

THE INFLUENCE OF WEATHER VARIABLES ON THE DENSITY

OF NOCTURNAL MIGRATION IN SPRING

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INTRODUCTION

Until the availability of radars that could detect birds migrating aloft at night, studies emphasizing the influence of meteorological variables on the density of nocturnal bird migration suffered because the techniques of study were either indirect (e.g., counting grounded migrants) or limited by certain weather variables (e.g., obscuring clouds in the case of moon-watching). Lack (1960a) reviewed more than 100 papers published between 1880 and 1958 that discussed the influence of weather variables on passerine migration, and he criticized all previous conclusions because most authors had used subjective judgment or univariate statistics to study a multivariate problem. Lack also concluded that radar provided the most adequate measurements of the density of migration. At least 12 papers emphasizing the influences of weather variables on bird migration have been published since Lack's review in 1960, and each is based on radar data and employs multivariate statistics. Four of these studies concern only spring migration (Lack 1960b; Nisbet and Drury 1968; Richardson 1971, 1974a); four concern only fall migration (Lack 1963a, Gruys-Casimir 1965, Able 1973, Richardson 1976); and four studies concern both spring and fall migration (Lack 1963b, Geil et al. 1974, Richardson 1974b, Alerstam 1976).

In this paper I analyze the influence of weather variables on the nocturnal migration of passerine birds in spring using multivariate statistics and review the conclusions of similar studies. The implications of the findings are discussed in terms of the relative contributions of exogenous and endogenous factors to the migratory behavior of birds.

METHODS

I used the WSR-57 radar at the National Weather Service station at Athens, Georgia, during the spring of 1969 to gather data on the density of nocturnal passerine migration. Pertinent details of this radar are thoroughly reviewed in Gauthreaux (1970). The peak amount of migration on each of 54 nights sampled from 15 March to 19 May was determined by a technique similar to that used by radar meteorologists to measure the intensity of rainfall (see Gauthreaux 1970, 1975). This method yields density measurements of bird migration detected by the radar that are highly correlated with those obtained by moon-watching (Lowery 1951), and the amount of migration can be expressed as the number of birds crossing a mile of front per hour, the migration traffic rate.

In the multivariate statistical analyses that follow the maximum density of nocturnal migration on a given night (TR) is the dependent variable. The independent variables are photoperiod (PP), surface wind direction (SWIND), surface wind velocity (SVEL), aloft wind direction at 305 m (1,000 ft) (AWIND), aloft wind velocity (AVEL), precipitation during previous daylight hours (PPT), percentage cloud cover (CLDS), cloud height (CLHT), dry bulb temperature (DTEMP), wet bulb temperature (WTEMP), relative humidity (RH), 24-hour change in dry bulb temperature (DLDTMP), 24-hour change in wet bulb temperature (DLWTMP), 24-hour change in relative humidity (DLRH), barometric pressure (BP), 24-hour change in

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barometric pressure (DLBP), general synoptic weather over station (GENW), precipitation during sample evening (NPPT), and magnetic storm activity (K). In all, 19 independent variables are included in the analysis. Unless noted, the weather variables are those recorded at the beginning of the sample evening (19:00 EST) at the Athens, Georgia, weather station. Any variable reflecting 24-hour change is the difference between the value of the variable at the 19:00 hour on the sample evening and the value at the 19:00 hour on the previous evening. The value assigned to the general synoptic weather pattern over the station was based on the comparison between the national weather map for the 19:00 hour and Figure 1. Wind direction is a circular variable and was linearized before analysis by assigning the value of zero to north winds and the value of 180 to south winds. For winds from the intermediate directions either westerly or easterly the values ranged from one to 179 (e.g., northeast and northwest winds had a value of 45, east and west winds had a value of 90, and so forth). The dependent variable (TR) originally showed a right-skewed and leptokurtotic (clumped) distribution without transformation, but a $\sqrt{TR+1}$ transformation normalized the distribution. Other details of this analysis follow the recommendations of Richardson (1974b).

The multivariate statistical analyses of the data included a multiple correlation procedure (CORR) using the Barr and Goodnight (1972) Statistical Analysis System (SAS) package, the stepwise regression (STEPWISE), and the maximum R procedures (MAXR) using the Barr and Goodnight (1972) SAS package, and the stepwise multiple discriminant analysis procedure using the BMD07M program (Dixon 1973). Stepwise multiple discriminant analyses were performed with the dependent variable (TR) divided first into two categories, zero migration and migration, and then into three categories, zero, medium, and heavy migration.

RESULTS AND DISCUSSION

The multiple correlation analysis showed that the night-to-night change in the density of migration was correlated positively with dry bulb temperature ($p < .0001$), general synoptic weather ($p < .0003$), surface wind direction ($p < .0004$), 24-hour change in dry bulb temperature ($p < .0006$), aloft wind direction ($p < .0007$), wet bulb temperature ($p < .0009$), 24-hour change in wet bulb temperature ($p < .0036$), and correlated negatively with aloft wind velocity ($p < .0060$) and surface wind velocity ($p < .0067$). The remaining variables were not significant at the 0.05 significance level.

Stepwise regression analysis generated the best predictive model with only four variables--dry bulb temperature, general synoptic weather, precipitation during the sample night, and velocity of aloft wind at 305 meters--explaining 54 percent of the night-to-night variance in migration density (Table 1). The model shows the following relationship between peak nightly migration density (TR) and the four weather variables:

$$TR = [-66.29 + 1.49(DTEMP) + 9.13(GENW) - 28.70(NPPT) - 0.95(AVEL)]^2 - 1$$

The included weather variables are significant at the 0.05 significance level. One variable alone, dry bulb temperature, explains nearly 40 percent of the variance in TR.

In an effort to examine the makeup of the variable general synoptic weather, a maximum R procedure was performed with GENW as the dependent variable and with migration density (TR) eliminated. With all the weather variables included, only 73 percent of the variability in synoptic weather was explained. It thus appears that general synoptic weather includes additional weather parameters not specified by the array of weather variables I have chosen for my analysis. In addition, a

stepwise regression analysis was performed to examine the most significant weather variables that contributed to the dependent variable, general synoptic weather. The resulting model contained only three variables: the direction of aloft wind, the velocity of aloft wind, and the 24-hour change in wet bulb temperature. The three variables accounted for 48 percent of the variance in synoptic weather, and the aloft wind direction alone accounted for 41 percent of the variance. When synoptic weather (GENW) was eliminated as an independent variable, the best regression model contained only two weather variables, surface wind direction and dry bulb temperature, and explained 44 per cent of the variation in nightly migration traffic rate.

In the first stepwise discriminant function analysis, I attempted to find the weather variables that were most important in discriminating between occasions with no migration and occasions with migration. Based on this analysis, the following variables contributed significantly ($p < .05$) to the discriminant model: dry bulb temperature, velocity of aloft winds, precipitation during the sample night, and general synoptic weather. Based on the discriminant model with these four variables, only two of the 17 cases of no migration were incorrectly classified (88% accuracy), and of the 37 cases of migration only four were misclassified (89% accuracy). When all 19 weather variables were included the misclassification in the migration category was reduced by only one case (92% accuracy). Thus four weather variables had almost the same predictor accuracy as all 19 weather variables.

When each case of no migration and migration is plotted using the first and second canonical variables, the separation of the two categories of migration traffic rate is clearly evident (Figure 2). The canonical variables incorporate the most important weather

variables that allow maximum discrimination between the two categories of migration. The canonical correlation coefficient (R_c) is 0.80, and the proportion of the variance in the discriminant function accounted for by the two groups is 64 per cent.

In the second stepwise discriminant function analysis I divided the dependent variable TR into three categories: zero migration, medium migration (traffic rates between 1 and 4500), and heavy migration (traffic rates above 4500). Only three variables were significant ($p < .05$): dry bulb temperature, general synoptic weather, and relative humidity. On the basis of this discriminant model with these three variables, three of the 17 cases of no migration were misclassified (82% accuracy), 13 of the 28 cases with medium migration densities were misclassified (54% accuracy), and two of the nine cases with heavy migration were misclassified (78% accuracy). When all 19 weather variables were included, only one case was misclassified in the zero migration category (94% accuracy), eight of the 28 cases in the medium migration category were misclassified (72% accuracy), and none were misclassified in the heavy migration category (100% accuracy). Figure 3 shows the plot of the cases in the three categories along the axes of the first and second canonical variables. As expected, the medium migration cases were the most poorly classified, probably because the limits of the category were somewhat arbitrarily defined. The canonical correlation coefficient (R_c) is 0.82 for the first canonical variable and 0.54 for the second canonical variable, and the proportion of the variance in the discriminant function accounted for by the three groups is 67 per cent.

In all the multivariate studies of weather influence on bird migration two patterns emerge. First, of the weather variables that have been shown to have a significant influence on the night-to-night variation in the amount of migration, two variables, temperature and wind, have rather consistently appeared. Aspects of the weather variable wind have been shown significant in every study. In my study both wind direction and dry bulb temperature were significantly cross-correlated (partial correlation coefficient 0.43, $p < .0016$ for direction of surface wind; partial correlation coefficient 0.59, $p < .0001$ for direction of aloft wind). When one considers the flight energetics of bird migration the importance of both temperature and wind is self-evident. The other pattern evident from multivariate studies of weather and bird migration concerns the percentage of night-to-night variability in the amount of migration explained by the array of weather variables. In spring (Table 2) the average percentage of explained variability is 52 per cent with a range from 40 per cent to 62 percent. In the fall (Table 3) the average explained variability is 47 per cent with a range from 26 per cent to 61 per cent. Thus weather conditions appear to be able to account for only about half of the variation in the amount of nightly migration. The remaining variability is probably dependent on the number of grounded migrants in the general area and on the internal conditions of these migrants relative to their readiness to migrate.

SUMMARY

Fifty-four nights of radar data were gathered and processed according to the methods of Gauthreaux (1970, 1975) yielding accurate estimates of migration traffic rates. The highest hourly migration

traffic rate for each night (the dependent variable) was analyzed in terms of 19 weather parameters (independent variables) gathered at the beginning of each night by several Statistical Analysis System (SAS) procedures: simple rank correlation, stepwise regression, and discriminant analysis. When necessary the data were transformed as recommended by Richardson (1974b).

Nine weather variables were found significantly correlated with migration traffic rate. Dry bulb temperature accounted for 37 per cent of the variation in migration traffic rate; the best model included four variables--aloft wind velocity, dry bulb temperature, synoptic weather, and nightly precipitation--that together explained 54 per cent of the variation in nightly migration traffic rate. When synoptic weather was eliminated the best regression model contained only two variables, surface wind direction and dry bulb temperature, and explained 44 per cent of the variation in nightly migration traffic rate.

The stepwise discriminant function analyses showed that dry bulb temperature, velocity of winds aloft, precipitation during the sample night, and general synoptic weather contributed most significantly to the discriminant model for predicting no migration or migration. The discriminant model for separating the categories no migration, medium migration, and heavy migration relied strongly on just three variables: dry bulb temperature, general synoptic weather, and relative humidity.

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TABLE 1
STEPWISE REGRESSION ANALYSIS FOR SPRING MIGRATION

| Number in Model | R-Square | Variables in Model ^a |
|-----------------|----------|---------------------------------|
| 1 | 0.38 | DTEMP |
| 2 | 0.44 | DTEMP GENW |
| 3 | 0.49 | DTEMP NPPT GENW |
| 4 | 0.54 | AVEL DTEMP NPPT GENW |
| 5 | 0.55 | AVEL DTEMP DLDTEMP NPPT GENW |
| 4 | 0.54 | AVEL DTEMP NPPT GENW |

^aThe variables in the above model have all been deemed significant at the 0.05 significance level.

TABLE 2
INFLUENCE OF WEATHER VARIABLES ON SPRING MIGRATION (MULTIVARIATE ANALYSES)

| | Temp | Wind | Cloud | Rel Hum | Bar Press | Precip | Gen Weath | R ² or R _C ² |
|---------------------------------|------|------|-------|---------|-----------|--------|-----------|---|
| Lack (1960b) | * | * | * | | | * | | |
| Lack (1963b) | * | * | * | | | | * | |
| Nisbet & Drury (1968) | * | * | | * | * | * | | 0.60 |
| Richardson (1971, 1974b) | * | * | * | | | | | 0.62 |
| Geil et al. (1974) ^b | * | * | | * | * | | | 0.61 |
| Geil et al. (1974) ^c | * | * | * | | | * | | 0.43 |
| Richardson (1974a) ^d | | * | | | * | | | 0.51 |
| Richardson (1974a) ^e | | * | | | | | | 0.40 |
| Alerstam (1976) | | * | | * | * | | * | 0.44 |
| Gauthreaux (1976) | * | * | | | | * | * | 0.54 |

^a Specific weather variables (e.g., 24-hour change in temperature, temperature departure from normal) are included in general variable (e.g., temperature); ^b March; ^c April; ^d offshore; ^e overland.

TABLE 3
 INFLUENCE OF WEATHER VARIABLES ON FALL MIGRATION (MULTIVARIATE ANALYSES)

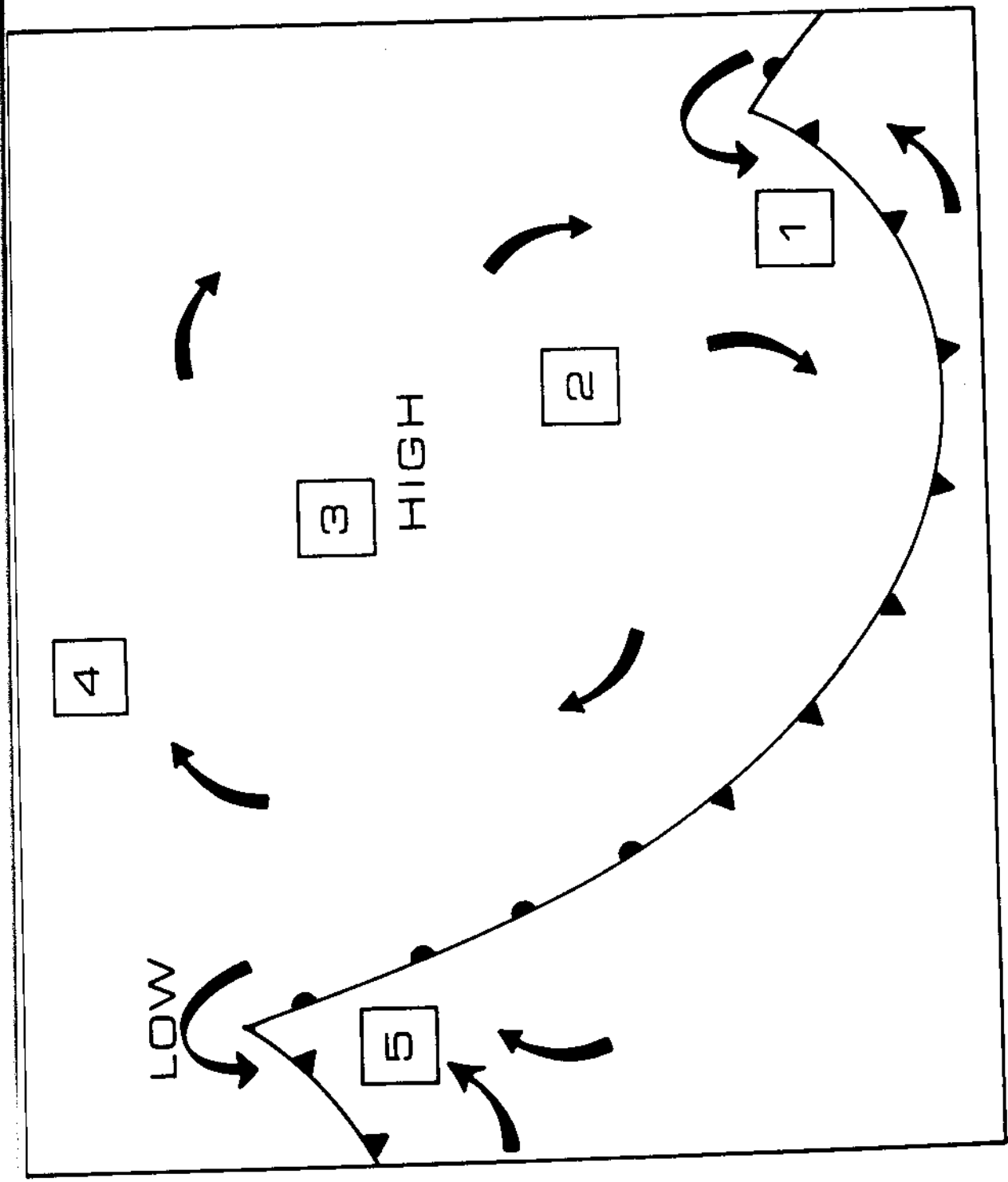
| | General Weather Variables ^a | | | | | | | | | | R ² or R _C ² |
|---------------------------------|--|------|-------|----------|---------|-----------|--------|-----------|----------|---|--|
| | Temp | Wind | Cloud | Visibill | Rel Hum | Bar Press | Precip | Gen Weath | Mag Dist | | |
| Lack (1963a) ^b | * | | | | | | | | * | | |
| Lack (1963a) ^c | * | * | * | | | | | | * | | 0.54 |
| Able (1973) | * | * | | | | | | | | | 0.44 |
| Geil et al. (1974) ^b | * | * | | | * | | | | | | 0.48 |
| Geil et al. (1974) ^d | * | | * | * | * | | | | | | 0.51 |
| Richardson (1974b) | * | * | | | * | * | * | | * | | 0.61 |
| Alerstam (1976) | * | * | * | * | * | * | | | * | * | 0.26 |
| Richardson (1976) | * | | | | | * | | | | | |

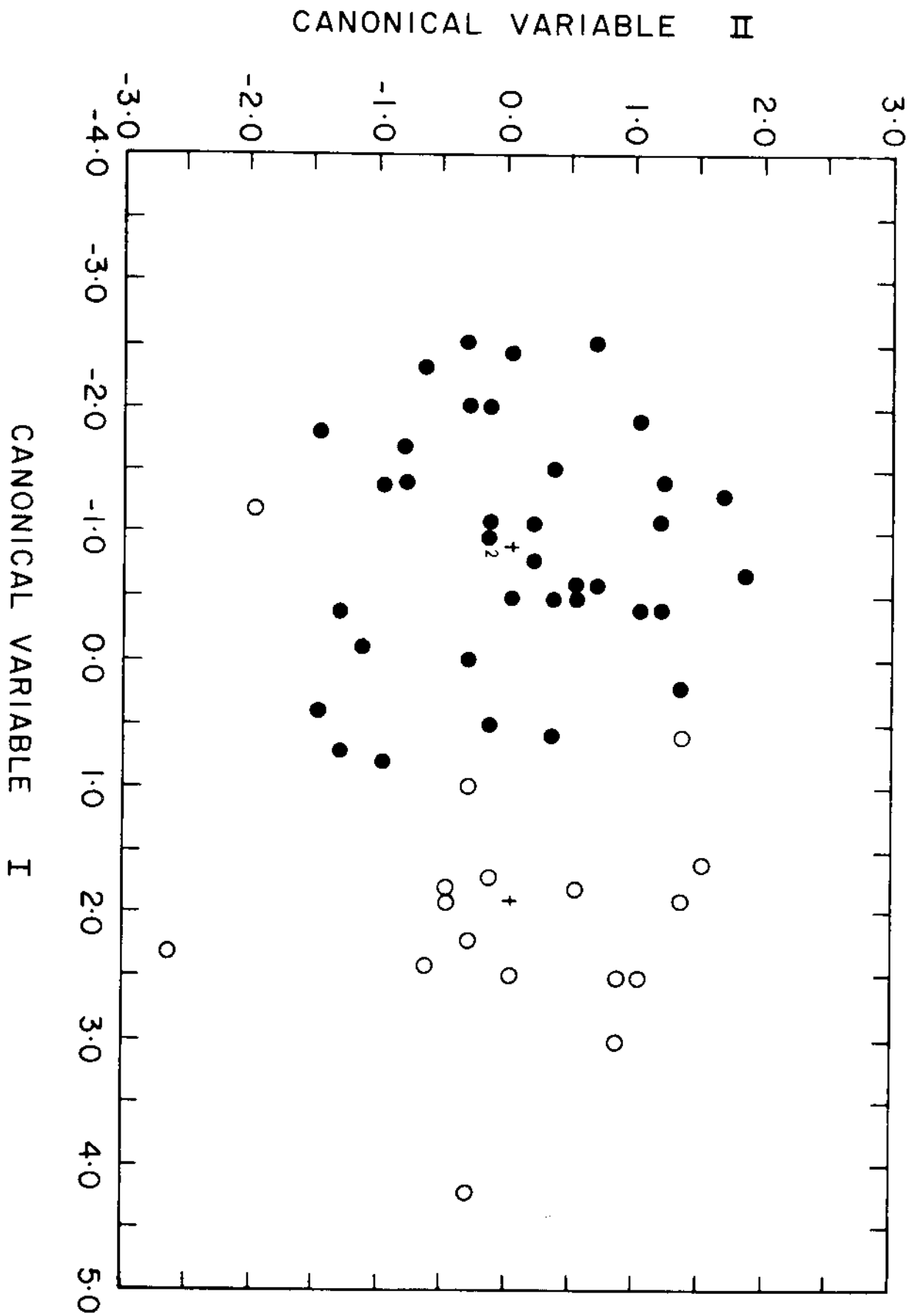
^a Specific weather variables (e.g., 24-hour change in temperature, temperature departure from normal) are included in general variable (e.g., temperature); ^b September; ^c October-November; ^d November.

Figure 1. Synoptic weather chart used to assign values to the variable general weather (GENW). The value (in square box) given to GENW was that most closely associated with the synoptic weather pattern over the study site based on examination of the actual surface weather map for 19:00 EST.

Figure 2. Discrimination between nights with no migration and migration on the basis of weather. Nights are plotted in relation to the first and second canonical variables. Open circles are cases of no migration, and solid circles are cases with migration.

Figure 3. Discrimination between nights with zero, medium, and heavy migration on the basis of weather. Nights are plotted in relation to the first and second canonical variables. Open circles are cases of no migration, half-shaded circles are cases of medium migration, and solid circles are cases of heavy migration.





CANONICAL VARIABLE II

