THE PHENOLOGY OF THE NESTING SEASON OF THE AMERICAN ROBIN (*TURDUS MIGRATORIUS*) IN THE UNITED STATES

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Populations of birds that breed in temperate climates adapt their breeding schedules to variations in the progression of the spring from year to year at one locality and also across climatic gradients in a broad geographic area. Since predictable relationships have been demonstrated between a mean daily temperature and the beginning of the period of egg-laying independently of the date (see Nice 1937 and Erskine 1971 for examples), it is possible that both annual and geographic variation in the initiation of the reproductive period are attributable to the fact that members of a given species begin nesting when the local climate reaches a certain mean daily temperature. To examine this hypothesis more thoroughly, we have compared the general trends of annual periodicity in climate in the United States with periodic reproduction in American Robins (*Turdus migratorius*). This involved analysis of records of 8544 nests. These data have been compiled since 1963 from information submitted by volunteer contributors to the Cornell Laboratory of Ornithology Nest-record Card Program and were made available to us through the kindness of David B. Peakall, Director. Quantitative data for factors that are obviously important to robins, such as the presence of mud for nest construction and the presence of soil invertebrates for food, are not available. If these in turn are a function of phenology, then a study of the climate-nesting season relationship is an indirect but valid approach.

We give the geographic pattern of the dates on which robins generally begin feeding nestlings. Then we give a three-dimensional presentation of the results of a principal component analysis of the environmental conditions at those times. Finally, the problem is reduced to a model demonstrating how a combination of climatic conditions can be used to predict when robins will nest. The model is also useful for generating hypotheses regarding the limits of the breeding range. This analysis is presented as an alternative or supplementary approach to the synecological one in which the distribution and behavior of a species are viewed as attributable to competition with coexisting species for the resources of the locality under consideration.

METHODS

Lack (1950) suggests that the most critical period of the nesting cycle is when adults are feeding nestlings, so we used data for only those nests that contained young. These were organized geographically into 51 two-degree latitude and longitude blocks, for which there was a minimum of 20 nests per block. To obtain a statistic that would represent the date on which robins generally begin feeding young in the nest we determined, for each block, the shortest continuous period that contained 90% of the nests with young (table 1). This is the period when the local environment puts a minimum of physiological stress on the adults and there is a maximum probability for the survival of parents and young (Immelman 1971). The day representing the beginning of this period was used in the subsequent analysis, and will be called "the beginning of the nestling period."

The IBM Stampede package contains functions that accept data for three coordinates. Surfaces are fitted and represented on annotated computer-generated contour maps. These techniques are useful in mapping (fig. 1) and in the display of continuously varying phenomena (fig. 3). In the first instance, the first two coordinates are latitude and longitude and the third is the data on the beginning of the nestling period. In this case an additional program was required to transform the latitude and longitude grid to fit a polyconic projection so that later it could be overlain on a map of the United States having the same projection. The contours were determined by continuous interpolations among points within a 5–6-degree scan.

ANALYSIS

GEOGRAPHIC PATTERN OF THE NESTLING PERIOD

Robins nest throughout most of the United States and Canada and into the mountains of México (A.O.U. Check-list 1957). Figure 1

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The Condor 76:159–168, 1974

TABLE 1. Summary of 8544 robin nests with young; organized into two-degree latitude and longitude blocks. Blocks are listed by tiers moving from east to west within a tier and with the northernmost tier as the initial entry.

Code no.	Center of block Lat.–Long.	City nearest center of block	No. of nests	Period containing 90% of nests with young			Mean noon dry-bulb temperature at beginning of period (°F)
				Begin (mo/day)	Length (days)	End (mo/day)	
1	49–119	Grand Coulee, Wash.	43	5/4	66	7/8	62.3
2	45–73	Burlington, Vt.	58	5/17	36	6/21	56.5
3	45–85	Mackinaw City, Mich.	187	5/28	57	7/23	58.6
4	45–87	Monominee, Wisc.	42	6/7	47	7/23	65.0
5	45–89	Rhinelander, Wisc.	126	5/6	59	7/3	54.1
6	45–91	Eau Claire, Wisc.	80	5/14	66	7/18	62.6
7	45–93	Minneapolis, Minn.	109	5/11	51	6/30	60.7
8	45–95	Willmar, Minn.	21	5/20	39	6/27	64.5
9	45–103	Rapid City, S.D.	75	5/25	51	7/14	67.5
10	45–109	Billings, Mont.	22	5/18	27	6/13	65.8
11	45–111	Bozeman, Mont.	27	5/25	68	7/31	68.0
12	43–71	Portsmouth, N.H.	1161	5/8	51	6/27	56.8
13	43–73	Bennington, Vt.	289	5/9	64	7/11	58.4
14	43–75	Utica, N.Y.	183	5/8	64	7/10	57.6
15	43–77	Geneva, N.Y.	493	5/7	76	7/21	54.8
16	43–79	Niagara Falls, N.Y.	243	5/5	70	7/13	51.0
17	43–83	Detroit, Mich.	160	4/30	71	7/9	55.3
18	43–85	Grand Rapids, Mich.	317	5/8	84	7/30	59.0
19	43–87	Milwaukee, Wisc.	151	5/10	68	7/16	55.5
20	43–89	Madison, Wisc.	815	5/4	66	7/8	53.6
21	41–71	Newport, R.I.	363	5/10	44	6/22	58.9
22	41–73	Bridgeport, Conn.	300	5/11	58	7/7	59.6
23	41–75	Easton, Penna.	437	5/7	60	7/5	59.0
24	41–77	Williamsport, Penna.	69	4/24	54	6/16	55.7
25	41–79	Pittsburgh, Penna.	134	5/5	59	7/2	60.8
26	41–81	Akron, Ohio	147	4/28	60	6/26	52.0
27	41–83	Findlay, Ohio	60	4/30	76	7/14	58.9
28	41–85	Fort Wayne, Ind.	90	5/4	45	6/17	58.8
29	41–87	Gary, Ind.	126	5/6	71	7/15	61.9
30	41–89	Peoria, Ill.	180	5/2	118	8/27	63.7
31	41–93	Ottumwa, Iowa	54	4/30	59	6/27	62.6
32	41–95	Omaha, Nebr.	20	5/9	34	6/11	66.4
33	41–97	Lincoln, Nebr.	206	5/5	81	7/24	66.6
34	41–99	Grand Island, Nebr.	45	5/15	60	7/13	69.1
35	39–75	Cape May, N.J.	173	5/3	79	7/20	56.7
36	39–77	Washington, D.C.	669	5/1	68	7/7	62.8
37	39–79	Front Royal, Va.	65	5/9	43	6/20	65.4
38	39–81	Parkersburg, W. Va.	39	5/2	66	7/6	64.3
39	39–85	Madison, Ind.	112	4/28	50	6/16	63.1
40	39–87	Terre Haute, Ind.	114	5/2	65	7/5	62.5
41	39–89	Effingham, Ill.	41	5/11	25	6/4	68.4
42	39–91	St. Louis, Mo.	89	5/2	77	7/17	67.2
43	39–95	Kansas City, Mo.	26	4/24	28	5/21	64.1
44	39–105	Colorado Springs, Colo.	68	6/2	52	7/23	70.6
45	39–121	Sacramento, Calif.	26	5/5	59	7/2	70.0
46	37–81	Bluefield, Va.	34	5/4	53	6/25	67.6
47	37–87	Bowling Green, Ky.	149	4/16	108	8/1	63.2
48	37–89	Cairo, Ill.	33	4/27	33	5/29	66.5
49	37–95	Joplin, Mo.	25	4/25	91	7/24	65.2
50	37–97	Wichita, Kan.	22	5/3	69	7/10	69.9
51	35–107	Albuquerque, N.M.	27	5/9	58	7/5	68.4

is a computer-generated map giving isolines for the dates of the beginning of the nestling period. This date occurs in the last 10 days of April in the southeastern extremity of the breeding range and shows a delay northward so that robins in New England begin having young in the nest in mid-May. There is an interesting dip in the contour lines around the Great Lakes, indicating that the breeding season of robins is delayed by the effects of the lakes upon the climate over a broad geographic area. Robins tend to nest later in the western states than in the east, but records from a few localities in California (not included in the analysis) suggest that the birds probably nest at approximately the same time along both

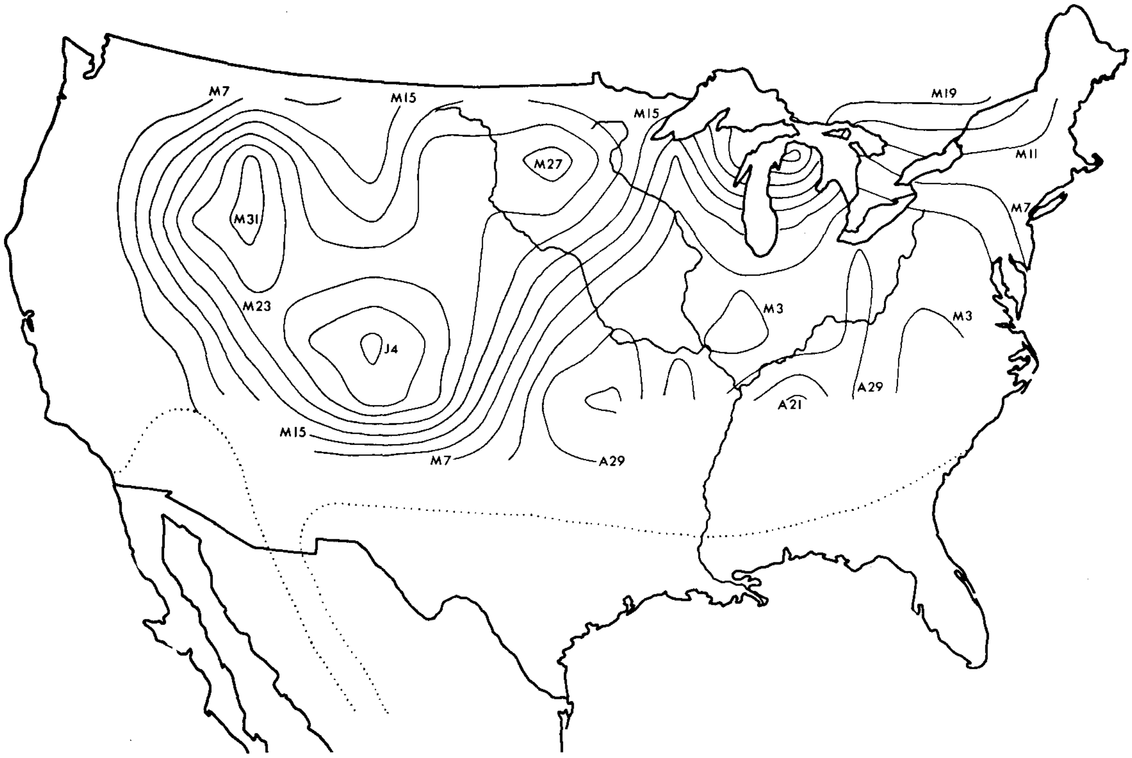

FIGURE 1. A computer-generated contour map giving isolines for dates of the beginning of the period when robins have young in the nest. A, April; M, May; J, June. The dotted line is the southern limit of the breeding range.

the Pacific and the Atlantic coasts. The two westernmost peaks of late dates correspond to the delayed nesting season of robins in the Rocky Mountains.

An examination of the length of the nestling period (table 1) reveals that, in general, it is greatest in the eastern and central states (80 days), shortest in the western mountains (50 days), and intermediate in New England (60 days). For a block centered on latitude 65° N and longitude 149° W, including Fairbanks, Alaska (but not included in this analysis) the length of the period is 27 days beginning 30 May.

RELATIONSHIP WITH TEMPERATURE GRADIENTS

In order to find how the pattern of the advance of the breeding season across the country is related to temperature, values for April and July mean noon dry-bulb temperatures were plotted on a map and linear interpolations were made to the centers of each of the 51 blocks. A second interpolation from the April and July values gave the mean daily temperature of the beginning of the nestling period for each block (table 1). If the beginning of the breeding season is correlated with a certain mean daily temperature, then the temperatures in table 1 would be expected to be very similar. But this is not the case. There is a 20°F (11°C) spread in the values and the standard deviation is intermediate between that for April and July (standard deviation from mean noon dry-bulb temperature: April, SD = 5.7; July, SD = 4.4; when the nestling period begins, SD = 5.1). In the eastern half of the United States, robins initiate the nesting season at successively cooler mean daily temperatures as the season progresses northward. The values for southern localities are mostly between 60 and 65°F (16 and 18°C), whereas the temperature for the northeastern states and the Great Lakes region are between 55 and 60°F (13 and 16°C). The mean daily temperatures at the time that robins begin feeding nestlings are highest in the western states. Thus the relationship between the initiation of the reproductive period by robins and the progression of temperatures in spring is not direct, and it is necessary to consider additional variables in order to find a predictive model for relating the breeding season to climate.

PRINCIPAL COMPONENT ANALYSIS

The procedure described above for determining the mean daily temperature at the be-

TABLE 2. Summary of 51 environmental situations under which robins begin feeding young.[a]

Variable	Units	Max.	Min.	Mean	Standard deviation	Coefficient of variation	Correlations with principal components			
							I	II	III	IV
Noon Dry-bulb Temperature	°F	70.6	51.0	61.9	5.1	8.2	0.88	0.31	−0.12	−0.28
Noon Wet-bulb Temperature	°F	58.1	45.0	51.0	3.0	5.9	0.64	0.74	−0.06	−0.15
Sunshine	hrs/30 days	334	198	254	25.7	10.1	0.86	−0.19	0.25	−0.06
Solar Radiation	langleys/day	613	327	447	50.5	11.3	0.81	0.03	0.19	0.49
Wind	mph	16.0	6.2	10.0	2.3	22.7	−0.45	0.32	0.81	−0.13
Precipitation	inches/30 days	4.3	1.2	3.0	0.70	23.6	−0.48	0.74	−0.29	0.09
Absolute Humidity	gr/ft^3	4.1	2.0	3.2	0.46	14.6	−0.13	0.89	0.08	0.17

[a] Sources of environmental data were Albright (1939), U.S. Department of Commerce (1965), Air Ministry Meteorological Office (1958) and Torok (1935).

ginning of the nestling period was repeated for the six additional environmental variables (table 2), including the maximal and minimal values for the seven environmental variables for the beginning of the nestling period within each of the 51 geographic blocks listed in table 1. Since the breeding range of the robin extends farther north than the areas considered, the minimal temperatures and maximal hours of sunshine per 30 days do not represent limiting factors. Robins in Canada and Alaska nest at lower temperatures and longer daylengths than robins in the United States. In fact, they nest northward to the treeline, so habitat requirements probably limit their breeding range in these areas.

The correlation matrix of the values of the seven climatic variables on the dates of the beginning of the nestling period was subjected to a principal component analysis. This procedure derives axes through the hypothetical seven-dimensional space, expressing variables that show covariation as single components. The new compound variables (components) can be defined by examining their correlations with the original variables (table 2), and the percentage of the total variance in the original data set that can be accounted for by the components is known. The environmental variables comprising each of the first four components are identified in table 3; the percentage of the variance accounted for by each is also shown. In the present case, Component I, accounting for 43.3% of the variance, is highly correlated with dry-bulb temperature, hours of sunshine, and solar radiation; Component II, accounting for an additional 30.3% of the variance, is highly correlated with absolute humidity, wet-bulb temperature, and precipitation; Component III, accounting for an additional 12.2% of the variance, is correlated with wind; and Component IV, accounting for 5.8% of the variance, represents an interaction between solar radiation and dry-bulb temperature. By means of these four components, it has been possible to account for 91.6% of the variance in the original seven-dimensional space.

A second advantage of this technique is that the derived components are orthogonal to one another and can be expressed graphically as axes on a plot. In figure 2 the first three components are used as axes and the fourth is expressed as the height of the triangles. Thus, this figure is a graphic representation of the varying combinations of climatic conditions under which robins begin feeding young. Numbers refer to the location of the blocks and are identified in table 1. The

TABLE 3. Identification of the principal components used as axes in figure 2 from the correlations in table 2 for the varying environmental conditions under which robins begin feeding young at different geographic localities.

Component	Identification	% Variance accounted for	Cumulative % variance accounted for
I	Dry-bulb Temperature, Hours of Sunshine Solar Radiation	43.3	43.3
II	Absolute Humidity, Wet-bulb Temperature, Precipitation	30.3	73.6
III	Wind	12.2	85.8
IV	Interaction between Solar Radiation and Dry-bulb Temperature	5.8	91.6

perspective of the plot (e.g., looking down on the plot, looking at the plot from the right) was determined by projecting different views on an IBM 2250 Display Unit. When a perspective was determined that displayed the data most clearly, a hard copy was made on a Calcomp Plotter. Figure 2 is a tracing of 37 of the 51 triangles on the plot. The remaining 14 were omitted because they overlapped other triangles and represented only redundancy among adjacent geographic blocks.

It is important to remember that the pattern in figure 1 has been disregarded in the principal component analysis, which considers the climate at the time of the beginning of feeding young independently of the date. Component I, labeled "Dry-bulb Temperature," increases from right to left. By mentally projecting the bases of the lines to it, one can confirm that robins begin feeding young at relatively low temperatures in the northeast (15, Geneva, N.Y.; 16, Niagara Falls, N.Y.; 26, Akron, Ohio) and relatively high temperatures in the west (11, Bozeman, Mont.; 44, Colorado Springs,

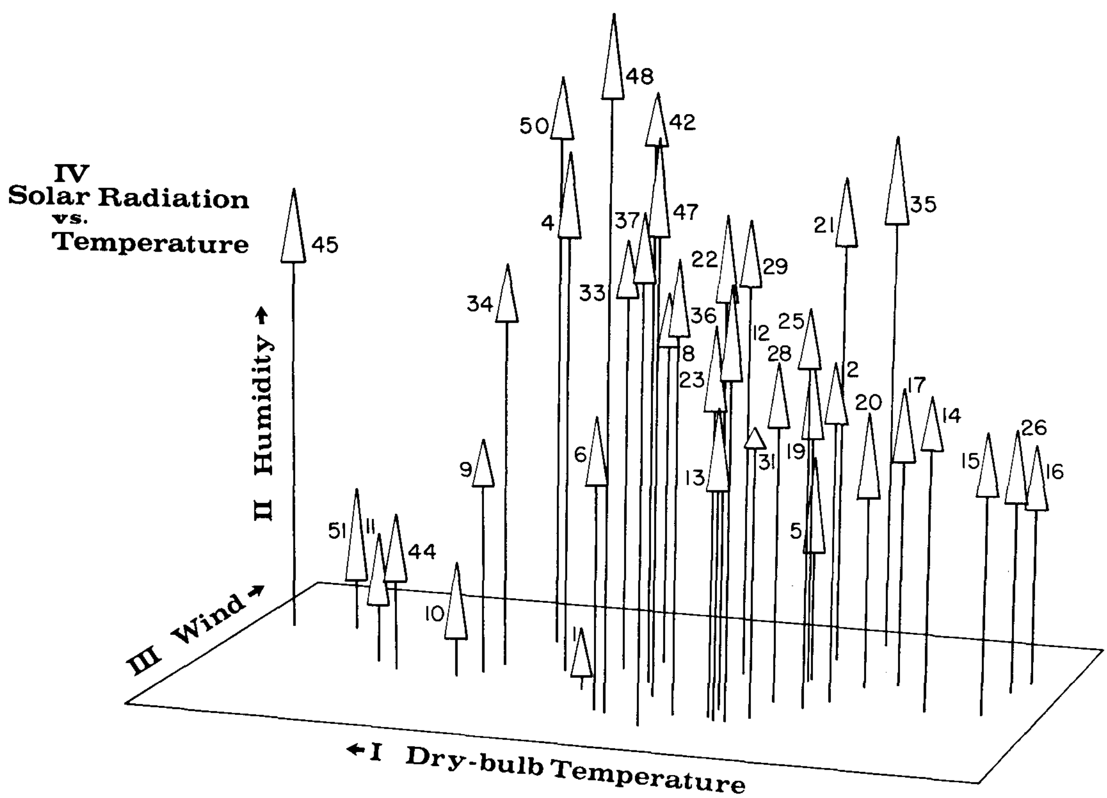

FIGURE 2. Results of a principal component analysis of the varying climatic situations under which robins begin feeding young. Data were obtained by extrapolating values for seven climatic variables (table 2) to the dates on which robins begin feeding young. Numbers refer to the geographic blocks identified in table 1. The axes are the first three principal components of the variation in climate; the fourth component is represented by the height of the triangle.

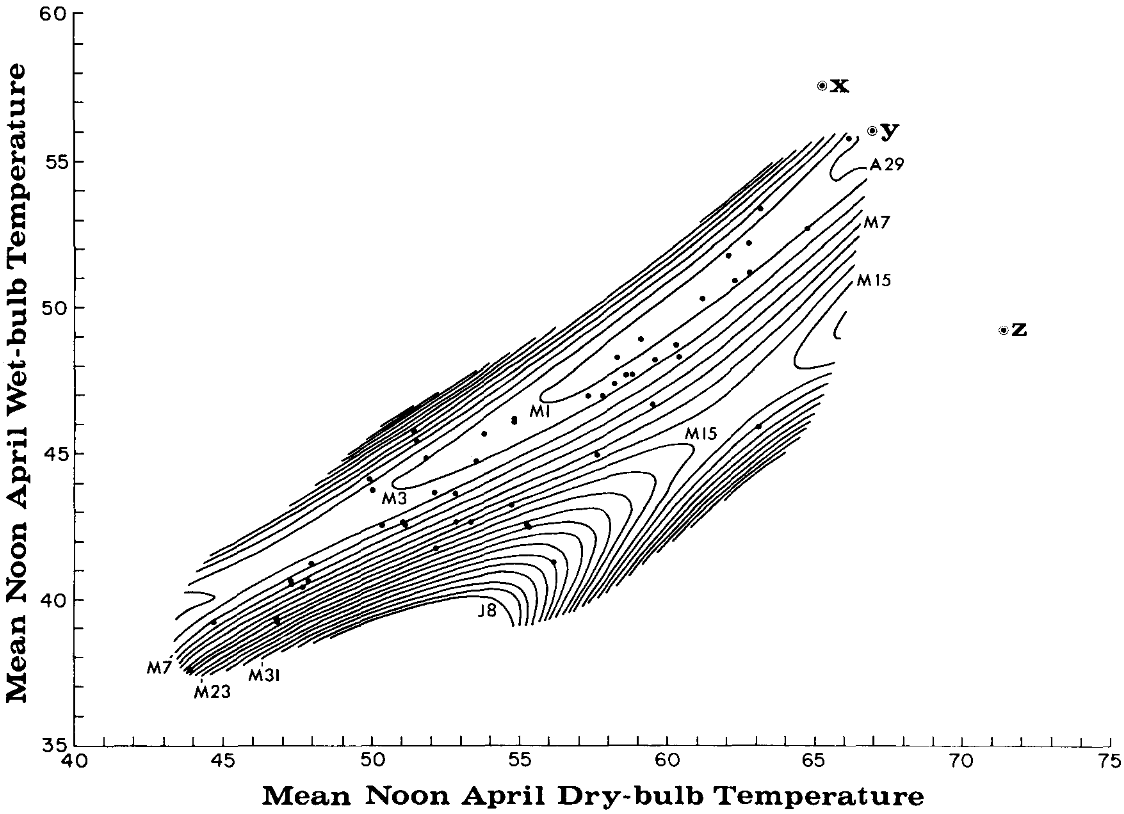

FIGURE 3. A computer-generated contour graph made by a third-degree polynomial fit of the dates on which robins begin feeding young to April dry-bulb and wet-bulb temperatures (°F) for 51 geographic blocks in the United States. The letters *X* and *Y* refer to blocks in the Southwest, beyond the normal breeding range of the species: *X*, Lat. 33, Long. 117 includes San Diego, California; *Z*, Lat. 31, Long. 107 includes El Paso, Texas. The letter *Y* refers to a block including Atlanta, Georgia, at the southeastern limit of the breeding range.

Colo.; 45, Sacramento, Calif.; 51, Albuquerque, N.M.). Component II, labeled "Humidity," increases from the bottom to the top of the figure so that the length of the line supporting the triangles expresses the amount of moisture in the air (absolute humidity) and other correlated variables (wet-bulb temperature and precipitation). Both the longest and the shortest vertical lines are near the center of the dry-bulb temperature gradient (48, Cairo, Ill.; 1, Grand Coulee, Wash.). Since warm air can hold more moisture than cool air, the pattern becomes cool-dry (even though the air may be saturated) in the northeast in the right side of the plot, warm-moist in the central southern region at the top center of the plot, and hot-very dry in the west at the lower left section of the plot. It is unfortunate that there are not more blocks for the western half of the country so that the pattern there could be examined in more detail. The distribution of the triangles along the first two axes accounts for 73.6% of the variance in the data and an additional 12.2% is attributable to Component III ("Wind"), which increases from front to back of the figure. Along this axis the highest values are for coastal localities (21, Newport, R.I.; 35, Cape May, N.J.) showing only that coasts are windy. We refrain from trying to interpret how this affects robins. The fact that blocks in the Great Plains (31, Ottumwa, Iowa; 33, Lincoln, Nebr.) have low values of Component IV (Solar Radiation vs. Temperature), expressed as the height of the triangles, means that the amount of radiation an area receives affects the climate independently of the covariation of solar radiation and temperature, and this effect is extreme in the Great Plains.

SEASONALITY MODEL

The next question is whether or not a combination of climatic variables can be used to predict the seasonality of the reproductive period in robins. If so, it might also be possible to discover whether climatic constraints and their ecological correlates limit the breeding range.

Correlations between the beginning of the nestling period and April values of the environmental factors are highest for April precipitation and April wet-bulb temperature ($r = -0.56$, df $= 49$, $\alpha = 0.05$). This means that within their breeding range robins nest earlier in areas that are both moist and warm in April.

A step-down multiple regression analysis with the beginning of the nestling period as the criterion variable, and April and July values of *all* of the environmental variables (table 2) as the predictor variables, indicates that something more than simple linear relationships are involved. When powers and products of the predictor variables were added as additional predictor variables, the remarkable result was that only functions of April dry-bulb and April wet-bulb temperature were retained by the step-down procedure. For example, April dry-bulb temperature times April wet-bulb temperature and either April dry-bulb temperature or April wet-bulb temperature were always retained regardless of the remaining variables in the predictor set. Hence, we felt justified in constructing a computer-generated contour map (fig. 3) representing the criterion variable only as a function of April dry-bulb and wet-bulb temperature. The contoured area represents a climate-space acceptable to robins and they respond in a predictable way within it. Moving along any particular contour line represents interchangeability of dry-bulb and wet-bulb temperature, while retaining the date at which feeding starts. Or, considering a fixed dry-bulb temperature, the date changes with wet-bulb temperature.

Robins at localities having a mean noon April dry-bulb temperature between 45° and 65°F begin feeding young in late April or early May, providing that the relative humidity is about 50%. If the relative humidity is either higher or lower than 50%, robins nest later. An extreme of this latter condition is shown at the base of the map (fig. 3) where wet-bulb temperatures are depressed by the dry air of the western localities and the birds do not begin feeding young until late in May or early June.

Figure 3 can be used (1) to predict when robins will begin feeding young in areas not considered in the analysis; (2) to predict new areas of range expansion; and (3) to explain the limits of the breeding range. The letters *X* and *Z* are temperature values for two places beyond the regular breeding range. They fall beyond the contoured climate space. The value *X* is for lat. 32°, long. 117°, which includes San Diego, California. Here the April wet-bulb temperature is too high for robins. The value Z is for lat. 31°, long. 107°, which includes El Paso, Texas. Here the April dry-bulb temperature is too high for robins. The value Y is for lat. 33°, long. 85°, which includes Atlanta, Georgia. This is at the southeastern border of the breeding range and robins have been expanding their range in this direction for several decades (Greene et al. 1945). The figure would have included lower temperatures if data from Canada and Alaska had been available.

DISCUSSION

An important consideration with respect to robins is the extent to which the breeding range is affected by the influence of man. Before towns were established by colonists, robins must have been restricted to natural areas having moist short grass for foraging and usually a medium-sized tree for a nest site. Since the nest is always held together with mud, there must be saturated soil within the territory at the time of nest-building. Robins probably nested mainly in woodland openings and wooded streamsides from the mountains of México to the treeline of the Appalachians and Rocky Mountains, and to the tundra of Canada and Alaska, but they must have been excluded by their habitat requirements from the southwestern deserts, the central prairies, and the denser parts of the eastern deciduous forest (Bent 1947). With the establishment of colonial towns near natural habitat, the birds accepted shade trees and even buildings for nest sites and lawns for foraging areas. As this situation continued, man has provided habitat for robins beyond their original breeding range. Within the past 20 years, robins have nested in certain parks, cemeteries, and older residential sections of towns as far south of the dotted line in figure 1 as San Antonio, Texas (Peterson 1960) and New Orleans, Louisiana (Lowery 1955). What appears to be a case of species adapting to new situations is actually a case of man creating suitable microenvironments and microhabitats for birds in new localities.

For the broadly uniform area of the eastern United States, there is generally a 3-day retardation of the breeding season of robins per degree of increasing latitude. This is consistent with data for the Starling (*Sturnus vulgaris*) in the same area (Kessel 1953), the Song Sparrow (*Melospiza melodia*) in west coastal North America (Johnston 1954), and for other species in Europe (Baker 1938). Since daylength varies with latitude, and recrudescence of gonads in male birds can be altered by experimentally varied photoperiods (see Immelman 1971, for recent review), the hypothesis that birds breeding in temperate regions use daylength as a proximate cue for periodic reproduction is initially attractive. However, in the case of robins, there are two serious disadvantages. First, the pattern of the progression of the breeding season across the continent as a whole is not highly correlated with latitude (fig. 1). In fact, robins in Colorado Springs, Colorado, at 39°N nest at the same time as robins in Fairbanks, Alaska, at 65°N. It is possible to avoid this difficulty by postulating that daylength affects breeding populations differentially. A second problem with assigning daylength a primary *zeitgeber* role for the timing of the breeding season in robins is that although adults return to the same breeding localities in successive years (Howell 1942; Roberts 1932), they wander across wide areas on the wintering grounds according to the severity of the weather and the availability of food (Speirs 1953). Wintering populations in Arkansas include birds that breed locally and birds that breed in Canada (James 1968). Since robins breeding in a given area disperse in winter throughout the southern United States and thus are subjected to different daylengths, and since wintering robins in a given area are drawn from very different breeding populations, it is difficult to assign control of the initiation of the nesting cycle to photoperiod alone. It seems more likely that photoperiod affects the reproductive readiness of robins and that other factors determine the initiation of the nesting cycle.

There is both field and experimental evidence that mean daily temperature affects the development of the reproductive organs in addition to the effects of daylength (Marshall 1949; Farner and Mewaldt 1952; Farner and Wilson 1957; Engels and Jenner 1956). Perhaps for each species there is an optimal daily temperature for the initiation of the nesting cycle. This hypothesis could account for the delayed nesting at higher altitudes, for annual variation at single localities, and even for instances of "unseasonal" nesting (Snow 1955; and others). The correlation between the date of the beginning of the nestling period and mean noon April dry-bulb temperature is significant ($r = -0.37$, $df = 49$, $P > 0.95$), but the results of this study show that a model that includes other environmental variables has more predictive power. Specifically, if dry-bulb temperature and wet-bulb temperatures are both known, it is possible to use the graphic model (fig. 3) to predict not only at what date robins will nest but also whether a given area is outside the potential breeding range. We assume that robins select the optimal combination of environmental conditions that permit a high probability of survival of parents and young. Since daylength, temperature, humidity, and aspects of the vegetation tend to vary concordantly in the spring, it is not possible to tell what proximal cues the birds use to begin the nesting cycle. All that is known is that if they use climate, they must use an integrated combination of factors because no one factor has a higher predictive power than a combination.

In addition to the suitability of the climate and correlated factors such as aspects of the vegetation, daylength, and availability of food for the young (Lack 1950), two other factors should be mentioned as potentially affecting the breeding season and the breeding range. MacArthur (1972) suggested that the southern limit of the range of the robin is determined by competition with other species of *Turdus* in México. He does not discuss how this competition operates or why robins are absent from Florida and south Texas, where no members of the genus are known to nest. Morton (1971) gives an example of a case in which predation may be more important than food availability in determining the reproductive period of the Clay-colored Robin (*Turdus grayi*). In spite of the complexity of factors potentially involved in any analysis of periodic reproduction, we believe that the inclusion of an examination of the responses to climatic gradients is a useful approach.

It would be impossible to obtain data such as that used here without a nationwide cooperative effort combined with a computerized data bank such as the Cornell Laboratory of Ornithology Nest-record Card Program. Peakall (1970) cautions that the data may be biased by the geographical distribution of observers, their enthusiasm, and variations in their expertise in the field. Nevertheless, the records constitute the only massive source of data on the nesting of birds in the conterminous United States. For other examples of studies based on data from this program see Peakall (1970) on the Eastern Bluebird (*Sialia sialis*), Howard (1967) on the American Robin (*Turdus migratorius*) in the northeast, and Erskine (1971) on the Common Grackle (*Quisculus quiscula*).

SUMMARY

By means of seasonality modeling, we have interpreted geographic variation in the beginning of the reproductive period of the robin in the United States as a complex response to climatic gradients in time and space. This in

turn must be related to proximate factors such as the phenological development of the vegetation, the availability of mud for nest construction, and food for nestlings. This approach ignores the possibility that the limits of the breeding range and the timing of the reproductive period are constrained by factors such as predation or competition with other species. It is presented as an alternate or supplementary method of defining some of the dimensions of that exclusive hyperspace called the "realized ecological niche." The next step in the logical development of this approach would be to design a study to quantify the extent to which the pattern described here is a function of community organization.

The analysis is based upon a data set of 8544 nests made available by the Cornell Laboartory of Ornithology Nest-record Card Program. A computer-generated map gives contoured lines for the dates of the beginning of the nestling period. In the eastern states there is a 3-day retardation of the breeding season per degree of increasing latitude. Robins nest at progressively cooler temperatures as spring progresses northward. In the western states where nesting is delayed, robins begin nesting at the highest mean daily temperatures. Although local temperatures and the beginning of the nestling period are significantly correlated, this study shows that by considering additional climatic variables and reducing the relationships to graphic form, the response of the breeding population across a wide geographic area can be described more precisely. A three-dimensional graph having axes determined by the principal components of seven climatic variables permits simultaneous comparisons of the various climatic conditions when robins begin the nestling period, independently of the date. The results of a step-down multiple regression analysis indicate that a combination of April dry-bulb and wet-bulb temperatures is the best predictor of the beginning of the nestling period. If the mean noon relative humidity is near 50% in April, the beginning of the nestling period will be in late April or early May, regardless of the dry-bulb temperature; if the mean noon relative humidity is either higher or lower than 50% in April, the beginning of the nestling period will be later. A graphic model of the climate space within which this response occurs, made by fitting a third degree polynomial surface of dates to a grid of April dry-bulb and wet-bulb temperatures, permits analysis of the limits of the breeding range and predictions about the probabilities of range expansion.

ACKNOWLEDGMENTS

We are very grateful to Allen W. Baker and James E. Dunn for assistance with analysis and to Linda P. Murphy for final drafting of the figures. This research was supported in part by the Eastern Deciduous Forest Biome, US/IBP, funded by the National Science Foundation under Interagency Agreement AG-100, 40-193-69 with the Atomic Energy Commission-Oak Ridge National Laboratory.

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Accepted for publication 16 March 1973.