BIRD STRIKE COMMITTEE EUROPE BSCE23/ WP52
London, 13-17 May 1996

USING GEOGRAPHIC INFORMATION SYSTEMS TO MODEL BIRD DISTRIBUTIONS AND POPULATIONS ON A CONTINENTAL SCALE

Russell P. DeFusco
Major, United States Air Force
Department of Biology
Unites States Air Force Academy, Colorado 80840
USA

SUMMARY

The objectives of this study were to use physiographic, geographic, and climatic correlates to describe the breeding and wintering distribution and abundance patterns of Turkey Vultures (*Cathartes aura*) in the continental United States and model the hazards posed to aircraft by these birds. Thirty years of data were correlated with remotely sensed and ground sampled environmental data in a raster-based geographic information system (GIS). Environmental factors evaluated include elevation, hydrography, thermal reflectance, temperature, precipitation, snow cover, number of frost-free days, vegetation types, and ecoregions, for each 1 Km^2 block of the continental United States. A GIS overlay process was used to determine statistical relationships between environmental factors and sampled vulture data. Vulture numbers were most strongly correlated with geophysical factors throughout their range and between seasons. Breeding vultures were most strongly positively correlated with heterogeneous and more open physiographic habitats. Wintering vultures were more strongly correlated with forested areas, presumably for thermal roosting cover. These techniques have helped better determine Turkey Vulture habitat requirements on a scale never before attempted, and can be used for other species in the future. Modeling techniques can be used to identify specific areas where birds pose potential hazards to aviation.

Key Words: Bird Populations, Radar, Migration, Avoidance, Local Movements, Electronic

USING GEOGRAPHIC INFORMATION SYSTEMS TO MODEL BIRD DISTRIBUTIONS AND POPULATIONS ON A CONTINENTAL SCALE

INTRODUCTION:

1. U.S. AIR FORCE INTEREST IN BIRD DISTRIBUTIONS:

Initiation of this project was prompted by a United States Air Force (USAF) need to avoid bird collisions with its aircraft. Each of the US military services suffers from these problems and every aircraft type from helicopters to fighters are vulnerable to bird strikes. Military aircraft are particularly vulnerable to bird strikes, as they routinely operate at low altitudes and high speeds. The USAF reports around 3,200 bird strikes each year (Merritt and Dogan 1992). These incidents have caused the loss of numerous jet aircraft, many with resultant fatalities, and have cost the Air Force an average of over 65 million dollars per year (DeFusco and Turner 1986, Thompson et al. 1986, DeFusco 1988, DeFusco et al. 1989, Merritt 1990, Merritt and Dogan 1992). Other services report similar bird strike rates. Bird strikes occur during all phases of flight, but are most likely to result in catastrophic accidents during low-level missions and on training ranges. Aircraft frequently operate in remote locations at altitudes from 100 to 300 meters above ground level, and from 350 to 600 knots indicated airspeed. Unlike in the airfield environment where birds may be dispersed, there is no way to control birds in the low-level environment. Aircrews are dependent upon information on bird distributions to avoid potentially hazardous areas. The USAF is upgrading its computerized Bird Avoidance Model (BAM) to provide this information to all Department of Defense agencies. The model must provide localized data on bird distributions and abundance throughout the continental United States (CONUS). This study was designed, in part, to provide information about vultures for inclusion in the upgraded Bird Avoidance Model.

The variety of birds struck by aircraft numbers in the hundreds, but several orders of birds pose the most serious hazards. Notable among these are the raptors (Falconiformes). In the United States, the species causing the single greatest hazard is the Turkey Vulture (*Cathartes aura*). This is due to a number of factors including its large body mass (over 2 kilograms), widespread distribution, and flight behaviors. Turkey Vultures usually make foraging and migratory flights at the same altitudes as military flight operations. Compounding this problem is the fact that vultures rarely take evasive action to avoid collisions. Adult vultures have no known airborne predators and certainly have not evolved to deal with the closure rates associated with aircraft encounters. Consequently, Turkey Vultures have been involved in over 200 collisions that cost the Air Force over 30 million dollars, 4 crashed aircraft, and 3 fatalities since 1989. Due to the significant hazard this bird poses to flight safety, the Turkey Vulture was chosen as a priority species to begin the modeling process. Funding for this project was provided by the U.S. Congress through the Department of Defense Legacy Resource Management Program. Funding for presentation of these results to the Bird Strike Committee Europe was provided by the Army Environmental Policy Institute through the USAF Institute for National Security Studies.

2. BIOGEOGRAPHY - SPECIES DISTRIBUTION AND ABUNDANCE PATTERNS:

Modeling Turkey Vulture distributions for bird strike avoidance must begin within the broader context of their biogeography. Understanding the forces shaping the present day distribution and abundance of a species demands an examination of their ecological and physiological requirements and constraints. The entire field of biogeography is dedicated to deciphering such patterns in an evolutionary and historical context.

Traditional biogeographical studies concentrate largely on the presence or absence of species within a defined region. These studies place a great deal of emphasis on the ranges of the organisms under study, with particular attention paid to the factors that limit these ranges. Species' ranges may be shaped by biotic interactions of competitors, predators, prey, parasites, or disease (Bartholomew 1958, MacArthur 1958, Sturkie 1965, Terborgh and Weske 1975, Brown and Gibson 1983). While biotic interactions may influence the proximate details of range boundaries, physical tolerances to abiotic factors may ultimately determine a species' range (Wardle 1981, Hayworth and Weathers 1984, Root 1988b). External abiotic environmental factors, such as physical barriers to expansion, temperature extremes, availability of water or other resources, may be the primary forces shaping species' biogeographic ranges (Andrewartha and Birch 1954, Udvardy 1969, Krebs 1985). For example, Root (1988b, 1989) argued that many winter bird distributions are limited by cold temperatures that prevent physiological tolerance beyond 2.4 times their basal metabolic rate (but see Castro 1989). Such traditional approaches focus on the two-dimensional ranges of species and often ignore the critical third dimension of species abundance patterns within their ranges (Udvardy 1969, Bock and Root 1981b, Brown and Gibson 1983). This third dimension may reveal much more of what is important to a population of organisms than the limits imposed at the extremes of their range.

Analysis of regional abundance patterns on a continental scale requires an enormous amount of data before coherent patterns are revealed. Fortunately, such databases exist in the form of the National Audubon Society's Christmas Bird Count (CBC) and the National Biological Survey's Breeding Bird Survey (BBS), each of which potentially can be used to describe bird species abundance patterns across North America. This study correlated these extensive databases with physiographic, climatic, and geographic variables, in an attempt to describe and interpret the breeding and wintering distribution and abundance patterns of Turkey Vultures in the continental United States.

2.1. The Christmas Bird Count:

Christmas Bird Counts are conducted over a 24-hour period during the two weeks surrounding Christmas day each year. Many thousands of volunteers participate in these annual counts and several million hours of observation have been recorded since counts began in 1900 (Bock and Root 1981b, Root 1988a). Observers record the center point of each established count circle by degrees and minutes of latitude and longitude. Participants are allowed to conduct surveys anywhere within a 12.1 kilometer radius of the center point. Parties of individuals may split up to simultaneously cover different parts of the count circle during the survey period. The total number of party hours are recorded in addition to the total number of each species observed during the survey. CBC results are reported in this study as the number of birds observed per party hour, per count circle, per year, to standardize results of counts with differing effort levels. Root (1988a) includes a more detailed description of CBC methodology and its history in the introduction to her book. Data are compiled by state and entered into a national database maintained by the National Biological Survey in Laurel, Maryland. Computerized data are available for each year from 1960 to present. All available data for each year through 1992 were used for this study. Figure 1 depicts the 2,026 CBC sites where at least one survey was conducted between 1960 and 1992. Turkey Vultures have been recorded at least once at 539 (26.6%) of these sites. Data range from a minimum value of 0.0 to a maximum of 3.57 vultures per party hour, per CBC circle, per year. For the purposes of this study, it was assumed that vultures were randomly distributed within any given count circle and that observers randomly or uniformly surveyed the area contained therein.

2.2. The Breeding Bird Survey:

The Breeding Bird Survey is a standardized survey conducted each year at various locations throughout the United States during the spring and early summer. The BBS was initiated in 1965 to develop a reliable index of North American bird populations (Bystrak 1981). Surveys are conducted along established routes on secondary roads in largely rural areas. The starting point of each route is recorded in degrees and minutes of latitude and longitude. The direction of the routes from the starting points are randomly selected, but repeated each year. Fifty, three minute stops are made at 0.79 kilometer intervals along each 39.4 kilometer route. Total numbers of each bird species seen or heard during stops are recorded for the route. Robbins and Van Velzen (1967) include a detailed description of BBS methodology. Data are compiled by state and entered into the national database maintained by the National Biological Survey in Laurel, Maryland. Survey results have been recorded each year from 1966 to present, and all available data from each year through 1992 were included in this study. Figure 2 depicts the 2,167 BBS sites where at least one survey has been conducted during the inclusive period for data analyzed in this study. Turkey Vultures have been recorded at least once at 1,589 (73.3%) of these sites. Data range from a minimum value of 0.0 to a maximum of 49.4 vultures per route, per year.

3. SUITABILITY OF CBC AND BBS DATA:

Much has been written about the use of Christmas Bird Counts and Breeding Bird Surveys to determine trends in population and geographic abundance patterns of various bird species (see Robbins and Van Velzen 1967, Tramer 1974, Bock and Lepthien 1975a,b,c, 1976; Lepthien and Bock 1976, Bock 1980, 1982; Arbib 1981, Bock and Root 1981a,b; Bystrak 1981, Drennan 1981, Faanes and Bystrak 1981, Geissler and Noon 1981, Robbins et al. 1986, Root 1988a, Pattee and Wilbur 1989, Butcher et al. 1990). There are potential problems with such survey techniques. The CBC in particular is loosely organized and not standardized in its format. Data may not be reliable for some species such as rarities and highly gregarious species (Root 1988a). The BBS was organized in a standard format to overcome some of these potential problems (Robbins and Van Velzen 1967, Bystrak 1981). Even so, uncommon and secretive species may be undercounted in some surveys, particularly with the BBS. Rare

Christmas Bird Count Sites

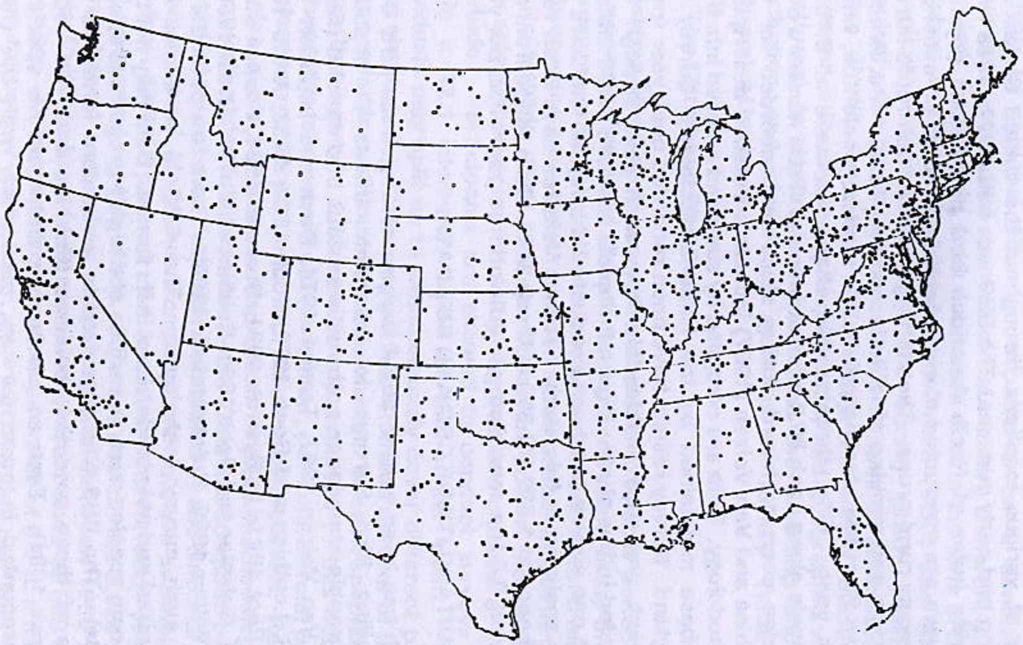

Figure 1. Locations of 2,026 Christmas Bird Counts conducted between 1960 and 1992. Surveys at these sites were used to determine winter Turkey Vulture distribution and abundance patterns in the continental United States.

Figure 2. Locations of 2,167 Breeding Bird Surveys conducted between 1965 and 1992. Surveys at these sites were used to determine summer Turkey Vulture distribution and abundance patterns in the continental United States.

species may actually be overcounted in the CBC as competition often arises between participants to record the most species in a count circle. Another criticism of the CBC is that it may occur too early in the season, when some birds are still migrating (Bock and Root 1981b). Despite such problems, most researchers conclude that these surveys, as they are long-term and large-scale, are useful for monitoring both trends in populations and distributions of most common species (Bock and Lepthien 1975a, Bock and Root 1981a, Butcher et al. 1990, O'Connor 1991). Concerns about reliability of data for common species are mitigated to a large extent by the sheer volume of available data.

Turkey Vultures are ideal for these type surveys as they are relatively common, highly conspicuous, easily identifiable, widely distributed, and therefore provide robust data sets. Analysis of previous surveys also reveal that Turkey Vulture populations are relatively stable, with little apparent changes in distribution (Brown 1976, Robbins et al. 1986, Pattee and Wilbur 1989). Variability in individual surveys due to population fluctuations, observer bias, and weather conditions is further mitigated by averaging data over a period of many years and, in the case of the CBC, by standardizing the data by party hours (Bystrak and Drennan 1975, Raynor 1975, Plaza 1978, Falk 1979, Bock and Root 1981b, Drennan 1981, Butcher et al. 1990). The size of these data sets reduces many of the concerns about non-standard statistical assumptions needed to analyze them (Drennan 1981).

METHODS:

1. GENERAL APPROACH:

This study was designed to determine if statistical relationships existed between Turkey Vulture distribution and abundance patterns and various environmental factors. It was necessarily assumed that Turkey Vultures are limited, as are all species, by a combination of external biotic and abiotic environmental factors which have led to their present day distribution patterns. Arrays of such factors were tested individually and collectively in this study. Surfaces depicting winter and summer abundances of Turkey Vultures were created using Christmas Bird Count and Breeding Bird Survey data. These surfaces were superimposed on various environmental data layers using Geographic Information System overlay procedures. Correlations were then generated between the layers to determine which variables best predicted Turkey Vulture abundance patterns.

2. CBC AND BBS DATA FORMAT AND TRANSFORMATIONS:

2.1. The Christmas Bird Count:

Christmas Bird Count data were provided by the National Biological Survey in digital format. These files were converted to American Standard Code for Information Interchange (ASCII) format and reduced to represent the coordinates of each circle with corresponding mean numbers of birds observed per party hour, per count circle, per year. These data were then entered into the Geographic Resource Analysis Support System (GRASS) Geographic Information System (GIS) by Kenneth Shepardson of Spectrum Sciences and Software, Inc., under contract with the USAF and subcontracted by the University of Colorado. GRASS is a public domain GIS software package originally developed by the U.S. Army for storage and analysis of data on land resources. The package is versatile in its ability to handle both raster and vector-based data models. Raster data models consist of numbered rows and columns of uniform cells, or picture elements (pixels), each coded with an individual value. Vector data models are points, lines, or area boundaries coded by coordinates of critical points that define an entity (see Peuquet and Marble 1990, Starr and Estes 1990, Maguire et al. 1991, Laurini and Thompson 1992).

Geographic coordinates of CBC count circles were converted into a Lambert Azimuthal Equal Area projection for conformity and spatial registration with data sets to be further described below. After overlaying CBC point data on the GIS projection, a surface was generated to interpolate values between known points (see Lam 1983). A grid of known and interpolated values was created with an inverse distance weighted interpolation algorithm using the 12 nearest points and a squared decay function. The algorithm is expressed as:

$$Z = \frac{\sum_{i=1}^{n} z_i/d_i^w}{\sum_{i=1}^{n} 1/d_i^w}$$

Where: Z = the value of the unknown point
n = the number of sample points used for interpolation
z = the value at the sampled point
d = the distance between the sample point and Z
w = the weighting factor

The resultant grid was converted into a raster format with each pixel given an individual value. These data were then imported into ARCINFO (Environmental Systems Research Institute, Inc., Redlands CA) for graphic display by James Zack of the GIS, Remote Sensing, and Cartography Lab at the University of Colorado.

2.2. The Breeding Bird Survey:

Breeding Bird Survey data were provided by the National Biological Survey in digital format. These files were converted to ASCII format and reduced to give the coordinates with the corresponding mean number of birds observed per route, per year. These data were then transformed into a Lambert Azimuthal Equal Area projection coordinate system by the same procedures described above for the CBC, and a surface created using the above inverse distance weighted interpolation algorithm.

2.3. CBC and BBS Areas Used for Correlational Analysis:

The GRASS program was used to generate a buffer with a 12.1 kilometer radius around the central coordinates of each CBC count circle. This buffer corresponded to the radius of the original count circles. The inclusive area within each circle was 441 square kilometers, represented by 441 pixels of 1 square kilometer each, in the raster data set as defined above. For purposes of conformity, and to limit the extensive area potentially covered by a 39.4 kilometer BBS route, the same 12.1 kilometer buffer was used surrounding the starting coordinates of each BBS route. A program to separate the individual survey sites within each clump of two or more overlapping circles was written and each area given a unique designator for further analysis. As it was impossible to distinguish effects of common or exclusive areas in overlapping circles, the correlational analyses to be described below treated each area as a separate entity.

3. ENVIRONMENTAL DATA FORMAT AND TRANSFORMATIONS:

Each of the following climatic, geographic, and physiographic factors were tested for statistical correlation with the CBC and BBS data sets.

3.1. Temperature:

Point data on temperature were obtained from the Global Historical Climatology Network (GHCN) through the Cooperative Institute for Research in Environmental Sciences (CIRES) at the University of

Colorado. These data were obtained from meteorological monitoring stations throughout the U.S. and the world (see Eischeid et al. 1991, Vose et al. 1992). Data from 1,528 temperature stations were used. The original data set included the name of the station, latitude and longitude coordinates, inclusive years, monthly mean and standard deviations for temperature, and several other categories. Data were converted into ASCII format and 30-year averages for the period of 1961 through 1990 calculated for relevant factors. These data were transformed to conform to the Lambert Azimuthal Equal Area projection described above. An interpolation program was performed to create a grid surface of temperature data for each square kilometer of the continental United States. The interpolation technique used for this application was the standard inverse distance weighted interpolator described above. Grids were generated for each of the following temperature parameters:

1. Mean monthly temperature for May for correlation with BBS data
2. Mean monthly temperature for December for correlation with CBC data
3. Mean annual temperature maximum for correlation with BBS and CBC data
4. Mean annual temperature minimum for correlation with BBS and CBC data

The resultant grids were then put in raster format and spatially registered with the CBC and BBS data sets. Overlays of the bird data on each of the above parameters were performed with the mean value contained within each 441 Km^2 CBC or BBS survey area used for analysis.

3.2. Frost-free Days:

Data on frost-free days were obtained from the National Climate Data Center in Asheville, NC. Thirty year mean data for the period of 1961 through 1990 were derived from 5,868 monitoring stations throughout the United States. The data were treated in the same manner as temperature data presented above. Bird data were overlaid on the frost-free day data with the mean number of frost-free days per annum contained within each survey area used for analysis.

3.3. Precipitation:

Point data on precipitation were obtained from the GHCN through CIRES and conform to standard data sets (Eischeid et al. 1991). Data from 1,877 precipitation stations were used in this application.

Formats for these data were the same and were treated in the same manner as the temperature data set. Grids were generated for each of the following precipitation parameters:

1. Mean monthly precipitation for May for correlation with BBS data
2. Mean monthly precipitation for December for correlation with CBC data
3. Mean annual precipitation for correlation with BBS and CBC data

Bird data were overlaid on each of the precipitation layers with the mean value contained within the survey areas used for analysis.

3.4. Snow Cover:

Snow cover data were obtained from the Northern Hemisphere Digitized Snow and Ice Cover Data Base through the National Oceanic and Atmospheric Administration (NOAA) National Snow and Ice Data Center in Boulder CO, and from 8,114 stations monitored by the National Climate Data Center. These databases provided the extent and depth of coverage of snow and ice on a weekly basis. Data were averaged for the last week of December over a period of 10 years from 1981 through 1990. Conversion of coordinate locations to the Lambert Azimuthal Equal Area projection were performed as previously described and a surface generated as above. Bird data from the CBC were overlaid on these data for correlation with the presence and depth of snow cover within each count circle.

3.5. Hydrology:

Hydrology data were obtained from the USGS EROS Data Center on the Conterminous U.S. Advanced Very High Resolution Radiometer (AVHRR) Companion Disc. The Digital Line Graph (DLG) hydrologic data on this disc were the USGS 1:2,000,000-scale DLG vector data digitized from the maps in the "National Atlas of the United States of America" (1970). All data on this disc conformed with the Lambert Azimuthal Equal Area projection and thus were spatially registered with other data sets and could be overlaid directly on them. Two files from this data set were used; a waterbody file and a stream file. The data were converted to raster format and the files merged for this application. Information was provided for all permanent and intermittent water sources and may have been too detailed for the scope of this study. In order to limit the extensive number of features contained in these data sets, only permanent water sources were considered for analysis. Vulture data from the CBC and BBS were overlaid on the permanent water body data set and a linear distance, in Km, from each survey area to the nearest water source calculated. Correlational analyses were performed to determine if vulture populations were related to the distance to water.

3.6. Elevation:

Elevation data were obtained from the EROS data center with the hydrology data. Elevation data on the disc were derived from a Digital Elevation Model (DEM) from the 30-arc second data set distributed by the National Geophysical Data Center (NGDC). Mean elevations for each 1km block were rounded to the nearest 20 feet (6.45 m). Survey areas were overlaid on the elevation data, and a mean elevation calculated for the area contained within each circle. The standard deviations among the 441 1-km blocks within each circle were also calculated as a measure of elevational heterogeneity or surface roughness. Analyses were performed to determine if there were statistical correlations between vulture populations and the two factors of absolute elevation and surface roughness.

3.7. Primary Productivity:

A measure of primary productivity can be derived from satellite multi-spectral imagery. The USGS EROS Data Center has compiled multi-spectral data from NOAA-11 AVHRR satellites which produce weekly and biweekly maximum normalized difference vegetation index (NDVI) composites for each 1 Km block of the conterminous United States. Composites were produced using the maximum NDVI value recorded during each week of the year to reduce the chance of cloud cover interfering with readings on any given date. These data were available on the 1991 AVHRR companion disk supplied by the USGS. NDVI is represented by the following formula:

$$NDVI = (NIR - R) / (NIR + R)$$

Where: NIR = Near Infrared (0.725-1.0m, AVHRR Channel 2)
R = Red (0.58-0.68 m, AVHRR Channel 1)

This index was used as it is directly related to photosynthetic activity and thus provided an weekly picture of primary productivity (Tucker 1978, Tucker et al. 1980, Curran 1980, Townshend et al. 1985). The maximum weekly value of NDVI recorded for each month was used in this study rather than summing the weekly values, or using values from specific dates, to limit the chance of cloud cover interfering with reflectance during any given week. This procedure biased the NDVI values to the highest recorded for each block, but allows direct comparison between sites, as all values are relative. Vulture survey data were overlaid on the NDVI surfaces and mean NDVI values for each survey area calculated. Breeding Bird Survey data were compared to the mean maximum NDVI recorded for the month of May for each survey site. Christmas Bird Count data were compared to the mean maximum NDVI recorded for the month of December for each survey site. Both surveys were compared to the sum of the maximum NDVI values for each month as an index of total annual productivity.

3.8. Thermal Reflectance:

Thermal reflectance data were derived from 1991 AVHRR satellite spectral imagery as provided by the USGS EROS Data Center. Data from the same dates as the NDVI readings were used to ensure peak readings were obtained on days with no interference from cloud cover. Bi-weekly data were available for each 1 Km block of the U.S. and were measured in watts per m^2. Peak readings for the months of May and December were used to create surfaces for correlation with the BBS and CBC data sets. The mean value contained within each survey area was used for analyses. This factor is not merely a measure of incident rays from the sun, but represents the amount of energy reflected from the Earth's surface. Reflected energy is dependent upon a number of surface features such as soil types, land forms, vegetation cover, and other factors. Thermal reflectance was used as it may be an indirect measure of thermals or orographic lift necessary for vultures to sustain foraging and migratory flights and therefore affect habitat selection.

3.9. Vegetation:

Vegetation data sets were created by the USGS EROS Data Center as part of ongoing research and development of a land-use characteristics data base for the United States (see Loveland et al. 1991, Brown et al. 1993). A preliminary copy of the database was provided on 8mm tape by Jesslyn Brown of the EDC. Vegetation classification was based on spectral characteristics derived from AVHRR satellite data and ground truthed for accuracy. Multitemporal indices, such as the NDVI described above, reveal chronological and spectral reflectance differences that were used to differentiate vegetation classes (see Barrett and Curtis 1976, Johannsen and Sanders 1982, Norwine and Greegor 1983, Goward et al. 1985, Townshend et al. 1985, 1987; Roller and Colwell 1986, Dale 1990, Brown et al. 1993). These techniques were used to classify vegetation for each 1km block in the conterminous U.S.

Vegetation was classified into 167 categories on the 1991 AVHRR companion disc. The CBC and BBS sites were overlaid on the vegetation imagery with the amount of each vegetation class by percent coverage calculated for each 441 square kilometer area. Statistical analyses were performed to determine if the presence of certain vegetation classes, or combinations of classes, could be used to predict the occurrence of vultures. It was presumed that vultures preferentially selected certain vegetation classes in their home ranges for cover or food sources. The extremely fine division of vegetation classes in this data set made correlation at this scale difficult at best, if not impossible. Examination of vegetation classes revealed many duplicate categories. This resulted from similar land uses in different parts of the country. For example, a soybean field in Alabama would show a markedly different temporal spectral reflectance over the course of a year compared to a similar field in Ohio. Clumping of vegetation classes as described below was also accomplished for coarser resolution.

Vegetation was also reclassified into 49 more general classes on the AVHRR companion disc. The percentages of each class within each survey area were calculated as above. Analyses of these data were accomplished in the same manner as the more specific vegetation classes. This test was conducted to determine if the vultures responded to cover types to a coarser degree than implied by the division into the 167 more specific vegetation classes described above.

The vegetation classes described above were also clumped into 8 very broad categories with the same analyses performed as above.

3.10. Ecoregions:

The AVHRR companion disk also included information on ecoregions. The ecoregions were as defined by the Environmental Protection Agency (EPA) and Major Land Resource Areas (MLRA) as compiled by the Soil Conservation Service (SCS). The ecoregion data were originally digitized from the "Ecoregions of the conterminous United States" (Omernik 1987) map and generally conformed to other such ecoregion designations (see Fenneman 1931, 1938; Barnes and Marshner 1933, Kuchler 1964, Anderson et al. 1976, Omernik and Gallant 1989). The ecoregions data set contained polygons based on common soils, land use, natural vegetation, landforms, and surface geology. These ecoregions are divided into 76 categories. This was a further aggregation of vegetation types but included other features which may have determined the presence of vultures and their abundance. The objective was to test whether vultures preferentially selected certain ecoregions. The difficult part of this evaluation is that many other factors described above covaried with this general characterization of the environment though no effort was made to separate these effects. Also, as ecoregions were discreet units, they could not occur in different areas of the country as might all other variables.

4. STATISTICAL APPLICATIONS:

Each of the analyses described below were performed using a GIS overlay process to determine the area of overlap between various data layers. Each of the 2,026 Christmas Bird Count circles, and the 2,167 Breeding Bird Survey routes were treated as individual samples. The value assigned each site was the mean number of vultures per party hour, per count circle, per year for the CBC, and the mean number of vultures per route, per year for the BBS. Environmental data layers underlying each bird survey site were represented as the mean value for each factor contained within the 441 km^2 bird survey area. Statistical analyses were performed using the SAS program (SAS Institute Inc., Cary NC) and S-Plus (Statistical Sciences, Inc., Seattle WA). Bivariate linear regressions were performed for each factor against CBC and BBS data sets. Environmental factor data that followed continuous distributions were analyzed using traditional statistical approaches (see Harris 1975, Zar 1984, Morrison 1990, Cressie 1991). For those data classified as discreet, regression analyses were run against the percentage of the 441 km^2 cells in each survey area containing each discreet variable. Statistical assumptions necessary to perform these analyses include the following, where Y = the number of vultures at each survey location, and X_i = the environmental factor tested*:

1. variable Y is measured at the interval or ratio scale,
2. variable X_i is measured without error, whereas any measurement error in Y is random,
3. the relationship between Y and X is linear,
4. the error variable has zero mean,
5. the error variable has constant variance,
6. all pairs of errors are uncorrelated, and,
7. the error variable is normally distributed.

(*adapted from Griffith and Amrhein 1991).

The assumption most likely violated from the above list was number three, that the relationships between environmental factors and Turkey Vulture numbers were linear. No doubt, sophisticated transformations of these numerical distributions could have improved the predictive power of the statistical techniques, but the correlations between vultures and the various environmental variables likely would not have changed. For the sake of simplicity and because of the large number of variables considered, other than ranking the BBS and CBC data, such transformations were not accomplished as part of this initial research analysis, but might be appropriate for follow-on research.

Multiple regression analyses including step-wise, backward, forward, and maximum R regression were then performed to find the best combination of predictors of Turkey Vulture abundance. These techniques were used as a screening mechanism to determine key variables from the list of environmental factors that best explained variability in the vulture data. These techniques were not used, and may not be appropriate, for determining the importance of each variable relative to other variables, but have the advantage of accounting for covariance between independent factors not possible with standard bivariate techniques (see James and McCulloch 1990). Results of these analyses were used to estimate the number of vultures expected at a site as a function of a combination of various environmental factors. E.g. $Y = f(X_i, X_{i+1}, X_n)$, where X_i = environmental factor.

Principal component analyses (PCA) also were performed on various subsets of these data to potentially simplify the modeling process. These procedures generated a greatly reduced number of variables represented by the resultant principal components, though describing the often complex components proved difficult. A substantial amount of the variation amongst the environmental variables could be explained by the first few principal components, and it was hoped that vultures numbers would correlate with these new variables. However, when the PCA scores were correlated with the CBC and BBS data, no improvement could be determined over the original variables. In fact, in most instances the results of the PCA scores explained less of the variance than the original variables. Thus, the original variables are described in these results despite the fact that many covary substantially with one or more of the other environmental variables.

RESULTS:

1. BIVARIATE REGRESSIONS:

Preparation of the environmental data sets resulted in over 300 variables for correlation with each of the vulture data sets. As it was unlikely that most of these variables were important in explaining the variance in the bird data, a screening process was necessary to limit the data set to a smaller list of key variables. Bivariate and multivariate analyses were used towards this end.

Standard bivariate regression analyses were performed for each environmental variable against the BBS and CBC data. Results from the 167-category vegetation data revealed that these divisions generally were too small to be meaningful at the scale of this study. Therefore, they were dropped from further analysis. Remaining variables were divided into geographic, climatic, and physiographic categories. Correlation coefficients and significance levels were calculated for each. Those variables with the highest absolute R values were designated key variables and used for further analyses (see Tables 1 and 2). An absolute R value above 0.06 was chosen as the cutoff point, as it formed a dramatic natural break among all variables considered. Correlations between vulture abundances and all key variables were significant at the 0.001 level for both the CBC and BBS. These significance levels were not surprising, given the enormous amount of data analyzed (n = 2,026 for the CBC and n = 2,167 for the BBS), but were reassuring in that the relationships explained could not be due to chance alone.

Table 1. Correlations between summer Turkey Vulture abundance from Breeding Bird Surveys and key environmental variables (n = 2,167, all R values significant at $p < 0.001$).

Geographic	R
May Thermal Reflectance	.198
Elevation Standard Deviation	-.104
Mean Elevation	-.152
Climatic	**R**
May Temperature	.375
Number of Frost-Free Days	.335
Minimum Annual Temperature	.321
Maximum Annual Temperature	.172
May Precipitation	.077

TABLE 1 continued

Physiographic	
Vegetation (49 category)	**R**
Savanna	.288
Cropland/Woodland	.222
Grassland/Shrubland/Woodland	.126
Desert Shrubs	.104
Southern Pine/Wetlands	.087
Grassland/Cropland	.087
Southern Pine	.083
Grassland/Chaparral	.069
Coastal Wetlands	.069
Coniferous Forest	-.063
Grassland	-.064
Rocky Mountain Mixed Forest	-.065
Northern Forest	-.066
Northern Hardwoods	-.070
Woodland/Pasture	-.088
Western Conifers	-.098
Cropland/Woodlots	-.114
Vegetation (8 Category)	**R**
Grassland/Cropland	.096
Wetlands	.068
Forest	-.085
Ecoregions	**R**
Central Texas Plateau	.328
South Texas Plains	.226
East Central Texas Plains	.211
Southern Deserts	.203
Central Oklahoma-Texas Plains	.138
South Central Plains	.121
Texas Blackland Prairies	.101
South Florida Coastal Plain	.088
Western Gulf Coastal Plain	.072
South & Cent Calif Plains and Hills	.071
South Central Plains	.071
Mid-Atlantic Coastal Plain	.066
Northeastern Highlands	-.062

TABLE 2. Correlations between winter Turkey Vulture abundance from Christmas Bird Counts and key environmental variables (n = 2,026, all R values significant at $p < 0.001$).

Geographic	R
December Thermal Reflectance	.168
Distance to Perm anent Water	.096
Elevation Standard Deviation	-.097
Mean Elevation	-.151
Climatic	**R**
December Temperature	.300
Number of Frost-Free Days	.273
Minimum Annual Temperature	.246
Annual Precipitation	.207
December Precipitation	.087
December Snow Accumulation	-.170
Physiographic	
December NDVI	.211
Annual NDVI	.113
Vegetation (49 Category)	**R**
Southern Pine	.307
Cropland/Woodland	.301
Savanna	.163
Mixed Forest	.120
Southern Pine/Wetlands	.119
Coastal Wetlands	.062
Cropland	-.069
Cropland/Grassland	-.069
Desert Shrubs/Grass	-.075
Woodland/Pasture	-.079
Cropland/Woodlots	-.122
Vegetation (8 Category)	**R**
Forest	.078
Wetlands	.062
Woodland/Savanna	-.066
Shrub/Chaparral	-.075

TABLE 2 continued

Ecoregions	R
South Central Plains	.211
South Florida Coastal Plain	.193
Southeastern Pla ins	.184
East Central Texas Plains	.170
South Central Plains	.158
Mid-Atlantic Coastal Plain	.114
Western Gulf Coastal Plain	.086
Oachita Mountains	.083
Texas Blackland Prairies	.076
Mississippi Vally Loess Plains	.069
Central Oklahoma-Texas Plains	.066

Results from these analyses revealed that Turkey Vulture abundances could be correlated with a variety of environmental factors. Vulture populations were most strongly correlated with geophysical factors, particularly temperature, during both summer and winter. Vulture abundances were positively correlated with several temperature variables, such as mean monthly temperatures, the number of frost-free days, minimum, and maximum annual temperatures. Mean monthly temperatures were the strongest predictors of all geophysical factors during both seasons. Vulture abundances also were positively correlated with measures of thermal reflectance between seasons. They were negatively correlated with both mean elevation and surface roughness (elevation standard deviation) in both seasons. Vultures abundances were positively correlated with monthly and annual measures of precipitation, but negatively correlated with winter snow cover.

Examination of physiographic correlates revealed consistent patterns in vultures' preference for certain ecoregions, but differences in preferences for vegetative cover types within these ecoregions between seasons. Turkey Vultures were most closely associated with the southern and Gulf coastal plains and the mid-Atlantic and Florida coastal plains during summer and winter. Breeding vultures were also associated with southern deserts and California plains and hills. Within these ecoregions, breeding Turkey Vulture abundances were most strongly positively correlated with heterogeneous and more open vegetative habitats. These cover types included savanna, shrubland, chaparral, grassland, and mixed croplands. They were most strongly negatively correlated with forested areas. During winter, by contrast, vultures were much more strongly associated with forested areas and tended to avoid more open areas such as grasslands and cropland unless these were interspersed with forested cover types. Wetlands also appeared important during winter. Wetland habitats occur primarily in the southeastern U.S. and are frequently associated with cover types such as southern pine forests. Interestingly, vulture abundances were positively correlated with measures of monthly and annual primary productivity (NDVI) during winter, but not during the summer. This likely reflected the longer growing season associated with southern wintering areas.

In general, absolute correlations between vulture abundances and environmental variables were lower than might have been expected. There are several possible explanations for this. First, and perhaps most importantly, is the inherent variability introduced by the CBC and BBS data collection methodology. Several authors have commented on these potential problems and have suggested that the BBS, as it is more rigorous in its approach, may be an improvement over the CBC (see Robbins and Van Velzen 1967). Examination of the relative R values for all variables between surveys supported these claims and suggested that the low correlation coefficients were likely influenced by the data collection methodology, though correlation coefficients of the reduced set of key variables were similar between surveys.

Second, local environmental conditions undoubtedly were important to vultures in selecting habitats. Some of these local effects were obscured when environmental conditions were examined at a continental scale. Similar studies which have pooled bird abundance data over much larger regional areas, and thus reduced inter-survey variability, demonstrate significantly higher correlations between various environmental factors and surveyed bird populations, due to the smoothing effect of pooled data (see Bock and Lepthien 1975a,c; Lepthien and Bock 1976, Bock and Root 1981a). Additionally, vultures may have responded to local environmental features below the resolution of this study. For example, Turkey Vultures often congregate at sites such as landfills, feedlots, and other food sources that could not be detected at the 1 kilometer scale used in this application.

Another possibility for the low correlation coefficient values is the nature of the Turkey Vulture itself. Turkey Vultures are generalist scavengers capable of exploiting a wide variety of food resources, and thus they are not limited to specific habitats. The techniques used in this study may reveal much stronger correlations if applied to more specialized species. Lastly, many of the correlation equations may not be strictly linear, and more sophisticated transformation techniques might have improved the statistical associations, though the observed relationships would remain significant. Examination of scatterplots revealed that the vulture data were skewed toward zero observed birds at a significant number of sites. As the statistical techniques used may be particularly sensitive to outliers, some of the variability may be explained by such sensitivities. To address this potential pitfall, bivariate regression analyses were repeated on ranked BBS and CBC data to more closely approach normality. Results from the ranked data set showed only a slight improvement in some of the correlation coefficients, and no improvement in most others. But most importantly, these transformations did not change the list of key variables nor substantially change their sequential positions relative to other variables.

Despite the comparatively low R values, results of these correlational analyses revealed consistent and interpretable patterns of Turkey Vulture abundances throughout their range, and between seasons. These results lend substantial insight into the habitat requirements of the Turkey Vulture.

2. MULTIPLE REGRESSIONS:

A series of multivariate analyses next were performed on various subsets of the original data to determine if some of the same key variables emerged as the best predictors of Turkey Vulture distributions. These analyses were used to screen variables as with the above bivariate regression analyses, but offered the added advantage of reducing the effects of covariance between factors. Covariance of factors could not be determined with bivariate analyses techniques. Stepwise, forward, backward, and maximum R regressions were performed against both ranked and unranked vulture data sets for this purpose. Each of these procedures was performed on the entire data set, key variables from the bivariate regression analyses, and on subsets of geographic, climatic, and physiographic variables. These analyses were used for screening predictors and to reduce the list of variables, but were not used to determine the relative importance of variables. Results from these analyses were complex, yet generally revealed consistent patterns that supported the findings from the bivariate regression analyses. For the sake of brevity, only highlights from these procedures will be presented here. Results of the maximum R regression procedure will be presented, as it may be the most robust of the techniques used (SAS Institute, Inc., Cary NC). However, the variables that emerged as best estimators of the bird data did not differ substantially between techniques.

Maximum R analysis is a stepwise procedure that sequentially adds variables to a regression model in order to maximize the residual variance explained at each step. Application of this procedure revealed that 40.40% of the total variance in the Breeding Bird Survey vulture data could be explained after 187 steps, beyond which no improvement occurred. Most of the cumulative variance was explained in the first few steps, however, and graphic display of these results showed that the line representing cumulative variance quickly became asymptotic approaching the maximum value (see Figure 3).

The first ten steps shown in Figure 3 accounted for 33.67% of the total variance in the vulture data, or 83.3% of the variance explained by the entire analysis. For the Christmas Bird Count, 27.86% of the total variance was explained after 223 steps. Again, most of the variance (22.34% of the variance in the vulture data, or 80% of the total variance explained by this procedure) was accounted for in the first ten steps.

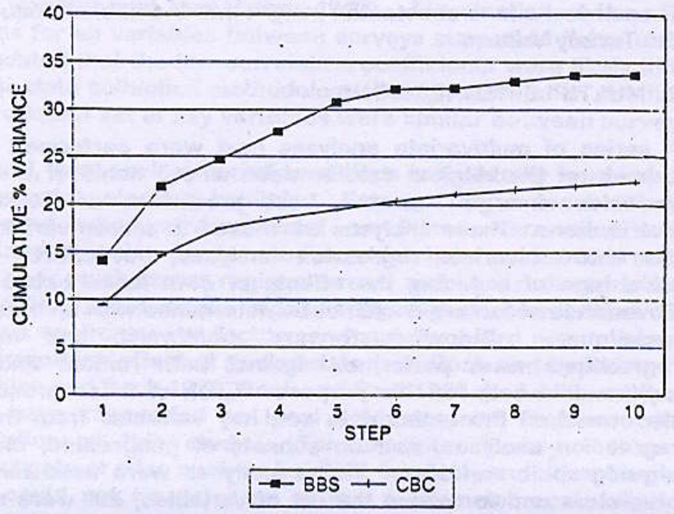

Figure 3. A comparison of results from multiple regression analyses on the BBS and CBC against environmental factors using a maximum R stepwise technique. The cumulative percent variance explained by the first ten steps of these analyses are represented for each survey.

As with the bivariate regressions, multiple regression analyses revealed that more variance could be explained for the Breeding Bird Survey and it may be a more reliable technique than the Christmas Bird Count. Nevertheless, some of the same key variables seemed to be important to the vultures in both summer and winter, and the results were consistent with the bivariate regression analyses previously performed. Consistent results between regression techniques were reassuring since related factors that covary statistically could have made interpretation of results more difficult. Table 3 lists the first ten variables added to each of these maximum R regression models for the BBS and CBC on a subset of the environmental data set including only the broadest of vegetation classes. These analyses again revealed that temperature variables were important predictors of vulture abundances during both summer and winter. Precipitation and the distance to permanent water also seemed important in these analyses. These results also supported the physiographic habitat preferences of vultures during both seasons, with more open or mixed habitats important in summer, and forested and wetland areas important in winter.

TABLE 3. Environmental variables added in the first ten steps of maximum R multiple regression models of the Breeding Bird Survey and Christmas Bird Count on Turkey Vulture abundances.

Breeding Bird Survey		Christmas Bird Count	
Step	Variable Added	Step	Variable Added
1	May Temperature	1	December Temperature
2	Annual Precipitation	2	Veg Class - Shrub/Chaparral
3	Veg Class - Barren	3	Minimum Annual Temperature
4	Minimum Annual Temperature	4	Annual Precipitation
5	May Precipitation	5	December Precipitation
6	Veg Class - Woodland/Savanna	6	December Thermal Reflectance
7	Veg Class - Shrub/Chaparral	7	December NDVI
8	Maximum Annual Temperature	8	Distance to Permanent Water
9	Number of Frost-Free Days	9	Veg Class - Wetlands
10	Distance to Pemanent Water	10	Veg Class - Forest

3. SUMMER VULTURE DISTRIBUTION:

The model surface generated from the BBS data revealed the summer distribution and abundance patterns of Turkey Vultures (Figure 4). Most birds inhabited the southern half of the United States. The highest concentrations of vultures were in broad areas of the southern plains through Texas, and the Florida peninsula, but significant breeding populations of vultures occurred at diverse locations throughout the country. High concentrations of vultures in areas such as California's central valley and northern coastal region, southern Arizona, the Ohio River valley, and the Chesapeake Bay region, as well as numerous more localized populations, were evident from these results. These procedures also revealed extensive areas where breeding Turkey Vultures were absent or scarce. Most notable were the mountainous areas of the north and west, and the northern Great Plains. Vultures also were rare in the densely forested areas of the New England states, particularly Maine. This analysis revealed a dramatically heterogeneous distribution and abundance pattern for breeding Turkey Vultures through the U.S. that could not be implied from more traditional range maps for this species.

4. WINTER VULTURE DISTRIBUTION:

The model surface generated from the CBC data using the above procedures revealed the winter distribution and abundance patterns of Turkey Vultures in the United States (Figure 5). Most populations inhabited the southeastern states. The heaviest concentrations of birds were in the southern plains of Texas and the southern Atlantic coastal plain through the Florida peninsula. Isolated concentrations of birds were evident in several areas of the country, such as the Snake River Birds of Prey area in Idaho, the southern Appalachians, and along the Chesapeake Bay.

Also revealed by this surface was the clear evidence that the vast majority of birds which summer in the western U.S. had departed the region for the winter. Most of these birds probably migrated to Central and South America. It was also possible that some of the vultures had not fully completed their migration at the time of the Christmas Bird Counts, as these counts occurred early in the winter season. This may have been particularly true in the southern states. Migratory, rather than wintering populations, may have been counted at some CBC locations if this was the case. Migratory behavior thus may have driven the habitat selection process at these sites.

DISCUSSION:

Turkey Vulture distribution and abundance patterns were correlated with a number of environmental factors both spatially and temporally. These distribution and abundance patterns were highly heterogeneous, and the result of interactions of many environmental variables that each contributed incrementally to the vultures' habitat requirements. Geophysical factors, especially those related to temperature, were the strongest predictors of vulture abundance and distribution patterns. Winter vulture populations correlated with the same host of geophysical factors of temperature, precipitation, elevation, and thermal reflectance as summer populations, albeit further south.

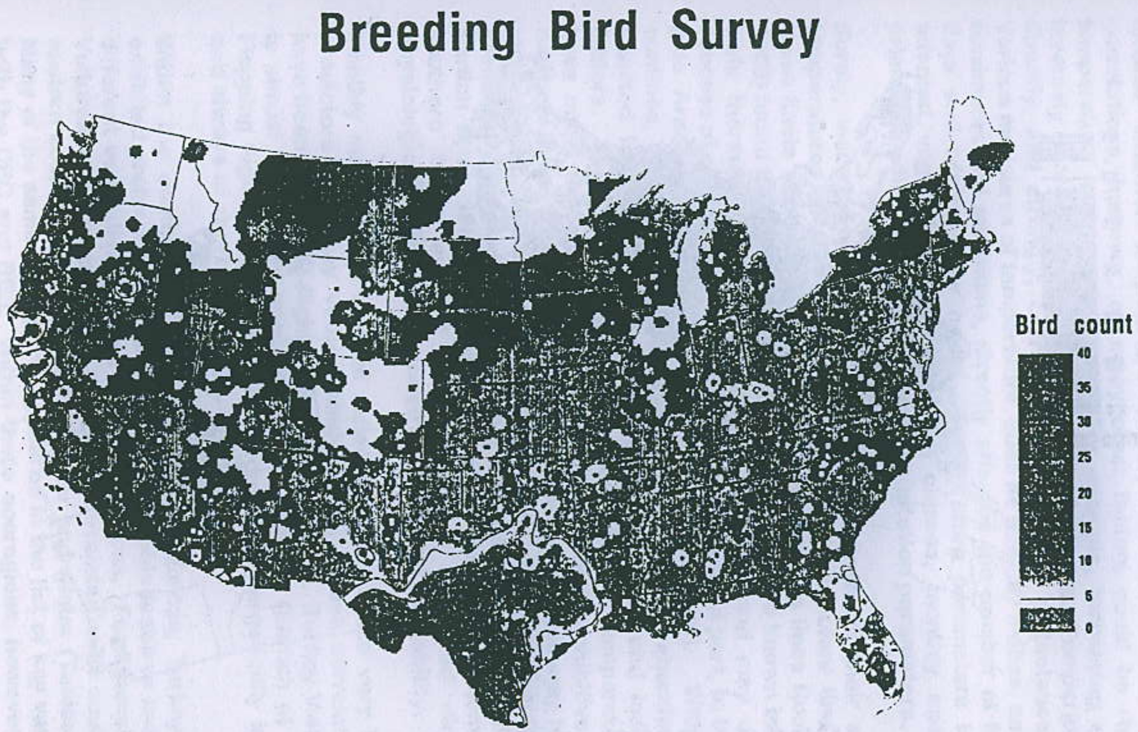

Figure 4. Interpolated surface depicting summer Turkey Vulture distribution and abundance in the United States. Data were derived from 2,167 Breeding Bird Survey sites. Smoothed contour lines are represented at 5 Turkey Vultures/BBS route/ year intervals.

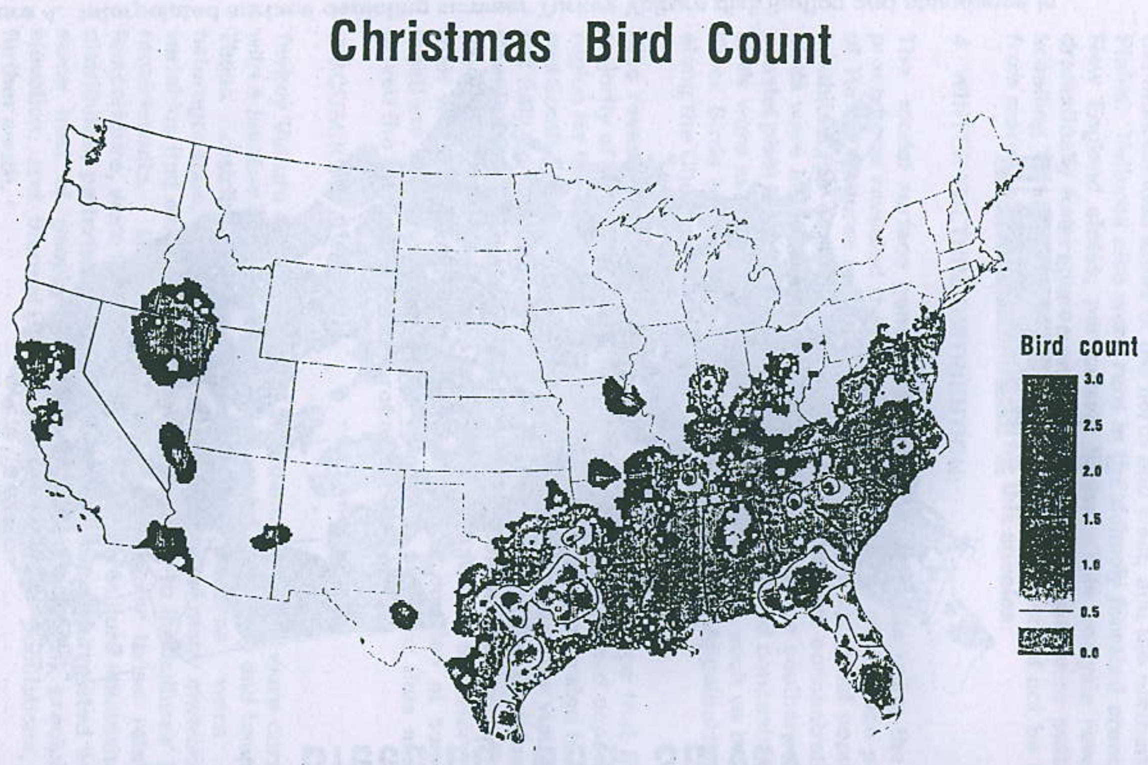

Figure 5. Interpolated surface depicting winter Turkey Vulture distribution and abundance in the United States. Data were derived from 2,026 Christmas Bird Count sites. Countour lines are represented at 0.5 Turkey Vultures/party hour/CBC circle/year intervals.

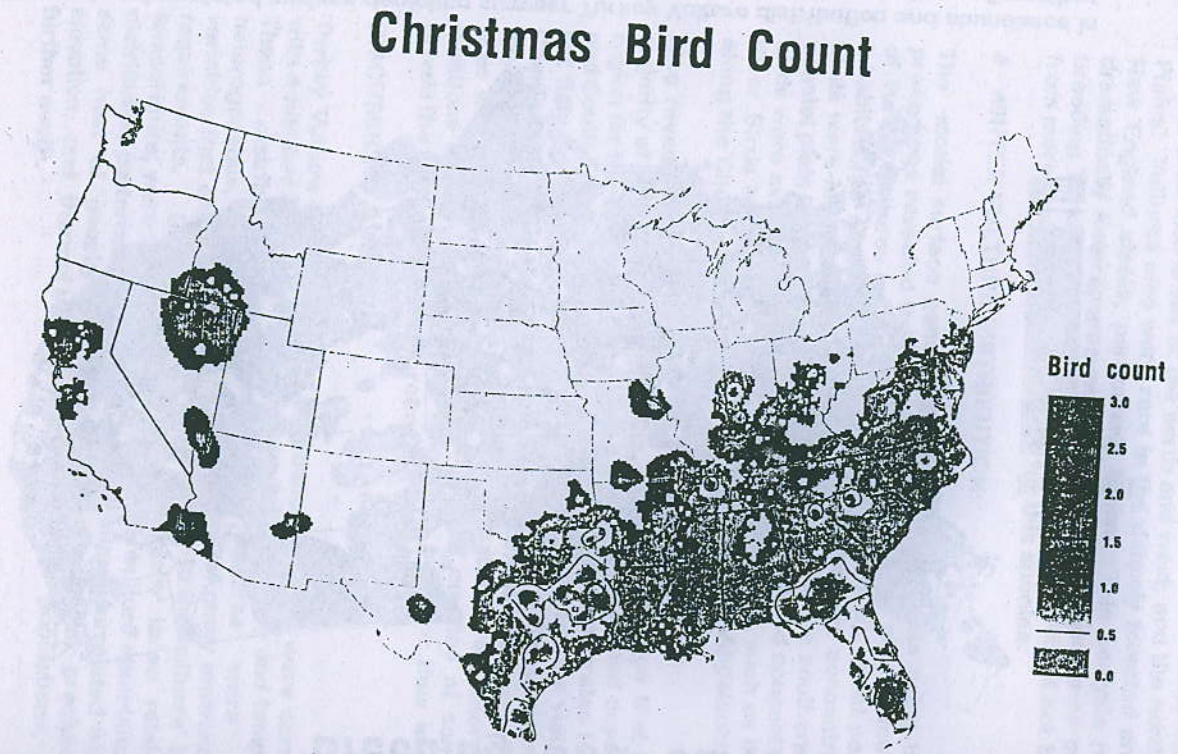

Figure 5. Interpolated surface depicting winter Turkey Vulture distribution and abundance in the United States. Data were derived from 2,026 Christmas Bird Count sites. Countour lines are represented at 0.5 Turkey Vultures/party hour/CBC circle/year intervals.

preferentially selected cover types that varied between summer and winter. During summer, the birds seemed to prefer heterogeneous habitats throughout their range such as shrubland, savanna, chaparral, or mixed croplands which are more open in nature. They avoided heavily forested areas at this time of year. Southern pine forests were used during summer, but these forests have much more open canopies than other forest classifications and are often associated with other cover types such as wetlands. Perhaps it is more difficult to observe or secure enough food to raise young in forested areas. Or, potential nest sites could be limited in heavy forests.

Deciphering the habitat preferences of wintering vultures was more problematic. The majority of Turkey Vultures that summered in the western U.S. departed the country for wintering grounds in Central and South America. This fact, combined with a sampling effort disparity between eastern and western North America, made the quality of available data very much lower in the west than the east, especially during winter. Examination of the continental U.S. as a whole, recognizing that the correlations were largely driven by eastern vulture populations, revealed that wintering birds exhibited a much stronger preference for forested areas than breeding vultures. Winter roost sites were likely chosen primarily for their thermal cover characteristics.

Dense vegetation providing communal nighttime roosting cover with thermal protection is important to Turkey Vultures during the winter, and forests were presumably favorable habitats (also see Wilkerson and Debbon 1980, Sweeney 1984, Fraser and Coleman 1989, Thompson et al. 1990).

Summarizing the major trends in these data, it is apparent that Turkey Vultures consistently demonstrated preferences for certain environmental factors in their selection of habitats throughout their range and between seasons. They sought similar geophysical conditions, but preferred different physiographic environments between seasons. Breeding vultures sought more heterogeneous and open habitats. Wintering vultures preferred more densely forested habitats. These preferences for various environmental factors could be used to predict the distribution and abundance patterns of Turkey Vultures in the continental United States and may help flight planners and route designers to avoid areas of potential bird hazards to flight safety.

CONCLUSIONS:

Results from this study demonstrated that environmental variables could be used to model and predict the distribution and abundance of Turkey Vultures on a scale never previously attempted, yet with relatively fine resolution. A clearer picture of Turkey Vulture habitat selection preferences has emerged. Turkey Vultures responded consistently to a variety of external biotic and abiotic factors throughout their range and between seasons. Results of these efforts have helped gain insight into this unique species and will also be used by the U.S. Department of Defense to minimize bird strike hazards to its aircraft. It is hoped that the techniques developed can be applied to other species and that this work can prompt further efforts to better understand the natural history and ecology of the Turkey Vulture and at the same time, make the skies safer for aircraft that share their airspace.

ACKNOWLEDGMENTS:

Many people have assisted immeasurably in collecting and preparing data for this project and the attached paper. I cannot begin to thank them all, but several deserve special mention here. Carl Bock of the Department of Environmental, Population, and Organismic Biology at the University of Colorado served as major professor and committee chairman for this project. Other committee members were David Chiszar, Wilson Crumpacker, Alexander Cruz, Charles Southwick, and Carol Wessman. They all provided invaluable advice and assistance in this project. Ronald Merritt, Michael Thompson, David Arrington, and Christine Atkins of the USAF Bird Aircraft Strike Hazard Team provided much of the bird strike statistics. Bruce Peterjohn provided the Breeding Bird Survey data from the National Biological Survey. James Lowe provided the Christmas Bird Count data from the National Audubon Society. Jesslyn Brown of the USGS EROS Data Center provided much information on several of the environmental data sets used herein. John Eischeid and Daniel Haynes of CIRES and the National Snow and Ice Data Center provided environmental data. Michael Hodgson of the Department of Geography at the University of Colorado provided much-needed assistance in addressing geographic information systems manipulations and spatial data analyses. Kenneth Shepardson of Spectrum Sciences and Software, Inc. provided the innumerable data transformations for the many and diverse data sets needed for this study. James Zack of the GIS, Remote Sensing, and Cartography Lab at CU produced the computer graphics in this paper. Mark Camara provided assistance with the numerous statistical procedures used in this project. I am indebted to them all.