SOLAR RADIATION, LIGHT INTENSITY, AND ROOSTING BEHAVIOR IN BIRDS

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Many investigators have commented on the apparent relationship of cloud cover, light intensity, temperature and sunset time to the time of roosting in many bird species (e.g., Davis 1955, Bliese 1955, Davis and Lussenhop 1970). There is general agreement that light levels are closely associated with the timing of roosting responses, but there is disagreement concerning the influence of cloud cover, temperature, and time of sunset on the daily onset and termination of roosting. We have obtained data that clarify the issue. Furthermore, we report a close relationship between the amount of daily solar radiation and the arrival time of birds at the roost. This latter relationship is important as a field verification of the circadian rule (Aschoff 1967).

MATERIALS AND METHODS

Observations were made on 21 afternoons during February and March, 1972, at a Brown-headed Cowbird (*Molothrus ater*) roost located in a bamboo (*Phyllosatachys* spp.) thicket on the campus of Clemson University, South Carolina. The roost contained on an average 1500 birds, and only "pre-roosting" and "roosting" behaviors were studied (Jumber 1956). The roost site consisted of a bamboo area of approximately 19 m^2 surrounded by four isolated trees; the bamboo was about 4 m high, and the nearby trees ranged from 10 to 16 m in height. All data were gathered 20 m from the roost. The following information was taken each day: general weather conditions; direction of flight into the roosting area; time of first flock arrival, peak of pre-roosting activity, first bird into the roost, peak of roosting activity and last bird into the roost. The light levels near the termination of roosting behavior were based on the light level required to activate a photocell-controlled light 2 m from the roost. We found that the light consistently turned on at an ambient light intensity of 64.56 lux (6 ft-candles). A Weston photometer (Model 703–67) was used for light measurements. Data on total daily solar radiation and average daily temperature were supplied by the National Weather Service office on campus.

RESULTS

Most of the flocks that arrived at the roost site contained from 10 to 30 birds, but occasionally flocks had 200 to 250 birds. The birds landed in the trees next to the roost (pre-roosting behavior) and did not fly into the bamboo thicket until nearly all the flocks had assembled in the nearby trees. On the average approximately 28 min elapsed between the arrival of the first and last flocks in the trees. Coincident with the arrival of the last flock, the birds that had assembled in the pre-roosting trees started to enter the roost. Figure 1 shows the plots of the time the first birds entered the roost, the time the

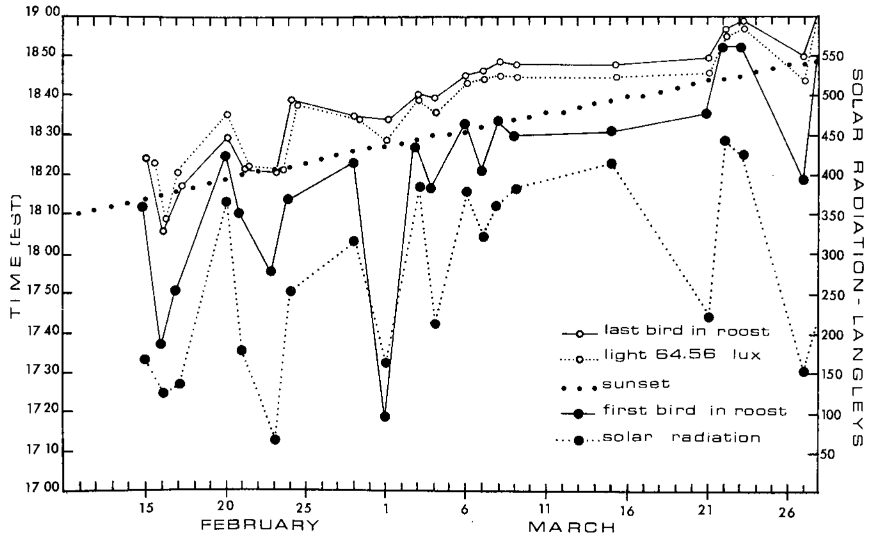

FIG. 1. Plots of first and last birds in roost in relation to daily amount of solar radiation, time of sunset, and time that light levels reached 64.56 lux. Twenty-one days were sampled from February 15 to March 28.

last bird entered the roost, the total daily solar radiation, and the time when ambient light intensity reached 64.56 lux. The curves for the first bird in roost (the same as peak number of birds in nearby trees) and the total daily solar radiation show very close correlation. The product moment correlation coefficient (Sokal and Rohlf 1969) for these two curves is +0.67 ($P < .001$). We found the degree of association between the time of onset of pre-roosting behavior and the amount of daily solar radiation to be equally strong. Similarly, the plots of the time when the last bird entered the roost and the time when ambient light levels reached 64.56 lux show a marked degree of association. The product moment correlation coefficient for these plots is +0.99 ($P < .001$).

Despite fluctuations in the curve for the times that the first birds entered the roost, the line that best fits the individual plot points shows a slightly greater slope (1.32) than that for the plot of sunset time (0.91). The overall seasonal timing of roosting may be related to the time of sunset, but the day-to-day variation in the time the first birds arrive at the roosting site and enter the roost is greatly influenced by the daily amount of solar radiation impinging on the birds. The termination of roosting events is similarly related to the time when light intensities reach low levels during twilight.

Figure 2 shows the relationships of average daily temperature to solar

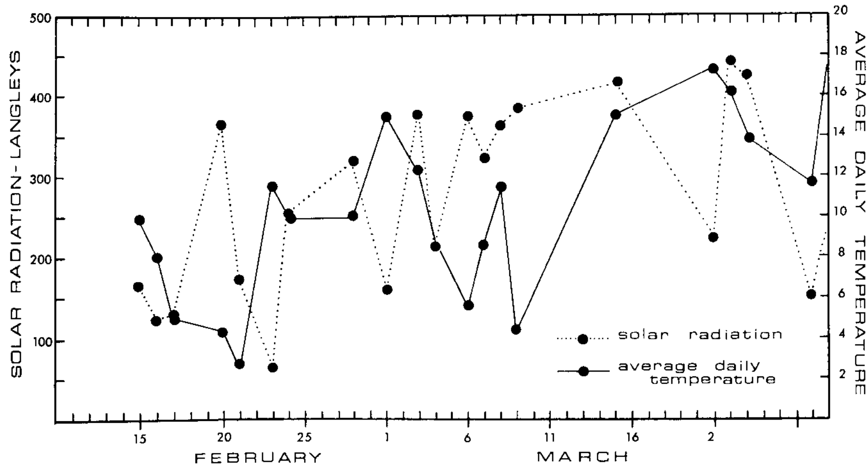

FIG. 2. Plots of average daily temperature (in degrees Celsius) in relation to the amount of solar radiation. The points represent the 21 days on which roosting data were acquired.

radiation. On warm days in winter, cloud cover increases while the amount of solar radiation decreases. In contrast, on cold days the weather is influenced by cold anticyclonic weather systems, the sky is generally clear, and the amount of solar radiation reaching the ground is high. Thus in winter in the Piedmont of South Carolina, the days with relatively high totals of solar radiation are the coldest; the days with relatively low daily totals of solar radiation are the warmest.

DISCUSSION

Light intensity, temperature, cloud cover, and time of sunset have been viewed as influential factors affecting the timing of roosting behavior in birds (Davis 1955), but these factors are interrelated and interdependent (Bliese 1955). Kluijver (1950) found that weather conditions had little influence on the time of roosting although the coefficients for cloudiness were about – 0.3. Light intensity and cloudiness have usually been the main factors correlated with roosting behavior (Bliese 1955), but some workers have pointed out that roosting birds forage longer (roost later) on cold days than on warm days (Radford 1954, Davis 1955), and this has advantages from an energetic standpoint. While these explanations are reasonable, there has been little attempt to discuss how the factors interrelate. The data we have gathered suggest a close relationship between the amount of solar radiation and the time birds stop foraging and begin their roosting behavior. The effects of temperature on roosting behavior may be indirect because the total daily solar radiation is inversely related to the average daily temperature. Moreover, the influence of the daily totals of solar radiation on the duration of activity periods follows the circadian rule (Aschoff 1960).

The circadian rule predicts that for a day-active species in constant conditions, an increase in light intensity will cause the organism to become more active during longer activity periods. Aschoff (1965, 1967) found that this influence also operated in cases of natural entrainment by photoperiod, and that the entrained organisms integrate more or less over the light intensities in both parts of a light cycle. We feel that the timing of roosting in day-active birds functions similarly; that is, the brighter the day (more solar radiation), the later the birds start towards the roost. This relationship would also explain the influence of cloud cover and light intensity reported by other workers. Nice (1943) found that the last evening song of Song Sparrows (*Melospiza melodia*) occurred 13 to 14 min after sunset on clear days and 3 min after the time of sunset on cloudy days, and Dunnett and Hinde (1953) found that Great Tits (*Parus major*) roosted earlier on cloudy days. It would appear then that the total daily amount of solar radiation reaching a bird during the course of a day is an important factor in determining its total behavioral energy budget, and this in turn regulates its activity cycle.

If the amount of solar radiation is an important factor in determining when foraging birds start toward their roost, what factor is responsible for the timing of the final events of roosting? Ambient light intensity after sunset appears to be responsible. Bünning (1973) has pointed out that light intensities during sunrise or sunset are too variable to serve as discrete reference points regulating activity rhythms, because the fluctuations of the light intensities during these phases of the solar day are much too great from day to day, depending especially on cloudiness. He found most suitable as reference points the values of light intensities between about 1 and 10 lux, occurring shortly before sunrise and soon after sunset. In this range of light intensity, the rates of intensity changes are the greatest, and the variations in time because of weather conditions usually do not exceed a few minutes. Bünning thinks an abrupt increase or decrease in intensity is more effective in controlling a physiological process than a gradual one. Our data support Bünning's postulate, for the variation in the times the last birds entered the roost is considerably less than the variation in the times the birds arrived in the vicinity of the roost.

The influence of changing photoperiods or varying daylengths on seasonal behaviors and physiological events is well documented. We suggest that the changing duration and quality (intensity) of light during the day might well have an equally important effect on the daily behavioral and physiological functions of animals in the wild.

SUMMARY

The timing of Brown-headed Cowbird (*Molothrus ater*) roosting behavior on 21 evenings during February and March, 1972, in the Piedmont of South Carolina was compared to the total daily amount of solar radiation, the time of sunset, and the ambient light levels during twilight. The movement of birds toward the roosting area was closely associated with the total daily amount of solar radiation, while the termination of roosting was more closely correlated to light intensity levels following sunset. The timing of roosting behavior in relation to the quantity and quality of light was in accordance with the circadian rule.

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