different intervals and the differences tested for significance (at the 95 per cent level) with a *t* test.

RESULTS

Egg-laying.—The pattern of activity pursued during incubation becomes established gradually during the egg-laying period. I have two recordings for the third last day of laying, two for the second last, and one for the last day of laying.

Four daily intervals were considered in analyzing the data for the egg-laying stage: (1) 0800 to 1400 hours, (2) 1400 to the beginning of the night rest, (3) night rest, and (4) end of night rest to 0800. The 0800 to 1400 interval has relatively short attentive periods (6–7 minutes), this being associated with midday activity, whereas the intervals before and after the night rest have long attentive periods (Table 1). The intervals

TABLE 1

MEAN LENGTH IN MINUTES AND NUMBER (IN PARENTHESES) OF VISITS TO NEST
DURING THE EGG-LAYING PERIOD

Day of laying[2]	*Interval*[1]				*Time of egg-laying visit*
	1	*2*	*3*	*4*	
Third last			291	42 (2)[3]	0225–0329
(two nests)	46		354	87	0158–0325
Second last	6 (9)[4]	44 (4)	289	33 (5)	0420–0518[5]
(two nests)	7 (5)[4]	36 (3)	303	34 (4)[4]	0402–0459[5]
Last		74 (2)	375	32 (4)	0317–0431[5]
(one nest)					

[1] See text for definitions.

[2] Includes the 24-hour period beginning with the stated day and ending on the succeeding day.

[3] Two visits to the nest were 21 and 64 minutes.

[4] Recording for interval incomplete.

[5] See text for further explanation.

before and after the night rest may last as long as four and one-half
to seven hours during the egg-laying period.

All the recordings indicate that the females sleep on the nest during the
egg-laying period, but I do not know if any heat is applied to the eggs.
The mean length of these night rests was 322 minutes (Table 1). This time
compares with a mean length of 451 minutes for the night rest during
incubation.

The two recordings for the third last day of laying show only three
visits to the nest for both nests. These three visits included, for each nest,
the night rest, the laying visit, and one additional visit. The visits when
eggs were laid occurred approximately between 0200 and 0330 and lasted
an hour or more (Table 1).

On the second last day of laying, the number of visits to the nest in-
creased markedly (Table 1), with attentive periods occurring during all
intervals of the day. On that day the females began a regular alternation
of attentive and inattentive periods, especially in the intervals preceding
and succeeding the night rest, when the attentive periods are very long
(longer, in fact, than those in the corresponding intervals during incuba-
tion). Hence, the diurnal pattern of nest attentiveness develops chrono-
logically around the night rest (the first instance of nest attentiveness
exhibited by the females).

The only recording for the last day of laying, unfortunately, is incom-
plete. However, it appears that the attentive pattern on the last day of
laying is similar to that of the second last day, at least in the intervals
preceding and succeeding the night rest. It was no longer possible to
identify the egg-laying visit accurately on the last two days of laying,

since there were a number of visits to the nest in the interval following
the night rest. However, if we assume that the longest visit during this
interval is the egg-laying visit then we can conclude that it lasts approxi-
mately an hour or longer (Table 1) and occurs sometime between 0315
and 0500.

The recordings for the second last day of laying were all obtained in
1961. In this year at least some incubating was being done on the second
last day of laying. I do not know if this is the case in all years. In 1960
(for which no nest recordings are available), some females did not visit
the nest for some days between the end of laying and the beginning of
incubation. Possibly the pattern of nest attentiveness in 1960 was not
established until later than it was in 1961.

Incubation.—The incubation activity of female Tree Sparrows follows
a regular and characteristic pattern of alternating attentive and inattentive
periods in any 24-hour day. The lengths of the attentive periods are
characteristic for each interval of the day and differ by a factor as great
as two. This pattern was followed by most of the females studied, although
the lengths of both attentive and inattentive periods varied greatly between
individuals. However the individual recordings were obtained on different
days, and the internal rhythmicity of the animals may be subject to varia-
tion by environmental conditions, although the effect of these was not
clearly understood.

To illustrate the diurnal pattern of variation in the length of attentive
and inattentive periods, I have subdivided the 24-hour day into six inter-
vals: (1) 1000 to 1400 hours, (2) 1400 to 1800, (3) 1800 to the beginning
of the night rest, (4) night rest, (5) end of night rest to 0600, (6) 0600 to
1000.

Intervals 3, 4, and 5 are variable in length. The night rest is an ex-
tended period of attentiveness, including sleep, while Interval 3, preceding
the night rest, includes between one and four attentive periods that are
usually at least twice as long as the attentive periods of the previous
intervals. Interval 3 lasts from one-half to two hours. The increase in
the length of the attentive periods is usually fairly abrupt and occurs be-
tween 1700 and 1800. Interval 5, succeeding the night rest, like Interval
3, also shows an attentive pattern which is distinctly different from that of
the intervals following it, but Interval 5 is more variable in length and
may include one to seven attentive periods that are twice as long or
longer than the regular daytime intervals. Further, unlike Interval 3, at
the termination of Interval 5 the pattern of attentiveness does not change
abruptly but frequently grades into the daytime pattern by a gradual
shortening of the attentive periods. It was not possible to delimit Intervals
3 and 5 in such a way that only the distinctly longer attentive periods are

TABLE 2

ACTIVITIES OF FEMALE TREE SPARROWS DURING THE INCUBATION PERIOD

	1961[1]				1962[2]		
Inter-val[3]	Length (in min.) of attentive periods (Mean and SE)	Lenth (in min.) of inattentive periods (Mean and SE)	Per cent time incu-bating	Mean temp. (°F)	Length (in min.) of attentive periods (Mean and SE)	Length (in min.) of inattentive periods (Mean and SE)	Per cent time incu-bating
1	14.5 ± 0.93	8.5 ± 0.41	60	59	12.1 ± 0.81	8.6 ± 0.75	57
2	15.4 ± 0.77	7.7 ± 0.40	64	59	13.0 ± 0.94	9.4 ± 0.68	59
3	26.6 ± 2.25	6.7 ± 0.81	76	59	29.7 ± 2.65	8.0 ± 0.80	72
4	425.7 ± 10.55	none	100	49	484.5 ± 11.03	none	100
5	23.2 ± 5.40	8.8 ± 1.02	71	47	25.9 ± 2.13	7.9 ± 0.50	73
6	16.9 ± 0.77	7.6 ± 0.12	65	55	16.5 ± 1.31	8.2 ± 0.47	63

[1] Based on 20 complete 24-hour recordings and 2 partial recordings.

[2] Based on 15 complete 24-hour recordings and 5 partial recordings. No temperature records available.

[3] See text for definitions.

included, since there was a great deal of variation among individuals and among days. Thus, these intervals were chosen in such a way that Intervals 1, 2, and 6 could be 4-hour intervals. Hence Intervals 3 and 5 may include some "standard" daytime activity or may omit some of the clearly distinctive activity preceding and succeeding the night rest.

A comparison of activities during incubation and the egg-laying periods will further clarify my previous statement that the incubation pattern becomes established gradually during the egg-laying stage. For the egg-laying stage, I used fewer intervals (four) than for the incubation period (six), since diurnal differences in attentive behavior were not as clearly differentiated in the former as they became during incubation. On the basis of the kind of activity, the interval 0800 to 1400 hours during egg-laying corresponds to Intervals 1, 2, and 6 during incubation, even though the latter includes more hours and thus more activity characterized by short attentive periods. The intervals preceding and succeeding the night rest are longer during the egg-laying stage with longer attentive periods than during incubation. On the other hand, the night rest is longer during incubation.

During incubation the visits (attentive periods) to the nest on any day varied in number from 25 to 56 and in mean duration from 12.1 to 29.7 minutes among the daily intervals. The mean lengths of the attentive periods were lowest during Interval 1, followed next by Interval 2 (Table 2), but the difference in the mean length of attentive periods between these two intervals is not statistically significant for either 1961 or 1962. The attentive periods in Interval 6 (Table 2) are significantly longer than

Intervals 1 and 2 for both years. Intervals 3 and 5, preceding and succeeding the night rest, both show significantly increased attentiveness over Intervals 1, 2, and 6. Undoubtedly this difference in attentiveness would be even more marked if Intervals 3 and 5 contained only the long attentive periods that characterize these intervals.

The night rest averaged 425.7 and 484.5 minutes in 1961 and 1962, respectively. This night rest was considerably longer than the quiescent period for male Tree Sparrows in the same area, which was three to four hours. The night rest for female Tree Sparrows at Eagle Creek is similar in length to the night rest for passerine species in temperate regions (Kendeigh, 1952: 164).

Although there appear (Table 2) to be differences in the mean lengths of the inattentive periods for different intervals of the day, none of these is statistically significant. The variation in environmental conditions among the established intervals is primarily due to fluctuations in temperature. Thus there is no apparent relation between environmental temperature and inattentiveness. Also, the inattentive periods remain relatively constant while the attentive periods vary throughout the day. Further, the percentage of time spent incubating in each interval is determined primarily by the lengths of the attentive periods and shows the same trend as the length of the attentive periods.

The incubation recordings were examined for variation in attentiveness related to the progression of incubation. However, there were no apparent trends for either increased or decreased attentiveness as incubation progressed, or if such trends did exist they were obscured by individual variation. Variation in day length (sunrise to sunset) did not appear to affect the length of the night rest or the time of retiring to or awakening from the night rest.

Hatching.—The recordings for activity of adults at the nest during the nestling stage became difficult to interpret after the second or third day of that stage, as already indicated. A further difficulty in interpreting the recordings from the nestling stage is introduced by the fact that the males help in feeding the young. Thus, the averages for the attentive periods during the first three days of the nestling stage may include some male attentive periods along with those of the females. However, the male's contribution of food to the nestlings is minimal or non-existent during the first few days after hatching (but see Baumgartner, 1937: 77) and it can be assumed that the number of male visits included are not great enough to affect the means seriously.

In analyzing attentive behavior during nestling stages, the same six intervals as were established for incubation were used. Table 3 shows that the mean attentive periods for each daily interval during early

TABLE 3

MEAN LENGTHS OF ATTENTIVE (A) AND INATTENTIVE (I) PERIODS (MINUTES)
FOR TREE SPARROWS DURING THE NESTLING STAGE

Date of record[2]	Day of nestling stage	Interval[1]										
		1		2		3		4	5		6	
		A	I	A	I	A	I	A	A	I	A	I
19 June 1961	0–1 day	18.2	6.8	14.5	2.9	12.5	3.4	320	44.5	8.5	14.8	5.8
17 June 1961	1–2 day	7.3	4.8	7.0	5.6	6.3	5.5	–	–	–	–	–
20 June 1961	2–3 day	16.5	5.7	10.9	5.2	12.7	3.5	308	26.1	5.5	10.1	5.1
	3–4 day	9.5	5.1	8.8	4.7	7.5	4.3	–	–	–	–	–
19 June 1961	2–3 day	5.7	9.5	–	–	–	–	222	–	–	–	–
20 June 1961	2–3 day	9.1	12.0	11.5	8.3	12.2	5.5	295	15.5	6.6	–	–
[23 June 1961	4–5 day	–	–	–	–	–	–	269	–	–	–	–
24 June 1961]	5–6 day	–	–	–	–	–	–	214	–	–	–	–
[23 June 1961	4–5 day	–	–	–	–	–	–	322	–	–	–	–
24 June 1961]	5–6 day	–	–	–	–	–	–	245	–	–	–	–
[22 June 1961	4–5 day	–	–	–	–	–	–	357	–	–	–	–
17 June 1962]	1–2 day	–	–	11.7	8.8	19.2	8.4	506	27.6	5.6	–	–
17 June 1962	1–2 day	10.0	5.8	–	–	–	–	–	–	–	–	–
18 June 1962	1–2 day	7.5	8.9	3.4	10.0	4.9	8.0	270	9.4	8.3	–	–
[20 June 1962	3–4 day	–	–	–	–	–	–	180	–	–	–	–
21 June 1962]	4–5 day	–	–	–	–	–	–	335	–	–	–	–
Averages		10.5	7.3	9.7	6.5	10.8	5.5	296	24.6	6.9	12.5	5.5

[1] See text for definitions.

[2] Date given is for Interval 1; Intervals 4, 5, and 6 would be the following day. Recordings in brackets are two for the same female.

nestling stage are shorter than they are during incubation, except for Interval 5 where they are similar in length. The mean inattentive periods are also slightly shorter for the nestling stage than those for the incubation period but this difference is not significant. The most interesting difference in patterns of attentiveness between incubation and nestling stages occurs in the interval preceding the night rest (Interval 3). Contrary to the situation in the incubation period, the interval preceding the night rest during the nestling stage has attentive periods that are about the same in length as during the daytime intervals from 0600 to 1800 hours. Interval 3 is considerably longer during the nestling stage, the time of retirement taking place between 1947 and 2218 hours (mostly between 2100 and 2130 hours), whereas the times of retirement during incubation occurred between 1648 and 2033 hours (mostly between 1900 and 2000 hours). The mean length of the night rest was shorter during the nestling stage, averaging 296 minutes as compared with 451 minutes for incubation. This shorter night rest results both from a later retirement and an earlier rising.

Effect of temperature on incubation pattern.—Only a portion of the 1961 incubation recordings and none of those from 1962 could be subjected

TABLE 4

Times when Temperature Rose Above 50° F and when Individual
Female Tree Sparrows Retired for the Night Rest

Date	A Temperature rose above 50° F[1]	B ♀ ♀ Retired at night[1]	Number of hours between A & B
6 June	0200	1700	15
9 June	0500	1900, 1900	14, 14
8 June	0500	1800, 1900	13, 14
15 June	0500	1800, 1900	13, 14
14 June	0600	1900	13
10 June	0600	1800, 1900	12, 13
13 June	0700	1900, 2000	12, 13
7 June	0800	2000	12
11 June	0900	2000	11

[1] Given as the nearest hour.

to examination for the effect of temperature, since complete temperature records are unavailable.

The mean length of visits to the nest was calculated for each of the intervals of the day (Table 2). Temperature readings were available for each hour of the day and these were averaged to give a mean temperature for each interval. When these mean lengths of visits to the nest were plotted against the mean temperature for each interval for each record, a scatter diagram resulted that indicated that there was no correlation between length of visit and air temperature *at that time*. The same was true when percentage of time spent incubating was plotted against average temperature.

When the length of the night rest was plotted against the mean temperature during the night, a trend was observed which suggested that a longer night rest occurred on cooler nights. Not enough data were available to verify the occurrence of this trend. More precise information on temperatures and microclimates at the nest site would be desirable to test this hypothesis. Possibly the time of occurrence of the minimum temperature has some bearing on this problem.

Female Tree Sparrows went to rest at widely varying times on different days. Some of this large variation seemed to be related to temperature conditions prevailing throughout the day. It was difficult to assess temperature conditions over a day, since temperature fluctuated widely. Thus, an exact analysis of the effect of temperature could not be made. However, I noted the time when the temperature on any day rose above 50°F. This relates to the approximate length of time when good feeding prevailed on that day (when insects were most active). It became apparent that on days when the temperature rose early in the morning, the birds tended to retire early in the evening (Table 4). Presumably on such a day the

TABLE 5

TIMES OF GOING TO REST AND AWAKENING FOR FEMALE TREE SPARROWS

	1961	1962
Mean and range of time for going to rest	1911 (1648–2110)	1927 (1831–2033)
Mean and range of time for awakening	0225 (0107–0441)	0324 (0222–0433)
Mean and range of length of night rest (minutes)	425.7 (346–539)	484.5 (375–602)

birds had a sufficiently good feeding opportunity so that it was unnecessary for them to stay up late, or they became tired earlier having become active earlier. On days when the temperature did not rise until later, the birds did not retire until late (Table 4). Thus, temperature probably acts in determining the length of the total daytime activity period but not in determining the length of the attentive and inattentive periods.

Annual variation in incubation pattern.—In comparing the incubation patterns of the two years it was evident that there were some differences in attentiveness. The most pronounced difference was in the length of the night rest, this being accounted for chiefly by a difference in waking time rather than in the time of retiring (see Tables 5 and 6). This difference in the length of the night rest was statistically highly significant, being longer in 1962 than in 1961. For the intervals preceding and suc-ceeding the night rest the mean lengths of the attentive periods were greater in 1962 than in 1961, but not significantly so. For the two midday intervals (1 and 2) the difference was reversed, the mean attentive periods being significantly greater in 1961 than in 1962. Possibly the lower midday attentiveness in 1962 was accounted for by a longer night rest or *vice versa*. The total percentage of time spent incubating in 24 hours did not differ significantly between the two years, 77 per cent (1961) and 76 per cent (1962), and we can assume that the value is relatively constant for the species, although the pattern in which this incubation is applied may vary according to annual differences in environmental conditions. The length of attentive periods during the morning interval (6) between 0600 and 1000 hours did not differ significantly between the two years.

Data were available for one banded female (four recordings in 1961,

TABLE 6

TIMES OF AWAKENING OF FEMALE TREE SPARROWS DURING THE INCUBATION PERIOD

Time interval	Number of birds awakening	
	1961	1962
0100–0200 hours	7	0
0200–0300 hours	12	5
0300–0400 hours	2	12
0400–0500 hours	1	2

TABLE 7

MEAN NUMBER OF SONGS BY MALES DURING DIFFERENT INTERVALS OF THE DAY

Intervals[1]	Songs/bird/hour		
	1960	1961	Mean
5	7	10	8.5
6	6	9	7.5
1	4	8	6.0
2	7	5	6.0
3	5	7	6.0

[1] See text for definitions.

one in 1962). This female showed a pronounced tendency for a longer night rest in 1962, but shorter daytime attentive periods, than in 1961. The percentage of time incubating, as well as the mean length of inattentive periods differ markedly too.

The mean lengths of inattentive periods were also compared for the two years. None of these is statistically different except for the afternoon interval between 1400 and 1800 hours. Thus, the inattentive intervals, usually synonymous with feeding intervals, are not as subject to variation as are the attentive periods. This fact is in accordance with the previous conclusion that the mean length of the inattentive periods did not differ significantly among the different daily intervals.

Possible explanations for this difference in the behavioral patterns of the two years are discussed later.

Relation of attentiveness of female to activity of male.—Male and female Tree Sparrows were often observed feeding quietly together during the incubation stage. This led me to question whether there was any relation between the song activity of males (attentiveness) and nest attentiveness of the female.

The song activity of male Tree Sparrows showed a highly irregular pattern, with large variations in singing from one diurnal interval (the same intervals used for incubating females) to the next, or even from one hour to the next. Cullen (1954: 40) refers to this pronounced variation in song activity as polyphasy. The interval of greatest song activity (considering number of songs per bird) of male Tree Sparrows during the incubation stage generally occurred from the end of the night rest to 0600 hours. This interval (Interval 5) is the time of day when the females showed prolonged attentive periods. Males awakened earlier than the females so that this interval is longer for them than it is for females. Generally, male song activity declined throughout the remaining intervals of the day (Table 7), with a slight increase toward evening. Thus, the times during the day when females are least attentive to the nest are the times
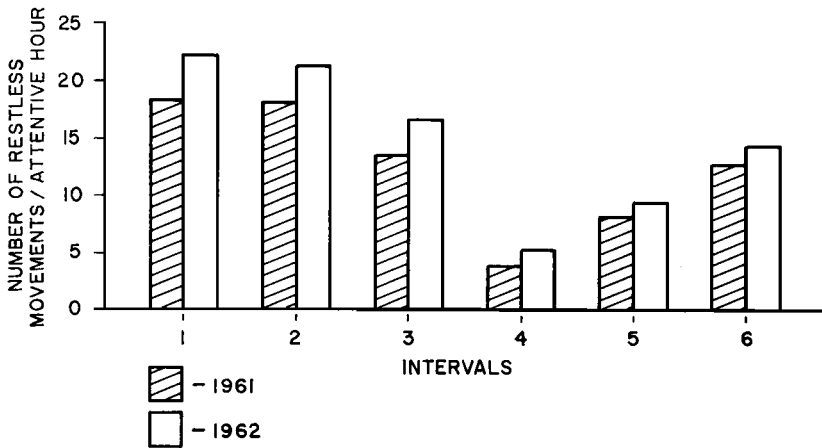
Figure 1. Diurnal restlessness of female Tree Sparrows during incubation. See text for definitions of intervals.

when the males are least active in their singing, but I do not know if there is any causal relationship. In view of the erratic behavior of the male, it seems that the internal rhythms of male and female Tree Sparrows operate independently.

Restlessness of incubating females.—During the attentive periods the recording needle is capable of recording light which falls instantaneously on the photo-resistors such as occurs when the hen stands up momentarily. Such risings from the eggs may indicate times when the female turns the eggs, but it may also just indicate restlessness and thus should be considered as such since it is impossible to distinguish between the two. The number of restless movements per attentive hour was highly variable both from day to day and from individual to individual. However, when the restless movements per attentive hour were averaged for all the recordings for each daily interval, a general pattern emerged. Most females followed this pattern, although the magnitude of this restlessness may differ considerably (Figure 1).

In the intervals between 1000 and 1400, and 1400 and 1800, the females show the greatest restlessness (Figure 1), followed next by a significantly lower restlessness in the interval preceding the night rest. Restlessness during the night rest was lowest, presumably because a high proportion of that interval represents actual sleep. Restlessness during Interval 5 was significantly higher than during the night but significantly lower than restlessness during any other interval of the waking day. Restlessness increases as the day progresses (Figure 1). In none of the intervals could I detect a trend toward greater or lower restlessness as incubation progressed.

If such a trend does exist it was obscured by the large amount of individual variation that is apparently present.

There is a noticeable difference in the mean number of restless movements per attentive hour between 1961 and 1962 for each interval (Figure 1), although the pattern of restlessness still follows the same trend throughout the day. This difference in magnitude, however, did not show significance. Thus some other explanation for the difference in restlessness was sought.

I compared the restlessness of females incubating four eggs with those incubating five eggs. A mean number of restless movements per attentive hour was calculated for each 24-hour incubation record, allowing comparisons between individuals and between days. The mean number of restless movements per attentive hour for females incubating 4-egg clutches and 5-egg clutches was 11.3 (range, 5.6–17.9) and 14.3 (8.9–23.1), respectively. The difference between these two mean values was statistically highly significant. No recordings for clutches of six eggs were available although these do occur among Tree Sparrows. The fact that the number of eggs in the clutch influences restlessness probably accounts for the annual difference in restlessness, since the 1961 data are composed of 12 recordings from five clutches of four eggs and 7 recordings from four clutches of five eggs, whereas the 1962 data are from 3 recordings of two clutches of four eggs and 13 recordings of eight clutches of five eggs.

There was no apparent relation between restlessness and mean daily temperature. However, mean daily temperatures during June, 1961, did not vary greatly, falling into the approximate range of 50° to 60° F. The mean maximum and minimum air temperatures for the period of incubation were 63° F (range, 58°–68°) and 41° F (31°–46°). The microclimates in the vicinity of the nests undoubtedly had less pronounced extremes than the air temperatures.

There was no change in restlessness that could be attributed to the progression of incubation. However, there were no recordings for any individual females that were continuous throughout the incubation period. Further, there was no relation between restlessness of an individual female and the percentage of time she was attentive in 24 hours.

DISCUSSION

In discussing the diurnal activity of female Tree Sparrows during incubation, it is necessary to differentiate between night rest (which is spent on the nest) and daytime attentiveness at the nest. Daytime activity is characterized by the rhythmic alternation of attentive and inattentive periods. This rhythmic pattern shows predictable variations between different times of the day. The most noticeable feature in the diurnal pat-

tern is the much stronger attentiveness in the intervals preceding and succeeding the night rest. During these two intervals the attentive periods are almost twice as long as the attentive periods during midday, while the inattentive periods (feeding periods) remain about the same. For Tree Sparrows the interval preceding the night rest lasts about one to two hours, while the interval succeeding the night rest may be as long as three to four hours. Kendeigh's (1952: 73) data on the House Wren (*Troglodytes aedon*) also show stronger attentiveness preceding and succeeding the night rest, but those intervals are considerably shorter than for the Tree Sparrow, each lasting only about one hour. Cox (1960: 18), Fautin (1941: 114), Kuusisto (1941: 41), and Verner (1965a: 19) also found such an increase in the early morning and evening attentiveness. This phenomenon of increased attentiveness preceding and succeeding the night rest is by no means a universal one among passerines. Davis (1960: 440) found no regularity or rhythm of the attentive and inattentive periods and stated that very long or very short attentive periods could occur at any time of day. The latter statement is probably true for most species but it seems biologically more meaningful to consider means in this case. Still other authors have found shorter attentive periods occurring in the early morning hours (Erickson, 1938: 291). The situation in the Wrentits, *Chamaea fasciata* (Erickson, 1938: 291), may be a special case since male and female relieve each other at the nest and do so more frequently during the early morning hours. What, then are the factors controlling the variation in the attentive-inattentive rhythm during the day for Tree Sparrows?

Nice (1937: 123) stated that hunger is the basis for the rhythm in incubation attentiveness. Kendeigh (1952: 86) also agreed with this view and thought that the time required to digest the particular diet and the size of the bird's "stomach" determine the length of the attentive period. Tree Sparrows are largely insectivorous during the breeding season (Baumgartner, 1937: 73). The availability of insect food throughout the day depends on temperature. If hunger terminates attentive periods, they would be shortest, and inattentive periods longest, when the birds are hungriest after the long night rest. Further, food is least available during the cool early morning hours and a relatively longer time is required to obtain food. These two factors together would lead us to speculate that the longest inattentive and shortest attentive periods occur in the interval succeeding the night rest. Thus inattentive periods should, perhaps, be longer. This is not the case. Thus, in regard to the hunger factor, we can say either that the birds are not as hungry in the intervals preceding and succeeding the night rest, or that some other factor determines the length of the attentive period during these time intervals.

The factor most often discussed in relation to nest attentiveness is

temperature. The question of the effect of temperature on incubation is important and unfortunately one that this particular study does not sufficiently elucidate. In the literature one finds statements indicating no relation between attendance and temperature (Davis, 1960: 439; Davis *et al.*, 1963: 356; Kuusisto, 1941: 45) or an inverse relation such that attendance decreases with increased temperature (Hann, 1937: 174; Kendeigh, 1952: 40; Kluijver, 1950: 120; Lawrence, 1953: 60; Prescott, 1964: 40; Verner, 1965a: 19). This diversity of opinion concerning the relation between temperature and attentiveness may be due to a different response to the temperature factor by different species as suggested by Skutch (1957: 81) and Eyster (1954: 23), or diurnal rhythm may be related to temperature only superficially through some other factor. For example, if diurnal rhythm were related to food availability, there would also be a superficial relation to temperature which would differ for species with different food habits.

Kendeigh's (1952: 41) curve for attentiveness of female House Wrens follows more or less inversely the curve for air temperature, except that the curve for air temperature lags behind the curve for attentiveness. Tree Sparrows show a similar relationship with temperature (Table 2). Here changes in mean temperature for each of the diurnal intervals also lag behind changes in the mean length of the attentive periods. The mean temperature for Intervals 1, 2, and 3 is 59° F (Table 2). Thus, the temperature during the interval preceding the night rest is about the same as during the daytime although attentiveness of female Tree Sparrows increases greatly. Thus, increased attentiveness is not correlated with decreased temperature in the evening. Interestingly, the night rest does not correspond to the interval of lowest temperature, again suggesting that nest attentiveness is not directly correlated with temperature. The interval of lowest mean temperature succeeds the night rest and has long attentive periods.

Eyster (1954: 20) stated that daily rhythm in passerines "appears to be inherent and capable of only limited variation due to external factors." Further, Verner (1965b: 132) thinks that selection should favor those individuals that forage at the best feeding time, thus leaving more time for other activities. He stated that not only temperature, but also light, plays an important role in making the optimum feeding time during mid-day; at this time insects are most active and light conditions are such that the feeding birds are able to perceive them best. It is at this time that the birds store most of the energy that is needed, not only for metabolism through the night but also to provide a surplus that allows for non-foraging activity in the early morning (Verner, 1965b: 132). This would be a plausible explanation of the observed incubation activity of female Tree

Sparrows where nest attentiveness continues to be a stronger instinct than feeding activity during the time of day when feeding is least efficient. Indeed, my data indicate that the time of evening retirement is determined by the quality of the feeding opportunity on any day. Hence, only daytime activity is ultimately related to the temperature and not the attentive behavior preceding and succeeding the night rest.

In comparing daily rhythms of activity of Tree Sparrows in a northern latitude with birds in temperate regions, another point of interest emerges. I have already pointed out similarities in the behavior of Tree Sparrows at Eagle Creek and House Wrens studied by Kendeigh (1952) near Cleveland, Ohio. The length of the night rest for the females of these two species is similar. (Kendeigh has not calculated average lengths of night rests during incubation, giving only the beginning and end in relation to sunset and sunrise drawn on a small-scale graph.) The mean length of the night rest during incubation for female Tree Sparrows averaged approximately 7 and 8 hours for two years. This is similar to the night rest for House Wrens during incubation as I am able to read it from the difference between Kendeigh's curves (1952: figure 15) for end and beginning of daily activity. Kuusisto (1941: figure 10) found the length of the night rest to vary between 6 hours 20 minutes and 9 hours 26 minutes for *Phylloscopus trochilus acredula* in Finland (at a latitude similar to central Alaska). In contrast to the similarity of the quiescent period of female passerines in northern and central latitudes there is a marked reduction in the length of the quiescent period of males (3 to 4 hours for male Tree Sparrows) at northern latitudes (Armstrong, 1954: 7; Franz, 1948: 318; Hoffman, 1959: 89; Tinbergen, 1939: 11; Wagner, 1958: table 6). These authors relate the increased activity of males in the arctic to the difference in light regime between northern and central latitudes superimposed on the normal increased excitability of males in the breeding season. Franz (1948: 323) and Kluijver (1950: 102) noted a difference in the length of quiescence of the sexes in central latitudes also. Franz (1948: 318) did not make any special mention of the fact that this difference in the activity of the sexes becomes much more pronounced at northern latitudes; this may be because he did not have data on the incubation activity of the females but only on the nestling period when the activity time of females increases considerably. Baumgartner (1937: 77) found the night rest for Tree Sparrows to be approximately six hours during the nestling period at Churchill, Manitoba. This time compares with a mean night rest of approximately five hours for 13 recordings I obtained during the nestling stage for Tree Sparrows at Eagle Creek. The increase in the active period of females at Eagle Creek during the nestling stage resulted primarily from an extension of evening activity. The similarity of the

timing of the incubation rhythm between the Tree Sparrow operating
under continuous daylight and the House Wren operating under a
regime of alternating light and dark intervals, leads me to speculate on
the existence of an endogenous rhythm in control of attentive behavior
during incubation and, further, that the light factor is not operative in
determining the pattern of incubation activity, although it may still be
an important "Zeitgeber" (Aschoff, 1960: 11) in keeping the rhythm
regular on a diurnal basis.. Then we must postulate a different rhythm to
account for the attentive behavior during the nestling stage. Franz (1948:
figure 14), Karplus (1952), and Wagner (1958: 52) have shown that the
daily feeding period is longer at northern latitudes than for the same
species at central latitudes and it may be that the light factor does influ-
ence the activity period during the nestling stage.

The incubation recordings showed that there were small but significant
differences in the pattern between two years expressed as a shorter night
rest in 1961 and relatively longer attentive periods on the nest during the day
than in 1962. The incubation recordings included approximately equal
dates and thus a difference in day length is not a likely cause for the varia-
tion. Two clear environmental differences existed between the two years,
but these may not be responsible necessarily for the observed differences
in behavior. First, 1961 was an "early" and 1962 a "late" season (dates
of first flowering of first flower to bloom, *Douglasia gormania*, were 16
May 1961 and 31 May 1962), and second, a difference in population
density existed (21 pairs per 100 acres in 1961, and 35 pairs per 100 acres
in 1962) (Weeden, 1965: table 1). Differences in phenology could pos-
sibly affect the relative availability of food and thus the number of times
the females must leave the nest to feed. Although I previously suggested
that a factor other than hunger is responsible for the decidedly longer
attentive periods in the intervals preceding and succeeding the night rest,
this is not to say that hunger is not responsible for determining the length
of attentive periods in the middle of the day when the birds might take
advantage of the optimal availability of food. The annual differences
in daytime attentiveness occurred only in the intervals between 1000 and
1800 hours and not in the intervals preceding and succeeding the night
rest. Differences in night rest may simply compensate for differences in
daytime attentiveness since the percentage of time spent incubating was
the same in the two years of the study.

Population density may influence the amount of social stimulation
that the individuals of the population receives. In many species of pas-
serine birds, some attentive periods of females are terminated when the
male sings or calls in the vicinity of the nest (Cox, 1960: 17; Hann,
1937: 173; Nice, 1937: 126), and these attentive periods are then shorter

than those that terminate without the interference of the male. I have no direct observations to verify that the male Tree Sparrow occasionally calls the female from the nest. At high densities, territories of Tree Sparrows are smaller (Weeden, 1965: table 1) and thus males and females are in closer proximity; perhaps females were called from the nest more frequently, resulting in shorter average attentive periods. If this were so, then the attentive periods preceding and succeeding the night rest could be expected to be shorter also.

Some observers have found that the incubation pattern changes as incubation progresses. No clearly chronological changes were seen for Tree Sparrows. There was much variation in the pattern, but this seemed primarily due to individual variation. Not only have different observers found changes in attentiveness during incubation, but some have noted changes in restlessness as incubation approached hatching (Fautin, 1941: 114). I was not able to discover a trend toward greater restlessness near hatching, and differences that I did find seemed to be due to differences in the number of eggs being incubated. Beer (1965: 15) found that an "optimal" number of eggs produced fewer risings and settlings in Black-billed Gulls (*Larus bulleri*) than did fewer or more eggs in the clutch. This might indicate that a comfort factor is involved.

The diurnal pattern of restlessness shows a relation to the pattern of actual nest attentiveness. Restlessness is lowest during the night rest and is significantly higher for all intervals of daytime activity. Throughout the daytime activity, restlessness increases gradually to a maximum level that prevails during the 1000–1800 hour intervals (Figure 1) but then decreases slightly in the interval preceding the night rest. Thus, short attentive periods correspond to high restlessness and undoubtedly these two factors are interrelated.

SUMMARY

Nest attentiveness was studied in Alaska (65°25′ N, 145°32′ E) by using photo-resistors mounted in the nests to indicate the presence or absence of the female by the amount of light striking the photo-resistor.

The pattern of activity of incubation became gradually established during the egg-laying stage. The first attentive interval was the night rest spent on the nest as soon as laying began, followed on the second last day of laying by the establishment of attentive periods preceding and succeding the night rest, and finally on the day of clutch completion by the establishment of daytime attentiveness.

During incubation the rhythmic alternation of attentive and inattentive periods varied throughout the day. The attentive periods were significantly longer in the intervals preceding and succeeding the night rest

than during midday. The mean length of attentive periods preceding and succeeding the night rest varied between 23 and 30 minutes, while the mean daytime intervals varied between 12 and 17 minutes. The mean length of inattentive periods varied between 6.7 and 9.4 minutes throughout the day. No change in this pattern was observed as incubation progressed.

Total daytime activity of female Tree Sparrows during the incubation period in continuous daylight was 16 to 17 hours, a value similar to that of passerine species in temperate regions. The total daytime activity of females at Eagle Creek was three to four hours shorter than that of male Tree Sparrows.

During the nestling stage the attentive periods were shorter but the total length of attentiveness throughout the day was greater. The interval preceding the night rest during the nestling stage continued to have short attentive intervals similar to those during midday.

Temperature apparently did not influence the length of the attentive or inattentive periods. It did, however, influence the total daytime activity. On warm days, when the birds had a good feeding opportunity, they tended to retire earlier than on cool days or on days when the temperature did not rise until late.

There were some significant annual differences in incubation pattern between 1961 and 1962, although the total time spent incubating was the same (76 to 77 per cent of the day). The night rest was longer, and daytime attentive periods shorter in 1962 than in 1961. The difference in night rest was accounted for chiefly in waking time.

Risings and settlings (restless movements) by the females during the attentive periods showed a pattern similar to nest attentiveness itself. At the time of day when the female Tree Sparrows show the strongest attentive instinct, they are the least restless. For example, restlessness is lowest during the night rest, somewhat higher but still relatively low in the interval succeeding the night rest, rises throughout the daytime intervals to its maximum but becomes much lower again during the interval preceding the night rest, when attentiveness has again increased.

LITERATURE CITED

ARMSTRONG, E. A. 1954. The behaviour of birds in continuous daylight. Ibis, **96:** 1–30.
ASCHOFF, J. 1960. Exogenous and endogenous components in circadian rhythms. Cold Spring Harbor Symposia on Quantitative Biology, **25:** 11–28.
BAUMGARTNER, A. M. 1937. Food and feeding habits of the Tree Sparrow. Wilson Bull., **49:** 65–80.
BEER, C. G. 1965. Clutch size and incubation behavior in Black-billed Gulls (*Larus bulleri*). Auk, **82:** 1–18.

BROWN, R. G. B. 1963. The behaviour of the Willow Warbler *Phylloscopus trochilus* in continuous daylight. Ibis, **105**: 63–75.

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

CULLEN, J. M. 1954. The diurnal rhythm of birds in the arctic summer. Ibis, **96**: 31–46.

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

DAVIS, J., G. F. FISLER, AND B. S. DAVIS. 1963. The breeding biology of the Western Flycatcher. Condor, **65**: 337–382.

ERICKSON, M. M. 1938. Territory, annual cycle, and numbers in a population of Wrentits (*Chamaea fasciata*). Univ. California Publs. Zoöl., **42**: 247–334.

EYSTER, M. B. 1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. Ecol. Monogr., **24**: 1–28.

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

FRANZ, J. 1948. Jahres- und Tagesrhythmus einiger Vögel in Nordfinnland. Zeits. f. Tierpsychol., **6**: 309–329.

HANN, H. W. 1937. Life history of the Oven-bird in Southern Michigan. Wilson Bull., **49**: 145–237.

HARDY, J. W. 1963. Epigamic and reproductive behavior of the Orange-fronted Parakeet. Condor, **65**: 169–199.

HOFFMAN, K. 1959. Über den Tagesrhythmus der Singvögel im arktischen Sommer. J. f. Orn., **100**: 84–89.

KARPLUS, M. 1952. Bird activity in the continuous daylight of the arctic summer. Ecol., **33**: 129–134.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Illinois Biol. Monogr., **22**: 1–356.

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

KLUIJVER, H. N. 1950. Daily routines of the Great Tit, *Parus m. major* L. Ardea, **38**: 99–135.

KUUSISTO, P. 1941. Studien über die Ökologie und Tagesrhytmik von *Phylloscopus trochilus acredula* (L.) mit besonderer Berucksichtigung der Brutbiologie. Acta Zool. Fenn., **31**: 1–120.

LAWRENCE, L. DE K. 1953. Nesting life and behaviour of the Red-eyed Vireo. Canadian Field Nat., **67**: 47–77.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow, I. Trans. Linn. Soc. New York, **4**: 1–246.

PALMGREN, P. 1949. On the diurnal rhythm of activity and rest in birds. Ibis, **91**: 561–576.

PRESCOTT, K. W. 1964. Constancy of incubation for the Scarlet Tanager. Wilson Bull., **76**: 37–42.

PUTNAM, L. S. 1949. The life history of the Cedar Waxwing. Wilson Bull., **61**: 141–182.

SKUTCH, A. F. 1957. The incubation patterns of birds. Ibis, **99**: 69–93.

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

TINBERGEN, N. 1939. The behavior of the Snow Bunting in spring. Trans. Linn. Soc. New York, **5**: 1–94.

VERNER, J. 1965a. Breeding biology of the Long-billed Marsh Wren. Condor,
    67: 6–30.
VERNER, J. 1965b. Time budget of the male Long-billed Marsh Wren during the
    breeding season. Condor, **67**: 125–139.
WAGNER, G. 1958. Beobachtungen über Futterungsrhythmus und Nestlingsentwick-
    lung bei Singvögeln im arktischen Sommer [Lat 67°30′ N]. Orn. Beob., **55**:
    37–54.
WEEDEN, J. S. 1965. Territorial behavior of the Tree Sparrow. Condor, **67**: 193–209.

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