EFFECTS OF WEATHER ON THE NOCTURNAL ACTIVITY OF WHITE-THROATED SPARROWS

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Many studies have demonstrated that temperature, wind speed and direction, barometric pressure, rain, and overcast are correlated with the daily amount of migration. Bagg et al. (1950) were the first to discuss in detail the association between the movements of large air masses and the amount of songbird migration. They found that in the spring, in North America east of the Rocky Mountains, most migration took place west of high pressure systems and east of lows, after the passage of a warm front and before the passage of the associated cold front. At this time the wind is generally from the south, the temperature is rising, and the pressure is falling. Other authors have subsequently made similar findings (e.g., Lowery and Newman 1955, Richardson 1966, 1971, Nisbet and Drury 1968).

In autumn the largest migrations have been observed east of a high pressure system, after the passage of a cold front (e.g., Hassler et al. 1963, Lowery and Newman 1966, Able 1973). At that time there are usually north winds, falling temperature, and rising pressure.

These observations suggest that birds can detect weather conditions (or some unknown factor correlated with the weather), and that this detection influences their subsequent behavior, particularly their "decision" whether or not to initiate a migratory flight.

Multivariate analyses have been used to explore the effect of individual weather variables on the volume of observed migration (Nisbet and Drury 1968, Able 1973). Using this method one can establish correlations but cannot specify which weather variables affect the birds' behavior.

Another approach has been to utilize laboratory experiments and observations to examine the relationship between weather variables and the nocturnal activity (*Zugunruhe*) shown by caged birds. This type of study assumes that the amount of nocturnal activity is related to the probability that a bird would initiate a migratory flight.

My study was designed to determine whether or not a relationship existed between weather conditions and the amount of nocturnal activity of caged White-throated Sparrows (*Zonotrichia albicollis*) using birds exposed as fully as possible to natural weather conditions.

METHODS

White-throated Sparrows were housed in outdoor 61 cm × 41 cm × 33 cm wire mesh cages. Activity was monitored by two activated perches in each cage which rested on microswitches, and only movement onto the two perches was recorded. I assumed that the fraction of total locomotor activity recorded on the perches was nearly constant from night to night because individual caged birds develop "characteristic and almost invariable" activity patterns (King 1961). Because a bird's activity on any night was compared only to its own activity in the same cage on other nights, individual differences in activity patterns were felt to be unimportant.

The birds used in this study were caught during migration either in Ithaca, N.Y. or at Island Beach, N.J. They were kept in captivity on natural Ithaca photoperiod for a period ranging from several days to several months prior to the period of recorded activity. Records of activity were accumulated for four migration seasons: spring 1970 (19 May–18 June), spring 1971 (8 May–29 June), fall 1970 (15 October–20 November), and fall 1971 (3 October–9 November). The spring 1970 data were collected from four birds. The data from the next three seasons were collected from eight birds for each season. The birds were fed a mixture of wild birdseed supplemented by "turkey starter crumbles" (Agway) and live mealworms. Food and water were replaced daily.

The activity cages were located in an open field in the Cornell Research Park, Ithaca, New York. This location was moderately well screened from nearby artificial lights. In spring 1970 the cages were placed about 20 cm apart in an outdoor aviary. No attempt was made to isolate the birds from each other either visually or acoustically. The aviary was protected on three sides and on top with plywood planks. This left the birds with a view of the sky up to an elevation of about 45° to the south. During the other three seasons (fall 1970, spring and fall 1971) the activity cages were placed individually on poles (2 m high, 3 m apart) near the aviary. Each cage had a thin (0.5 mm) plastic cover as protection from rain, but the cages were open on all sides. The "clear" plastic cover allowed some vision through it of blurred images, and I could locate the sun's position through it.

Activity for the spring 1970 season was recorded on an Esterline-Angus event recorded (chart speed = 7.6 cm/hr). If the amount of activity was high, exact quantitative information was impossible from this type of record because the marks on the chart blended into one another. In such cases I made two estimates of the amount of activity using arbitrary but objective criteria. The low estimate assumed that the marks were just touching. The individual marks were 0.4 mm wide, and the saturated areas were quantified by dividing their width by 0.4 mm. The high estimate, which was derived from several observations of simultaneous chart recordings and jump counts considered a 1 mm saturated area to be 10 jumps. These two estimates produced activity scores that were highly correlated, and only the low estimate was used in the computer analysis. To avoid this imprecision, activity in fall 1970 and 1971 and spring 1971 was recorded with digital counters. The counters were activated after evening nautical twilight and left on for a constant interval. This interval was calculated so that the counters would shut off one half hour before dawn nautical twilight on the shortest night of the season. Consequently, the interval from the time the counters shut off until dawn varied. This variation was considered to be unimportant because the Esterline-Angus records revealed very little activity in the hours just prior to dawn. This procedure minimized differences in amount of activity resulting from differences in daylength.

WEATHER DATA

Thermograph and relative humidity charts were obtained from the Cornell meteorology department (see appendix 1 for definitions of weather variables). Wind, rain, and visibility information (visibility, opacity, fog) came from the Tompkins County Airport, which is within 0.8 km of the research area, pressure was recorded on a barograph in nearby Langmuir Laboratory, and K-values of magnetic disturbance were obtained from the Geophysical Observatory, Frederick, Md.

Temperature, wind direction, rain, barometric pressure, and relative humidity have been shown to be correlated with numbers of observed migrants. Visibility, opacity, and fog are all possible measures of the availability of visual navigation cues and therefore might affect a bird's "decision" to migrate. Magnetic intensity has been correlated with the amount of nocturnal activity of caged migrants (Shumakov 1967).

Temperature has a daily cycle imposed upon longer changes, and it is not known how a bird might monitor such a system. For that reason, I used three measures of temperature in my analysis: the highest and lowest reading for the day (midnight to midnight) and the reading two hours before sunset. Two measures of pressure change (4 hr and 24 hr) were also used in order to separate long and short term trends.

METHODS OF ANALYSIS

I measured activity in two ways: the number of perch hops on each night, and the change in the amount of activity from the previous night. This second measure of activity was included because factors other than weather may affect the amount of nighttime activity (e.g., changes in the bird's physiological condition). The direction of the changes in the amount of activity caused by other factors is probably constant over days or even weeks. For example, a bird's motivation to migrate may increase slowly throughout a season until migration takes place. Such an effect would gradually increase the amount of activity through the season. Seasonal trends in amount of activity were large in fall 1970, and spring 1971 but not in spring 1970 or fall 1971. Some changes in the amount of activity caused by the weather are assumed to be daily changes. When daily changes in activity are the criteria, the effect of other factors is filtered out.

The changes in activity from the previous night were plotted on a generalized weather map that represents an idealized picture of common weather situations (Richardson and Haight 1970). For each night the position of the experimental area was determined in relation to ambient pressure systems, fronts, etc. and plotted on the map. Each map represents a cumulation of many nights of activity, and nights close together on the map have similar weather conditions.

The rank correlation test (Sokal and Rohlf 1969) was used to determine whether correlations existed between activity and individual weather variables. Also, each night of activity was placed into one of several categories for each weather parameter. For example, there were nights when temperature increased, decreased, or remained the same from the previous night. (See appendix for a description of the categories for each weather variable.) In this way the amount of activity or the change in activity could be compared, for example, on nights with south vs. north winds. The significance levels for differences in amounts of activity or changes in activity were measured with the Mann-Whitney U test when comparing two categories and the Kruskall-Wallis test when comparing more than two categories. All statistical tests were nonparametric because interval data for spring 1970 were lacking and because there was no reason to assume normality in the activity data for any of the seasons. These tests were run on a IBM 360 computer with a FORTRAN program written by W. John Richardson.

RESULTS

GENERAL WEATHER MAP

The changes in activity scores for each group of birds were plotted on the generalized weather maps. Figure 1 shows a pressure system divided into four regions. Type one regions are the warm sectors of a low, and type two regions are on the west side of a high. Both of these areas generally have southerly winds and are associated with much spring migration. The type three region is behind a cold front and has northerly winds and falling temperatures. Under these conditions in the spring very few birds migrate (see references in introduction). The type four region is also behind a cold front, but in this case the wind is from the west instead of the north or northwest. The number of migrants varies under these conditions; sometimes there is much migration, sometimes none.

Spring nocturnal activity of the caged White-throated Sparrows from this study was nonrandom with respect to weather (fig. 2). These birds showed more nights of increased activity as opposed to decreased activity in situations favorable for migration and more nights of decreased activity as opposed to increased activity in those situations unfavorable for migration (table 1). A chi square test of the combined results for both spring seasons

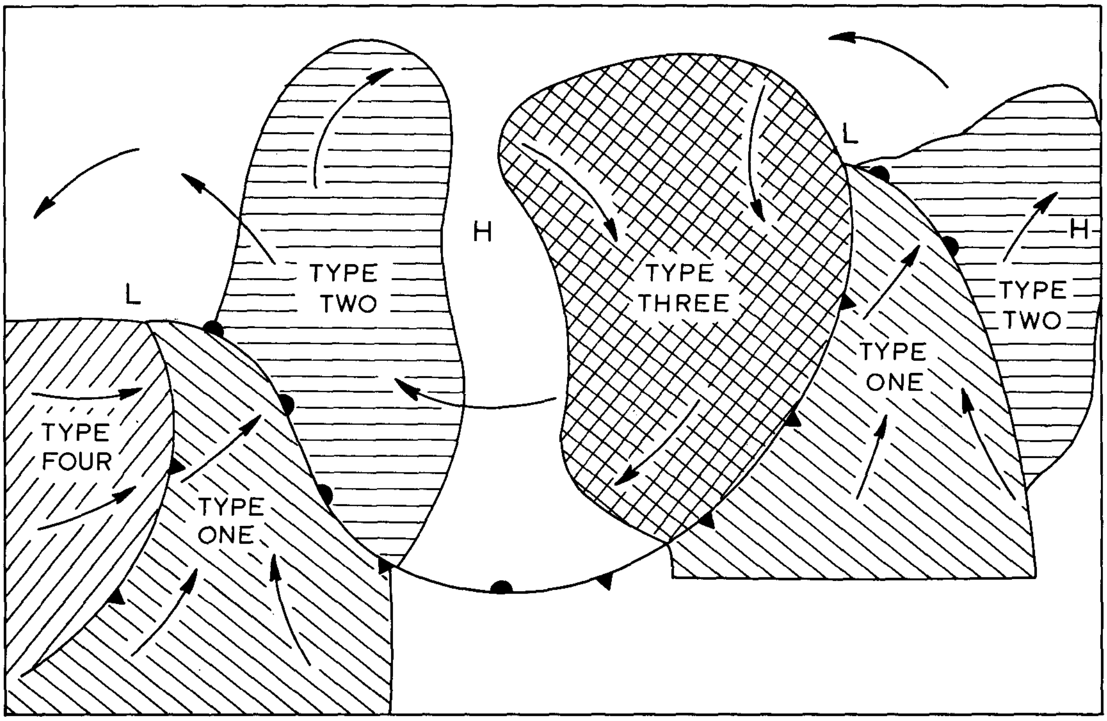

FIGURE 1. An idealized weather map showing regions of similar weather conditions. Explanation of numerical regions is in the text.

showed that the probability that these results were due to chance is less than 0.05 ($\chi^2 = 3.92$, df = 1). The corresponding results for the fall groups, however, were nonsignificant ($\chi^2 = 1.82$, df = 1, $P = 0.9$).

INDIVIDUAL WEATHER VARIABLES

Table 2 shows the significant correlations between daily weather parameters and average daily activity for the four seasonal groups of birds. Table 3 gives the analogous correlations between *changes* in weather parameters and *changes* in average daily activity of the birds.

In both the spring groups *change* in high temperature, increased high temperature, and a south wind were significantly positively correlated with either high or increasing activity levels. Likewise both spring groups showed a significant negative correlation with the pressure trend. These results agree with those obtained from the general weather map analysis.

TABLE 1. Number of nights of increased and decreased activity for several seasons and weather conditions (expressed for regions of weather map).

		Region of Map			
Season	Activity	1	2	3	4
Spring 1970	Increased	4	3	0	1
	Decreased	2	4	5	1
Spring 1971	Increased	4	11	5	2
	Decreased	1	2	8	3
Fall 1970	Increased	1	7	3	0
	Decreased	1	5	3	1
Fall 1971	Increased	2	3	2	0
	Decreased	4	4	3	1

TABLE 2. Results of tests of significance comparing average activity with individual weather parameters.[a]

	Season				
Weather parameter	Spring 70	Spring 71	Fall 70	Fall 71	Test
High temperature	—	**P	**P	*P	C
Low temperature	—	**P	**P	*P	C
Increased high temperature	*P	—	—	—	M
Increased SS-2 temperature	**P	—	—	—	M
Relative humidity	—	*P	**P	—	M
South wind	*P	*P	—	—	M
Visibility	—	**N	**N	*N	C
Pressure	—	*N	—	—	C

[a] Symbols: P, a positive correlation; N, a negative correlation; *, $P < .05$; **, $P < .01$; C, rank correlation test; M, Mann-Whitney U test; —, no significant correlation; SS-2, 2 hr before sunset.

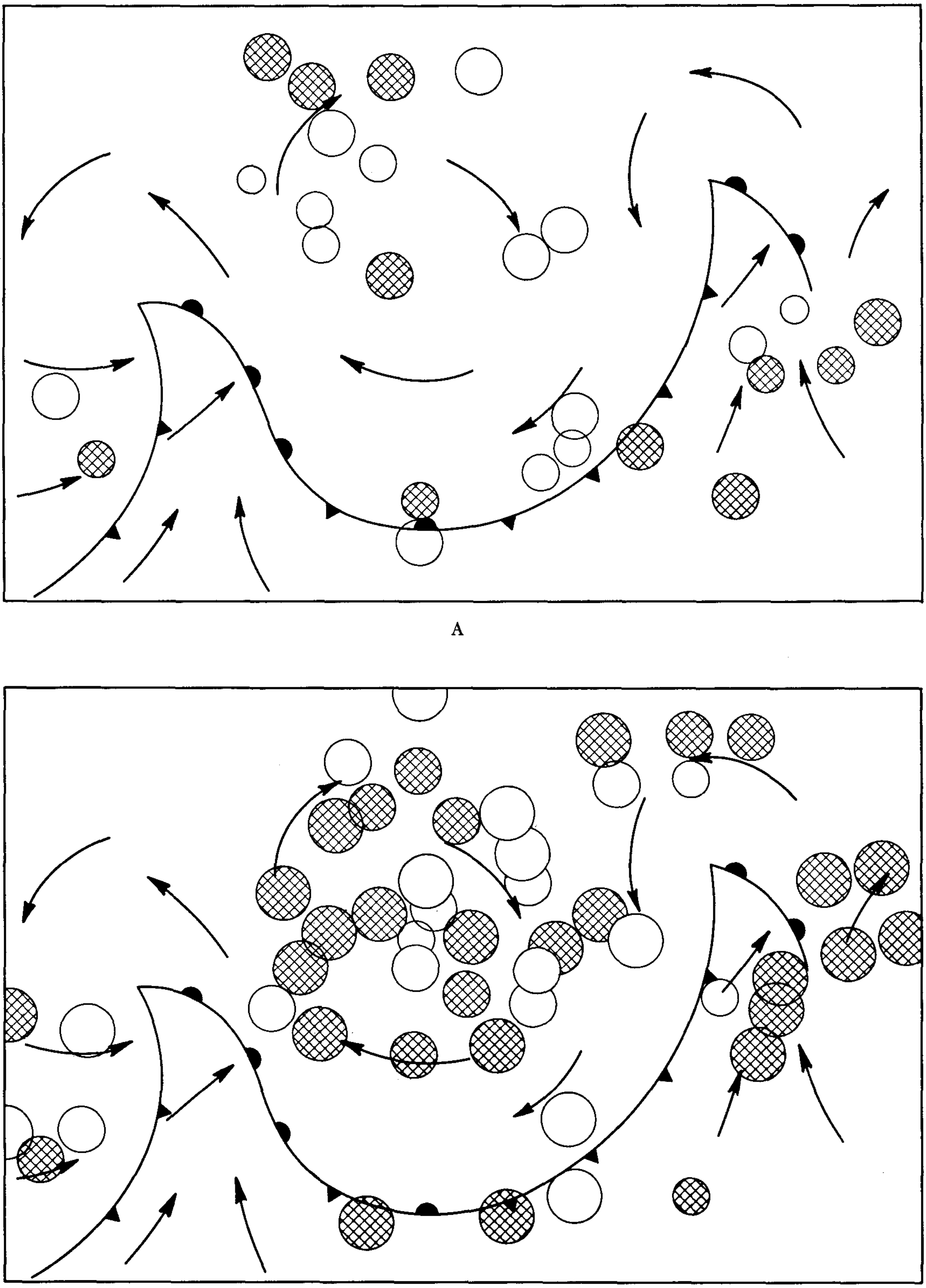

FIGURE 2. Nights of activity plotted on an idealized weather map. Open circles are nights of decreased activity. Cross-hatched circles are nights of increased activity. Size of circles indicates size of change in activity on a logarithmic scale. A—spring 1970; B—spring 1971.

TABLE 3. Results of tests of significance comparing *change* in average activity with individual weather parameters.[a]

Weather parameter	Season Spring 70	 Spring 71	 Fall 70	 Fall 71	Test
Change in high temperature	*P	**P	—	—	C
Change in low temperature	*P	—	—	—	C
Increased high temperature	*P	*P	—	—	M
Increased low temperature	*P	—	—	—	M
Increased SS-2 temperature	*P	—	—	—	M
Change in relative humidity	—	—	*P	—	C
South wind	*P	—	—	—	M
Opacity (total overcast)	—	—	*P	—	M
Pressure trend	*N	*N	—	—	C

[a] Symbols: as in Table 2.

The activity of both groups of the fall birds showed significant positive correlations with high and low temperatures, and significant negative correlations to low visibility. It is important to note that the correlation with temperature is only with high temperatures and not with increasing temperatures. These and other features of tables 2 and 3 are discussed below.

Some of the significant correlations obtained in this study appear to result from seasonal trends in both the amount of activity and the weather variable. Two of the groups had large long-term activity trends. The spring 1971 group had a steady increase in activity throughout the observation period, and the fall 1970 group showed a progressive decrease in activity. Both trends would tend to produce correlations with weather variables that have a yearly cycle. For example, since temperature also increases through the spring and decreases throughout the fall, we might expect that the amount of activity would be correlated with the temperature for the two seasons with long-term trends. These temperature-activity correlations are significant for the fall 1970 and spring 1971 groups, but not for the spring 1970 group, which showed a fairly constant amount of activity throughout the season. The fall 1971 group, which had less of an activity trend, had a less significant correlation with temperature.

The correlations between change in activity and change in temperature yield further evilence. These daily changes have no seasonal trend. The two spring groups have significant correlations with changing temperature whereas the two fall groups do not.

Two criteria were used to determine those correlations that were considered spurious: (1) the presence of the correlation in the groups that had marked seasonal trends in activity (spring 1971, fall 1970) and not in the spring 1970 or fall 1971 group; and (2) the disappearance of the correlation when examining the daily change in activity and the weather variable. These criteria indicated a positive spring 1971 activity-humidity correlation, positive fall 1970 and 1971 activity-temperature correlations, and negative spring 1971, fall 1970 and 1971 activity-visibility correlations to be spurious.

INDIVIDUAL BIRDS

The results of the previous sections are based on the average activity of groups of birds. Such group results could be due to several combinations of causes; for instance, a significant positive correlation could be the result of either similar correlations in all of the individuals in the group or of very strong correlations in some individuals and no correlations in others. Nonsignificant results could be caused either by nonsignificant results in all the individuals or by significant results in opposing directions (i.e., some positive correlations and some negative).

When the activity of individual birds was examined, very few of the statistical tests yielded significant correlations. In addition, I did not find that some individuals had significant correlations with several weather variables, and that others had activity unrelated to weather. The significant group correlations seemed to be produced by the summations of weak correlations of most of the individuals in that group.

Also the individual results were more consistent for the spring seasons than the fall seasons. Most of the spring birds responded to temperature, wind direction, and pressure in similar ways. The fall birds, however, often responded very differently to individual weather parameters. This resulted in fewer significant group correlations in the fall.

DISCUSSION

Although some weather variables were measured at points up to several miles from the activity cages, I do not consider this to be a serious problem for two reasons. First, the locations of both the activity cages and the weather instruments were flat open areas, and

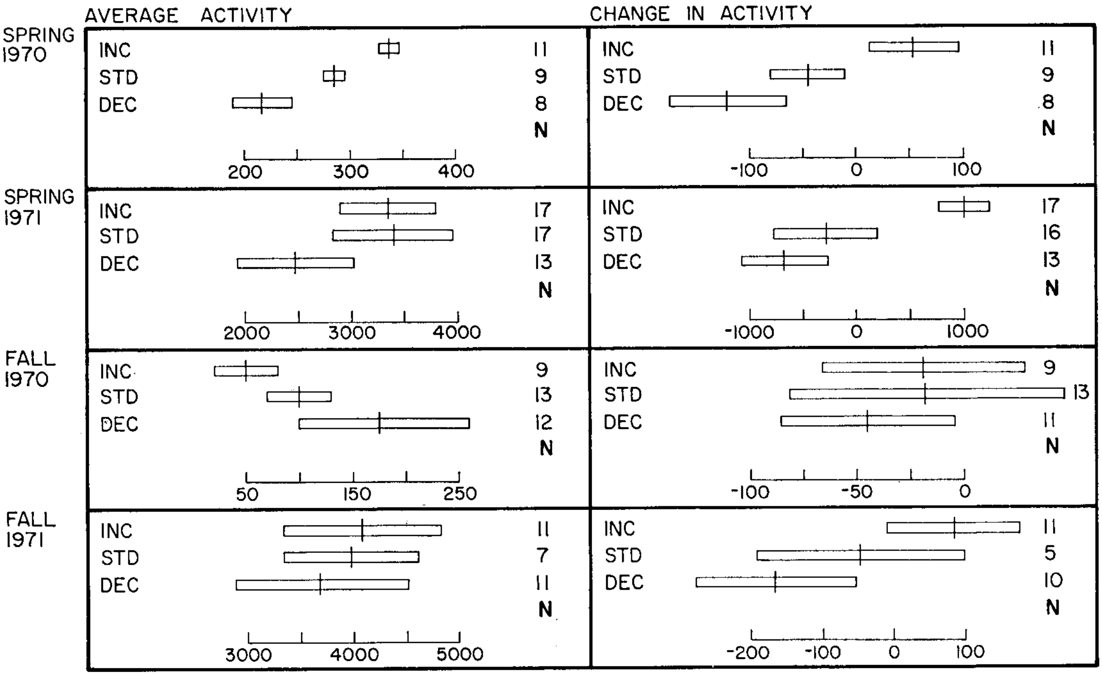

FIGURE 3. Relationship of activity to the highest temperature of the day. Vertical lines indicate means. Bars denote standard error of the mean. Both measures of activity are expressed in jumps/night. N = the number of nights in each category. INC—increased temperature; STD—steady temperature; DEC—decreased temperature.

any differences in conditions between them were probably very small. Second, the correlations reported in the literature between observed migration and weather were obtained from data that were often collected at one location and compared to the volume of migration at a different location. In addition, the observed migration progressed over a large area if radar was used. Able (1973) reported that the magnitude of migration departing from within 25 nautical miles of his radar station was significantly correlated ($r = .995$) with the maximum traffic rate, which consisted of birds that had been flying up to four hours. The fact that birds observed in such a study took off from widely divergent locations suggests that any weather changes which influenced these birds must have been very similar over large areas.

SPRING RESULTS

The spring results are similar to correlations between weather and the amount of migration observed in the field. Temperature, wind direction, and pressure have been consistently related to the amount of migration (see introduction). If the amount of activity is a measure of the probability that a bird would have initiated a migratory flight, high activity should be associated with high or increased temperature, falling pressure, and south winds in the spring and with low or decreased temperature, rising pressure, and north winds in the fall. In this study, the spring results fulfill these predictions but the fall results do not. In the spring: (1) nocturnal activity and temperature were significantly ($P < 0.05$) positively correlated, (2) nocturnal activity was significantly ($P < 0.05$) greater with south winds than with north winds, and (3) nocturnal activity was significantly ($P < 0.05$) greater will falling barometric pressure from 16:00 to 20:00 prior to the activity than with rising pressure. Furthermore, the generalized weather maps show that in the spring activity increases under synoptic weather conditions where migration is reported to be common, and decreases under conditions where there is little migration. If the amount of migration observed in the field is determined by the average migratory motivation of individual birds, then it would appear that the amount of nocturnal activity can be used as a measure of migratory motivation in the spring.

The previously-cited studies of migration involved observations of many species, and in many cases the species could not be identified. However they suggest that the responses

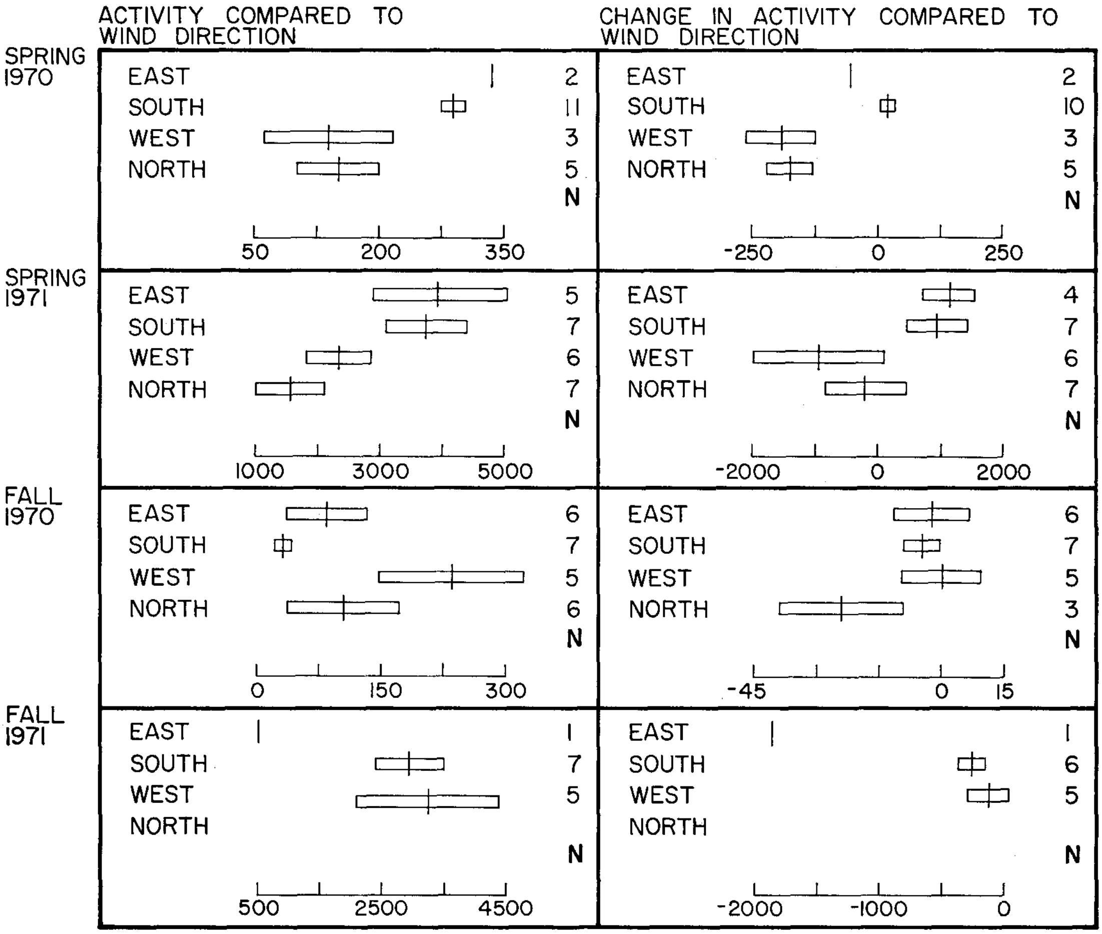

FIGURE 4. Relationship of activity to surface wind direction. Vertical lines indicate means. Bars denote standard error of the mean. Both measures of activity are expressed in jumps/night. N = the number of nights in each category.

of many species of passerines to weather are similar. Therefore they are useful in describing the general relationship between the migration behavior of *Zonotrichia albicollis* and weather changes.

Although some of the correlations were significant for one year and not the other, the relationships between weather and activity during both spring periods were very similar (figs. 3 and 4). For example, spring 1970 and spring 1971 had significantly more activity on nights with south winds than on nights with north winds. In addition, change in activity was significantly related to wind direction for the 1970 group. The change in activity did not differ significantly with north vs. south winds for the 1971 group, but the results were consistent: south winds—average increase of 965 perch registrations, north winds—average decrease of 229 perch registrations from the previous night. This consistency implies that the spring correlations were not due to chance.

FALL RESULTS

The results for the fall groups are very different. Activity was random with respect to synoptic weather conditions. Excluding spurious results, the correlations with temperature, wind direction, and pressure were not significant. The only significant weather-activity correlations were with opacity and relative humidity for the fall 1970 group (table 3).

The fall groups, in addition to having far fewer significant results (19 spring, 10 fall), showed much less consistency in their relationship to weather parameters (figs. 3 and 4). This suggests that the birds' responses to weather are very different in the spring and fall. Apparently caged *Zonotrichia albicollis* show more nocturnal activity on nights with favorable migration weather in spring, but do not do so in the fall.

This conclusion is unsatisfying because field studies find that migration is correlated with weather in the fall. The fall results may be an artifact of my experimental setup, but other workers (Weise 1956, Helms 1965) using Z. *albicollis* also found better correlations with weather in the spring than in the fall. In addition, the migration behavior of Z. *albicollis* differs between the spring and fall. Spring migration is usually accomplished in less time, and there seem to be differences in the relative importance of various navigational cues used by this species in the spring and fall (S. Emlen, pers. comm.).

IMPLICATIONS FOR FURTHER WORK

This study demonstrates short-term correlations between the amount of spring nocturnal activity and weather variables. Significant correlations were found between the amount of activity and individual variables without grouping the data, and also between the day to day changes in both the weather variables and activity.

The fact that a high rate of activity is associated with the same weather conditions as a high rate of migration suggests that the activity shown by a caged migrant is related to the probability that migration would have been initiated, and that both are influenced by weather conditions. This relationship could be partially tested by simultaneously monitoring migration and the activity levels of caged migrants.

One explanation for the short-term correlations found in this study and not in others (Mascher and Stolt 1961, Helms 1965) is that the birds used in this study were exposed as much as possible to the natural weather conditions. Perhaps testing birds inside (e.g., Mascher and Stolt 1961) even if windows are open to the outside (e.g., Helms 1965) alters the natural situation enough to block a natural response to weather variables. Helms (1963) stated that the removal of a natural environment progressively blocks these natural responses.

In addition, changes in activity from the previous night might be a better measure of activity than absolute amount because the latter might be affected by factors other than weather.

Although the activity of a group of birds showed significant correlations with several weather variables, almost none of the results for individual birds were statistically significant because of a high variance in behavior. An analysis of variance was not possible because the data were not distributed normally, but the lack of significant results for individual birds suggests that a substantial variation in activity was caused by factors other than weather.

By changing the birds' environment in the laboratory, it may be possible to determine which weather variables affect the amount of activity if natural conditions can be sufficiently simulated. However, my study indicates that such experiments would have to be performed on fairly large groups of birds to yield statistically significant results because of the large variance in the behavior of individual birds.

SUMMARY

White-throated Sparrows (*Zonotrichia albicollis*) were kept in outdoor activity cages for two spring and two fall migratory seasons in order to examine the relationship between activity and weather. Activity was compared with synoptic weather conditions. The weather-activity maps showed a nonrandom relationship between activity and synoptic weather conditions in the spring. Activity increased from the previous night in areas on the map representing weather conditions in which radar studies show much spring migration takes place, and decreased in areas where radar shows there is little forward spring migration. In addition, the amount of activity and the change in activity from the previous night were compared to individual weather variables. Significant correlations were obtained in the spring between activity and temperature, surface wind direction, and change in barometric pressure. In the fall the synoptic map did not show a clear relationship between activity and weather. Neither were there the expected significant correlations between activity and wind direction, temperature, and pressure. Possible reasons for the unexpected fall results are discussed.

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APPENDIX. Definition of weather variables.

Pressure—Barometric pressure in inches of mercury. A reading was taken at 8 P.M. each day. *Rising*: an increase of .05″ or more from the reading on the previous day. *Falling*: a decrease of .05″ or more from the reading on the previous day. *Steady*: a change of less than .05″ from the reading on the previous day.

Pressure trend—the change in pressure in the four hours from 16:00 to 20:00 preceding the night of activity.

High temperature—the highest reading of the day (midnight to midnight). *Rising*: an increase of 5° or more from the reading on the previous day. *Falling*: a decrease of 5° or more from the reading on the previous day. *Steady*: a change of less than 5° from the reading on the previous day.

Low temperature—the lowest reading of the day (midnight to midnight). The categories are the same as for high temperature.

SS-2 Temperature—the reading at 2 hr before sunset; the categories are the same as for high temperature.

SS-2 Temperature with respect to normal—SS-2 temperature compared to the average temperature for that day calculated from 10 years of data.

Humidity—the relative humidity measured in percentage at 2 hr before sunset each day. *Rising*: an increase of 5% or more from the reading on the previous day. *Falling*: a decrease of 5% or more from the reading on the previous day. *Steady*: a change of less than 5% from the reading on the previous day.

Wind—the direction from which the surface wind is blowing at 8 P.M. each day. 0° or 360° = north. *North*: a wind from 316° to 45°. *East*: a wind from 46° to 135°. *South*: a wind from 136° to 225°. *West*: a wind from 226° to 315°. *Calm*: a wind less than 1 mph.

Visibility—the surface visibility in miles recorded at the Tompkins County Airport, 0.8 km from the study site.

Opacity—the fraction of the sky covered by opaque clouds, measured in tenths.

Rain or Fog—the presence or absence of these recorded at the Tompkins County Airport at 8 P.M.

K-value—the size of the magnetic disturbance measured at the geophysical observatory in Frederick, Maryland.

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