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BETWEEN 20 November 1949 and 31 March 1950, the feeding patterns of the House Sparrows (*Passer domesticus*) that frequented a feeding station in suburban St. Paul, Minnesota, were observed. These observations were made in order to obtain an understanding of how weather conditions affect feeding and the survival of these birds. The feeding station was located on the north side of a building, where it had some protection from the wind and was not disturbed by people or dogs. Bread and other foods that could not be carried away were kept on the station constantly. No other species of bird was observed using the station. The weather data were taken from the records of the St. Paul weather station.

Forty-nine of the House Sparrows were banded with colored bands, and four others had natural marks that allowed the identification of 53 individuals. These marked birds showed that the individuals using the feeding station were from several flocks. These flocks were usually composed of from 5 to 15 birds, although larger groups were seen occasionally. The birds apparently traveled considerable distances, as one individual appearing at the feeding station frequently was also observed feeding at a riding stable about 0.9 miles away.

So far as was possible, the number of House Sparrows on the feeding station was recorded at 15-minute intervals throughout the day. The first observation of the day was usually made about a half hour before sunrise and the last about a half hour after sunset. Some 3,328 counts were made, totaling 12,848 bird observations. Since the day length during the period of study varied from about 8 hours and 32 minutes to about 12 hours and 39 minutes, it was not possible to make direct chronological comparisons. To make these comparisons, the period between sunrise and sunset was divided arbitrarily into 15 equal parts, and all observations falling within one of these periods were averaged.

In order to establish a base from which to compare the feeding patterns during extremes in weather conditions and day length, the entire set of observations were combined by period of the day (see Figure 1).

A small number of birds, usually singles or groups of twos or threes, arrived at the feeding station a little before sunrise. Shortly after sunrise the flocks would arrive, and the morning peak was reached immediately. The average number of birds at the station then decreased steadily

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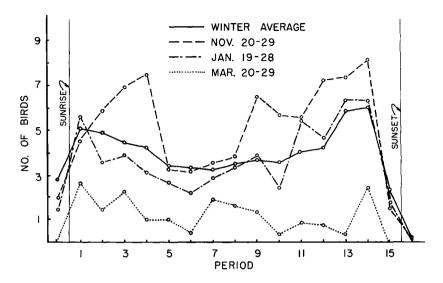


Figure 1. Average number of birds observed on the feeding station during each period of the day for the entire winter and the intervals of 20 to 29 November, 19 to 28 January, and 20 to 29 March. The curve for the winter average is based on 3,328 counts with 12,848 bird observations. The 20-29 November curve is based on 234 counts with 1,230 bird observations. Not less than 10 counts were made for any period. The 19-28 January curve is based on 275 counts with 1,038 bird observations. Not less than 11 counts were made for any period. The 20-29 March curve is based on 185 counts with 219 bird observations. Not less than 6 counts were made for any period.

through the fifth period, with the lowest number of birds being found during the seventh period. This was followed by a gradual increase in feeding activity through the 12th period. A sharp increase in numbers came during the 13th period, with the afternoon peak being reached in the 14th period. Only about a third as many birds remained feeding during the 15th period as in the preceding one. Only occasionally did a bird remain after sunset. During the winter the House Sparrows fed throughout the day, with the morning and evening peaks being only 1.6 and 1.9 times as great, respectively, as the midday low.

While intensity of feeding was not measured, it was evident that it was greater among those birds on the station during the peak periods than during the midday low. Those birds arriving before sunrise and those remaining after the afternoon peak were usually voracious feeders.

It is difficult to separate the several factors that have modifying effects on winter feeding habits. However, by taking a large series of observations, one can show trends, even though the absolute amounts of change

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in relation to a given factor cannot be determined. To facilitate the analysis of the data in relation to day length and season, the total period was divided into 10-day intervals. The average number of birds present per observation for each period was calculated for each of these intervals. Three 10-day intervals were selected for comparison. These typify the short day intervals of early winter and midwinter and the longer day intervals of late winter. The undescribed intervals between these change gradually from one to the other.

During the first series of observations (see Figure 1), 20 to 29 November, with an average of about nine hours between sunrise and sunset, the morning peak came during the fourth feeding period following a steady build-up that started just before sunrise. This was followed by an abrupt drop to the midday low in feeding activity. The curve for the morning peak contrasts with the winter average, in that build-up was more gradual and the decrease to the midday low in feeding activity was abrupt. The midday low was also relatively lower and of shorter duration than that for the all-winter average. An early afternoon peak in number of birds came during the ninth feeding period, followed by a minor drop and then an increase to the afternoon peak during the 14th period. The build-up to the afternoon peak and the subsequent drop followed the same pattern as that of the winter average, except that there were only about a fifth as many birds present during the 15th as during the 14th period.

The 19 to 28 January interval, with an average of about 9 hours and 20 minutes between sunrise and sunset, contrasts with the November period of similar day length primarily in that the morning peak comes abruptly as in the all-winter average. An indication of a possible ninth-period peak is also present here. The late-afternoon peak is somewhat more pronounced than that of the early-winter period.

The 20 to 29 March interval typifies the longer day periods of late winter. These periods differ from the short day intervals and the allwinter average in that there are three feeding peaks with well-defined troughs between them. There is also a considerably shorter period of intense feeding activity during the early morning and late afternoon. The feeding during the long day intervals is also more leisurely and erratic.

The differences observed between the early- and midwinter intervals undoubtedly reflect changes in the daily temperature. The differences seen between the early- and late-winter periods, where the average daily temperatures were not greatly different, are undoubtedly due to the increased length of the feeding period. In order to facilitate the analysis of the temperature data, the average temperature for each day was calculated. The data were then grouped in six categories covering about 5.5 degrees C each. The average daily temperatures varied from -25 to  $6^{\circ}$  C. The groups of data from days having -25 to  $21^{\circ}$  C, -14 to  $-9^{\circ}$  C, and -3 to  $2^{\circ}$  C are summarized in Figure 2 and will be discussed in detail.

When the temperatures averaged between -3 and  $2^{\circ}$  C, the birds started arriving at the feeding station a little before sunrise and reached a morning peak during the first feeding period. The number of birds feeding dropped off some after this morning peak and was then somewhat erratic until in the late afternoon. The late-afternoon peak came during the 13th and 14th periods. Nearly all of the birds were gone during the 15th period, and none was seen after sunset. The feeding pattern for the day differed from the winter average in that the morning peak was relatively lower and in that the midday low in numbers came immediately before the afternoon high in feeding activity. During these

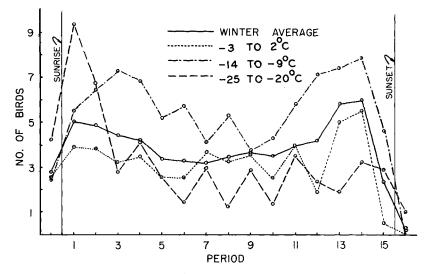


Figure 2. Average number of birds observed on the feeding station during each period of the day for the entire winter and for those days having average temperatures of -3 to  $2^{\circ}$  C, -14 to  $-9^{\circ}$  C, and -25 to  $-20^{\circ}$  C. The curve for those days averaging from -3 to  $2^{\circ}$  C is based on 604 counts with 2,029 bird observations. Not less than 21 counts were made for any period. The curve for those days averaging from -14 to  $-9^{\circ}$  C is based on 841 counts with 4,809 bird observations. Not less than 38 counts were made for any period. The curve for those days averaging from -25 to  $-20^{\circ}$  C is based on 274 counts with 945 bird observations. Not less than 16 counts were made for any period.

relatively warm days, with the exception of during the late-afternoon peak, feeding was rather leisurely and somewhat erratic. The individual birds would land on the feeding station and feed for a minute or so and leave. Sometimes they would leave the area and at others just land in the nearest tree to preen and dress their feathers. While on the feeding station there was considerable squabbling and fighting.

During those days when the average temperature was between ---14 and -9° C, the hirds started arriving just before sunrise, followed by a steady build-up until the morning peak was reached during the third feeding period. This was followed by a well-defined midday low. The afternoon build-up in rumbers started to develop during the 10th feeding period and reaches as peak during the 14th feeding period. This feeding pattern varied from the one just described in that the morning feeding peak was more pronounced and continued to build up until the third feeding period instead of dropping after the first period. The afternoon feeding peak started about two feeding periods earlier than during the warmer period and did not quit as abruptly after the maximum was reached during the 14th feeding period. The feeding pattern differed from the winter average in that the morning and afternoon peaks were relatively higher. During the days with an average temperature of between -3 and  $2^{\circ}$  C. only an occasional bird was seen on the station during the last period before sunset, while during the days averaging between -14 and -9° C. there were as many birds as were usually seen during the midday low. Also birds were occasionally seen after sunset. Feeding intensity differed from that of the warmer days in that feeding during the morning and afternoon peaks was a little more intense.

The feeding pattern during the days that averaged between -9 and  $-4^{\circ}$  C and -21 and  $-15^{\circ}$  C was quite similar to that observed on days averaging between -17 and  $-9^{\circ}$  C.

During the coldest days, when the average temperature ranged from -25 to  $-21^{\circ}$  C, birds started arriving at the feeding station as soon as it was light enough to see. Thus there was a considerable number of birds feeding by sunrise. Peak numbers of birds were reached during the first feeding period. There then was a steady drop in numbers until the sixth feeding period and by erratic occurrence at the feeding station throughout the rest of the day with only a slight tendency toward an afternoon feeding peak. A few birds were usually seen at the feeding station after sunset. This feeding curve varied from the others in that the major feeding period was during the early morning and in that there was but a slight indication of the usual afternoon peak. Also birds were commonly seen after sunset. The behavior of the birds was also con-

Auk Vol. 78 siderably different when they were on the station. They fed constantly and paid very little attention to each other. When they finished feeding, they flew to the nearest tree and sat quietly with their feathers fluffed out. They seldom moved until ready to feed again.

Two birds with leg and one with wing injuries were observed during the early part of the study. These all disappeared by the time the average daily temperatures reached  $-20^{\circ}$  C. Direct injury to the birds did not appear until minimum temperatures reached about -29° C. On four occasions, birds were seen on the station with what appeared to be frozen eves. The eve appeared white, and the lid was not closed over it. These birds, two of which were banded, failed to reappear at the station. Two birds were observed to freeze to death on the feeding station. This occurred in the latter part of January, when the minimum temperatures for the day reached -31 and -32° C, respectively. These birds arrived at the station before sunrise and started to feed immediately. However, their feeding activity lacked its usual vigor, and they would sit with their feathers fluffed out more than the other birds. After about an hour on the station, they ceased to feed and then sat quietly with their eyes partially closed until they died.

Observations, although not in as much detail as those on temperature and day length, were made on the effect of wind, rain, and snow on feeding behavior. When the feeding station was exposed to the wind, the birds would arrive at the station as usual but would feed rapidly and leave for more protected areas. This was the case even during the warmer days. Rain also caused the birds to feed rapidly and leave the station. Fighting and loafing on and near the station were curtailed by both of these factors. Snow appeared to have no effect on the birds' activity except to restrict the areas available for feeding. Except for the very few days when the average daily temperature was above  $2^{\circ}$  C, the ground was covered with snow. During these warmer days, the birds would feed a little at one area and move on to another. For this reason, too few observations were made to discuss this temperature range.

The birds that were observed at the station after sunset usually showed abnormal behavior, and it was assumed that these birds were sick. One marked bird was observed at the station after sunset for two days in a row, skipped one day and was observed again on the fourth day after sunset. This individual was not seen again. Throughout the winter, there was a steady decline in the average number of birds observed on the feeding station (see Figure 3). It is probable that much of this decline is due to mortality. If so, this is a high rate and may not be typical for the area as a whole. Auk Vol. 78

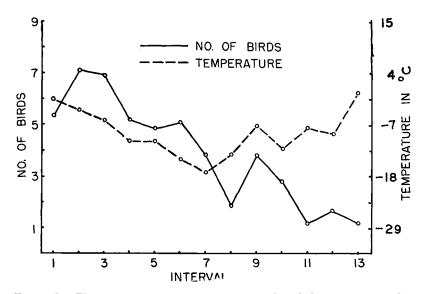


Figure 3. The average temperature per interval and the average number of birds per observation for each interval.

## Discussion

The critical temperature at which the House Sparrows' metabolic rate is at a minimum has been shown to be about 37° C (Kendeigh, 1944). At temperatures below this point, the birds are able to maintain themselves without increased food intake by increasing their insulation until the temperature drops to about 15° C (Steen, 1958). At temperatures below 15° C, the metabolic rate increases as the environmental temperature drops. Rowan (1925) showed that juncos were unable to gather enough food to survive when the temperatures dropped to  $-47^{\circ}$  C. Kendeigh (1949) believed that the House Sparrow reached its maximum rate of energy intake at about -20° C. Stevenson (1933) showed that Song Sparrows and Field Sparrows with full stomachs will void the last of this material in from 2.2 to 2.5 hours. After this period, a bird would either have to obtain a new supply of food or live off its body reserves. Baldwin and Kendeigh (1955) have shown that this takes place, since there is considerable daily variation in body weight of small birds. The maximum weight is reached during the late afternoon. This stored energy is used during the night, and the minimum weight is reached by early morning when feeding starts again. Wild birds are also heavier in the winter than in the summer, and this additional weight gives them a greater reserve during periods of extreme cold stress.

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To help conserve this energy, the metabolic rate and body temperature of birds normally drop at night (Benedict and Fox, 1933, and Miller, 1939). Steen (1958) concluded that birds subjected to extremely cold weather survive the long winter night by balling up and remaining motionless to conserve heat and by elevating their metabolism and lowering their body temperature.

Kendeigh (1944) found that House Sparrows were able to tolerate extremely low temperatures (presumably between -30 and  $-40^{\circ}$  C and in the postabsorptive state) for only about six hours, after which there was a rapid decline in metabolism resulting in death.

During the present study, the period between sunrise and sunset, which is usually slightly longer than the period during which most of the birds are active, varied from about 8 hours and 32 minutes to about 12 hours and 39 minutes. During January, when most of the very cold weather occurred, the period between sunrise and sunset ranged from 8 hours and 40 minutes to 9 hours and 45 minutes. Thus, the birds had to survive from about 14 to 15 hours without obtaining food and probably from 12 to 13 hours in the postabsorptive state.

Baldwin and Kendeigh (1938) showed that during July small birds have a major feeding period in the morning and a minor feeding period in the late afternoon. There was very little feeding during the middle of the day. During the winter, there are two major feeding periods, with the afternoon period being the time of greatest feeding activity. There was also fairly heavy feeding during the middle of the day. It was only when the average daily temperature dropped below  $-20^{\circ}$  C that the major feeding activity came in the morning. It appears that these shifts in feeding patterns allow the birds to obtain the amount of energy required for survival.

Kendeigh (1949) has shown that the gross energy intake increases as a straight line with decrease in temperature until temperatures as low as  $-30^{\circ}$  C are reached. However, the completeness of digestion and absorption decreases with the quantity of food ingested (Brody, 1945). When existing under starvation conditions, birds die with higher body weights when exposed to very low temperatures than when exposed to higher temperatures (Kendeigh, 1934). This is probably due to the fact that food reserves cannot be made available fast enough to maintain the body temperature at the lower environmental temperatures.

Most studies have either involved the effect of temperature on the rate of food intake and degree of digestion or on the survival time while the bird is in the postabsorptive state. The information from these laboratory studies indicates that if the House Sparrows were exposed Auk Vol. 78

continuously to the low environmental temperatures often found in this region, they could not survive. However, the birds hunt for protected areas in which to roost and loaf and thus avoid these extremely low temperatures during much of the day.

When the average daily temperature drops below about  $-20^{\circ}$  C, the daily feeding pattern shifts considerably from that seen at higher temperatures. It would appear that considerable stress is placed on the House Sparrows and that this is probably approaching the limit of their temperature tolerance.

## SUMMARY

Between 20 November 1949 and 31 March 1950, 3,328 observations were made of House Sparrows on a feeding station. Typically, the birds started feeding at about sunrise and reached a morning peak soon thereafter. Feeding was somewhat erratic during the middle of the day, with a second feeding peak coming about an hour before sunset.

At average daily temperatures of below  $-20^{\circ}$  C, the major feeding peak took place early in the morning, with the birds starting to feed well before sunrise. At these colder temperatures there was little build-up in the afternoon, although individuals did not leave the station until well after sunset.

Rain and wind caused a decrease in feeding activity.

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