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Wading Bird Foraging Patterns in the Southern Everglades: Correlations to Land Elements and Surface Water Pattern

ABSTRACT

Foraging patterns of colonial wading birds (*Ciconiiformes*) in the 4300 sq km of the southern Everglades in Florida are described for 93 sampling dates during 1985 to 1995 based on observations from a systematic aerial sampling program. Sampling occurred primarily during the winter months (Dec-May) for each year with a mid-summer (August) sample. Additional months were included at the beginning of the program as well as just after hurricane Andrew. An index of bird abundance is used to examine temporal and spatial patterns as well as explore correlations with landscape and surface water coverage patterns. Location and counts of Great Egret (*Casmerobous albas*), Snowy Egret (*Egretta thula*), Great Blue Heron (*Ardea herodias*), Great White Heron (*Ardea herodias occidentalis*), White Ibis (*Eudimicus alba*), Glossy Ibis (*Eudimicus niger*), Wood Stork (*Myrcia americana*) and Roseate Spoonbill (*Ajaj ajaj*) were collected. Feeding guilds were created by pooling the above into the following: short-legged, tactile feeders (White Ibis, Glossy Ibis), long-legged, tactile feeders (Wood Storks, Roseate Spoonbills) and long-legged, visual feeders (Great Blue Herons, Great White Herons, Great Egrets).

The estimated numbers of wading birds demonstrated a peak in January, 1993 with 90,035 birds, with a minimum estimated number of 1327 birds for May, 1990. All species and feeding guilds experienced declines from December to May, although the year-to-year pattern was not always consistent. Only a fraction of this temporal pattern can be attributed to hydrology changes, although it is clear that bird abundance was positively correlated with the fraction of total area classified as being of intermediate between wet or dry. Spatial patterns of bird occurrence was highly correlated with bird abundance which was also highly correlated with water condition changes which were themselves correlated to vegetation and other landscape patterns.

This study clearly demonstrates the complexity of patterns of resource usage of colonial wading birds in the southern Everglades. More...

just two) which can rapidly change these maps.

The multidimensional classifications are attempts to examine a more parsimonious characterization of the study area than by considering all possible cross-classifications of the land element themes. The Hierarchical Landscape Classification (HLC) is the result of a traditional geographic information system analysis of the multiple layers. The Statistical Cluster Classification (Table 6) is the result of a traditional cluster analysis of the land element themes.

Table 2: Land element themes defined from existing maps.

Table 3: Land element categorizations based on aerial observations.

Table 4: Landscape classification based on multivariate analysis of land element themes.

Table 5: Major land element theme categories for each level of the Statistical Cluster Classification.

Surface Water Condition

During the monthly bird counts, each study cell was also qualitatively classified by the third observer in the plane into a surface water condition category based on the amount of the cell area covered by surface water. From 1985 through 1987, surface water conditions were classified into one of three categories: dry (absence of surface water), transitional, (a mixture of wet and dry) or wet (continuous surface water). From August, 1988 through May 1996, a five category classification scheme was used, consisting of dry/dry (absence of surface water and no groundwater visible in solution holes or ponds), dry/wet (absence of surface water but groundwater present in solution holes or ponds), dry transitional (ground surface area mostly dry but small, scattered pools of surface water present and groundwater visible in solution holes or ponds), wet transitional (ground surface area mostly wet but small, scattered dry areas present and groundwater visible in solution holes or ponds) and wet (continuous surface water over the area). For this report, the 1988-96 five category metric was recoded to the 1985-87 three category metric by considering the dry/dry and dry/wet categories as dry, the dry/transitional as transitional, and the wet/transitional and wet categories as wet. The range of surface water condition patterns can be seen in Figure 14 where patterns for May of four years, 1990, 1991, 1995 and 1996 demonstrate how the dry season can end predominately wet, predominately dry or two different type of intermediate condition.

An index of water level condition was developed to characterize dry season surface water coverage as another categorization in the development of the HLC. The number of dry season months, averaged across all study years, that a grid cell remained in the "wet" category was defined as the average annual dry season condition for that cell. The index of dry season condition (Figure 15) for each cell was computed as the average annual dry season condition computed *using only those years for with water levels were determined to be normal* ('85-'88, '90-'93, '96).

Data Analysis

Abundance

Location and cell count data of foraging colonial wading birds during each multi-species aerial survey were collected on the following species: Great Egret (*Casmerobous albas*), Snowy Egret (*Egretta thula*), Great Blue Heron (*Ardea herodias*), Great White Heron (*Ardea herodias occidentalis*), White Ibis (*Eudimicus alba*), Glossy Ibis (*Eudimicus niger*), Wood Stork (*Myrcia americana*) and Roseate Spoonbill (*Ajaj ajaj*). Pooled data were available for Small Dark Herons and Small White Herons without individual species identification. Data collected on each individual species were also pooled by feeding guilds.

Feeding guilds are defined as species with similar feeding methods and habitat utilization. These were defined as: Short-Legged Tactile Feeders (White Ibis, Glossy Ibis); Long-Legged Tactile Feeders (Wood Storks, Roseate Spoonbills); and Long-Legged Visual Feeders (Great Blue Herons, Great White Herons, Great Egrets). These guilds are somewhat arbitrary, as no two species are precisely the same in terms of habitat utilization or responses to hydrological or other environmental changes.

Two approaches to estimating bird density and computing a corresponding confidence interval are appropriate for these data. The ratio method of population estimation (Jolly, 1969; Krebs, 1989) assumes that each transect is an independent sampling unit, count data in the cells along a transect are subsamples, and the spatial arrangement of counts in cells along the transect is not used in computing confidence intervals. This approach assumes 35 unequal length sampling units available for estimating the standard error of the estimator, which usually results in computing wide confidence intervals. The discrete nature of these count data are also disregarded and normality is assumed.

The second approach, and the one reported here, incorporates the spatial information obtained in the cell counts and models the correlation between counts of neighboring cells. Using Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM) methodology (Appendix A), density estimates and associated confidence intervals were computed for the whole study area. These estimates were then converted to an overall abundance estimate. Note that these estimates were not adjusted for visibility biases and hence are very likely underestimates of the true area abundance. This approach was considered acceptable since the objective of this study was more to compare estimates across time than to accurately estimate abundance. It is assumed that the effects of visibility bias in the aerial transect methodology are consistent throughout the time period of the study, hence making comparisons across time appropriate.

In this study, it was unlikely that all cells on a transect would be equally correlated. Two main reasons are offered: cells on the east and west edge of a transect can be up to 80 kms apart and wading birds tend to aggregate when foraging. The extent of correlation in bird counts over the study area was initially assessed using a General Linear Mixed Model (GLMM, Appendix A, Littell et. al, 1996). Various formulations of this model were computationally too difficult to fit for even the project high-end UNIX workstation (IBM RISC/System 6000 running AIX with 160Mb memory). A set of non-nested models (Table 6) were constructed and fit to a subset of dates selected to represent the range of conditions encountered in the study. Based on these results the model used to estimate density for each date and each species was the Autoregressive AR(1) model. It incorporated correlation in counts among neighboring cells along a transect while assuming independence among cell counts from different transects.

Table 6. Models used to examine various dependence structures within the bird count data.

The models listed in Table 6 are of quite different structures and are not hierarchical, hence there is no method to statistically determine which model fits best. Instead, models were compared using their Schwartz's Bayesian Criterion (BIC) values for four example dates. The BIC value facilitates comparison of non-hierarchical models by adjusting the fraction of total variance (deviance) explained by the model for differences in the number of parameters estimated by each model. Larger values of BIC indicate a better model fit. Since the assumption of normally distributed errors is critical to inference with general linear mixed models, bird counts were transformed to $\log_e(\text{count}+1)$. The same approach but using a more appropriate generalized linear mixed model (GLMM, see Appendix A also) was computationally infeasible with available computer technology.

The spherical model with nugget effect had the largest number of parameters, most complex correlation structure and highest BIC values (see Table 7); however, it took hours of computational time to estimate model parameters for just one date for one species. This model was simply too complex for screening 93 dates for 13 species/guild combinations. A large jump is seen in the BIC when comparing the Autoregressive AR(1) model to the independence model. The jump in BIC was much smaller when comparing the Autoregressive AR(1) fit to any of the other more complex models. This was not unexpected, since counts were made in sequential cells along aerial transects would be expected to be more correlated between neighboring cells on a transect to counts of cells on different transects. For these reasons, the Autoregressive AR(1) correlation structure was chosen for estimating bird densities.

Table 7. Schwartz's Bayesian Criterion values for alternate GLMM models for selected dates, all species combined.

Statistical inference with mixed linear models requires the assumption of normally distributed errors. Usually for count data, a $\log_e$ transformation is applied and log counts are assumed to be normal. However, the natural log transformation can distort the correlation relationships among counts and produce unacceptable negative variance estimates. Using a generalized linear mixed

model (GLMM) it was possible to assume the more appropriate discrete exponential family of distributions (e.g. Poisson) for the count data while also incorporating the Autoregressive AR(1) structure for expected counts along each transect. A property of the Poisson distribution is that the variance of cell counts is a positive multiple of its expected value. For spatially distributed points, if the point pattern is random, cell counts should be Poisson distributed which makes the mean and variance of the counts the same. By allowing the variance of counts to be a multiplier of the expected count, a more flexible and general model is used. This extra variability assumption is examined by estimating the overdispersion parameter and testing whether it is significantly different from one. An overdispersion parameter equal to one indicates that counts follow the Poisson distribution, and is indicative of a random spatial pattern. An overdispersion parameter much greater than one indicates that the counts are aggregated or clustered. Significant overdispersion will affect the estimates of the standard errors and associated test statistics. The software used to fit this GLMM(Poisson) model (GLIMMIX macro in SAS, Littell, et al, 1996) automatically adjusts the standard errors and test statistics to account for overdispersion. Using the results of this model fitting, a program was constructed to estimate the density (birds/km²) and associated 95% confidence interval.

Associations Among Guild/Species Counts

Species associations and feeding guilds associations were examined using the Jaccard index (Pielou, 1984) calculated for each pair of species for each date. The Jaccard index was chosen over others such as Dice or Ochia because of its ease of interpretation for these data. An index value of 0 indicates no association while a value of 1 indicates perfect association. The index only measures presence/absence and does not compare densities of the birds. If two species were not seen at all during an entire survey the indices were not computed. The index was plotted over time to look for trends. A test for strongly associated species pairs was performed (Ludwig and Reynolds, 1992).

Surface Water Condition Stability

The stability of the surface water condition pattern in each cell over the dry season was assessed by examining the change in water condition classification for neighboring months: December to January, January to February, February to March, March to April, April to May, May to August, and August to December. No change in condition class between consecutive months indicated a 'stall' classification for that grid cell. A "reversal" classification was recorded when the second of two such consecutive values represented a wetter category than the first. "Progressive drying" was recorded when the second value represented a drier category than the first value.

A weighted kappa statistic (Agresti, 1984, Cohen, 1960) was used to index persistence of a surface water condition over a two month interval for the whole study area. This index ranges between values of 0 and 1, with a value of 0 indicating persistence consistent with no association in category assignment between the two months, and a value of 1 indicating perfect persistence of pattern, i.e. no cells changed category, a very non-random situation. As the kappa index goes to

zero, fewer cells have the same category in the second date than they had in the first date. The occasional negative weighted kappa value indicates a change pattern displaying no consistent pattern but which has less agreement than would be expected by chance. The weights are used to account for the fact that the probability of going from say "wet" to "transitional" may not be the same as the probability of going from "wet" to "dry".

The proportion of "transitional" cells and "wet" cells that did get drier (P_D), the proportion of "dry" cells and "transitional" cells that did get wetter (P_W), and a "change potential index" (CPI) were all used to examine the direction of change in surface water condition. All of these were used to examine the question of whether cells got drier or wetter as the year progressed. Computational details for these measures are given in Appendix C. CPI values range from -1 to 1, with positive values indicating a drying trend and negative values indicating a wetting trend. Temporal patterns in CPI, P_D and P_W were examined graphically.

Decomposition of Total Variability in Bird Counts and Importance of Environmental Correlates

The major objective of the data analysis was the search for temporal trends and spatial patterns in wading bird counts. A generalized linear modelling approach was used to assess the importance of long-term temporal trends and inter-year cycles in explaining total variability in wading bird counts. The residuals from these models represented unexplained temporal and spatial variability. The importance of land element theme classifications (Table 3 and 4) and landscape classifications (Table 5) in describing average spatial pattern was further examined by including these variables one-at-a-time as covariates in the log-linear models. Because these environmental correlates were only available as snapshot images for one period of time, it was not expected that they would explain a very significant fraction of the total temporal/spatial variation in counts.

Surface water condition was also used as a covariate in the model to examine its importance in explaining both temporal trends and spatial pattern of counts. Because surface water condition was measured concurrent with bird counts, it was expected that this measure would present the best opportunity for describing bird count patterns and trends.

Finally, the recently developed tree regression methodology (Chambers and Hastie 1992, Appendix D) was used to further examine the conditions under which high and low bird counts could be expected. This analysis approach combines regression models with hierarchical cluster analysis techniques to systematically decompose the time averaged transect/cell data into groups. The groups have different overall averages and the pooled within group variance in average cell counts is much less than the total variance for all cells.

RESULTS

Abundance

Total observed wading birds summed over all 93 sampling dates is presented in Table 8 along with the distribution of these counts to feeding guilds and individual species. These numbers are misleading since they do not take into account the spatial and temporal variability in estimated counts, but are presented here as an indication of the total sampling yield for the effort presented.

Table 8: Total counts and percentages by feeding guild and species.

Using the GLMM(Poisson w/Autogressive AR(1)) models discussed in the methods section, estimated abundance and associated 95% confidence intervals were computed. Time plots of the estimates and confidence intervals are presented in Figures 17 to 21. An indication of the degree of temporal variability in these estimates can be obtained from Table 9.

- Figure 17: Time series plot of all species estimated abundance and 95% confidence bars.
Figure 18: Time series plot of long legged tactile feeders estimated abundance and 95% confidence bars. Time series plots of individual species in this guild are also provided.
Figure 19: Time series plot of long legged visual feeders estimated abundance and 95% confidence bars. Time series plots of individual species in this guild are also provided.
Figure 20: Time series plot of short legged visual feeders estimated abundance and 95% confidence bars. Time series plots of individual species in this guild are also provided.
Figure 21: Time series plot of small dark and small white heron estimated abundance and 95% confidence bars.

Table 9: Table of minimum and maximum estimated species abundance by feeding guild and species.

Associations Among Guild/Species Counts

Table 10: Jaccard index, averaged over time, for association between guilds with associated variance of this index over time measured as the standard deviation.

Table 11: Jaccard index, averaged over time, for association between individual species with associated variance of this index over time measured as the standard deviation..

Surface Water Condition Stability

Each transect/cell on a survey date was classified as "dry", "transitional" or "wet". The proportion of the 1075 cells allocated to each water condition class forms a simplex. Simplex data can be plotted on a triangle, where the nodes of the triangle represent 100% of the cells in one of the three classes. The water condition proportions are presented in Figure 22 with line segments connecting temporal neighbors and arrows indicating the direction of time. The general pattern is one of a cycle. Starting in August the study area was predominately wet. There was a tendency for the percentage of dry cells to increase from December to May then decrease dramatically in August. At the same time, the percentage of wet cells decreased from December to May with a subsequent dramatic increase in August. The path from predominately wet to predominately dry was usually through a predominately transitional stage. The fact that the path is not a simple open form (circle) but is "filled" suggests that there was a lot of variation among years in the actual cycle.

Figure 22: Water condition fractions pattern as a simplex.

A graph of the weighted kappa statistics (Figure 23a) showed a consistent year-to-year pattern in water condition persistence. The level of agreement in consecutive classifications for transitions: Dec-Jan, Jan-Feb, Feb-Mar, Mar-Apr, Apr-May is constant for most years, with less agreement observed for the May-August transition, and only moderate agreement for the August to December transition.

Figure 23: Weighted kappa statistics, Average Drying and Wetting Proportions and Average Change Potential Index

A graph of the drying proportion, P_D , shows no clear dry season trend, but a trend could be hidden by the large amount of variation observed. P_D drops from May to August then rebounds from August to December. The wetting proportion, P_W , shows the opposite trend. The change potential index, CPI, does not demonstrate a trend during the dry season but there is a decrease from May to August and subsequent increase from August to December except for 1994.

Decomposition of Total Variability in Bird Counts and Importance of Environmental Correlates

Temporal Trend

With 93 sample dates over 12 years, it is possible to describe gross annual trends in estimated abundance (computed for the whole study area), decompose this annual trend into wet/dry seasonal effects and even further explore within season trends. Annual cycles in these patterns were examined using linear regression and by computing the proportion of total annual variability which could be explained by an average annual cycle. An inter-annual wet season/dry season

comparison was added to the model. The remaining within season variability was further decomposed into a within season average trend and a residual variation. Results of the variance decomposition analysis are given in Table 12.

Table 12: Decomposition of total variability in bird counts.

Spatial Pattern

Within each date, bird counts were distributed spatially to the 1075 sample cells in very non-random patterns. Analysis of spatial pattern begins with an examination of general spatial aspects of bird counts, then proceeds to an exploration of the correlations of bird counts to landscape aspects and surface water condition. The measure of the importance of these factors is the fraction of total count variation explained.

General Spatial Pattern

Summarizing spatial pattern with one statistic is extremely difficult. In fitting the GLMM(Poisson) model to the count data, an extra dispersion parameter was estimated. This parameter is interpreted as a measure of non-randomness of counts. Large values of the extra dispersion parameter are indicative of sample dates for which guild/species counts were aggregated more than would be expected from a random spatial pattern. Similarly, small extra dispersion parameters are indicative of a more uniform distribution of counts than would be expected. Time plots of estimated overdispersion are presented in Figures 24 to 28.

Figure 24: Estimated extradispersion by date for all species combined.

Figure 25: Estimated extradispersion by date for long legged tactile feeders.

Figure 26: Estimated extradispersion by date for long legged visual feeders.

Figure 27: Estimated extradispersion by date for short legged visual feeders.

Figure 28: Estimated extradispersion by date for small dark and small white herons.

Correlations to Land Elements

The degree to which land elements categorizations explain within date variability in bird counts was measured by adding each aspect as a covariate in the GLM(Poisson) model. Each land element theme examined provided clues to possible reasons for overall pattern of transect/cell counts observed. As a land element categorization was added to the model as a covariate, the unexplained within date variation was reduced. The percent reduction is presented for each land element theme in Table 13.

Table 13. Importance of land element themes in describing spatial pattern.

A landscape element which is not important in describing overall spatial pattern via the GLM(Poisson) model, might still provide important spatial information for specific months or

even years. This possibility was examined by computing a measure of association for each landscape element theme using a Chi-square test of homogeneity statistic to examine whether relative abundance in each category followed the relative fraction of area assigned to that category. High values of this measure indicated a sampling date for which bird utilization of the landscape did not match up with the relative distribution of space defined by the landscape theme. The individual tables can be further examined to determine where bird counts were less than expected (under-utilization) and where bird counts were greater than expected (over-utilization) (see Table 15).

Table 15. Patterns of significant over- or under-utilization of cells with land element classifications.

Correlations to Landscape Classifications

Table 15 Importance of HLC and SCC in describing spatial pattern.

Correlations to Surface Water Condition

Table 16 Importance of Surface Water Condition in describing temporal and spatial patterns.

Table 17. Patterns of significant over- or under-utilization of cells with surface water condition classifications.

Tree Regression Results

Not included at this time.

DISCUSSION

APPENDIX A

Linear Model Methodology

Generalized Linear Model

A generalized linear model (a GLM) (McCullagh and Nelder 1989) was used to examine the proportion of variability attributed to temporal and spatial effects for each species. Let n_{tcym} denote the number of birds observed in the c^{th} cell of the t^{th} transect during the y^{th} year and m^{th} month. The index c runs from 1 to the number of cells in transect t , call this C_t . The index m depends on the year. Let M_y denote the set of months sampled in year y , and let L_y denote the number of months sampled in year y . The n_{tcym} are assumed to be independent random variables with an exponential dispersion family probability density (mass) function described as:

$$f(n_{tcym}; \theta_{tcym}, \phi_{tcym}) = \exp \left(\frac{n_{tcym} \theta_{tcym} - b(\theta_{tcym})}{a(\phi_{tcym})} - c(n_{tcym}, \phi_{tcym}) \right).$$

Letting $\theta_{tcym} = \mu_{tcym}$, $b(\theta_{tcym}) = (\mu_{tcym}^2)/2$, $a(\phi_{tcym}) = \sigma_{tcym}^2$, and $c(n_{tcym}, \phi_{tcym}) = -(n_{tcym}^2/\sigma_{tcym}^2 + \log(2\pi\sigma_{tcym}^2))/2$, the probability mass function for Normally distributed data is obtained. Here, μ_{tcym} is the expected value for the data in the c^{th} cell of the t^{th} transect during the y^{th} year and m^{th} month, and σ_{tcym}^2 is the variance. While the count is not usually assumed to follow the normal distribution, in some cases the square root or natural log of the count + 1 might be reasonably assumed to be normal. In this paper, this is referred to this as the GLM(Normal) model. For this probability density function we have that:

$$\text{Mean}(n_{tcym}) = \mu_{tcym} \quad \text{and} \quad \text{Var}(n_{tcym}) = \sigma_{tcym}^2.$$

Letting $\theta_{tcym} = \log(\mu_{tcym})$, $b(\theta_{tcym}) = \mu_{tcym}$, $a(\phi_{tcym}) = \phi_{tcym}$, and $c(n_{tcym}, \phi_{tcym}) = -\log(n_{tcym}!)$, the probability mass function for the Poisson distributed counts is obtained. Here, μ_{tcym} is the expected count for the c^{th} cell of the t^{th} transect during the y^{th} year and m^{th} month, and ϕ_{tcym} is a measure of variance called the over-dispersion parameter. The parameter ϕ measures how much the variability in the counts differs from the variability expected for observations from a Poisson distribution. In this paper, this is referred to as the GLM(Poisson) model. For this probability density function we have that:

$$\text{Mean}(n_{tcym}) = \mu_{tcym} \quad \text{and} \quad \text{Var}(n_{tcym}) = \mu_{tcym} \phi_{tcym}.$$

The GLM(Poisson) model as specified above is overparameterized since there are actually two parameters for each observation. For inference purposes, the mean and over-dispersion parameterization must be simplified. This is done by relating the expected mean count to temporal and spatial variables by equating the log of μ_{tcym} to a linear function of temporal and spatial regressors. That is:

$$\log(\mu_{tcym}) = \alpha + \beta_1 y + \beta_2 y^2 + \beta_3 \sin\left(\frac{2\pi}{12}m\right) + \beta_3 \cos\left(\frac{2\pi}{12}m\right) + s(t,c)$$

and

$$\phi_{tcym} = \phi \quad (a \text{ constant})$$

This model dictates that the log of the mean number of birds per cell is modeled by three components. The first component represents the overall spatial and temporal average count. The second and third components ($\beta_1 y + \beta_2 y^2$) measure long-term trends in average count modeled as a linear and quadratic function of year. The fourth and fifth terms use sine and cosine functions to model a sinusoidal cycle having a period of twelve months. These terms assess inter-year trends in monthly counts averaged over all transect and cell counts. The last component ($s(t,c)$) refers to a general spatial function defined for all values of t and c . Its purpose is to assess the impact of a spatial categorization or classification, such as basin or pond density, on the expected count. The first two components combined measure the proportion of total count variability which can be attributed to temporal effects. The last component in the model allows us to measure the proportion of total count variability attributed to spatial effects which can be explained by a spatial categorical or classification variable.

Thus, the proportion of variability in bird counts can be partitioned into temporal and spatial effects by fitting reparameterized GLM(Poisson) models of increasing complexity, by adding the above components to the model one at a time. In normal model analysis of variance, the differences between the residual deviance (error) would be called the Type 1 sums of squares. The sequence in which variables were added to the model is: intercept, year, month, and spatial variable. Table 1 shows an example of an analysis of deviance table. For this example, the proportion of variability explained by temporal effects is calculated in the following manner. First the difference in deviances between the intercept-only model and the model containing the year and month terms is computed ($100-70=30$). Second, this difference in deviances is divided by the deviance of the intercept model ($30/100 = .30$). This final number (.30) is the proportion of variability explained by temporal effects. The proportion of variability explained by spatial effects when temporal effects have been accounted for is calculated in a similar fashion. First, the difference in deviances between the full model (year, month, and spatial variable) and the model

with only year and month terms is calculated ($70 - 50 = 20$). Next, this difference in deviances is divided by the deviance of the intercept only model ($20/100 = 0.20$). The final number (0.20) is the proportion of variability explained by the spatial variable when temporal effects have been accounted in the model. This can be written in a table as given below.

Variable	Deviance
Intercept	100
Year	80
Month	70
Spatial Variable	50

Computations for fitting the GLM(Poisson) models were performed using the SAS procedure GENMOD (SAS Institute Inc 1996). The GLM(Normal) model was not used in this paper, but would be fit using the SAS procedure, GLM (SAS Institute Inc 1996).

Generalized Linear Mixed Model

A generalized linear mixed model (GLMM) (Wolfinger and O'Connell 1993) is a broader class of generalized linear models. They were used in this paper to 1) determine the nature of spatial correlations to include in the abundance estimation model and 2) to estimate bird abundance for each species and date combination.

The initial screening models were developed from the GLM(Normal) model. In this case the $z_{tcym} = \log_e(n_{tcym} + 1)$ were assumed to follow a normal family of probability density functions with dependency in transect and cell observations taking a number of forms (see Table 5). The different models specified quite different correlation structures as follows:

Model Name	Correlation Structure
Independence	$Var(z_{tcym}) = \sigma_{ym}^2$ $Cov(z_{tcym}, z_{t'c'ym}) = 0 \quad \text{for } t \neq t'; c \neq c'$

Compound Symmetry, within a transect	$ar(z_{tcym}) = \sigma^2_{ym} + \phi^2_{ym}$ $Cov(z_{tcym}, z_{t'c'ym}) = \phi^2_{ym} \quad \text{for } t = t', c$
AR(1) within independent transects	$Var(z) = \sigma^2_{ym}$ $Cov(z_{tcym}, z_{t'c'ym}) = \sigma^2_{ym} \phi_{ym}^{ c-c' } \quad \text{for } t = t'$ $Cov(z_{tcym}, z_{t'c'ym}) = 0 \quad \text{for } t \neq t'$
AR(1) with random transects	$Var(z) = \sigma^2_{ym} + \psi^2_{ym}$ $Cov(z_{tcym}, z_{t'c'ym}) = (\sigma^2_{ym} + \psi^2_{ym}) \phi_{ym}^{ c-c' } \quad \text{for } t = t'$ $Cov(z_{tcym}, z_{t'c'ym}) = \psi^2_{ym} \quad \text{for } t \neq t'$

Spherical, no nugget effect	$Var(z) = \sigma_{ym}^2$ $Cov(z_{t_{cym}}, z_{t'_{c'}_{ym}}) =$ $[1 - 1.5(d_{t_{c'}_{c'}}/\rho_{ym}) + 0.5(d_{t_{c'}_{c'}}/\rho_{ym})^2] \quad \text{for } d_{t_{c'}_{c'}} <$ $Cov(z_{t_{cym}}, z_{t'_{c'}_{ym}}) = \sigma_{ym}^2 \quad \text{for } d_{t_{c'}_{c'}} \geq$ $d_{t_{c'}_{c'}} = \sqrt{(t-t')^2 + (c-c')^2}$
Spherical, with a nugget effect	$Var(z) = \sigma_{ym}^2 + \psi_{ym}^2$ $Cov(z_{t_{cym}}, z_{t'_{c'}_{ym}}) =$ $[1 - 1.5(d_{t_{c'}_{c'}}/\rho_{ym}) + 0.5(d_{t_{c'}_{c'}}/\rho_{ym})^2] \quad \text{for } d_{t_{c'}_{c'}} <$ $Cov(z_{t_{cym}}, z_{t'_{c'}_{ym}}) = \sigma_{ym}^2 \quad \text{for } d_{t_{c'}_{c'}} \geq$ $d_{t_{c'}_{c'}} = \sqrt{(t-t')^2 + (c-c')^2}$

For the final estimation model, the $n_{t_{cym}}$ were assumed to follow the same exponential family probability density function described for GLM(Poisson), but a dependency in the transect and cell observations for a particular sample date is modeled using a covariance structure given by:

$$Var(n_{t_{cym}}) = \mu_{ym}\phi_{ym}$$

This model specifies that observations within the same transect are correlated and cell counts

$$\text{Cov}(n_{tcym}, n_{t'c'ym}) = \mu_{ym} \phi_{ym} \varphi_{ym}^{|c-c'|} \quad \text{for } t = t'$$

$$\text{Cov}(n_{tcym}, n_{t'c'ym}) = 0 \quad \text{for } t \neq t'$$

along a transect that are closer together are more correlated than observations farther apart. Cell counts of two different transects are assumed independent. When $\varphi = 0$, this model simplifies to the GLM(Poisson). We refer to this as the GLMM(Poisson) model. The SAS macro GLIMMIX (Littell, Milliken, Stroup, and Wolfinger 1996) was used to compute estimates of the unknown parameters μ , ϕ , and φ . The parameter estimation procedure also provides standard error estimates for these parameter estimates. Using the estimate for average density, μ , bird abundance, a_{ym} , for the y^{th} year and m^{th} month was calculated by:

$$a_{ym} = \frac{N \mu_{ym}}{p_c}$$

where $N = 1075$ is the number of cells sampled on one date and p_c is 0.15 representing a 15% coverage of each cell in the aerial sampling. A confidence interval for a was also computed.

APPENDIX B

Statistical Cluster Classification Development

The land element themes (Tables 2 and 3) contain different categorizations of the 1,075 cells in the study and hence each provides a separate spatial characterization. The Statistical Cluster Classification (Table 4) was developed using standard statistical cluster analysis methods applied to eight of the land element themes (elevation, soil type, specific vegetation, basin, physiographic region, watershed, pond density, and ground surface features). The goal in developing this classification was to create groups such that cells within a class have similar land element theme values, and at the same time, cells in different classes differ as much as possible in as many of these land element categories as possible.

A two-step cluster procedure was used to create the classifications. In the first step, a hierarchical clustering procedure was used to create an initial set of cluster groups. This method uses a measure of distance or similarity to group cells. Since all eight land element variables in the analysis are categorical, a similarity measure based on indicator variables for land element variable levels was used. Thus, for example, seven indicator variables were created for elevation (call them e_1 to e_7). If a cell was classified in the i^{th} elevation category, then e_i was set to 1, otherwise e_i equaled 0. Distance between two cells was defined as Euclidean distance using all of the indicator variables. As an example, suppose the distance between two cells is based on physiographic region and pond density. The table below shows physiographic region and pond density along with the associated indicator variables for two hypothetical cells. $Ph_1 - Ph_3$ and $Po_1 - Po_3$ are the indicator variables associated with physiographic region and pond density respectively.

Cell	Physiographic Region	Pond Density	Ph_1	Ph_2	Ph_3	Po_1	Po_2	Po_3
1	1	2	1	0	0	0	1	0
2	1	3	1	0	0	0	0	0

The Euclidean distance between cells 1 and 2 is

$$[(1-1)^2 + (0-0)^2 + (0-0)^2 + (0-0)^2 + (1-0)^2 + (0-1)^2]^{1/2} = 2^{1/2}$$

This distance function counts the number of land element variables for which cells differ, multiplies the count by two, and takes the square root of the product.

The hierarchical clustering technique starts with 1,075 groups. Each group contains one observation. The two groups with the smallest distance are merged into one group. The merging process continues until it is deemed prudent to stop the process. Distance between groups is computed as the average distance between all pairs of cells between the two groups.

A characteristic of the hierarchical clustering implemented in this analysis is that once a cell is classified into a group, the cell can never leave the group. In the second step, the initial cluster groups were reconstructed using a K-means clustering algorithm (Johnson and Wichern 1992) which produces groups which were internally more consistent. The input to the k-means procedure is the number of groups created from the hierarchical procedure and each group's centroid (vector of majority values for the category code for each land element). The k-means procedure calculates the distance between a cell and the centroid of all the groups and assigns the cell to the group with the nearest centroid.

APPENDIX C

Computing drying (P_D) and wetting (P_W) proportions and the change potential index (CPI).

Let n_{ij} be the number of cells meeting both row and column conditions. That is, n_{11} is the number of cells which were dry in both Month 1 and Month 2. These counts can be arranged in the following table.

		Month 2		
		Dry	Transitional	Wet
Month 1	Dry	n_{11}	n_{12}	n_{13}
	Transitional	n_{21}	n_{22}	n_{23}
	Wet	n_{31}	n_{32}	n_{33}

The drying (P_D) and wetting (P_W) proportions and the change potential index (CPI) are computed as follows:

$$P_D = (n_{21} + n_{31} + n_{32}) / (n_{21} + n_{22} + n_{23} + n_{31} + n_{32} + n_{33})$$

$$P_W = (n_{12} + n_{13} + n_{23}) / (n_{11} + n_{12} + n_{13} + n_{21} + n_{22} + n_{23})$$

$$CPI = P_D - P_W$$

APPENDIX D

TREE REGRESSION METHODOLOGY

A tree regression analysis was performed on the count data for each species/guild combination to determine if there were cells which demonstrated consistently high or low counts over time. The analysis was performed on the sum of cell counts for dry season months only. Let $n_{tc..}$ represent the total dry season count for transect t , cell c . Let $X = [X^{(1)}, X^{(2)}, \dots, X^{(p)}]_{(t \times c) \times p}$ denote a vector of the predictor variables, in this case the land element themes, categorizations, and classifications. The measurement space, denoted Ω , for X is defined as the set of all possible combinations of values for the vector X . In the analyses using the GLM(Poisson) and GLMM(Poisson) models, the objective was to examine the relationship between $n_{tc..}$ and X using a real-valued predictor function defined on Ω .

When the exact form of the predictor equation is not known, and the dimensionality of X is such that some form of variable selection is required. Assuming a linear predictor, either a stepwise or best subsets selection algorithm is usually recommended. In the case of the GLMM(Poisson) model, this process did not result in increases in the percent variability explained. In addition, the complexity of the relationships assumed increases dramatically once one increases the number of covariates in the model.

Tree-based regression was used as an alternative to the normal variable selection methodologies. Like other robust regression techniques, tree-based regression facilitates development of predictors when its general form is not known.

In tree-based regression, the measurement space, Ω is partitioned by repeated binary splitting of subsets of Ω into two descendent subsets, starting with Ω itself. The partition of Ω is usually represented as a binary tree (Figure xxx), denoted T , with nodes, T_k , $k = 1, 2, \dots, K$. This binary recursive partitioning of Ω is done in such a way that the within node variability in observed response (total cell count) is minimized. That is, the added residual variance of the two descendent nodes is less than the residual variance in the original ancestor.

If we let Ω_k be that subset of Ω represented in the k^{th} node, then the value of the predictor function for node k is the mean of the observed responses in that node. If one designates the set of all transect/cells in the node T_k by $\{(t,c) \in T_k\}$, then the average response for this node is

$$f(x|x \in \Omega_k) = \bar{n}(x) = \bar{n}(T_k) = \frac{\sum_{(t,c) \in T_k} n_{tc..}}{\sum_{(t,c) \in T_k} 1}$$

In this way, the prediction surface (i.e. expected total cell counts) is approximated by a step

function defined on all transect/cell combinations, whose value depends on which node, T_k the combination falls into. Each subset of Ω_k really translates to a set of transect/cells, each having similar values for some subset of land element themes. The model assigns to each of these transect/cells a expected count value which is the average of all total counts all included transect/cells.

The residual sums of squares (or deviance) associated with $f(x)$, for the sample (n_{tc}, x_{tc}) is

$$R(f) = \sum_{all(t,c)} (n_{tc} - f(x_{tc}))^2 \quad (1)$$

For node T_j of tree T , define the associated residual sums of squares or residual deviance as:

$$r(T_j) = \sum_{(t,c) \in T_j} (n_{tc} - \bar{n}(T_j))^2 \quad (2)$$

The residual sums of squares for tree T is the sum of all terminal node-associated sums of squares. That is, if $T_j^*, j = 1, 2, \dots, k^*$ are the terminal nodes of tree T , then

$$R(T) = \sum_{j=1}^{k^*} \sum_{(t,c) \in T_j} (n_{tc} - \bar{n}(T_j^*))^2 \quad (3)$$

The measure of improvement observed by splitting node T_j into nodes $T_{j'}$ and $T_{j''}$ is given by

$$r(T_j) - r(T_{j'}) - r(T_{j''}) \quad (4)$$

Using this measure of improvement, the best split at a node is that split which most successfully separates the high response values from the low ones. That is, for a successful split, $\bar{n}(T_{j'}) < \bar{n}(T_j) < \bar{n}(T_{j''})$ and $R(\text{unsplit tree}) > R(\text{split tree})$.

Candidates for splits are defined through the individual components of X . Let X be composed of p components, that is the tc^{th} observation is $x'_{tc} = \{x^{(1)}_{tc}, x^{(2)}_{tc}, \dots, x^{(p)}_{tc}\}$. For an ordinal, interval or ratio component, say $X^{(l)}$, splits can be created as

$$\begin{aligned} T_{j'} &= \{(t,c) | x^{(l)}_{tc} < x^0\} \\ T_{j''} &= \{(t,c) | x^{(l)}_{tc} > x^0\} \end{aligned} \quad (5)$$

for each observed value of x^0 in the domain of $X^{(l)}$. Similarly, if $X^{(l)}$ is a nominal scale variable with observed levels $C_l = \{C_{l1}, C_{l2}, \dots, C_{lu}\}$, then splits are created as

$$\begin{aligned}
T_{j'} &= \{(t,c) | x_{ic}^{(t)} \in C', C' \subset C\} \\
T_{j''} &= \{(t,c) | x_{ic}^{(t)} \in \bar{C}', \bar{C}' \subset C, \bar{C}' \cap C' = \emptyset, \bar{C}' \cup C' = C\}
\end{aligned} \tag{6}$$

For each subset Ω_k , the split, which maximizes the improvement in residual sums of squares is chosen from among all possible splits across all components. In this way, each component is examined at each opportunity to split. This partitioning of Ω is usually performed until either 1) each terminal node has fewer than a prespecified number of observations (usually 5) or 2) the variability in each terminal node is less than some small value, usually defined to be 1% of the variance of the root node. This results in a tree which is much larger than the data can support. As with over-specification in multiple linear regression, the final predictor function is over-optimistic in that the estimate of residual variance is much smaller than it should be.

To correct for over-optimistic trees, the maximum-sized tree is pruned back to a smaller tree. Our objective is to simplify the tree without significantly sacrificing goodness-of-fit. The pruning process produces a nested sequence of trees determined by recursively snipping off the least important branches. Importance is measured by a cost-complexity index

$$R_\alpha = R(T) + \alpha |T| \tag{7}$$

where $|T|$ = number of nodes in tree T , and α is the cost-complexity parameter. For a given value of α , the optimal subtree minimizes the cost-complexity index. Optimal subtree residual variance decreases and tree size increases monotonically as α decreases. Venables and Ripley (1994) use Mallows's C_p statistic to suggest using $\alpha = K\hat{\sigma}^2$ where $\hat{\sigma}^2$ is the residual mean square for the maximum size tree and K is a value between 2 and 6.

Supplemental information on optimal tree size is obtained by examination of tree prediction error using a 10-fold cross-validation process. Here the data are divided into 10 roughly equal parts and a tree is developed using 9 parts with prediction error (residual variances) computed on the tenth part. This is done in the 10 possible ways, with prediction error averaged for optimal subtrees for specified values of α . A plot of prediction error by optimal subtree size is not necessarily monotonically decreasing but trees with minimum prediction error are candidates for optimal tree.

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Figure 1. Map of southern Everglades and Big Cypress National Preserve with sampling grid and flight line.



