WINTER ACTIVITY PATTERNS OF BLACK-CAPPED CHICKADEES IN INTERIOR ALASKA

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The Black-capped Chickadee (*Parus atricapillus*) is a year-round resident of the mixed deciduous/spruce woodland association of the taiga forests of interior Alaska and thus has proved its ability, in spite of its small size (10–14 g), to withstand the environmental extremes occurring in that region. To learn something of its adaptability, I studied the winter activity patterns of the chickadee near Fairbanks, Alaska. Observations were based primarily on the feeding activity of wild birds about an artificial feeder, and data have been examined in relation to daylength, light intensity, ambient temperature, sky cover, solar radiation, precipitation (which fell as snow during the periods of the study), and wind velocity.

STUDY AREA AND METHODS

The site of the feeding station was in deciduous woods (primarily paper birch, *Betula papyrifera*; quaking aspen, *Populus tremuloides*, and several species of willow, *Salix*, shrubs) at about 230 m elevation on a south-facing slope at 64°53′ N. Lat. and 147°49′ W. Long., about 8 km northwest of Fairbanks and overlooking the broad, flat Tanana Valley.

Some of the environmental factors of the region can indeed be extreme. With Fairbanks only 190 km south of the Arctic Circle, sunlight duration (sunrise to sunset) varies from 22 hr 02 min on the 21st of June to 3 hr 38 min on the 21st of December and changes as rapidly as 7 min per day during part of the year.

Data from the U.S. Department of Commerce (1973) show that temperature extremes have ranged from + 36°C in June 1969 to – 52°C in January 1969; the mean temperature during July, however, is 14°C and during January is – 24°C. At any time from late October through March, temperatures below – 34°C may occur, as may above-freezing temperatures. It is not infrequent for temperature shifts of over 27°C to occur within a 24-hour period. During periods of cold weather, there is often a conspicuous vertical stratification of temperatures; the dense, cold air settles into the valley where the typical absence of wind during these cold periods allows stratification to occur. Temperatures at the feeding station, for instance, average about 5°C warmer during the winter than those at the National Weather Service station at Fairbanks International Airport, some 95 m lower in elevation; and, in the early days of a cold snap (before the valley fills with cold), temperatures may be more than 10°C warmer than in the valley bottom.

Precipitation in the Fairbanks area averages only 29.2 cm annually; 9.9 cm fall from October through March, mostly as snow. The mean annual snowfall is 168.5 cm, and the ground is usually snow-covered from about 10 October until the last week of April.

From November 1960 through February 1967 I monitored, with varying degrees of regularity and intensity, the daily activity patterns in winter of Black-capped Chickadees at several feeders located in a birch tree about 3 m outside a large window of my home. Food consisted primarily of sunflower seeds (*Helianthus anuus*), suet, and peanut butter and was available at all times. Observations were entirely visual until 17 February

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1964—I sat beside the window and tabulated the number of birds present at the feeding station at a given time. In the morning I was present in time to record the first arrival, and then, depending on the time available, remained to record subsequent arrivals until at least 5 to 10 birds had arrived. In the evening I began observations while substantial numbers were still feeding and recorded numbers remaining as individuals left for their roost sites, finally recording the departure of the last bird.

On 17 February 1964 the peanut butter feeder was automated so that chickadee visits to the peanut butter (the favored food) were recorded on an Esterline-Angus Model AW Graphic Ammeter recorder located inside the house. The 29-cm-high peanut butter feeder was hung inside a wood-mesh cage with a mesh size that excluded all birds but the Black-capped Chickadee. The feeder had 6 feeding loci, 3 arranged in a vertical row on each side. Under each locus, functioning as a perch, was a microswitch sensitive enough that the weight of a chickadee would close it, activating the pen on the recorder. The closing of each additional microswitch increased the amperage reaching the pen, causing it to scribe a longer line on the chart, so it was possible to determine the feeding times of 1 to 6 chickadees by examining the charts. Charts were run at the rate of 30.5 cm per hour.

The feeder loci were only 9 cm apart, so aggressive behavior among the birds usually limited the number simultaneously at the feeder to 2 or 3. Aggressive behavior was suppressed during extreme cold, however, and then all perches were sometimes used. Use of the recorder provided information on the time of first and last feeding each day and a relative picture of the intensity of feeding throughout the day. Lost in comparison to visual methods, however, was information on any differences in timing of arrival vs feeding, on actual numbers of birds present at the feeding station (as opposed to numbers at the peanut butter feeder loci), and the actual light intensity at the times of morning arrivals and evening departures. Between February 1964 and the end of the study, many of the data were gathered via the automated feeder, but from time to time these recordings were supplemented with visual observations.

Because I was working with a wild, free-ranging population of chickadees, knowledge of the population under study was not as good as would have been desirable. Four times during the study, each time in early spring, I trapped and banded all chickadees using the feeders; numbers in different years varied from 25 to 48 birds. As is typical of Black-capped Chickadees, however, the population was composed of small flocks which ranged over a fairly large area, and not all birds visited the feeding station every day. Especially in later years, too, when neighbors constructed other feeding stations, flocks traveled from one station in the neighborhood to another for feeding. A fluid population of varying size, however, should not significantly affect data on first arrival and last departure times or the length of the activity day as recorded at the feeder, but individual variation undoubtedly plays a minor role. Some individuals consistently arrived earlier or later than the main population, perhaps because of closer roosting sites, perhaps because of a somewhat different synchronization (phase angle) of endogenous rhythms to the light cycle, sexual differences, different physiological states, etc. Even with marked birds, however, it was impossible to read color combinations during twilight periods and hence to identify individuals.

Simultaneously with making observations on the activity patterns of the chickadees, environmental data were gathered. Maximum and minimum daily temperatures were recorded at the feeding station throughout the study. Temperature and sky cover at the time of each set of observations were tabulated, and the occurrence of wind or precipita-

tion was noted. Whenever possible, a series of light intensity readings was made, corre-sponding to times of morning arrivals and evening departures.

For light intensities, a photo cell (a light-dependent resistor), set about 3 cm back into a 2.2 cm diameter tube, was permanently mounted on the top of the inside of a window frame; the opening of the tube was directed at an angle of about 50° toward the ground outside. The light readings were read from an ohmmeter with an expanded scale calibrated to that of a Gossen Lunasix light meter. All readings were taken against a snow surface, and hence the relative light intensities recorded were of light reflected at a constant angle from a white surface. Comparative readings were obtained for reflected and incident light, so I can convert my readings to either luces or foot candles; the lux readings are used in this paper.

Statistical analyses have been employed in an attempt to determine the relative im-portance of various environmental factors on the chickadee's activity patterns. These factors are so interrelated that it would be impossible otherwise to determine their indi-vidual effects. Light intensity, for instance, is related to the daily light cycle, in that it is basically determined by the position of the sun in relation to the horizon; and it is further affected by variability in sky cover, with overcast days being darker at any given time. Temperature is also affected by sky cover, with overcast days in winter tending to be warmer than clear days. And solar radiation has interrelationships with the daily light cycle, light intensity, sky cover, and temperature.

The Biomedical Computer Program "BMDO2R—Stepwise Regression" (Dixon 1973) was used for most of the analyses. In addition to computing stepwise multiple linear re-gressions, this program provides a matrix of correlations, and I have used results from both types of analyses. In the regression analyses, I used every possible ordering of the independent variables for each dependent variable. The various environmental factors included as independent variables accounted for 93% of the variation in my data for the length of the activity day, 86% for the time of first activity relative to the beginning of morning Civil Twilight (sun 6° below horizon), 85% for the time of last activity relative to the end of evening Civil Twilight, and 79% for feeding intensity. These rela-tively high percentages lend credence to the results of the analyses.

Some preliminary stepwise regression analyses were made to determine which events in the daily activity cycle to use as "first" and "last" activity (when heard? when ar-rived? when they fed?), which temperatures to use (temperature at time of beginning and end of activity? yesterday's mean temperature? today's mean temperature?), which sky cover data (mine? National Weather Service data on average daily sky cover? on total opaque sky at the time of first and last activity?), and which solar radiation data (National Weather Service data on total daily solar radiation for yesterday? for today?).

In choosing the event to mark the first and last activity of the day, I decided to lump all types of observed activity in order to obtain as many data points as possible. My data were insufficient for separate analyses of all the individual activities, and 317 lumped observations made between 24 October and 2 March showed little more variability (SD = 7.25 min) than 251 "first arrived" observations made during the same period (SD = 6.92 min). Therefore, first and last activity as used in this paper refer to the time the first or last bird, respectively, was seen at the feeder site, was recorded at the mechanized feeder, or was heard.

Temperature measurements showed considerable interdependency (today's mean tem-perature showed an 84% correlation with yesterday's mean temperature and a 95% correlation with the temperature at last activity; temperature at first activity showed an 76% correlation with yesterday's mean temperature); based on regression analyses, how-

ever, temperatures at the time of first and last activity were selected, although the mean temperatures for the preceding 24-hour period also exerted a significant effect (P < .001). My sky cover readings, rating cloud cover from 1 to 5, appeared most influential (see discussion under *Effect of Sky Cover*), as did yesterday's total solar radiation in relation to first activity and today's total solar radiation in relation to last activity.

Data on intensity of feeding are from 69 days for which full-day recordings were obtained after the feeder was automated in 1964. Feeding intensity was determined by calculating the total number of bird-minutes per unit time (either per day or per minute) spent by chickadees at the feeder. These data, of course, are measures of feeding in a free-ranging population, so data given below are all relative and represent only a portion (hopefully a representative sample) of the population's feeding activity. Because of varying numbers of birds using the feeder in different years, direct comparison of even relative feeding intensities between years is not possible, although comparison of general daily activity patterns is feasible.

Several sets of data have been used in the analyses of this study so as to maximize the data base, since information on all factors was not obtained every day. For example, the early discussion on length of activity day is based solely on 161 days where data for both morning and evening were available, whereas later discussions are based on all days where either morning or evening data were available.

RESULTS AND DISCUSSION

Much has been learned about the daily activity patterns of birds since Palmgren's (1935), Paatela's (1938), Franz's (1943, 1949), Wagner's (1958), and Hoffmann's (1959) early observations of birds at northern latitudes. We now know that endogenous rhythms are major controlling factors in the daily and annual cycles of birds and that these rhythms are synchronized with environmental rhythms (primarily the daily light cycle) through entrainment to a Zeitgeber (Aschoff 1967). Studies using specific measurements of a number of environmental factors affecting avian activities under natural conditions have been undertaken (e.g., Leopold and Eynon 1961, Morton 1967a and b, Davis and Lussenhop 1970, and Krantz and Gauthreaux 1975), as have controlled experimental studies of these factors (see Aschoff 1965, Menaker 1971, and others cited below). The reaction mechanism of organisms to environmental factors cannot readily be determined under natural conditions, but the daily and seasonal activity patterns of the Black-capped Chickadee in this study compare so well to the oscillator model theory of endogenous rhythms that there is little doubt that the major environmental factors of light and temperature are influencing activity through their effect on endogenous rhythms.

General Seasonal Pattern of Diurnal Activity Cycle

Fig. 1 shows the times of first and last activity on days for which data were obtained from 1960 through 1967 as well as the beginning of morning Civil Twilight and the end of evening Civil Twilight. During the summer and early
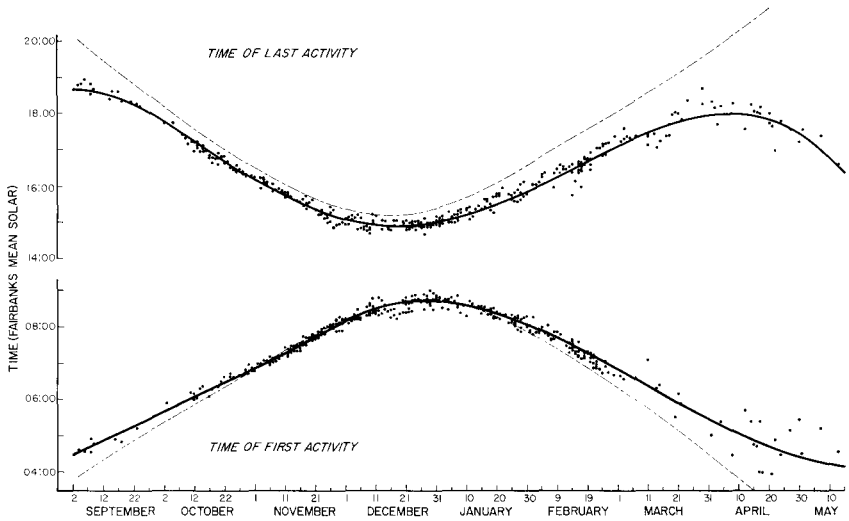
Fɪɢ. 1.   Times of first and last activity of chickadees recorded from 1960 through 1967. Times have been adjusted for longitude and are true solar times. The dotted lines represent the times of the beginning of morning Civil Twilight and ending of evening Civil Twilight, respectively; the solid lines are best-fit polynomial curves, adjusted somewhat by eye.

autumn, morning activity began after the beginning of Civil Twilight. Within a few days of 1 November, first activity began to occur prior to the beginning of Civil Twilight; and, except during occasional periods of cold stress (see below), chickadees generally continued to become active before the beginning of Civil Twilight until sometime during the first few days of January, after which they again usually remained at roost until after the beginning of Civil Twilight. (During the unusual winter of 1960–61, when temperatures were relatively warm and cloud cover relatively low, chickadees continued to become active before the beginning of Civil Twilight until the third week of January.) Activity ceased prior to the end of Civil Twilight throughout the year, and it ceased even before sunset from sometime during the first half of February until mid-September.

Regression analyses showed that the daily light cycle (= time of beginning and ending of Civil Twilight) is by far the dominant environmental factor affecting the chickadee's activity cycle (P < 0.001). The time of 249 first activity observations made between September and May showed a 93.1% correlation with the time of the beginning of morning Civil Twilight and a 96.0% correlation of 193 last activity observations over the same period with the ending of evening Civil Twilight.

The seasonal shifts in the time of first and last activity in relation to changing daylengths, defined as extending from the beginning of morning Civil Twilight to the end of evening Civil Twilight, appear to be adaptational responses to mean annual environmental stresses. In general, as seen in Fig. 1, as daylengths get shorter during the fall and early winter, the activity day gets proportionately longer in relation to the length of day. Not only did chickadees begin activity earliest in relation to morning Civil Twilight at and just prior to the winter solstice, but they had a longer activity day relative to daylength during November, which may be an adaptation for increased feeding and caching activity prior to the most stressful days of winter. (These longer days are apparent in Fig. 1 for the last third of November, in spite of the consistently cold temperatures that occurred during that period during all years of the study—lower temperatures which acted to shorten the activity day.) After the winter solstice, almost as soon as daylengths begin increasing, the activity day decreases relative to daylengths, in spite of the fact that environmental conditions are still severe during January and February. At least 2 influences may be operating here: the autumnal drive toward increased feeding and caching should no longer be operative, and the bird's physiology is beginning to shift toward breeding. (In some years, birds began singing as early as 16–18 December, and in most years they were singing regularly by 1 January.)

Length of Activity Day

Regression analyses of 161 days where both morning and evening data were available showed that daylength was the most important factor determining the length of the activity day ($P < 0.001$), with 53% of the variability in the length of the activity day explained by this factor alone. Other factors which proved significant, after adjusting for all other independent variables, were temperature and day of the year. The activity day is shorter at cold temperatures than at warmer temperatures and vice versa ($P < 0.01$). The significance of the day of the year ($P < 0.001$), after the effects of daylength and temperature have been accounted for, is apparently due in part to the longer activity days observed during late fall and early winter and in part to the shorter activity days relative to daylength that occur progressively after early January as compared to those before the winter solstice.

Average daily sky cover (cloudiness) did not prove statistically significant in its effect on the length of the activity day in the analyses of these 161 days; but, as discussed below, light intensity and sky cover, after adjusting for all other independent variables, affect the times of first and last activity and hence, to some extent, the length of the activity day.

For these 161 days, today's total solar radiation showed a 70% positive

correlation with the length of the activity day (the greater the total radiation the longer the activity day), but after the effects of daylength and the day of the year had been accounted for, the additional effect of solar radiation became insignificant. What at first appeared to be an effect of solar radiation was really the result of (1) longer days allowing greater time for accumulation of total solar radiation and (2) the longer days being in the spring and fall when the sun is higher in the sky.

Effect of light intensity.—After the daily light cycle per se (accounted for in my analyses by using activity relative to Civil Twilight as a dependent variable), light intensity exerts the greatest influence on the time of beginning and ending of daily activity of the chickadee ($P < 0.001$). On dark days, activity begins later and ends earlier than on bright days. Delays of up to 5 or 10 min in the commencement of morning activity due to darkness are not unusual. On 23 December 1962, when it took 20 min longer than on the preceding day to reach "threshold" light intensities, first activity also occurred 20 min later; similarly, a 12-min difference between the time of first activity on 27 and 28 December 1960 is ascribable to a parallel delay in light intensities reaching comparable levels.

The sensitivity of chickadees to light intensities appears to change during the year; and, as one would expect, these changes show a direct relationship to the seasonal shifts in the interrelationships of the daily light cycle and the daily activity cycle. Many avian studies have shown seasonal shifts in the time of beginning and ending of various activities relative to the sun's position; and, recently, Pohl (1972) has demonstrated a seasonal change in the sensitivity of the circadian system to light in Redpolls (*Acanthis flammea*). Fig. 2 shows the light intensity at first and last activity for chickadees on all days for which data are available from 1960–1967. As with other species that have been studied (Aschoff and Wever 1962, Leopold and Eynon 1961 and references therein), light intensities in the morning at first activity are considerably lower than in the evening when activity ceases. The range of light intensities relative to activity times is quite great (due in large part to temperature influences), but the best-fit polynomial lines for both morning and evening show a clear trend and the trend lines for morning and evening are similar. In general, the chickadees begin and end their daily activities at lowest light intensities during the last half of November and the first half of December (perhaps until 21 December)—again during the period of decreasing daylengths prior to the winter solstice and during the period of food caching. Dunnett and Hinde (1953), with captive Great Tits (*Parus major*) in England, also found that dawn emergence times were slightly earlier in late November and December relative to sunrise than in October and subsequently. During this period, the Fairbanks chickadees begin their activity in the morning at
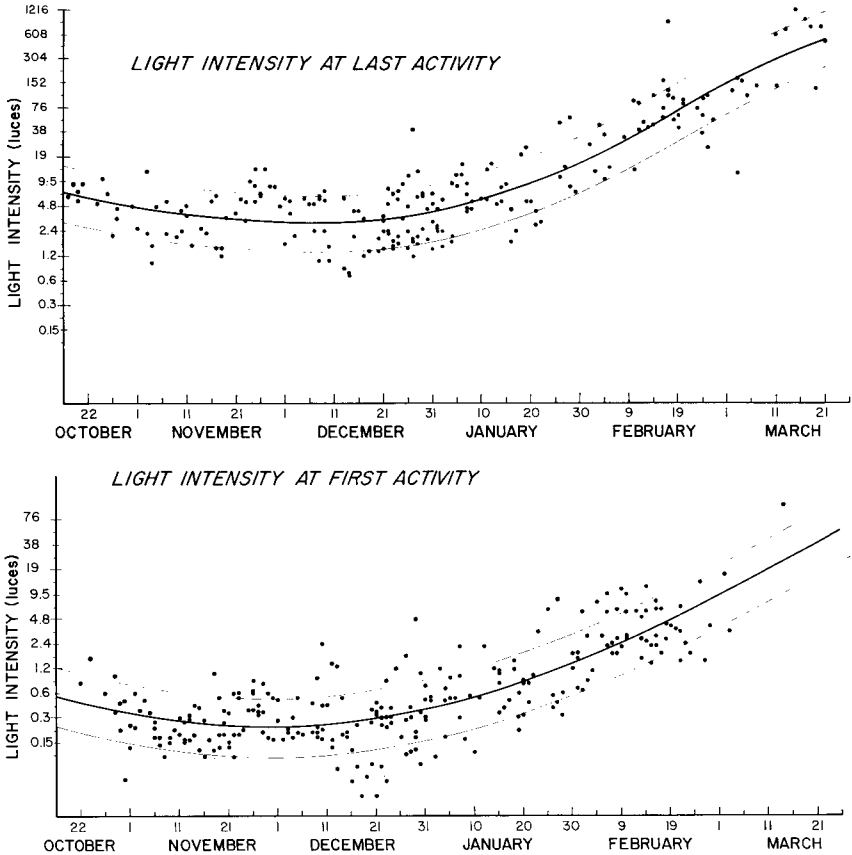
FIG. 2. Light intensity at the time of first and last activity, 1960–1967. The center lines are the best-fit polynomial curves for first and last activity, and the lines on either side are the distance of one standard deviation from the best-fit lines.

light intensities that seem marginal for vision—most commonly at 0.15–0.23 lux, and the end of their activity day is in the 2.4–4.8-lux range. At these light intensities, chickadees sometimes appear to "stumble" about the tree branches, as if it were too dark to see—in spite of the fact that this behavior sometimes occurs in the evening at light intensities far brighter than those at which they functioned adequately in the morning or at another season. After late December, the birds begin and end their activity day at steadily increasing light intensities (see Fig. 2).

The lower light intensities at which the chickadees begin and end their daily activities at a given time of year appear to represent a threshold for

activity, a threshold that differs in level morning and evening, at various times of year, and perhaps with temperature. As indicated above, on dark mornings, activity begins correspondingly later, and vice versa in the evenings. The fact that chickadees began activities at the lowest light intensities observed during the study during the unusually warm, cloud-free December of 1960 suggests a possible relationship between environmental temperatures and the shifting threshold of the bird's sensitivity to various levels of light intensity.

Effect of temperature.—On cold days, first activity occurs later relative to the beginning of morning Civil Twilight and the last activity earlier relative to the end of evening Civil Twilight than on warm days, and vice versa. This effect of temperature appears to be a more or less graduated one, with weeks or months of colder mean temperatures showing correspondingly shorter activity days than equivalent warmer periods, although there is some evidence that temperature is more influential, even critical, during extreme cold.

The influence of temperature on the activity period is difficult to demonstrate, largely because light, which is such a dominant factor, interrelates in several ways with temperature. In winter at Fairbanks, meteorological conditions are such that days are either dark (overcast) and relatively warm or are bright (clear) and cold, and these sets of conditions act in opposition to each other in relation to the length of the activity day. Also, when cold temperatures delay the beginning of activity in the morning, the brighter light at first activity is a function of lateness due to temperature rather than a response of the bird to light intensities; the reverse is true when birds roost earlier, and hence at brighter light intensities, on cold days than on warm days. When light was not included in the analyses, temperature showed a significance at the $P < 0.001$ level in its effect on the time of beginning and ending of daily activity relative to Civil Twilight. Also, as indicated above, other statistical analyses relative to the total length of 161 activity days showed temperature significant at the $P < 0.01$ level. Regression analyses of mid-winter data (20 Nov. to 10 Jan.), when environmental stresses are most severe, showed temperature to have almost 2.5 times the influence on the timing of first activity that it had during early and late winter, although temperature was significant at the $P < 0.001$ level during both periods.

In Fig. 1, the times of first activity for 364 observations and last activity for 332 observations made throughout the study are plotted by the day of the year, and best-fit curves, fitted in part mathematically and in part by eye, have been drawn through the points. A rough, overall indication of the effect of temperature can be obtained by averaging the temperatures at the time of first or last activity, respectively, for those days in which activity began or ended later than the mean time, as indicated by the best-fit curve, and comparing these mean temperatures with those days on which activity began or ended earlier than

TABLE 1

MEAN TEMPERATURES (± SD) AT TIME OF FIRST ACTIVITY*

First activity relative to mean time	November	December	January
Later than mean time	– 19.1°C ± 9.8 (n = 52)	– 22.2°C ± 14.3 (n = 34)	– 18.6°C ± 10.3 (n = 35)
	P < 0.2	P < 0.01	P < 0.2
Earlier than mean time	– 12.7°C ± 6.0 (n = 34)	– 13.3°C ± 8.8 (n = 49)	– 14.8°C ± 9.7 (n = 22)

* Using t-test for unpaired observations, unequal variances, and small, unequal sample sizes to test means of adjacent groups (Cochran and Cox 1957). P = probability of getting sample means as different as those observed if temperature was not an influence.

the mean time. The results (Tables 1 and 2) suggest that timing of the first and last activity are, indeed, related to temperature, with data showing greater statistical significance during December, the coldest month.

A further refinement, accounting for the effect of light intensity, can be made by analyzing first and last activity in relation to light intensity and temperature. (Other things being equal, the later the time of first activity—or the earlier the time of last activity—the greater the light intensity.) Using the best-fit polynomial lines in Fig. 2 as the mean light intensity at first or last activity, respectively, mean temperatures above (brighter) and below (darker) this line were calculated. Additional lines were drawn the distance of one standard deviation (= 1.18 lux at first activity, 1.09 lux at last activity) on either side of the best-fit line, and mean temperatures at first and last activity, respectively, were calculated for these further subdivisions. In spite of the great variability

TABLE 2

MEAN TEMPERATURES (± SD) AT TIME OF LAST ACTIVITY*

Last activity relative to mean time	November	December	January
Later than mean time	– 13.1°C ± 7.7 (n = 28)	– 13.1°C ± 6.5 (n = 32)	– 16.0°C ± 9.9 (n = 34)
	P < 0.01	P < 0.001	P < 0.01
Earlier than mean time	– 23.6°C ± 9.7 (n = 17)	– 24.5°C ± 12.7 (n = 42)	– 23.9°C ± 6.7 (n = 17)

* Data analyzed as in Table 1.

TABLE 3

MEAN TEMPERATURES (± SD) IN RELATION TO LIGHT INTENSITY AT TIME OF FIRST ACTIVITY*

	November	December	January
More than 1 SD brighter (later) than mean	$-27.0°C \pm 3.7 (n = 10)$	$-41.1°C \pm 5.9 (n = 9)$	$-25.6°C \pm 9.1 (n = 6)$
	$P < 0.001$	$P < 0.001$	$P < 0.2$
1 SD brighter (later) than mean	$-19.2°C \pm 7.9 (n = 27)$	$-15.5°C \pm 6.2 (n = 18)$	$-17.7°C \pm 10.4 (n = 18)$
	$P < 0.01$	$P > 0.3$	$P < 0.3$
	-------- MEAN LIGHT INTENSITY --------		
1 SD darker (earlier) than mean	$-13.6°C \pm 7.2 (n = 32)$	$-14.5°C \pm 9.1 (n = 31)$	$-13.3°C \pm 9.0 (n = 15)$
		$P < 0.02$	$P < 0.1$
More than 1 SD darker (earlier) than mean	$(n = 0)$	$-9.2°C \pm 4.6 (n = 14)$	$-12.6°C \pm 9.2 (n = 9)$

* Data analyzed as in Table 1.

in the data, the trends shown in Tables 3 and 4 illustrate the influence of temperature on the timing of the first and last daily activity in chickadees.

Under natural conditions, periods of extreme or widely fluctuating conditions best illustrate relationships. Specific examples of the effect of temperature on chickadee behavior are presented in Fig. 3, where changes of the time of first activity during abrupt and severe shifts in environmental temperatures are shown for brief periods in December 1961 and December 1964. Here, again, it shows that cold temperatures in the morning delay the beginning of the daily activities when compared to warmer temperatures.

Aside from causing shorter activity days, severe cold snaps appeared to affect chickadees in other ways. On mornings preceded by precipitous temperature drops, first activity times were not only later, but were more irregular than usual; instead of taking 5 to 8 min for a substantial number of chickadees to arrive at the feeder site, it would take 10 to 15 min. Another effect was that fewer birds used the feeding station, and, the more severe and longer the cold snap, the more this effect was evident. Either the birds were less active and fed less or their feeding radius was so reduced that few reached the feeder.

TABLE 4

MEAN TEMPERATURES ($\pm$ SD) IN RELATION TO LIGHT INTENSITY AT TIME OF LAST ACTIVITY*

	November	December	January
More than 1 SD brighter (earlier) than mean	$-26.5°C \pm 7.9\,(n = 8)$	$-42.8°C \pm 6.7\,(n = 8)$	$-24.5°C \pm 6.5\,(n = 9)$
	$P < 0.1$	$P < 0.001$	$P < 0.4$
1 SD brighter (earlier) than mean	$-20.1°C \pm 6.9\,(n = 13)$	$-25.7°C \pm 8.9\,(n = 22)$	$-21.2°C \pm 9.7\,(n = 12)$
	$P < 0.02$	$P < 0.001$	$P < 0.2$
----------------- MEAN LIGHT INTENSITY -----------------			
1 SD darker (later) than mean	$-9.8°C \pm 6.9\,(n = 8)$	$-12.5°C \pm 4.9\,(n = 26)$	$-15.6°C \pm 8.2\,(n = 14)$
	$P < 0.3$	$P < 0.2$	$P < 0.1$
More than 1 SD darker (later) than mean	$-5.6°C \pm 5.2\,(n = 6)$	$-10.1°C \pm 5.2\,(n = 13)$	$-10.2°C \pm 7.4\,(n = 15)$

* Data analyzed as in Table 1.

Johnson (1957) commented that Fairbanks Black-capped Chickadees were quiet, inconspicuous, and flew less during cold snaps. At my feeder site in late December 1961, when temperatures between 26 and 29 December remained in the $-46°$ to $-51°C$ range ($-49°$ to $-53°C$ in the valley bottoms, Fairbanks International Airport readings), birds using the feeder were so few that I feared a die-off. However, when temperatures bounced back to $-28°C$ on the morning of 30 December, the birds returned and my notes recorded that they were *"much* more lively."

Several things, here, suggest that environmental temperatures may be influencing the chickadee's behavior by acting on an endogenous rhythm. Recently, limited experimental data with House Finches (*Carpodacus mexicanus*) (Enright 1966), Chaffinches (*Fringilla coelebs*) (Pohl 1968a and b), and House Sparrows (*Passer domesticus*) (Eskin 1971) have shown that environmental temperatures affect the endogenous circadian rhythms of homeotherms; and the shorter activity days in the present study caused by colder temperatures are in the direction predicted by the oscillator model theory of endogenous rhythms (Aschoff 1965), as is the apparent reduction of activity on
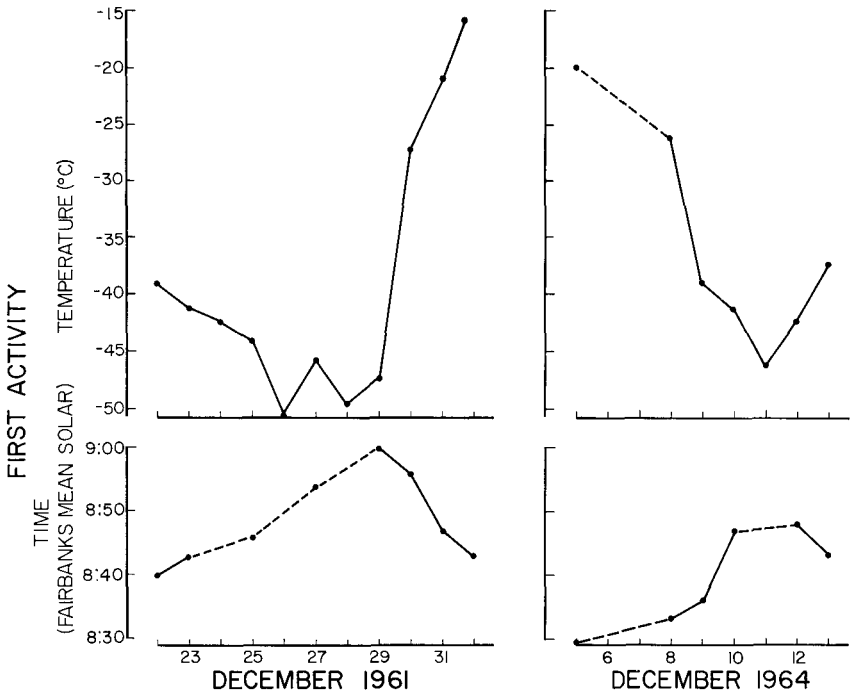
FIG. 3. Times of first activity relative to temperature during abrupt and severe changes of temperature in December 1961 and December 1964. Cold temperatures delayed the beginning of activity compared to warmer temperatures. Dotted lines have been used where intermediate data points are lacking.

cold days. Also, the irregularity of commencement of first activity with sudden changes of temperature is suggestive of phase-shifting of endogenous rhythms.

Regardless of the underlying response mechanism, all of these temperature effects on the activity pattern of the chickadee make it appear that, during periods of extreme cold stress, energy levels are better maintained under conditions of reduced activity rather than traveling distances for food or extending feeding periods. Recently, Chaplin (1974) in New York and Grossman (1975) at Fairbanks have even reported hypothermia in Black-capped Chickadees. Behaviorally on these cold days at Fairbanks, the chickadees fluff their feathers, until they resemble little balls, and withdraw their legs until they are entirely enveloped by the fluffed feathers. Hoar frost frequently develops about their heads from their breath, and excreta "steams" as it drops through the cold air to the ground.

Lawrence (1958) found that Black-capped Chickadees in central Ontario (46°N) also emerged later in the morning and roosted earlier on very cold days. She also noted that on mornings when temperatures were below − 29°C, instead of feeding intensely early in the morning as on milder days, the chickadees sought sites sheltered from wind and exposed to the rays of the sun, apparently improving their energy balance behaviorally.

Markgren (1963) found that Bean Geese (*Anser fabalis*) spent much of their time in an inactive, sleeping position during inclement winter weather in Sweden, and Raveling et al. (1972) observed that Canada Geese (*Branta canadensis*) reduced their activity at low winter temperatures in southern Illinois. Raveling et al. (op. cit.) noted that larger-sized subspecies began inactivity at lower temperatures than the smaller ones and suggested that "inactivity is the most adaptive response to severe cold and functions to conserve energy."

Effect of sky cover.—Sky cover, after adjusting for the effects of light intensity, exerts a significant effect (P < 0.001) on the time of first activity relative to morning Civil Twilight, the chickadees beginning their activity earlier on clear mornings than on cloudy ones. Sky cover may have some influence on the time of last activity relative to evening Civil Twilight (later on clear afternoons) (P < 0.10), but much less so than in the morning.

In examining the effect of sky cover, I worked with several sets of data. I used my own observations made at the feeding station; because the station was on a south-facing, wooded slope and because my observation window faced southward, my sky cover observations were essentially of the southern half of the sky. The other sets I used were from the National Weather Service: total opaque sky at the time of first and last activity and, for last activity, the average daily sky cover from sunrise to sunset. Average daily sky cover appeared to have no effect on the timing of last activity, and total opaque sky cover showed less influence, both morning and evening, than the southern sky from which I recorded my data. It appears, then, that the birds were responding to the part of the sky that they could see, i.e., the southern sky seen from their vantage point on a south-facing slope.

There are 2 possibilities for the differing effect of sky cover in the morning and the evening. The first is that the sky cover may have more of an effect in the morning than in the evening. The other possibility is that, while the sun rises in the southeast and south during the winter in Fairbanks—in the portion of the sky most visible to the chickadees using the feeder site—it sets in the southwest or west, behind a hill and in a part of the sky less completely visible to the birds. If the birds are responding to the effects of a brighter sky or some other effect caused by the sun in addition to cloud cover per se, then responses might differ between the morning and evening.

Leopold and Eynon (1961) noted that early in the year in Wisconsin some birds appeared to require more light for daybreak song on cloudy mornings. They failed to recognize, however, that cloud cover, over and above its effect on light intensity, could affect activity and that the increased light at daybreak song was the result of lateness caused by sky cover.

Effect of solar radiation.—Solar radiation appears to influence the chickadee's activity period at Fairbanks, although not strongly, perhaps because there is so little of it during the portion of the year included in this study. Average total daily solar radiation, in langleys, at Fairbanks in October is around 80; in November, 25–35; in December, about 5; in January, 15–20; in February, 80–95; and in March, over 200.

The effect of today's total solar radiation on the length of 161 activity days analyzed did not prove statistically significant after the effect of daylength and the day of the year had been considered. On the other hand, analyses of today's total solar radiation (after adjusting for all other factors) in relation to last activity relative to Civil Twilight for 90 days between 10 October and 2 March showed a small but significant effect ($P < 0.05$), with roosting occurring earlier when total solar radiation for the day had been greater. While not statistically significant ($P > 0.10$), the same trend showed in data for 228 mornings, i.e., when yesterday's total solar radiation was greater, first activity relative to Civil Twilight occurred later. In other words, over the period of 10 October through 2 March, increased total solar radiation tended to shorten the day.

When I repeated these latter analyses, but restricted the period to 20 November through 10 January, the severest part of the winter, the effect of solar radiation was reversed. That is, the chickadees tended to begin activity earlier and roost later relative to Civil Twilight ($=$ longer days) with increased solar radiation. Again, the effect was statistically significant in my evening data ($P < 0.025$), but not in the morning ($P > 0.10$). (The difference in the significance of solar radiation between morning and evening data is undoubtedly related, at least in part, to the time difference between the time the solar radiation was received and the time activity began or ended. Roosting birds are under the immediate influence of today's total solar radiation, whereas there is a lapse of 12–18 hours between receipt of yesterday's total solar radiation and the first activity of the day.)

Thus, during the relatively longer and warmer days of early and late winter, activity days are shorter when there is more solar radiation; but, during the short, cold days of mid-winter, the length of the activity day is increased slightly when more solar radiation is received. Since the energy balance in very cold weather may be best maintained by inactivity (see *Effect of temperature*), it appears that increased solar radiation, little as

it is at this stressful time of year, may improve the energy balance enough to allow slightly longer foraging days.

I cannot provide specific illustrations of the effect of solar radiation from my study, only the statistical evidence cited above. The apparent importance to Black-capped Chickadees of solar radiation in extreme cold temperatures was observed by Lawrence (1958) in central Ontario, however, where she watched fluffed birds perched facing the sun, even on cloudy days, and birds basking high in trees on sunny days.

Krantz and Gauthreaux (1975) found a close correlation in the day-to-day variation in the time of arrival at the roost of Brown-headed Cowbirds (*Molothrus ater*) in South Carolina with the daily amount of solar radiation, later arrival being associated with greater solar radiation. Morton (1967b) found that White-crowned Sparrows (*Zonotrichia leucophrys*) in Washington reduced their feeding activity under conditions of direct insolation (or under artificial short-wave infrared radiation) and concluded that the radiant energy received alleviated the energy costs of thermoregulation in cool situations.

Effect of precipitation.—Snow falling at the time of first and last activity appears to exert a slight effect on the timing of these activities, snow causing first activity to begin later and last activity to end earlier relative to Civil Twilight.

Specific examples of the effect of snow are hard to isolate because of the dominant influence of light and sky cover; conditions are almost always dark and cloudy when it is snowing, and each of these factors contributes individually to later first activity times relative to Civil Twilight. First activity times on the mornings of 28, 29, and 30 December 1960, however, provide a good illustration of the effect of falling snow. The morning of 28 December was dark, overcast, and 0°C, and the first chickadees arrived at the feeder just after 8:32 at 0.10 lux; the next 3 birds arrived within 2.5 min. Snow fell on the morning of 29 December, but, in spite of the snow, light reached intensities equivalent to those on the 28th 8 min earlier; skies were overcast and the temperature was − 3°C. Except for the quick visit of a single bird at 8:25 (0.10 lux), there was no activity at the feeder until 8:34 (0.42 lux), and it took another 5 min before the fourth bird had arrived. In my notes, I wrote, "8 min brighter than yesterday, in spite of snow, but chickadees *very* slow in arriving. Late, irregular, extended arrival period, and some never showed up at the feeder." The morning of 30 December was overcast, − 8°C, but without snow, and light intensities were similar to those on the 29th. The first bird arrived at 8:20 (0.02 lux) and the fourth bird had arrived by 8:34, reconfirming that falling snow was apparently a delaying factor on the morning of 29 December.

Another example of delay in morning activity apparently due to snow shows up in observations from 13 and 14 December 1960. Both mornings were overcast and light intensities were almost identical; temperatures were $-3°C$ on 13 December and $8°C$ on 14 December. It was snowing on the morning of 14 December, and chickadees arrived at the feeder 6 min later (0.22 lux brighter) than on the preceding day.

Statistically, the effect of snow can be isolated a bit better from the other influencing environmental factors. However, snow fell during only 28 of my morning and only 24 of my evening observation periods, and the influence is so slight (less than 0.4% of the variability in my data attributable solely to falling snow) that, while definite trends are visible, data are insufficient for statistical significance. The effect on the timing of first activity during the longer days of early and late winter (114 mornings, 24 October–19 November and 11 January–1 March) may have been significant ($P < 0.10$), although data for mid-winter were not ($P > 0.10$). Evening data lacked statistical significance ($P > 0.10$), but the data showed a consistent trend in the direction of falling snow causing earlier roosting.

Kluijver (1950) reported that in the Netherlands rain and snow delayed emergence of Great Tits *(Parus major)* in the morning and that rain often caused earlier retirement in the evening. Odum (1942) reported earlier roosting in Black-capped Chickadees in New York on snowy days. Williams (1941) found a tendency for Chestnut-backed Chickadees *(Parus rufescens)* in California to come to roost at somewhat higher light intensities ($=$ earlier) on rainy days.

Effect of wind.—Wind at the time of first activity tends to delay the beginning of morning activity relative to Civil Twilight. The effect is so slight (less than 0.15% of the variability in my morning data attributable solely to wind) and observations so few (only 22 mornings had wind) that my data are not significant, statistically. All the statistical results, however, show the same delaying trend in the morning due to wind. A specific illustration of this delaying effect is provided by a comparison of conditions on the mornings of 1 and 2 November 1962. It was overcast and $-1°C$ on 1 November; the first bird arrived at the feeder at 6:40 and 3 birds were present by 6:45. It was overcast and $-2°C$ on 2 November, with gusty surface winds. It took 4 min longer on 2 November for light intensities to reach levels equivalent to 1 November, but the first bird did not arrive until 11 min later, at 6:51; 4 birds were present by 6:53.

I am unable to make anything out of my data (20 observations) regarding the influence of wind on the timing of last activity relative to Civil Twilight.

During periods of actual observation, the only consistent pattern I was able to discern relative to wind was that the birds had less tendency to move
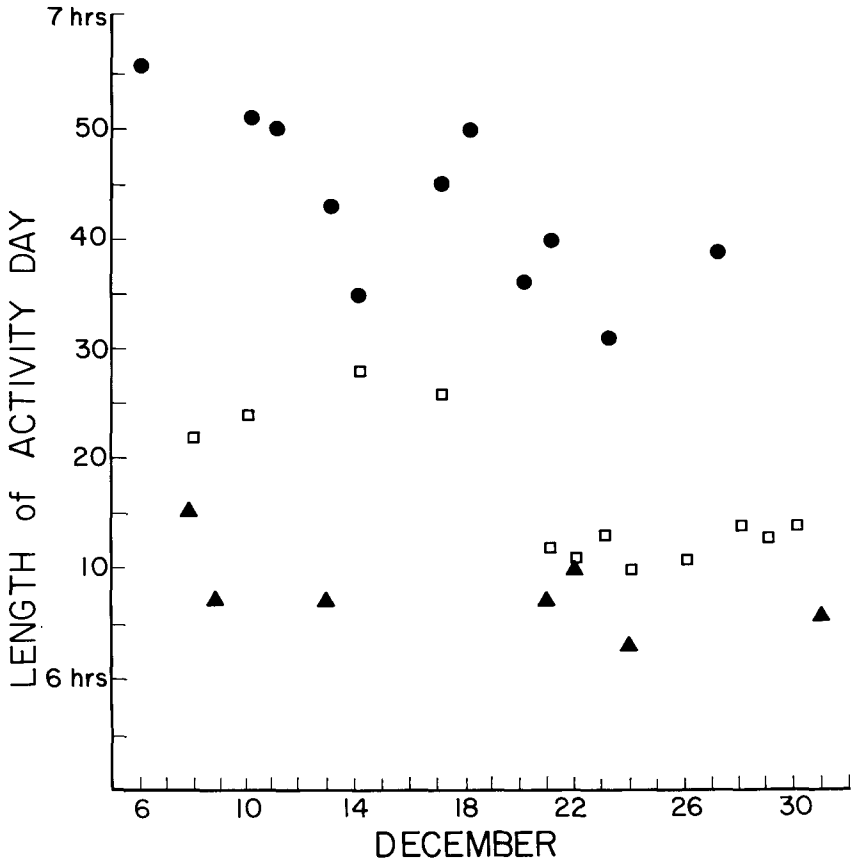
Fig. 4. Length of activity days during December of 1960 [●], 1963 [□], and 1964 [▲]. The longest activity days occurred during the relatively warm, cloud-free December of 1960, and the shortest during the relatively cold, cloudy December of 1964 (cf. Table 5).

about in relatively windy weather than on calmer days and that during periods of gusts the birds either remained tightly perched or temporarily disappeared from the scene, presumably seeking shelter. The morning of 10 January 1961, for example, was a windy, gusty day of − 27°C, and I noted that the birds "seem directly affected by wind gusts; they disappear with every strong gust."

Leopold (1949) noted that Black-capped Chickadees in Wisconsin avoided windy situations; and Kluijver (1950) found that the first morning appearance of the Great Tit in the Netherlands was delayed by strong winds, and, at least in March, that such winds had a tendency to cause early retirement.

TABLE 5

COMPARISON OF THE AVERAGE MONTHLY TEMPERATURES AND AVERAGE PERCENT SKY
COVER FOR THE VARIOUS DECEMBERS OF THE STUDY*

	Av. Monthly Temperatures (°C)	Av. Percent Monthly Cloud Cover
Dec. 1964	– 29.7	72
1961	– 29.3	57
1966	– 24.9	69
1962	– 18.9	65
1963	– 12.8	75
1960	– 11.7	62

* The shortest activity days occurred in 1964 and the longest in 1960, with activity days being intermediate in length in the other years.

Interrelationships of environmental factors.—All these main environmental influences act on the birds simultaneously, and when individual factors are additive (e.g., possibly low light intensities, complete sky cover, and cold temperatures), the response of the bird is greater than if some of these factors occur in opposition, tending to dampen the individual effects. Some of these interrelationships can be demonstrated in relation to the differing lengths of mid-winter activity days in different years. The shortest mid-winter days were in 1964–65, the longest in 1960–61, and the other years clumped between these extremes (Fig. 4). Unfortunately, I lack complete, pertinent environmental data from my own observations, but much of the annual variation seems explainable even with the more generalized weather data from the National Weather Service. From this source, in Table 5, are listed the average monthly temperatures and the average percent cloud cover for December of the various years. Average cloud cover can be used here as a rough measure of light intensity and sky cover, which are additive in their effects. December 1964 was the coldest and the cloud cover almost the greatest, whereas December 1960 was the warmest and the cloud cover almost the least; the additive effects in each instance apparently resulted in the shortest and longest activity days, respectively.

The relative influence of several of the environmental factors on the chickadee's activity period appears to change during the winter. This shift is most evident from my morning data. Light intensity is by far the most important factor influencing the time of first activity relative to Civil Twilight throughout the winter, but it accounts for more of the variability in early and late winter than in mid-winter (62% vs 52%). Sky cover is the second most influential factor in early and late winter, but drops to third in mid-winter.

Temperature is the second most influential factor during the short, cold days of mid-winter. In the evening, light appears to have more influence on the time of last activity in mid-winter than during early and late winter, and the same is true of the influence on last activity of the time of first activity relative to Civil Twilight.

In comparing statistically the influence of the various environmental factors on the time of beginning and ending of activity relative to Civil Twilight, it became evident that each factor exerts less influence in the evening than in the morning, although light intensity and temperature are still highly significant. This difference again suggests the involvement of an endogenous rhythm, a rhythm that is "set" in the morning and then largely runs its course until activity ceases in the evening. A comparison of the effects of morning environmental factors and evening environmental factors on the time of last activity relative to the end of evening Civil Twilight shows that the light intensity at the time of last activity is the most important factor ($P < 0.001$), accounting for over 30% of the variability after all other factors have been taken into account. The apparent influence on last activity of the time of first activity relative to the beginning of morning Civil Twilight is also highly significant ($P < 0.001$), but accounted for only about 3% of the variation.

Feeding Intensity

Amount of feeding per activity day.—Temperature is the most significant factor affecting feeding intensity ($P < 0.001$); 77% of the variability in daily feeding intensity was attributable solely to temperature, with today's mean temperature being far more influential than yesterday's mean temperature. Feeding intensity showed a 41% negative correlation with daylength ($P < 0.001$), but, after the effect of temperature had been accounted for, daylength was not significant (mid-winter days are cold as well as short). The same situation existed with average sky cover, i.e., average sky cover showed an 11% negative correlation with feeding intensity (the less cloud cover the greater the feeding intensity) ($P < 0.001$), but when temperature was taken into account (colder on clear days), sky cover was no longer significant.

Solar radiation, whether today's or yesterday's total solar radiation, showed a 20% negative correlation with feeding intensity (less radiation, greater feeding intensity) ($P < 0.001$), but after temperature and day of year were considered (cold days are clear with greater solar radiation; mid-winter days are cold and short), solar radiation per se did not show a statistically significant effect on feeding intensity.
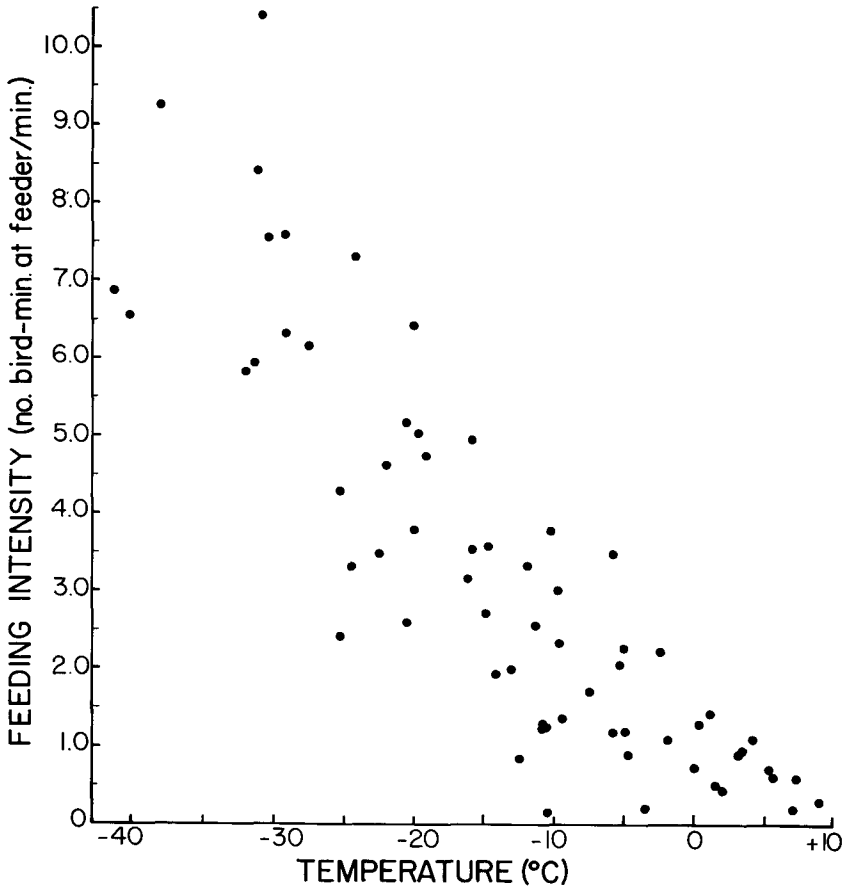
Fɪɢ. 5. Feeding intensity relative to daily mean temperatures, 1964–1967. Feeding intensity was derived by dividing the total bird-minutes spent at the feeder per day by the total number of minutes in that activity day.

Figure 5 illustrates the general relationship between environmental temperatures and feeding intensity. Shown clearly is the negative correlation between feeding intensity and temperature. This figure includes data from all years after the feeder was mechanized, and a considerable amount of the vertical scatter is due to the differing size of the population in different years, i.e., a smaller population will spend fewer total bird-minutes per activity day at the feeder than a larger population at any given temperature.

Daily pattern of feeding intensity.—The pattern of 2 daily activity peaks, described by many authors, including Lawrence (1958) for Black-capped
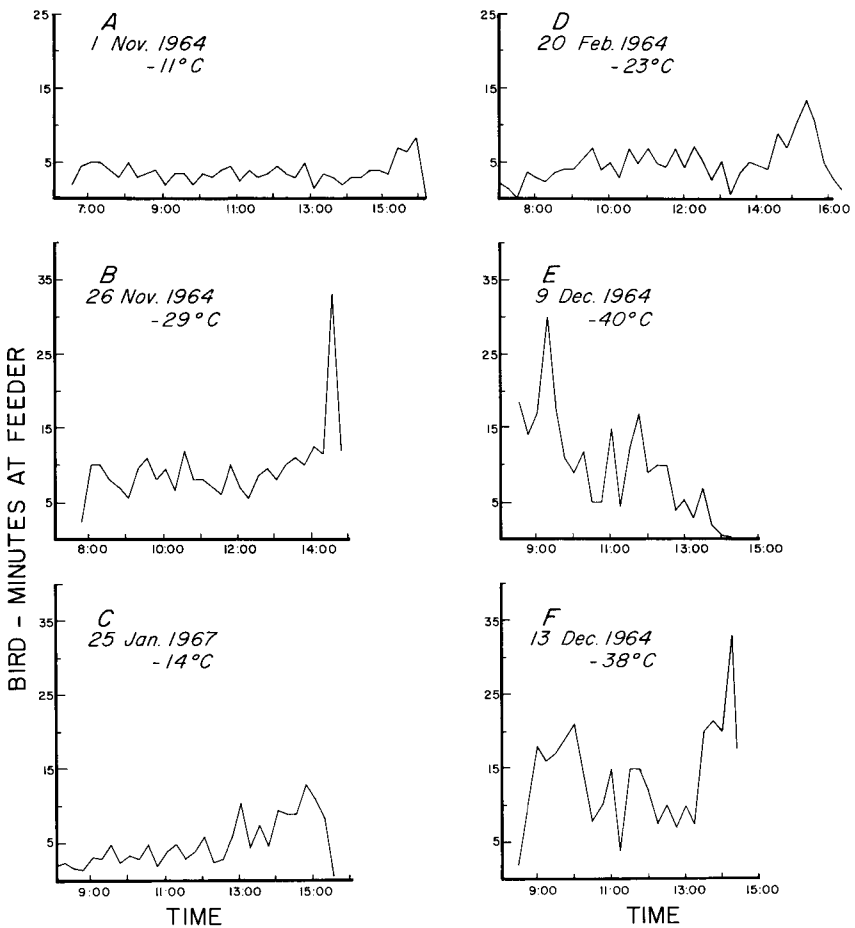
FIG. 6. Typical daily patterns of feeding intensity in chickadees at Fairbanks, Alaska. The total number of bird-minutes spent at the feeder is summed for each 15-min period during the activity day.

Chickadees in Ontario, was not apparent in most of the recordings made of the Fairbanks chickadee population. In fact, the only consistent pattern shown in the recordings was a tendency from mid-October to the end of February for a period of increased feeding activity to occur just before the birds went to roost (Fig. 6 A–D); 37 of the 50 recordings made during this time of year showed this tendency. The intensity peak was most conspicuous during the last 20 to 30 min before roosting, but on many days a gradual increase began as early as noon.

Before mid-October and after the end of February, when the feeder was not used as heavily as during the intervening months, no pattern of feeding intensity was discernible from the recordings.

On the 3 severest days for which I obtained full-day recordings, 2 distinct patterns were exhibited. On 2 days, 9 and 31 December 1964, with mean daily temperatures of $-40°C$ and $-41°C$, respectively, a period of high intensity feeding occurred in the morning; and, thereafter, intensity decreased throughout the remainder of the day (Fig. 6 E). On the other day, 13 December 1964, there was both a morning and an evening peak (Fig. 6 F); the mean daily temperature of $-38°C$ was a substantial warm-up from the $-42°C$ of the several preceding days. The morning peak of all 3 days can undoubtedly be explained by the need for food (energy) after the chickadees had been roosting for some 18 hours at these extremely low environmental temperatures. The reason for the lack of an evening peak on 9 and 31 December is less clear, however, but appears temperature related. Perhaps the birds obtained sufficient food early in the day, allowing them to conserve energy later in the day by inactivity (see above discussion regarding shorter activity days at cold temperatures). The resumption of the evening peak on 13 December may have been the result of the relative amelioration of environmental temperatures.

CONCLUSIONS

Several apparently adaptive responses of the Black-capped Chickadee to the environmental conditions of interior Alaska are evident from this study of activity patterns. The synchronization of the activity day with seasonal changes in the daily light cycle is one aspect of this adaptiveness. Such synchronization with the light cycle is essentially universal in living organisms but the timing and means of synchronization are unique to species and geographic locality. In interior Alaska, Black-capped Chickadees respond to different minimal levels of light intensity at different seasons of the year. In general, response to light intensities is such that activity days are longer in relation to daylength during the shorter, colder days of winter than at other seasons. In addition, the Fairbanks chickadees respond to lowest mean light intensities during the last half of November and the first half or more of December, with the result that their activity days are relatively even longer (1) during the November period of food caching and (2) prior to the winter solstice. While such synchronization is undoubtedly based on an evolutionary response to mean annual environmental conditions, it is noteworthy that during the warm December of 1960 chickadees responded directly with the longest mid-winter days of the study, beginning activities at the lowest light intensities of the study

Other responses which appear adaptive in nature are evident in relation to cold temperatures. Not only are there the general reactions of shorter activity days and greater feeding intensities with colder temperatures, but during mid-winter the amount of activity appears to decrease with extreme cold. These combined responses indicate that chickadees conserve energy by reducing activity during cold periods, especially during severe cold in mid-winter, through shorter feeding days and reduced activity; the fact that even slight increases in solar radiation in mid-winter tend to lengthen the activity day supports this contention.

With such responses, the tiny Black-capped Chickadee is better able to withstand the long nights and extreme cold of northern latitudes.

SUMMARY

Daily activity patterns of Black-capped Chickadees (*Parus atricapillus*) were studied about an artificial feeder near Fairbanks, Alaska, from September to May, 1960–1967. The daily light cycle was the dominant environmental factor determining the daily activity period. Activity days were longer relative to daylength before the winter solstice than after.

Light intensity was the second most influential factor. Chickadees began activity in the morning at lower light intensities than those at which they ended activity in the evening, and they began and ended activity at lower intensities during the last half of November and the first half of December than at other times of year.

At cold temperatures, chickadees had shorter activity days than when it was warmer, but their feeding intensity was greater; they apparently conserved energy by reducing activity during cold periods.

Even after accounting for the effects of light intensity, chickadees began activity in the morning earlier on clear than cloudy mornings. Solar radiation tended to result in shorter activity days during early and late winter, but longer activity days during mid-winter. Snow and wind appeared to have only slight effects on activity patterns.

The relative influence of several of the environmental factors appeared to change during the winter, and each factor exerted more influence on the timing of first activity than of last activity.

ACKNOWLEDGMENTS

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REQUESTS FOR ASSISTANCE

Shorebirds.—In 1976 the Canadian Wildlife Service will again be carrying out extensive banding and color-marking of shorebirds in James Bay. Last year a highly successful program resulted in over 70 reports of color-marked birds in eastern North America and South America from amongst c. 4000 banded in southern James Bay. Much valuable information on migration routes is being obtained and observers are again asked to look out for and report any color-dyed or color-banded shorebirds that they may see. Reports should include details of species, place, date, color-marks, and, if possible, notes on the numbers of other shorebirds present. For color-dyed birds, please record the color and area of the bird that was dyed. For color bands and standard metal leg bands, please record which leg the bands were on, the colors involved, and the relative position of the bands if more than 1 was on a leg (e.g. right leg, blue over metal, etc.). All reports will be acknowledged and should be sent to: Dr. R.I.G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1A 0H3.

Semipalmated and Least sandpipers.—In 1976 and 1977 the Surinam Forest Service plans to color-band large numbers of Semipalmated and Least sandpipers along the Surinam coast, northeastern South America. The objective of this study is to obtain more information about the origin of the birds visiting Surinam and about their migration routes to and from this country. All birds will be banded above the tarsus ("knee") with a standard aluminum Fish and Wildlife Service band and 2 orange color-bands of about the same size as the aluminum band. Should you see any of these birds, please write to: Arie L. Spaans, Surinam Forest Service, P.O. Box 436, Paramaribo, Surinam, South America. Mention species, location and date of observation, the position of the aluminum and color-bands (left or right, and, if more than 1 band is on a leg, which band is above and which below), and number of color-banded birds involved.