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ENVIRONMENTAL FACTORS INFLUENCING TURKEY VULTURE DISTRIBUTION AND ABUNDANCE: A GEOGRAPHIC INFORMATION SYSTEM APPLICATION STUDY

RUSSELL P. DEFUSCO

1994
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ENVIRONMENTAL FACTORS INFLUENCING TURKEY VULTURE DISTRIBUTION AND ABUNDANCE: A GEOGRAPHIC INFORMATION SYSTEM APPLICATION STUDY

by

RUSSELL PAUL DEFUSCO

B.S., United States Air Force Academy, 1981
M.S., Colorado State University, 1983

A thesis submitted to the
Faculty of the Graduate School of the
University of Colorado in partial fulfillment
of the requirement for the degree of
Doctor of Philosophy
Department of Environmental, Population,
and Organismic Biology

1994
This thesis for the Doctor of Philosophy degree by
Russell P. DeFusco
has been approved for the Department of
Environmental, Population, and Organismic Biology
by

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Dr. Carl E. Bock

Dr. Alexander Cruz

Date April 6, 1994
Environmental Factors Influencing Turkey Vulture Distribution And Abundance: A Geographic Information System Application Study.

Thesis directed by Professor Carl E. Bock

ABSTRACT:

The objective of this study was to use physiographic, geographic, and climatic correlates to describe and interpret the breeding and wintering distribution and abundance patterns of Turkey Vultures (Cathartes aura) in the continental United States. Thirty years of data from the National Audubon Society's Christmas Bird Count and the National Biological Survey's Breeding Bird Survey were correlated with remotely sensed and ground sampled environmental data in a raster-based geographic information system. Environmental factors evaluated include elevation, hydrography, thermal reflectance, temperature, precipitation, snow cover, number of frost-free days, vegetation types, and ecoregions, for each 1 Km² block of the continental United States. A geographic information system overlay process was used to determine statistical relationships between individual and combinations of environmental factors, and sampled vulture data.
numbers were most strongly correlated with geophysical factors, especially a positive relationship with temperature, throughout their range and between seasons. Breeding vultures were most strongly positively correlated with heterogeneous and more open physiographic habitats, such as shrubland, savanna, chaparral, and mixed croplands. 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.
ACKNOWLEDGEMENTS:

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 and Michael Thompson 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.
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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. 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). 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 dependant upon information on bird distributions to avoid potentially hazardous areas. The USAF is producing a computerized Bird Avoidance Model (BAM) to provide this information. 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 final 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 cost the Air Force over 21 million dollars, 3 crashed aircraft and 2 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 to the Air Force by the U.S. Congress through the Department of Defense Legacy Resource Management Program.
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 which 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. For example, Bock and Bock (1974) found abundance patterns correlated with vegetation, and Bock and Root (1981a) found North American vulture winter abundance patterns positively correlated with estimates of primary productivity, the number of frost-free days, and annual precipitation.

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.

a. 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.

b. 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
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.
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.

Attributing vulture observations to the starting point of each route results in some imprecision in the data set. Precise location is not recorded for individual bird observations. Assuming the birds are randomly distributed at the local level, the mean distance for birds observed on any given route is one half the total route length and may be in any direction from the starting point.

Robbins (1981b) documented Turkey Vulture observations as increasing during the final hour of BBS surveys, which would indicate that most vultures are sighted more than half way through the survey routes. Vulture home ranges should cover this area however, and more precise location of observations may not be meaningful at the scale of this study.
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.
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 Leptien 1975a,b,c, 1976; Leptien 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 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 Leptien 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).

TURKEY VULTURE ECOLOGY AND NATURAL HISTORY:

Any study of this nature requires at least a general understanding of the biology and natural history of the species. Little is known about many aspects of Turkey Vulture life histories, particularly their abundance.
patterns at local levels. A brief summary of relevance to this study is offered below.

1. **Turkey Vulture Distribution:**

Turkey Vultures are common birds that occur almost ubiquitously throughout North America south of Canada, though by no means are they evenly distributed. These birds are also common throughout Central and South America and may be found south to the Straits of Magellan (Bent 1937). Figure 3 depicts the breeding and wintering ranges of North American Turkey Vultures. Extralimital birds, possibly displaced juveniles, may be found considerably north of these boundaries, particularly along the west coast to Alaska. As Figure 3 indicates, Turkey Vulture summer range encompasses virtually the entire continental United States. Breeding vultures may be found in all habitats in this range (Bent 1937, Snyder and Snyder 1991), though they are uncommon in some areas. Most notably, there are but infrequent records of vultures breeding in the central or northern Great Plains. Turkey Vultures are also scarce in the high mountains of the west as compared to lowlands, foothills, and coastal areas. Turkey Vultures are certainly capable of surviving in these areas however, and I observed solitary birds soaring and feeding at elevations above 4,500 meters in Colorado during this study.
Most North American Turkey Vulture populations are considered migratory, and a significant, though unquantified, number of Turkey Vultures that summer in the continental United States spend their winters in subtropical and tropical regions (Smith 1980, 1985; Pattee and Wilbur 1989). Winter range of the Turkey Vulture covers considerably less of the continental U.S., and is generally restricted to the southern states and coastal areas.

Figure 3. Breeding and wintering ranges of the Turkey Vulture in North America. (Source: Snyder and Snyder 1991).
2. Feeding Behavior and Prey Items:

New World vultures in general, and Turkey Vultures in particular, with rare exception, are incapable of securing and killing live prey. They are dependent therefore on a stable supply of carrion. Turkey Vultures feed on a wide variety of carrion throughout their range but preferentially select small-sized prey (Prior and Weatherhead 1991). In fact, they may be incapable of penetrating the skin of large carcasses without the aid of other animals or prolonged periods of putrefaction (Coleman and Fraser 1987). Avoidance of larger prey may be due, in part, to the presence of competitors (Hiraldo et al. 1991a,b). The availability of suitable carrion may be the ultimate determinant of both the distribution patterns and abundance of the species throughout its range.

A diverse array of carrion from natural sources provides the bulk of Turkey Vulture forage, but human sources also contribute to their diet. Turkey Vultures are frequently seen at landfills, feedlots, and food processing facilities and may especially benefit from road-killed animals. Carrion gleaned from roads may be particularly important during winter (Yahner et al. 1986, Thompson et al. 1990).

Turkey Vultures locate much of their food visually, but they are adept at finding food sources through even the densest of rainforest canopies (Chapman 1929, 1938; Snyder
and Snyder 1991). They accomplish this through a highly developed sense of smell, which is rare among birds (Stager 1964). At one time, Los Angeles County, California engineers found leaks in gas pipelines by pumping ethyl mercaptan and spotting where Turkey Vultures gathered (Stager 1967). Other vulture species such as the Black Vulture \textit{(Coragyps atratus)} and the King Vulture \textit{(Sarcoramphus papa)} often locate food by visually following Turkey Vultures to the source. Turkey Vultures may benefit from these associations by the assistance these birds give in tearing apart carcasses, though they are sometimes displaced from carcasses by other species (Bent 1937). Turkey Vultures also may use olfactory cues to aid in navigation during migration (see Waldvogel 1989).

3. Roosting and Nesting:

Turkey Vultures often roost communally, particularly in winter, and sometimes with Black Vultures (Bent 1937, Koford 1953, Sweeney and Fraser 1986, Wilbur and Jackson 1983, Coleman and Fraser 1989b). Nighttime roost sites are selected with favorable microclimates, near food sources, and where favorable soaring conditions exist (Thompson et al. 1990). Roosts often are in patches of living or dead trees in these areas, though solitary perch sites sometimes are used.

New World vultures usually breed well apart from one another. They do not build nests, but merely scrape out a
hollow for their eggs (Newton 1979, Davis 1983, Palmer 1988). Turkey Vultures lay an average of two eggs (Bent 1937), usually in holes or caves in rocky outcroppings or cliffs (Bjorklund 1990). They also may nest in hollow logs, under dense vegetation, or in barns and sheds where more preferred sites are lacking (Bent 1937, Newton 1979, Cringan and Horak 1989).

4. Habitat Selection:

Since Turkey Vultures are able to feed on a diversity of carrion, and nest and roost in diverse sites, they are capable of using a variety of habitats. They are not uniformly distributed throughout their range however, and clearly exhibit preference for some habitat types over others. Whether these preferences are the result of physiological constraints, or availability of necessary resources, is not clearly understood.

Human influences and land uses may have major positive and negative effects on Turkey Vulture habitat selection, and may also influence migration routes (Halliman 1922, Lee 1978, Peacock 1980, Heintzelman 1986, Cringan and Horak 1989, Williams and Colson 1989). While vultures are somewhat intolerant of disturbance, particularly during breeding cycles, they also benefit in many ways from human activity. In western North America, poor range management may benefit vultures by providing ample food sources in the form of livestock carcasses (Kochert et al. 1988, Kochert
1989), though these are not their preferred prey items. Chemical contamination and disturbance in these and other agricultural areas may have an offsetting detrimental effect (Young 1989). Vultures are expanding their ranges in the northeastern United States in both summer and winter, possibly due to the increase in deer populations, poultry operations, and restrictions on organochloride pesticides (Coleman and Fraser 1989a). Vultures may also be attracted to diverse areas with extensive road networks as a result of their use of road-killed carrion (Bagg and Parker 1951, Wilbur 1983). Such human influences clearly affect the distribution and abundance of Turkey Vultures within their historical range.

While several studies have contributed to the knowledge of Turkey Vulture habitat requirements, overall, little is known about habitat selection by these birds at the local level. This project was specifically designed to address the issue of habitat selection during summer and winter.

**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:

   a. The Christmas Bird Count:

Christmas Bird Count data were provided by the National Biological Survey in digital format containing three files. The first gave the coordinates of each count circle by year, with the total number of vultures observed. The second provided effort data including the total number of party hours spent on each count circle by year. The third was a list of all count circles where Turkey Vultures had never been recorded. These files were merged in 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 (see Appendix A for parameters of this projection). 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.

b. The Breeding Bird Survey:

Breeding Bird Survey data were provided by the National Biological Survey in digital format consisting of two files. The first gave the geographic coordinates of the starting point of each route with the number of vultures observed by year. The second was a list of coordinates for each route where vultures had never been observed. These files were merged in 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.
projection coordinate system by the same procedures described above for the CBC, and a surface created using the above inverse distance weighted interpolation algorithm.

c. 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. The resultant images produced from these manipulations showed that there was considerable overlap of survey sites, despite efforts by CBC and BBS organizers to avoid such situations. This was particularly true for regions of the country with dense human populations (see Figures 4 and 5). 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.

Figure 4. Christmas Bird Count sites in the northeastern United States. Each circle represents an area with a 12.1 Km radius surrounding the central coordinates of individual sites. Note the significant overlap of count circles.
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.

23
a. 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.

Brown and Eischeid (1992) and Eischeid and Diaz (1993) demonstrated that at continental scales, the differences between various interpolation techniques may be negligible for temperature and precipitation data. The above interpolation formula was used for simplicity over other
methods (see Delfiner and Delhomme 1975, Isaaks and Srivastava 1989). Grids were generated for each of the following temperature parameters:

1. Mean monthly temperature for May for correlation with BBS data (Figure 6)
2. Mean monthly temperature for December for correlation with CBC data (Figure 7)
3. Mean annual temperature maximum for correlation with BBS and CBC data (Figure 8)
4. Mean annual temperature minimum for correlation with BBS and CBC data (Figure 9)

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 Km² CBC or BBS survey area used for analysis. The raster images, and particularly the overlying contour lines depicted in the figures, were smoothed for graphic display to ease the visual interpretation of data, but the interpolated surfaces, and not the smoothed data, were used for statistical correlation analyses. Each of the subsequent figures in this text were treated in the same manner for visual display purposes.
Figure 6. Thirty-year mean temperatures for the month of May in °C. This interpolated surface was derived from 1,528 meteorological monitoring stations throughout the United States. Smoothed contour lines are represented at 2.5°C intervals.
December Mean Temperature

Figure 7. Thirty-year mean temperatures for the month of December in °C. This interpolated surface was derived from 1,528 meteorological monitoring stations throughout the United States. Smoothed contour lines are represented at 2.5°C intervals.
Figure 8. Thirty-year mean extreme maximum annual temperatures in °C. This interpolated surface was derived from 1,528 meteorological monitoring stations throughout the United States. Smoothed contour lines are represented at 5°C intervals.
Figure 9. Thirty-year mean extreme minimum annual temperatures in °C. This interpolated surface was derived from 1,528 meteorological monitoring stations throughout the United States. Smoothed contour lines are represented at 5°C intervals.
b. 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 (Figure 10). 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.

c. 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 (Figure 11)
2. Mean monthly precipitation for December for correlation with CBC data (Figure 12)
3. Mean annual precipitation for correlation with BBS and CBC data (Figure 13)
Number of Frost-free Days per Annum

Figure 10. Thirty-year mean number of frost-free days per year for the continental United States. This surface was derived from 5,868 meteorological monitoring stations. Smoothed contour lines are represented at 30 day intervals.
Figure 11. Thirty-year mean precipitation for the month of May in millimeters accumulation. This interpolated surface was derived from 1,877 meteorological monitoring stations throughout the United States. Smoothed contour lines are represented at 25mm intervals.
Figure 12. Thirty-year mean precipitation for the month of December in millimeters accumulation. This interpolated surface was derived from 1,877 meteorological monitoring stations throughout the United States. Smoothed contour lines are represented at 25mm intervals.
Figure 13.  Thirty-year mean annual precipitation in millimeters accumulation. This interpolated surface was derived from 1,877 meteorological monitoring stations throughout the United States. Contour lines are represented at 200mm intervals.
Bird data were overlaid on each of the precipitation layers with the mean value contained within the survey areas used for analysis.

d. 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 (Figure 14). Bird data from the CBC were overlaid on these data for correlation with the presence and depth of snow cover within each count circle.

e. 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
Figure 14. Ten-year mean snowfall for the month of December in millimeters accumulation. This interpolated surface was derived from 8,114 meteorological monitoring stations throughout the United States. Smoothed contour lines are represented at 100mm intervals.
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 (Figure 15). 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.

f. 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) (Figure 16). 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
Permanent Waterbodies

Figure 15. Permanent waterbodies in the continental United States as obtained from the USGS data base. Hydrologic features are represented in raster format with 1Km pixel size as derived from the original vector-based files.
Figure 16. Elevation map of the continental United States in meters above sea level. Mean elevations for each 1Km block were used to generate this surface from the USGS database. Smoothed contour lines are represented at 500m intervals.
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.

g. Primary Productivity:

A measure of primary productivity can be derived from satellite 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:

\[
\text{NDVI} = \frac{(\text{NIR} - \text{R})}{(\text{NIR} + \text{R})}
\]

Where: NIR = Near Infrared (0.725-1.0 µm, AVHRR Channel 2)

\[
\text{R} = \text{Red (0.58-0.68 µm, AVHRR Channel 1)}
\]

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 (Figure 17). Christmas Bird Count data were compared to the mean maximum NDVI recorded for the month of December for each survey site (Figure 18). Both surveys were compared to the sum of the maximum NDVI values for each month as an index of total annual productivity (Figure 19).

h. 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 m². Peak readings for the months of May and December were used to create surfaces for correlation with
May Normalized Difference Vegetative Index

Figure 17. Normalized Difference Vegetation Index for the month of May. This unit less index was used as a measure of primary productivity. Data were derived from NOAA-11 AVHRR satellite imagery at 1 km resolution. Smoothed contour lines are represented at 10 NDVI-unit intervals.
Figure 18. Normalized Difference Vegetation Index for the month of December. This unitless index was used as a measure of primary productivity. Data were derived from NOAA-11 AVHRR satellite imagery at 1Km resolution. Smoothed contour lines are represented at 10 NDVI-unit intervals.
Annual Normalized Difference Vegetative Index

Figure 19. Annual Normalized Difference Vegetation Index for the United States. This unitless index was used as a measure of primary productivity. Data were derived from NOAA-11 AVHRR satellite imagery at 1Km resolution. Smoothed contour lines are represented at 200 NDVI-unit intervals.
the BBS and CBC data sets (Figures 20 and 21). 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.

i. 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 Gregeor 1983, Goward et al. 1985, Townshend et al. 1985, 1987; Roller and Colwell 1986, Dale 1990, Brown
Figure 20. Thermal reflectance for the month of May in watts per m$^2$. Data were derived from NOAA-11 AVHRR satellite imagery at 1Km resolution. Smoothed contour lines are represented at 25 W/m$^2$ intervals.
December Thermal Reflectance

Figure 21. Thermal reflectance for the month of December in watts per m². Data were derived from NOAA-11 AVHRR satellite imagery at 1Km resolution. Smoothed contour lines are represented at 25 W/m² intervals.
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. These classes are listed in Appendix B. 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 classes listed in Appendix B 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. These classes are listed in Appendix C and depicted in Figure 22. 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 as listed in Appendix D with the same analyses performed as above.

j. 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 as listed in Appendix E and depicted in Figure 23. This was a further aggregation of vegetation types but included other features
Figure 23. Ecoregions of the continental United States. Ecoregion designations are as defined by the EPA and SCS and provided by the USGS. Number classes correspond to those named in Appendix E.
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 km² 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 km² 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. \( Y = f(X_i, X_{i+1}, X_j) \), where \( X_i = \) environmental factor.

Principal component analyses (PCA) also were performed on various subsets of these data to potentially simplify the modelling 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.

5. Eastern Versus Western North America:

In order to determine if metapopulations of vultures responded differently to environmental factors in different parts of their range, each of the above statistical analyses were performed on eastern versus western subsets of the data. The continent was divided at 100° W longitude. This was a simple division as it formed the central meridian of the Lambert Azimuthal Equal Area projection used for all data layers in this study (see Appendix A). It divided the continental United States into roughly equal areas, with approximately 3.73 million Km² west, and 4.04 million Km² east of this line. Perhaps most importantly,
the hundredth meridian forms a rough biogeographical transition zone for numerous North American species, genera, and families with east-west distribution patterns (see Pielou 1979, Brown and Gibson 1983).

RESULTS:

1. Summer Vulture Distribution:

The interpolated surface generated from the BBS data revealed the summer distribution and abundance patterns of Turkey Vultures (see Figure 24). 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
Figure 24. 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.
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.

2. Winter Vulture Distribution:

The interpolated surface generated from the CBC data using the above procedures revealed the winter distribution and abundance patterns of Turkey Vultures in the United States (see Figure 25). 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
Figure 25. Interpolated surface depicting winter Turkey Vulture distribution and abundance in the United States. Data were derived from 2,026 Christmas Bird Count sites. Contour lines are represented at 0.5 Turkey Vultures/party hour/CBC circle/year intervals.
this was the case. Migratory behavior thus may have driven the habitat selection process at these sites.

Some minor problems with the procedure used to create these graphics are evident in Figure 25. The GIS used to generate this image was incapable of representing non-integer values, and therefore, some of the area surrounding the distribution patterns depicted actually contained non-zero values, but were lost due to rounding of data values. Also, peak values in sparsely sampled areas of the country often overwhelmed surrounding areas due to limitations of the interpolation algorithm (reference the area at the Idaho-Nevada boarder). Interpolating between sampled points also resulted in a smoothed surface which may not have accurately represented the more heterogeneous distribution of birds in nature. For these reasons, the above procedures were only used as a starting point for the research conducted in this study, with the ultimate objective to significantly refine both the resolution and the accuracy of predicted Turkey Vulture distribution patterns. Nevertheless, the procedures used in this study, and the resultant graphics, gave a much more refined picture of Turkey Vulture distribution and abundance patterns than was possible from traditional species range maps.

3. 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).

<table>
<thead>
<tr>
<th>Geographic</th>
<th>R</th>
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<tbody>
<tr>
<td>May Thermal Reflectance</td>
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<tr>
<td>Elevation Standard Deviation</td>
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<td>Mean Elevation</td>
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<td>Southern Pine/Wetlands</td>
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</tr>
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<td>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 &lt; 0.001).</td>
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<tr>
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<td>Wetlands</td>
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<td>Central Oklahoma-Texas Plains</td>
<td>.066</td>
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Results from these analyses revealed that Turkey Vultures 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 Leptien 1975a,c; Leptien 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.
4. **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 which emerged as
best estimators of the bird data did not differ substantially between techniques.

Maximum R analysis is a stepwise procedure which 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 26).

The first ten steps shown in Figure 26 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 26. 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. Environmental variables added at each step in this model are listed in the table accompanying the text.

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>
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<th>Variable Added</th>
<th>Christmas Bird Count</th>
<th>Step</th>
<th>Variable Added</th>
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<td></td>
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</tr>
<tr>
<td>2</td>
<td></td>
<td>Annual Precipitation</td>
<td>2</td>
<td></td>
<td>Veg Class - Shrub/Chaparral</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>Veg Class - Barren</td>
<td>3</td>
<td></td>
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</tr>
<tr>
<td>4</td>
<td></td>
<td>Minimum Annual Temperature</td>
<td>4</td>
<td></td>
<td>Annual Precipitation</td>
</tr>
<tr>
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<td></td>
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<td>5</td>
<td></td>
<td>December Precipitation</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>Veg Class - Woodland/Savanna</td>
<td>6</td>
<td></td>
<td>December Thermal Reflectance</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>Veg Class - Shrub/Chaparral</td>
<td>7</td>
<td></td>
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</tr>
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<td>8</td>
<td></td>
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</tr>
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<td></td>
<td>Number of Frost-Free Days</td>
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<td></td>
<td>Veg Class - Wetlands</td>
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<td>10</td>
<td></td>
<td>Distance to Permanent Water</td>
<td>10</td>
<td></td>
<td>Veg Class - Forest</td>
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</table>

71
5. **Eastern Versus Western North America:**

Eastern and western subsets of the vulture data were analyzed to determine if these birds responded differently to environmental factors in different parts of their range. Examination of Figures 1 and 2 revealed a great disparity in sampling effort between east and west for both the BBS and CBC, with the eastern half of the continent much better sampled than the west. Of the 2,167 Breeding Bird Survey sites, 1,409 (65%) were east and 758 (35%) west of the hundredth meridian. The Christmas Bird Count sites were even less uniformly distributed, with 1,459 (72%) of the 2,026 sites east of the hundredth meridian and 567 (28%) west. Compounding this problem was the fact that the environment itself was much more variable in nearly every aspect in the west than the east. Consequently, it was expected that the statistical relationships and the resultant mathematical models would be much stronger, and the significance levels and correlation coefficients higher in the east than the west.

Each of the bivariate and multivariate regression analyses performed on the intact data sets described above were repeated on the split data sets except that ecoregions were dropped at this stage as they could not occur in more than one region. The statistical relationships were indeed stronger in the east than the west, due to different sample sizes, though results were much closer for the CBC than the
BBS. Some of the correlations that were highly significant for the intact data set were no longer significant when split east and west, particularly for the western CBC. This pattern was seen for nearly every analysis technique performed on the east-west split data sets. Despite this fact, the key variables that emerged as best estimators of vulture distribution generally were consistent between east and west. Table 4 lists, in order of importance from their respective correlation coefficients, the key western and eastern variables for the Breeding Bird Survey. Table 5 does the same for the Christmas Bird Count.

Results from the above analyses revealed very consistent patterns of vulture response to all geophysical factors throughout eastern and western North America and between seasons. Again, temperature factors emerged as the strongest correlates with Turkey Vulture abundances, followed by monthly thermal reflectances, and negative correlations with elevation variables. These results were also consistent with those from the continent as a whole. Minor changes in the list of vegetation classes correlated with vulture abundances were seen. Most of these changes were additions to the list of classes used by the birds and were not surprising since vegetation types were not uniformly present in the eastern and western U.S. For example, wetlands were important to vultures in the east during summer, but not in the west. However, when the
vegetation map was examined, it revealed wetlands as a very scarce habitat type and thus was not available to vultures in the west. Overall, the vegetation classes most highly correlated with summer vulture abundances were very similar to those in the continental analysis.

**TABLE 4.** Correlations between summer Turkey Vulture abundance from Breeding Bird Surveys and key environmental variables in the western and eastern United States (n = 785 west and 1,409 east, R values indicated after each factor are > 0.06 and significant at p < 0.001).
### TABLE 5. Correlations between winter Turkey Vulture abundance from Christmas Bird Counts and key environmental variables in the western and eastern United States (n = 567 west and 1,459 east, R values indicated after each factor are > 0.06 in east and > 0.02 in west and significant at p < 0.05, except p > 0.05 where noted by †).

<table>
<thead>
<tr>
<th>CHRISTMAS BIRD COUNT</th>
<th>WEST</th>
<th>EAST</th>
</tr>
</thead>
<tbody>
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<td>December Thermal Reflectance</td>
</tr>
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<td>Mean Elevation</td>
<td>-.02</td>
<td>Distance to Permanent Water</td>
</tr>
<tr>
<td>Distance to Permanent Water</td>
<td>-.04</td>
<td>Elevation Standard Deviation</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean Elevation</td>
</tr>
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<td><strong>Climatic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minimum Annual Temperature</td>
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<td>December Temperature</td>
</tr>
<tr>
<td>December Temperature</td>
<td>.06†</td>
<td>Number of Frost-Free Days</td>
</tr>
<tr>
<td>Number of Frost-Free Days</td>
<td>.06†</td>
<td>Minimum Annual Temperature</td>
</tr>
<tr>
<td>December Precipitation</td>
<td>.03†</td>
<td>Annual Precipitation</td>
</tr>
<tr>
<td>December Snow</td>
<td>-.05</td>
<td>December Precipitation</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maximum Annual Temperature</td>
</tr>
<tr>
<td><strong>Physiographic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetation (8 Category)</td>
<td></td>
<td>Vegetation (8 Category)</td>
</tr>
<tr>
<td>Grassland/Cropland</td>
<td>.02†</td>
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</tr>
<tr>
<td>Forest</td>
<td>-.02</td>
<td>Woodland/Savanna</td>
</tr>
<tr>
<td>Woodland/Savanna</td>
<td>-.05</td>
<td></td>
</tr>
</tbody>
</table>

During winter, an interesting disparity occurred in the correlation between vulture numbers and forest areas in the eastern versus western United States. Eastern vulture populations were positively associated with forests, but western populations were negatively correlated. Examining the distribution of forests in the western U.S., which are primarily in northern and mountainous regions, it was apparent that these vegetative features were not present within the geophysical boundaries vultures required during the winter. This likely explained the apparent disparity.
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.

Various temperature parameters were those most strongly correlated with Turkey Vulture abundances throughout their range. It was unclear whether temperature alone was the reason for these correlations, however, as many other factors could be related to temperature in complex ways. For example, increasing elevation inversely related to temperature at fixed latitudes. Temperature also directly, and strongly, correlated with thermal reflectance values. Various measures of temperature, such as monthly means, and annual maximums and minimums, directly affected the number of frost-free days and winter snow cover. Temperature parameters indirectly affected
vegetation coverages and classes, monthly and annual primary productivity, and various precipitation parameters.

Surely, vultures were constrained at the limits of their range by temperatures to an unquantified degree, but no clear line defining these limits could be identified, unlike the strong lines Root (1988b, 1989) found for other species. Turkey Vultures are known to exhibit a wide thermoneutral range, from 26 to 40°C, and may owe their success at occupying a broad geographical area, in part, to this ability (see Arad and Bernstein 1988, Arad et al. 1989). Within these confines, Turkey Vultures displayed a wide range of abundances that resulted from preferences for many interrelated and independent factors. For example, snow cover and extreme temperatures may have made detection and procurement of food prohibitive in more northern areas (Jackson 1903). Additionally, vultures may have been incapable of sustained soaring flight in the absence of sufficient lift created by heating of the Earth’s surface (see Pennycuick 1972, Ehrlich et al. 1988). Perhaps this may have forced them to more southern areas even if they were not restricted directly by physiological temperature constraints or food availability.

Monthly measures of thermal reflectance were also very important predictors of Turkey Vulture abundances. These correlations may have been due to the flight behavior of vultures. Turkey Vulture flight is almost exclusively
accomplished by soaring (Ehrlich et al 1988). Flapping flight in these birds is uncommon, energetically inefficient, and always of short duration.

Vultures are remarkably efficient at capturing even the slightest of updrafts to aid in foraging and migratory flights. They have a locking mechanism to maintain their wings in an extended position which results in minimal muscular energy expenditure during flight. Their wings are broad with a low aspect ratio (length to width) and low wing loading (body weight relative to surface area) which enables minor deflective updrafts to be exploited for soaring flight. Wing surfaces of this design suffer from significant aerodynamic drag, a factor which is reduced somewhat by the slotted wing tips which minimize vortices produced in flight and which provide extreme sensitivity to air currents (see Pennycuick 1972, Henty 1977, Heintzelman 1986, Ehrlich et al. 1988). These characteristics make Turkey Vultures critically dependant on thermals or deflective updrafts for any sort of sustained flight, such as during migrations (see Broun and Goodwin 1943, Heintzelman 1975a, Kerlinger and Guathreaux 1983, 1985; Kerlinger et al. 1985, Kerlinger and Moore 1989).

Meteorological conditions that produce thermals or updrafts are absent over water and Turkey Vultures do not migrate, and rarely fly for even short distances, over most water bodies. Turkey Vultures blown off course frequently
drown when they fall exhausted into the water, and they have been documented taking refuge on ships and off-shore platforms (Mote 1969). Such reluctance to fly over water may have served to confine many of the high wintering vulture concentrations seen in the Florida peninsula. This may have also partially explained the concentration of vultures along Gulf Coastal areas, as they were forced westward on their migration to avoid flying over water. Some vultures might have sustained longer migrations to avoid intraspecific competition in occupied wintering areas. It has been documented that northern Turkey Vulture populations migrate farther than southern populations (Stewart 1977, Heintzelman 1986). "Leap-frog" migrations occurred in some regions, as breeding populations progressively further north migrated farther south to find unoccupied wintering areas (Salomonson 1955, Moreau 1972, Stewart 1977, Newton 1979, Fraser and Coleman 1989). These birds may well have been migrating during the Christmas Bird Counts. Thus, migratory, rather than wintering behavior, may have driven the habitat selection process in the southern U.S.

In western North America and along the Appalachians, vultures use updrafts when mountains are oriented along the direction of migration. Such "leading line" migration may be especially evident where mountain ranges are single, narrow, and steep, with wide valleys on each side (Hoffman
Many raptor species migrate along such terrain features, and may become more concentrated by weather conditions (Broun 1951, 1963; Mueller and Berger 1961, 1967; Richardson 1978, Fuller and Mosher 1981, Robbins 1981a, Elkins 1983, Alerstam 1990). Well-defined ridge systems (Will 1980, Broun 1935, 1939, 1949; Poole 1934, Heintzelman 1975b), broken mountains (DeGarmo 1953, Hoffman 1981), hilly terrain (Gerrard and Hatch 1983), and even river bluffs (Mengel 1965, Reese 1973) are used to aid in migration by generating deflective updrafts. The majority of raptor migration surveys are conducted along these leading lines (Bednarz and Kerlinger 1989).

In areas where suitable topographic features are absent, Turkey Vultures may rely solely on thermals and are significantly dispersed over the terrain. Horizontal convective patterns or "thermal streets" (see Pennycuick 1972, Smith 1980) may enable vultures to glide long distances without losing altitude, though it is difficult to distinguish these features from vertical convective currents which may exceed one kilometer in diameter (Hardy and Ottersten 1969, Konrad 1970).

Pennycuick (1972) hypothesized that raptors may spread out during migrations in order to increase the chance of encountering favorable air currents. Turkey Vultures often locate thermals by observing other birds rising in convective air columns. Such "broad front" migrations are
well documented by radar and visual observation studies (Heintzelman 1975a, Kerlinger and Gauthreaux 1983, 1985; Kerlinger et al. 1985). Surface features that aided in leading line and broad front migrations may have been key environmental features for vultures surveyed during the CBC throughout their range.

It would be misleading to imply from the above discussion that winter vulture abundance in the southern United States were largely the result of counts of migrating birds, as this was certainly not the case. However, resident and wintering Turkey Vulture populations in these areas may have been supplemented by migrating birds. This may have explained some of the peak values seen along migratory routes within traditional wintering areas. Surveys conducted later in the winter, after all migration had occurred, might have addressed this issue.

Within the confines of larger geophysical forces, Turkey Vultures exhibited preferences for certain physiographic features and selected different vegetative habitats between seasons. For example, Turkey Vultures were most highly positively correlated with southern and eastern ecoregions during both summer and winter (Tables 1 and 2). Many of the same ecoregions appeared in the list of key variables for both the CBC and BBS. Within these ecoregions, however, vultures 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, especially when comparing eastern and western subpopulations. 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 the sampling effort disparity discussed in the results section, made the quality of available data very much lower in the west than the east, especially during winter (see Table 5). 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. Thompson et al. (1990) reported that winter vulture roosts were in forested patches but were closer to
clearings, human residences, roads, and permanent streams, and occurred in areas with significantly more conifers, land surface ruggedness and interspersion of cover types than random sites. Studies by Prior and Weatherhead (1991) in Ontario suggested that Turkey Vulture roost sites did not operate as centers for food information transfer. Intraspecific competition, preference for small-sized carrion, and low degree of kin association made proposed benefits of information transfer much less applicable to these birds than for other species of scavengers. Winter roost sites were thus likely chosen primarily for their 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). This pattern was seen in the correlation coefficients and key variables for the eastern but not for the western United States. Perhaps the lack of good thermal roost sites during winter contributed to the migratory nature of western vulture populations. Research on vulture habitat selection on their southern wintering grounds may help address these speculations.

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.

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. Air Force 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.
LITERATURE CITED:


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Stager, K.E. 1964. The role of olfaction in food location by turkey vultures (Cathartes aura). Los Angeles County Museum Contribution Sci. No. 81.


APPENDIX A. Lambert Azimuthal Equal Area projection parameters*

Parameters:
- Radius of sphere: 6,370,997.0 meters
- Longitude of central meridian: 100 00 00 West
- Latitude of origin: 45 00 00 North
- False easting: 0
- False northing: 0
- Units of measure: Meters
- Pixel size: 1,000 meters

For the Conterminous United States
- Center of pixel (1,1): (-2050000, 752000)
- Number of lines: 2,889
- Number of samples: 4,587
- Minimum bounding rectangle:
  - Lower left: (-2050500, -2136500)
  - Upper left: (-2050500, 752500)
  - Upper right: (2536500, 752500)
  - Lower right: (2536500, -2136500)

In decimal degrees of latitude and longitude:
- Lower left: (-119.9722899 23.5837576)
- Upper left: (-128.5300591 48.4030555)
- Upper right: (-65.3946489 46.7048989)
- Lower right: (-75.4163527 22.4793919)

In degrees, minutes, seconds of latitude and longitude:
- Lower left: (-119 58 20 23 35 02)
- Upper left: (-128 31 48 48 24 11)
- Upper right: (-65 23 41 46 42 18)
- Lower right: (-75 24 59 22 28 46)

*From the Conterminous U.S. AVHRR Companion Disc purchased from the USGS Earth Resources Observation System (EROS) Data Center (EDC).
APPENDIX B. Vegetation categories defined on USGS AVHRR companion disc.

0. No data
1. Cropland: corn, soybeans, cotton, sorghum
2. Cropland/grassland: sorghum/small grains, bluestem, wheatgrass
3. Cropland: spring wheat
4. Cropland: rice, soybeans, corn, cotton
5. Cropland: winter wheat, sorghum
6. Cropland: mixed dryland (sorghum, small grains)
7. Cropland: Irrigated agriculture
8. Cropland: mixed crops (wheat, corn)
9. Cropland: irrigated ag, dryland wheat, corn, soybeans
10. Cropland/woodland: small grains, big sage, wheatgrass, ponderosa
11. Cropland: small grains, sorghum, cotton
12. Cropland: mixed crops (wheat, corn, fruit, vegetables)
13. Cropland: winter wheat, sorghum
14. Cropland: irrigated agriculture
15. Cropland: irrigated agriculture, winter wheat, sorghum
16. Cropland: irrigated agriculture
17. Cropland: soybeans
18. Cropland: mixed crops (wheat, sorghum, alfalfa, oats)
19. Grassland/cropland: native pasture, mixed small grains
20. Cropland: irrigated agriculture
21. Grassland/cropland: wheatgrass, needleandthread, wheat, peas, lentils
22. Grassland/cropland: bluestem, wheatgrass, wheat/sorghum
23. Cropland: mixed crops (wheat, sorghum, alfalfa, oats)
24. Cropland: corn, soybeans
25. Cropland: irrigated agriculture
26. Cropland: irrigated agriculture
27. Cropland: cotton, soybeans, rice, corn
28. Cropland: corn, soybeans, alfalfa, flax, wheat
29. Cropland: irrigated agriculture
30. Cropland: wheat, soybeans, corn
31. Cropland: corn, soybeans
32. Cropland: irrigated agriculture
33. Cropland: soybeans, cotton, corn, rice
34. Cropland: wheat, soybeans, corn, pasture
35. Cropland: irrigated agriculture
36. Cropland/pasture: corn, soybeans, pasture/hay
37. Cropland: irrigated agriculture
38. Cropland: soybeans, cotton, rice, corn
39. Cropland/woodland: sorghum, cotton, small grains, oak, mesquite
40. Cropland/woodland: soybeans, cotton, rice corn, oak, tupelo
41. Cropland/woodland: riparian woods, irrigated ag, bluegrama
42. Cropland/woodland: corn, soybeans, flax, wheat, n. hardwoods
43. Cropland/woodland: soybeans, corn, peanuts, cotton, oak, pine
44. Cropland/woodland: soybeans, cotton, rice, corn, oak, tupelo
45. Cropland/woodland: pasture/crops, doug fir
46. Cropland/woodland: soybeans, corn, peanuts, cotton, oak, pine
47. Cropland/woodlots: corn, soybeans, sorghum, mixed woodlots
48. Cropland/woodland: mixed oak, pine, soybeans, corn, peanuts,
49. Woodland/cropland: n. hardwoods, corn, soybeans, flax, wheat
50. Cropland/woodland: citrus, pasture, slash/longleaf pine
51. Cropland/woodland: soybeans, corn, peanuts, cotton, loblolly, slash
52. Cropland/woodland: soybeans, corn, peanuts, cotton, loblolly, slash
53. Cropland/woodland: pasture/crops, doug fir, oak
54. Woodland/crop/pasture: maple, birch, beech, corn, soybeans
55. Woodland/cropland: Mixed oak, pine, soybeans, corn, cotton, peanuts
56. Cropland/woodlots: forage crops, hay, woodlots, oak, maple
57. Cropland/woodland: loblolly, slash, oak, gum, soybeans, corn, cotton
58. Grassland: wheatgrass, needlegrass, needleandthread
59. Grassland: wheatgrass, blue grama, needleandthread
60. Grassland: wheatgrass, blue grama, needleandthread
61. Grassland: wheatgrass, needelegass, needleandthread
62. Grassland: wheatgrass, needlegrass, fescue, bluestem
63. Grassland: bluestem, indiangrass, switchgrass
64. Desert shrubs: saltbrush, greasewood, shadscale
65. Desert shrubs: bursage, saltbrush, greasewood
66. Desert shrubs: creosote, mesquite, saltbrush, sand sage
67. Desert shrubs: saltbrush, sand sage
68. Desert shrubs: dropseed, sand sage, creosote
69. Desert shrubs/grass: sand sage, ricegrass, blue grama, dropseed, creosote
70. Desert shrubs/grass: blue grama, wheatgrass, buffalograss, sand sage
71. Desert shrubs/grass: dropseed, sand sage, creosote, blue grama
72. Desert shrubs/grass: grammagrasses, wheatgrass, creosote, sand sage
73. Desert shrubs: saltbrush, greasewood, big sage
74. Desert shrubs/grass: blue grama, buffalograss, sand sage, oak
<table>
<thead>
<tr>
<th>Number</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>75</td>
<td>Desert shrubs/grass: big sage, wheatgrass</td>
</tr>
<tr>
<td>76</td>
<td>Desert shrubs/grass: greasewood, sage, needlegrass</td>
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<tr>
<td>77</td>
<td>Desert shrubs/grass: greasewood, sage, rabbitbrush,</td>
</tr>
<tr>
<td></td>
<td>needlegrass</td>
</tr>
<tr>
<td>78</td>
<td>Desert shrubs/grass: big sage, rabbitbrush, wheatgrass,</td>
</tr>
<tr>
<td></td>
<td>fescue</td>
</tr>
<tr>
<td>79</td>
<td>Desert shrubs/grass: wheatgrass, needleandthread,</td>
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<tr>
<td></td>
<td>sage, greasewood</td>
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<tr>
<td>80</td>
<td>Grassland: wheatgrass, needlegrass, needleandthread</td>
</tr>
<tr>
<td>81</td>
<td>Desert shrubs/grass: big sage, rabbitbrush, wheatgrass,</td>
</tr>
<tr>
<td></td>
<td>fescue</td>
</tr>
<tr>
<td>82</td>
<td>Desert shrubs/grass: bluestem, blue grama</td>
</tr>
<tr>
<td>83</td>
<td>Desert shrubs/grass: blue grama, buffalograss, big</td>
</tr>
<tr>
<td></td>
<td>sage, saltbrush</td>
</tr>
<tr>
<td>84</td>
<td>Desert shrubs/grass: grama, buffalograss, wheatgrass,</td>
</tr>
<tr>
<td></td>
<td>creosote, mesquite</td>
</tr>
<tr>
<td>85</td>
<td>Desert shrubs/grass: big sage, wheatgrass, fescue</td>
</tr>
<tr>
<td>86</td>
<td>Grassland/pasture: blue grama, wheatgrass,</td>
</tr>
<tr>
<td></td>
<td>buffalograss</td>
</tr>
<tr>
<td>87</td>
<td>Desert shrubs/grass: grama, tobosa, creosote</td>
</tr>
<tr>
<td>88</td>
<td>Cropland/grassland: bluestem, grama, wheatgrass,</td>
</tr>
<tr>
<td></td>
<td>grains</td>
</tr>
<tr>
<td>89</td>
<td>Cropland/grassland: winter wheat, sorghum, grama,</td>
</tr>
<tr>
<td></td>
<td>buffalograss</td>
</tr>
<tr>
<td>90</td>
<td>Cropland/grassland: small grains, sorghum, blue grama</td>
</tr>
<tr>
<td>91</td>
<td>Western deciduous: aspen, mountain shrubs, grasses</td>
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<tr>
<td>92</td>
<td>Western deciduous: aspen, mountain shrubs</td>
</tr>
<tr>
<td>93</td>
<td>Mixed forest/crop: oak, hickory, mixed pine, mixed</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
</tr>
<tr>
<td>94</td>
<td>Northern hardwoods: beech, birch, maple, spruce, fir</td>
</tr>
<tr>
<td>95</td>
<td>Woodlands/pasture: beech, birch, maple, oak, pasture</td>
</tr>
<tr>
<td>96</td>
<td>Mixed hardwoods: oak, hickory, poplar, beech, walnut</td>
</tr>
<tr>
<td>97</td>
<td>Coniferous forest: subalpine conifer, pasture</td>
</tr>
<tr>
<td>98</td>
<td>Coniferous woodlands: ponderosa, chaparral, pinyon,</td>
</tr>
<tr>
<td></td>
<td>juniper</td>
</tr>
<tr>
<td>99</td>
<td>Southern pine/wetlands: slash, longleaf pine, oak,</td>
</tr>
<tr>
<td></td>
<td>palm, mangrove, wetlands</td>
</tr>
<tr>
<td>100</td>
<td>Northwest conifer/past: doug fir, Pacific silver fir,</td>
</tr>
<tr>
<td></td>
<td>w. hemlock</td>
</tr>
<tr>
<td>101</td>
<td>Western pine forest: w. white, ponderosa, lodgepole</td>
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<tr>
<td>102</td>
<td>Western pine forest: w. white, ponderosa, lodgepole</td>
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<tr>
<td>103</td>
<td>Western conifer: w. white, ponderosa, lodgepole,</td>
</tr>
<tr>
<td></td>
<td>juniper</td>
</tr>
<tr>
<td>104</td>
<td>Northwest forest: w. white, ponderosa, doug fir,</td>
</tr>
<tr>
<td></td>
<td>lodgepole</td>
</tr>
<tr>
<td>105</td>
<td>Rocky Mtn mixed forest: pinyon, juniper, grasses,</td>
</tr>
<tr>
<td></td>
<td>ponderosa</td>
</tr>
<tr>
<td>106</td>
<td>Conifer forest: lodgepole, doug fir, alpine tundra</td>
</tr>
<tr>
<td>107</td>
<td>Northwest conifer: w. white, ponderosa, lodgepole,</td>
</tr>
<tr>
<td></td>
<td>doug fir, w. hemlock</td>
</tr>
<tr>
<td>108</td>
<td>Conifer forest: w. white, ponderosa, doug fir,</td>
</tr>
<tr>
<td></td>
<td>lodgepole</td>
</tr>
<tr>
<td>109</td>
<td>Western conifer: w. white, ponderosa, lodgepole</td>
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</tbody>
</table>
110. Western conifer: w. white, ponderosa, lodgepole
111. Western conifer: w. white, ponderosa, lodgepole
112. Northwest conifer: doug fir, Pacific silver fir
113. Western conifer: w. white, ponderosa, lodgepole, doug fir
114. Western conifer: w. white, ponderosa, lodgepole
115. Northwest conifer: doug fir, Pacific silver fir
116. Northern forest/bogs: spruce, pine, wetlands, n. hardwoods
117. Western conifer: w. white, ponderosa, lodgepole, doug fir
118. Southern pine: loblolly, longleaf, slash, shortleaf
119. Southern pine: loblolly, longleaf, slash, shortleaf, oak
120. Northwest forest: w. hemlock, w. redcedar, doug fir, sitka spruce
121. Western mixed forest: ponderosa, sugar pine, doug fir, oak
122. Conif/mixed forest: ponderosa, aspen, mtn shrubs
123. Western mixed forest: lodgepole, w. white, doug fir, aspen
124. Western mixed forest: lodgepole, w. white, doug fir, aspen
125. Western mixed forest: lodgepole, w. white, doug fir, aspen
126. Northern mixed forest: maple, beech, birch, jack/red pine
127. Western mixed forest: lodgepole, doug fir, aspen
128. Western mixed forest: sugar pine, oak, chaparral, ponderosa, doug fir
129. Northern forest: oak, maple, ash, white spruce, jack pine
130. Western mixed forest: ponderosa, sugar pine, doug fir, oak
131. Northern mixed forest: maple, birch, beech, spruce, fir
132. Northern forest: maple, birch, beech, jack/red/white pine
133. Rocky Mtn mixed forest: ponderosa, lodgepole, aspen
134. Western mixed forest: lodgepole, w. white, ponderosa, aspen
135. Western mixed forest: ponderosa, sugar pine, doug fir, oak
136. Northern forest: oak, maple, ash, jack pine, red pine
137. Western mixed forest: ponderosa, sugar pine, doug fir, oak
138. Western mixed forest: ponderosa, sugar pine, doug fir, oak
139. Western mixed forest: ponderosa, sugar pine, doug fir, oak
140. Mixed forest: loblolly, slash, shortleaf, oak, gum, poplar
141. Western mixed forest: ponderosa, sugar pine, doug fir, oak
142. Northwest mixed forest: w. hemlock, w. red cedar, doug fir, oak
143. Subalpine forest/tundra: lodgepole, alpine tundra, ponderosa, w. white oak
144. Grassland/woodland: grasses, ponderosa, lodgepole
145. Grassland/chaparral: annual grasses, manzanita, oak, pine
146. Grassland/woodland: lodgepole, ponderosa, grasses
147. Grass/shrubs/woodland: bluestem, sand sage, blue grama, pinyon, juniper
148. Desert shrubs/woodland: oak, sage, prairie grasses
149. Conifer woodland: ponderosa, lodgepole, wheatgrass, sage
150. Grassland/chaparral: annual grasses, manzanita, oak, pine
151. Grassland/chaparral: annual grasses, manzanita, oak, pinyon, juniper
152. Savanna: oak, bluestem, indiangrass, switchgrass
153. Grassland/chaparral: annual grasses, manzanita, oak, pinyon, juniper
154. Desert shrubs/woodland: pinyon, juniper, grasses, sage
155. Western woodlands: w. white, ponderosa, lodgepole, oak, sage, pasture
156. Subalpine forest: lodgepole, doug fir, aspen
157. Conifer forest: lodgepole, doug fir, aspen, w. white, ponderosa
158. Woodland/pasture: w. hemlock, w. red cedar, doug fir, sitka, pasture
159. Water: water
160. Coastal wetlands: fresh/saltwater marsh
161. Coastal wetlands: fresh/saltwater marsh, bald cypress, mangrove
162. Coastal wetlands: fresh/saltwater marsh, bald cypress, mangrove
163. Coastal wetlands: fresh/saltwater marsh, bald cypress, mangrove
164. Barren: barren
165. Alpine tundra: alpine tundra
166. Alpine tundra: alpine tundra
167. Alpine tundra: alpine tundra
APPENDIX C. Reclassified vegetation categories defined on USGS AVHRR companion disc.

1. Alpine tundra
2. Barren
3. Coastal wetlands
4. Conif/mixed forest
5. Conifer forest
6. Conifer woodland
7. Coniferous forest
8. Coniferous woodlands
9. Cropland
10. Cropland/grassland
11. Cropland/pasture
12. Cropland/woodland
13. Cropland/woodlots
14. Desert shrubs
15. Desert shrubs/grass
16. Desert shrubs/woodland
17. Grass/shrubs/woodland
18. Grassland
19. Grassland/chaparral
20. Grassland/cropland
21. Grassland/pasture
22. Grassland/woodland
23. Mixed forest
24. Mixed forest/crop
25. Mixed hardwoods
26. Northeast mixed forest
27. Northern forest
28. Northern forest/bogs
29. Northern hardwoods
30. Northern mixed forest
31. Northwest conifer
32. Northwest conifer/pasture
33. Northwest forest
34. Northwest mixed forest
35. Rock Mtn mixed forest
36. Savanna
37. Southern pine
38. Southern pine/wetlands
39. Subalpine forest
40. Water
41. Western conifer
42. Western deciduous
43. Western mixed forest
44. Western pine forest
45. Western woodlands
46. Woodland/cropland
47. Woodland/pasture

104
APPENDIX D. Reclassified vegetation categories as derived from USGS AVHRR companion disc.

<table>
<thead>
<tr>
<th>New Class #</th>
<th>Class Name</th>
<th>Old Class #s</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>Alpine Tundra</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>Barren</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>Wetlands</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>Forest</td>
<td>4, 5, 6, 7, 8, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 37, 38, 39, 42, 43, 44, 45</td>
</tr>
<tr>
<td>5</td>
<td>Grassland/Cropland</td>
<td>9, 10, 11, 12, 13, 18, 19, 20, 21, 22</td>
</tr>
<tr>
<td>6</td>
<td>Shrub/Chaparral</td>
<td>14, 15, 16</td>
</tr>
<tr>
<td>7</td>
<td>Woodland/Savanna</td>
<td>17, 36, 46, 48, 49</td>
</tr>
<tr>
<td>8</td>
<td>Water</td>
<td>41</td>
</tr>
</tbody>
</table>
APPENDIX E. Ecological regions defined on USGS AVHRR companion disc in the following format:

<table>
<thead>
<tr>
<th>Numerical designation</th>
<th>Ecoregion name</th>
<th>Terrain features</th>
<th>Potential natural vegetation</th>
<th>Land use/land cover</th>
<th>Soils</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Coast range</td>
<td>Low to high mountains</td>
<td>Spruce/cedar/hemlock, Douglas fir, redwood</td>
<td>Forest and woodland mostly ungrazed</td>
<td>Udic soils of high rainfall areas</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>2.</td>
<td>Puget lowland</td>
<td>Tablelands with moderate relief, plains with hills</td>
<td>Cedar/hemlock, Douglas fir</td>
<td>Mosaic of forest, woodland, pasture, and cropland</td>
<td>Alfisols, inceptisols, mollisols, spodosols</td>
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<td>3.</td>
<td>Willamette Valley</td>
<td>Plains with hills, or open hills</td>
<td>Cedar/hemlock/fir, mosaic of oakwoods and cedar</td>
<td>Cropland with interspersion of pasture, woodland</td>
<td>Xeric mollisols, vertisols, alfisols</td>
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<td>4.</td>
<td>Cascades</td>
<td>High mountains</td>
<td>Silver and Douglas fir, fir/hemlock/spruce/cedar</td>
<td>Forest and woodland grazed</td>
<td>Udic soils of high rainfall amounts</td>
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<td>5.</td>
<td>Sierra Nevada</td>
<td>High mountains</td>
<td>Mixed conifer forest, lodgepole pine</td>
<td>Forest and woodland grazed</td>
<td>Urgisols (xerults)</td>
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<td>6.</td>
<td>Southern and central California plains and hills</td>
<td>Irregular plains, tablelands, low mountains</td>
<td>California oakwoods, chaparral, California steppe</td>
<td>Open woodland grazed</td>
<td>Light-colored soils of subhumid regions</td>
</tr>
</tbody>
</table>
7. Central California valley
   Flat plains
   California steppe, tule marshes
   Irrigated agriculture, cropland with grazing
   Recent alluvial soils

8. Southern California mountains
   High mountains
   Chaparral, California oakwoods, juniper/pinyon
   Forest and woodland mostly ungrazed
   Immature shallow soils, entisols

9. Eastern Cascades slopes and foothills
   Tablelands, plains, low and high mountains
   Western ponderosa pine
   Forest and woodland grazed
   Xeric soils of moderate rainfall areas

10. Columbia basis
    Irregular plains, tablelands, open hills
    Wheatgrass/bluegrass/fescue, sagebrush steppe
    Mostly cropland, cropland with grazed land.
    Xerolls, channeled scablands

11. Blue Mountains
    Low to high open mountains
    Grand fir/Douglas fir, ponderosa pine, spruce/fir
    Forest and woodland grazed
    Soils of interior mtns, mollisols, inceptisols

12. Snake River basin/high desert
    Tablelands, plains with hills
    Sagebrush steppe, saltbrush/greasewood
    Desert shrubland grazed, irrigated agriculture
    Aridisols, aridic mollisols

13. Northern basis and range
    Plains with low mountains, open high mountains
    Great basis sagebrush, saltbrush/greasewood
    Desert shrubland grazed
    Aridisols
14. Southern basin and range
Plains with low mountains
Creosote, creosote/bur sage, paloverde/cactus
Desert shrubland grazed and ungrazed
Aridisols

15. Northern Rockies
High mountains
Cedar/hemlock/pine, spruce/fir
Forest and woodland mostly ungrazed
Interior mountain soils with acidic rock types

16. Montana valley and foothill prairies
Mixed
Foothills prairie (wheatgrass/fescue/needlegrass)
Subhumid grassland and semiarid grazing, irrigated
Dark-colored soils of semiarid regions

17. Middle Rockies
High mountains
Douglas fir, spruce/fir, alpine meadows
Grazed and ungrazed forest and woodland
Alfisols

18. Wyoming basin
Plains with hills or low mountains
Sagebrush steppe, wheatgrass/needlegrass, juniper
Desert shrubland grazed, some irrigated agriculture
Argids, orthents

19. Wasatch and Uinta mountains
High mountains
Conifers
Forest and woodland grazed
Dark-colored soils of subhumid regions

20. Colorado plateaus
Tablelands with considerable relief
Saltbrush/greasewood/blackbrush, pj woodland, sage
Open woodland grazed, desert shrubland grazed
Light-colored soils of arid regions
21. Southern Rockies
High mountains, tablelands with high relief
Spruce/fir, alpine meadows
Forest and woodland grazed
Borals

22. Arizona/New Mexico plateau
Tablelands with considerable relief
Grama/galleta steppe, great basin sage, saltbrush
Subhumid grassland and semiarid grazing
Aridisols, entisols

23. Arizona/New Mexico mountains
Low to high mountains
Pine/Douglas fir, pj woodland, spruce/Arizona pine
Forest and woodland grazed, open woodland grazed
Dry aridisols, dry mollisols

24. Southern deserts
Plains with high hills to high mountains
Grama/tobosa shrub-steppe, shrub-savanna
Desert shrubland grazed
Aridisols, rock outcrops

25. Western high plains
Smooth to irregular plains
Grama/buffalograss
Cropland, cropland with grazing, irrigated
Dry mollisols

26. Southwestern tableland
Tablelands with moderate to considerable relief
Grama/buffalograss, sand sage/bluestem, mesquite
Subhumid grassland and grazing, some cropland
Mixed

27. Central Great Plains
Irregular plains
Bluestem/grama prairie, bluestem, buffalograss
Cropland, cropland with grazing, some irrigation
Dry mollisols
28. Flint hills  
Open hills  
Bluestem prairie  
Subhumid grassland and semiarid grazing  
Mollisols (halpudolls)

29. Central Oklahoma-Texas plains  
Irregular plains  
Oak/hickory-bluestem prairie mosaic  
Cropland with pasture, woodland and forest  
Alfisols

30. Central Texas plateau  
Tablelands w/ moderate relief, plains w/ high hills  
Juniper/oak savanna, mesquite/oak savanna  
Open woodland grazed, subhumid grassland  
Dry alfisols, dry vertisols

31. Southern Texas plains  
Smooth to irregular plains  
Mesquite/acacia savanna, mesquite/live oak savanna  
Open woodland grazed, subhumid grassland  
Vertisols

32. Texas blackland prairies  
Irregular plains  
Bluestem/needlegrass, bluestem/buffalograss  
Cropland  
Vertisols

33. East central Texas plains  
Irregular plains  
Oak/hickory  
Woodland and forest with some cropland and pasture  
Dry alfisols

34. Western gulf coastal plain  
Flat plains  
Bluestem/cordgrass prairie  
Mostly cropland, cropland with grazing  
Vertisols
35. 
South central plains
Irregular plains
Oak/hickory/pine
Woodland and forest with some cropland and pasture
Moist ultisols

36. 
Ouachita mountains
Open high hills to open low mountains
Oak/hickory/pine
Forest and woodland grazed
Moist ultisols

37. 
Arkansas valley
Plains with hills
Varied forest oak/hickory/pine, oak/tupelc, cypress
Cropland with pasture, woodland and forest
Alfisols, sandstone/shale soils

38. 
Boston mountains
Low mountains
Oak/hickory
Forest and woodland grazed
Ultisols

39. 
Ozark highlands
Open hills, high hills
Oak/hickory, oak/hickory/pine
Cropland-pasture-woodland-forest mosaic
Ultisols

40. 
Central irregular plains
Irregular plains
Bluestem prairie-oak/hickory mosaic
Cropland with grazing land, cropland
Mollisols

41. 
Northern Montana glaciated plains
Irregular plains
Gram/needlegrass/wheatgrass
Cropland, cropland with grazing
Associations of brown, regosol, and solonetz
42. Northwestern glaciated plains
Irregular plains, plains with hills
Wheatgrass/needlegrass
Cropland, cropland with grazing
Cool moist mollisols

43. Northwestern Great Plains
Plains with low to high hills, tablelands
Wheatgrass/needlegrass, grama/needlegrass
Subhumid grassland and semiarid grazing land
Mixed

44. Nebraska sand hills
Open hills
Bluestem/sandreed prairie
Subhumid grassland, semiarid grazing land
Psamments

45. Northeastern Great Plains
Smooth to irregular plains, tableland
Wheatgrass/needlegrass
cropland with grazing land
Warm dry mollisols

46. Northern glaciated plains
Flat to smooth plains
Wheatgrass/bluestem/needlegrass prairie
Cropland
Borolls

47. Western corn belt plains
Irregular plains
Bluestem prairie
Cropland
Moist warm mollisols

48. Red River valley
Flat plains
Bluestem prairie
Cropland
Aquolls
49. Northern Minnesota wetlands
   Flat plains
   Conifer bog (spruce/larch/arborvitae)
   swamp, marshland
   Soils with restricted drainage

50. Northern lakes and forests
   Smooth to irregular plains, plains with hills
   Great Lakes spruce/fir, pine/northern hardwoods
   Forest and woodland mostly ungrazed
   Podzolic

51. North central hardwood forest
   Irregular plains
   Maple/basswood, northern hardwoods (maple/birch)
   Cropland with pasture, woodland, and forest
   Podzolic

52. Driftless area
   Open hills
   Oak savanna (bluestem/oak), maple/basswood
   Cropland with pasture, woodland, and forest
   Podzolic

53. Southeastern Wisconsin till plains
   Irregular plains (10-50% with standing water)
   Maple/basswood, oak savanna, bluestem prairie
   Cropland
   Udalfs

54. Central corn belt plains
   Smooth plains
   Mosaic of bluestem prairie, panic, oak/hickory
   Cropland
   Mollisols

55. Eastern corn belt plains
   Smooth plains
   Beech/maple
   Cropland
   Alfisols
Southern Michigan/northern Indiana till plains
Irregular plains
Oak/hickory, beech/maple
Cropland with pasture, woodland, forest
Grey-brown podzolic

Huron/Erie lake plain
Flat plains
Elm/ash
Cropland
Humic Gley

Northeastern highlands
Low mountains, open low mountains
Northern hardwoods/spruce
Forest and woodland mostly ungrazed
Sodosols

Northeastern coastal zone
Irregular plains, plains with low to high hills
Appalachian oak forest
Woodland and forest with some cropland, pasture
Inceptisols

Northern Appalachian plateau
Open hills, tableland
Northern hardwoods (maple/birch/beech/hemlock)
Forest and woodland mostly ungrazed
Inceptisols

Erie/Ontario lake plain
Irregular plains
Beech/maple, northern hardwoods
Cropland with pasture, woodland and forest
Alfisols

Northern central Appalachians
Open high hills to open low mountains
Northern hardwoods, northern hardwoods/spruce
Forest and woodland mostly ungrazed
Frigid inceptisols
63. Middle Atlantic coastal plain  
Flat plains  
Oak/hickory/pine, s. floodplain forest, mixed forest  
Woodland and forest with some cropland/pasture  
Aquults

64. Northern piedmont  
Irregular plains with low to high hills  
Appalachian oak  
Cropland with pasture, woodland and forest  
Mesic udalfs and udults

65. Southeastern plains  
Smooth to irregular plains  
Oak/hickory/pine, southern mixed forest  
Mosaic of cropland, pasture, woodland, forest  
Ultisols

66. Blue Ridge Mountains  
Low mountains, open low mountains  
Appalachian oak  
Forest and woodland with some cropland, pasture  
Hapluuds, dystrochrepts

67. Central Appalachian ridges and valleys  
Open low hills to open low mountains  
Appalachian oak  
Mosaic of cropland/pasture with woodland, forest  
Mesic inceptisols

68. Southwestern Appalachians  
Open low to high mountains  
Oak/hickory/pine, mixed (maple/oak/linden/tulip)  
Mosaic of cropland, pasture, woodland and forest  
Hapludults

69. Central Appalachians  
High hills to low mountains  
Mixed mesophytic forest, oak, northern hardwoods  
Forest and woodland mostly ungrazed  
Mixed
70. Western Allegheny plateau
Low to high hills
Mixed mesophytic forest, Appalachian oak
Woodland and forest with some cropland/pasture
Alfisols

71. Interior plateau
Plains with hills, open hills, tablelands
Oak/hickory
Mosaic of cropland/pasture/woodland
Udalfs, udults

72. Interior river lowland
Irregular plains and open hills
Oak/hickory
Mosaic of cropland/pasture/woodland/forest
Wet mollisols, alfisols

73. Mississippi alluvial plain
Flat plain
Southern floodplain forest (oak/tupelo/bald cypress)
Cropland, cropland with grazing, woodland, swamp
Wet inceptisols

74. Mississippi valley loess plains
Irregular plains
Oak/hickory, oak/hickory/pine
Cropland with pasture, woodland, and forest
Fragiudalfs, hapludalfs

75. Southern central plain
Flat plains (10-50% standing water)
Southern mixed forest (beech/sweetgum/magnolia/pine)
Forest and woodland grazed, some cropland, swamp
Wet soils (aquods, aquents, aquepts, aquults)

76. Southern Florida coastal plain
Flat plains (>50% covered by standing water)
Palmetto prairie, everglades
Marshland, swamp
Wet soils (emists, aprists, aquents, aqualfs)