SPATIAL STATISTICAL MODELING IN BIOLOGY

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Keywords: Bayesian, Cokriging, Convolution, Generalized linear model, Generalized linear mixed model, GIS, GLMM, Hierarchical, Kriging, LMM, Maximum likelihood, Markov random fields, Markov chain Monte Carlo, MCMC, Mixed model, Poisson, REML, Spectral, Variogram

Contents

1. Introduction
2. Gaussian Random Process Models
2.1. Linear Mixed Model Framework
2.2. Covariance models
2.3. Estimation and Prediction
2.3.1. Bayesian Estimation
2.4. Markov Random Field Spatial Models
2.4.1. Gaussian Markov Random Field Model
3. Non-Gaussian Random Process Models
3.1. Generalized Mixed Model Framework
3.2. Spatial GLMM Estimation and Prediction
3.2.1. Spatial GLMM Example: Mapping Bird Counts
4. Multivariate Spatial Models
4.1. Cokriging
4.2. Hierarchical Models
5. Spatiotemporal Models
6. Computation
6.1. High-Level or Low-Level Language
6.2. Bayesian Computation
6.3. Geographic Information Systems
6.4. Technology
7. Future Directions
7.1. Nonstationary Spatial Processes
7.2. Multivariate Non-Gaussian Formulations
Acknowledgments
Glossary
Bibliography
Biographical Sketches

Summary

Spatial modeling is increasingly prominent in the biological sciences as scientists attempt to characterize variability of processes that are spatially indexed. This chapter shows that the mixed model framework is useful for characterizing spatial statistical

methodology. In particular, the classical geostatistical approach known as kriging can be cast as a linear mixed model. Furthermore, the generalized linear mixed model provides a natural framework for extending the methodology to allow modeling of non-Gaussian spatial processes. The mixed model framework is also useful for describing multivariate spatial models and many spatiotemporal models. These are discussed in the chapter as well as specific issues related to covariance modeling, estimation and prediction, computation, and Bayesian methodologies.

1. Introduction

Since its inception as a discipline, statistics has provided tools by which scientists can better understand complex processes. Primarily this is because statistics is concerned with the study of variability, and all natural processes exhibit variability. As scientists seek to answer ever more challenging questions concerning processes that vary over space, the traditional statistics methods that one might learn in introductory statistics courses are not sufficient to adequately account for this variability. However, at least in principle, relatively simple extensions to simple statistical concepts such as linear models and regression provide the foundation for basic spatial statistical analysis.

Although not universally true, objects in close proximity are more alike. Consequently, one must include the effects of spatial proximity when performing statistical inference on such processes, or at least show that there is no need to do so. Including these spatial effects is important for efficient estimation of parameters, prediction, and the design of sampling networks. As a simple illustration, consider some spatial process, denoted by Y, at three locations, A, B, C such that A and B are very close together in space (i.e., adjacent plots in a field trial) and C is widely separated from both A and B. Assume the spatial process has zero mean and variance σ^2 at all spatial locations. It is then the case that

$$\text{var}[Y(A) - Y(B)] = 2\sigma^2 - 2\text{cov}[Y(A), Y(B)] \text{ and}$$
$$\text{var}[Y(A) - Y(C)] = 2\sigma^2 - 2\text{cov}[Y(A), Y(C)].$$

If the covariance is positive and decreases with distance (that is, things close together are more alike), then $\text{cov}[Y(A), Y(B)] > \text{cov}[Y(A), Y(C)]$ and thus $\text{var}[Y(A) - Y(B)] < \text{var}[Y(A) - Y(C)]$. Clearly, inference on the differences should include the effects of the spatial dependence. Such effects of spatial dependence in statistical inference have been known for a very long time. In fact, one of the arguments in favor of randomization for agricultural field trials is to mitigate the effects of such dependence. However, in many environmental and biological applications, one typically considers observational studies in which randomization is not a viable option. It is in these situations that one seeks to model the spatial dependence through the use of random field models.

The later twentieth century and beginning of the twenty-first century has seen a tremendous growth in spatial statistical methodological development and application. This is primarily a function of the rapid progression of computational technology,

hardware, software and algorithms, and the need to solve challenging problems. The corresponding propagation of Bayesian methodology into mainstream statistics has been responsible for a sizeable portion of this development. Although there is still an undercurrent of tension between traditional frequentist proponents and Bayesian proponents, most practicing statisticians recognize the advantages and disadvantages of both views and approach spatial modeling from a pragmatic perspective, using the methodology appropriate for the given problem. Thus, in this chapter, we consider a broad range of methodologies from both traditional and Bayesian perspectives.

Kriging and its derivatives constitute the most common class of spatial models used in diverse disciplines such as crop and soil science, geology, atmospheric science, and more recently in ecology and the biological sciences. Many software packages have "kriging" routines, and kriging is the core of many contemporary graduate level courses on spatial statistics. Much of the terminology common in spatial statistics today first arose within the field of geostatistics.

Kriging can be viewed as arising under a linear mixed model (LMM). LMMs have been intensively studied and have a well developed theory. Thus, understanding the basics of conventional mixed models is helpful for understanding spatial statistical models. In fact, it can be argued that the LMM perspective is natural since LMMs are widely used in biological, medical and epidemiological fields, particular in relation to *longitudinal* data, of which spatial data are a special case. When viewed from an LMM perspective, estimation and prediction of spatially correlated processes poses no additional complexity beyond that required for LMMs. This is in contrast to conventional developments of kriging, where these problems were derived independently, essentially outside of the field of statistics. Because of this, many ad hoc procedures exist within the geostatistical paradigm, and the terminology is cluttered with jargon. Conversely, linear mixed models are well-known to both statisticians and practitioners of statistics alike, and so this formulation is often simpler as an introductory framework. An additional benefit of the LMM development is that extension to non-Gaussian problems is straightforward by way of the generalized linear mixed model (GLMM) extension of the normal, linear case. The discipline of disease mapping makes widespread use of GLMMs within a spatial modeling context.

This chapter focuses on Gaussian spatial models as considered from a LMM approach, along with classical and Bayesian estimation issues. An important part of such modeling is related to the specification of realistic covariance structures, and so a discussion of this topic is included as well. We consider extensions to non-Gaussian spatial models, as well as multivariate and spatio-temporal processes. Finally, we present some topics in which there is substantial current research interest. Computational issues will be discussed as they arise.

2. Gaussian Random Process Models

Consider a spatial process $Y(\mathbf{s})$ where $\mathbf{s} \in D$, some domain in d-dimensional Euclidean space. In this chapter, we will only consider two-dimensional spatial processes. Furthermore, we assume that the process $Y(\mathbf{s})$ has a Gaussian (normal)

distribution with mean $\mu(\mathbf{s})$ and is correlated so that $c_y(\mathbf{s},\mathbf{s}') \equiv \text{cov}[Y(\mathbf{s}), Y(\mathbf{s}')]$ for some $\mathbf{s},\mathbf{s}' \in D$ where $\mathbf{s} \neq \mathbf{s}'$. We refer to such a process as a Gaussian random process or Gaussian random field.

2.1. Linear Mixed Model Framework

The classical linear mixed model generalizes the traditional linear model to include random effects. In the present context, we will equate the random effect to a correlated spatial process. A common statement of the LMM is:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{H}\alpha + \epsilon \qquad (1)$$

where $\mathbf{y}$ is an $n \times 1$ vector of responses, $\mathbf{X}$ and $\mathbf{H}$ are known matrices of independent, explanatory, or regression variables ($n \times p$ and $n \times q$, respectively, β is a $p \times 1$ vector of regression coefficients or *fixed effects*, and α and ϵ are $q \times 1$ and $n \times 1$ random vectors, respectively). Typically, columns of $\mathbf{H}$ are *indicator* variables, so that each observation is associated with a particular element of α. The usual assumption on these random effects is multivariate normality:

$$\begin{bmatrix} \alpha \\ \epsilon \end{bmatrix} \sim \text{N}\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \Sigma_\alpha & 0 \\ 0 & \Sigma_\epsilon \end{bmatrix} \right).$$

In spatial statistics one often finds the use of Gau (Gaussian) for N (normal))

In many statistical problems, including spatial statistics, one often assumes independence of the random errors, in which case $\Sigma_\epsilon = \sigma_\epsilon^2 \mathbf{I}_{n\times n}$, where $\mathbf{I}_{n\times n}$ is the n-dimensional identity matrix. The variance component σ_ϵ^2 is *measurement error variance*, and may additionally include effects of small-scale spatial variability – that is, anything unexplained by the random effect. In the field of geostatistics, σ_ϵ^2 is called the "nugget effect".

The application of this model to spatial settings is straightforward. Suppose that the response vector is spatially indexed, so that $\mathbf{y} = [y(\mathbf{s}_1),\ldots,y(\mathbf{s}_n)]'$ for spatial locations $\mathbf{s}_i, i = 1,\ldots,n$. Let the elements of α represent "spatial effects", then Σ_α is a $q \times q$ *spatial* covariance matrix where q is the number of spatial locations. In many spatial statistical problems $q = n$; i.e., there is a single response observation at each site, in which case $\mathbf{H} = \mathbf{I}_{n\times n}$. This is the essence of the model used in conventional kriging applications. The other consideration in the context of spatial applications is that prediction of "unobserved" data is of primary interest. This is in contrast to most mixed-model applications, where the primary interest is in estimation of the vectors β, perhaps the variance components σ_α^2 and σ_ϵ^2, and, to a lesser extent, α.

For the model (1) note that $\alpha \sim \text{N}(0, \Sigma_\alpha)$ and $\epsilon \sim \text{N}(0, \Sigma_\epsilon)$. One can think of this model

hierarchically, as

$$\mathbf{y} \mid \alpha \sim \mathrm{N}(\mathbf{X}\beta + \mathbf{H}\alpha, \Sigma_\epsilon) \quad (2)$$
$$\alpha \sim \mathrm{N}(0, \Sigma_\alpha). \quad (3)$$

The joint distribution is given by $f(\mathbf{y}, \alpha) = f(\mathbf{y} \mid \alpha) f(\alpha)$. One can obtain the marginal distribution for $\mathbf{y}$ by integrating out the random effects, $f(\mathbf{y}) = \int f(\mathbf{y} \mid \alpha) f(\alpha) d\alpha$, which is easily shown in this case to be

$$\mathbf{y} \sim \mathrm{N}(\mathbf{X}\beta, \Sigma_\alpha + \Sigma_\epsilon). \quad (4)$$

Thus, the marginal model (4) follows from the hierarchical formulation (2) and (3). In traditional LMM applications (e.g., longitudinal analysis) it is often convenient (and arguably more general) to proceed in terms of the marginal model, without the need for specific inference or estimation concerning the random effects. That is, one accounts for spatial dependence but is not interested in the underlying process that generates such dependence. However, for most traditional spatial applications, one is interested in performing inference on the random effects (spatial process) and the hierarchical formulation is more appropriate.

One might think of α as discrete levels of a random factor, but it is more often regarded, in spatial problems, as a *spatial random process*. Instead of the discrete multivariate normal model specification given in (1), one might instead write $y(\mathbf{s}) = \sum_j x_j(\mathbf{s})\beta_j + \alpha(\mathbf{s}) + \epsilon(\mathbf{s})$ and $\alpha(\mathbf{s}) \sim \mathrm{N}(0, \sigma_\alpha^2)$, with $\mathrm{cov}[\alpha(\mathbf{s}), \alpha(\mathbf{s}')] = \sigma_\alpha^2 r_\alpha(\mathbf{s}, \mathbf{s}')$, for some correlation function $r_\alpha()$, thus relating *observed* "levels" of the random process y with *unobserved* levels (those values which we wish to predict) of the spatial random effects process, a subtle but important aspect with regard to spatial problems. The distinction between the more traditional, vector representation (common in statistics), and the "process" representation (common in geosciences) is more a matter of tradition.

2.2. Covariance models

The essence of spatial statistics is spatial correlation, and consequently it is important to model this aspect of the problem adequately. Unfortunately, there are many limitations (having to do with both data and covariance models) which make this a difficult task. To guarantee that the covariance matrix is positive definite, the spatial covariance matrix Σ_α is assumed to be of some parametric form, indexed by the parameter θ (possibly a vector). To be more precise, the spatial covariance matrix is expressed as $\Sigma_\alpha(\theta)$. Much of the detail concerning *implementation* of contemporary spatial statistics focuses on the choice of the covariance function, and estimation of its parameters.

The covariance function describes the spatial association between the random effect at any two locations in space, say $\mathbf{s}$ and $\mathbf{s}'$:

$$\text{cov}[\alpha(\mathbf{s}),\alpha(\mathbf{s}')] = c_\alpha(\mathbf{s},\mathbf{s}';\theta).$$

If the variance of α is homogeneous, we may write $c_\alpha(\mathbf{s},\mathbf{s}') = \sigma_\alpha^2 r_\alpha(\mathbf{s},\mathbf{s}';\theta)$ where $r_\alpha()$ is the *correlation function*, being scaled by the variance component σ_α^2. Since elements of α are indexed by space, the covariance function allows one to "fill-in" the elements of $\Sigma_\alpha(\theta)$. Thus, given c_α, spatial parameters θ, and any two locations in space, $\mathbf{s}$ and $\mathbf{s}'$ (sample locations, or not), the covariance between $\alpha(\mathbf{s})$ and $\alpha(\mathbf{s}')$ may be determined.

Typically, assumptions are imposed on the process to facilitate estimation of parameters (as will be discussed further below), but also because there is a severe shortage of more general covariance models. The two usual assumptions are *second-order stationarity* and *isotropy*, the former being *translation invariance* of the second-moment structure of α, and the latter being *rotation invariance*. Normally the stationarity assumption would imply a similar constraint on the first moment structure, but we have assumed α to have mean 0, accommodating any mean nonstationarity in $\mathbf{X}\beta$. Thus, under these assumptions, the covariance between any two points is only a function of the *distance* separating them:

$$\text{cov}[\alpha(\mathbf{s}),\alpha(\mathbf{s}')] = \sigma_\alpha^2 r_\alpha(\| \mathbf{s}-\mathbf{s}' \|;\theta),$$

where $\| \mathbf{s}-\mathbf{s}' \|$ is the distance between points $\mathbf{s}$ and $\mathbf{s}'$, say Euclidean, geographic distance, etc.. This simplified correlation structure conveniently dictates the covariance between observed and unobserved values of y for which predictions are desired, a quantity required to formulate the predictor (discussed below). A common correlation model is the exponential model given by

$$r_\alpha(\| \mathbf{s}-\mathbf{s}' \|;\theta) = \exp\left(\frac{-\| \mathbf{s}-\mathbf{s}' \|}{\theta}\right).$$

There are many other models in widespread use.

In geostatistics, spatial modeling is often considered in terms of the *variogram* rather than the covariance. The variogram is an alternative description of spatial dependence and is defined as:

$$2\gamma(\mathbf{h}) \equiv \text{var}[\alpha(\mathbf{s}+\mathbf{h}) - \alpha(\mathbf{s})], \qquad (5)$$

for all $\mathbf{s},\mathbf{s}+\mathbf{h} \in D$, where D is the spatial domain of interest and $\mathbf{h}$ is some spatial lag. Note that the variogram must satisfy the condition of conditional-negative semidefiniteness to guarantee that all model-based variances are nonnegative. As with the covariance function, when the process is isotropic, the variogram is only a function of distance, so $2\gamma(\mathbf{h}) = 2\gamma(\| \mathbf{h} \|)$. Under the condition (5) and if the mean is constant, the process is said to be *intrinsically stationary*. The class of processes that are second-

order stationary are a subset of those that are intrinsically stationary. In fact, if the process is second-order stationary, then there is a simple relationship between the variogram and the covariance function, $2\gamma(\mathbf{h}) = 2[c(0) - c(\mathbf{h})]$. In general, the condition of second-order stationarity is sufficient for most processes of concern to the biological and environmental sciences. Thus, the remainder of this chapter assumes second-order stationarity.

2.3. Estimation and Prediction

A common method of parameter estimation under the mixed model is maximum likelihood estimation from the marginal distribution of $\mathbf{y}$. Under the simplifications discussed above, the marginal distribution of $\mathbf{y}$ is:

$$\mathbf{y} \sim \mathrm{N}(\mathbf{X}\beta, \sigma_\alpha^2 \mathbf{R}_\theta + \sigma_\epsilon^2 \mathbf{I}).$$

Letting λ be the vector of second-moment parameters, $(\sigma_\alpha^2, \sigma_\epsilon^2, \theta)$, and setting $\Sigma(\lambda) = \sigma_\alpha^2 \mathbf{R}_\theta + \sigma_\epsilon^2 \mathbf{I}$, the log likelihood is:

$$l(\mathbf{y} \mid \beta, \lambda) = -\frac{1}{2}\log(|\Sigma(\lambda)|) - \frac{1}{2}(\mathbf{y} - \mathbf{X}\beta)'\Sigma(\lambda)^{-1}(\mathbf{y} - \mathbf{X}\beta).$$

To obtain parameter estimates for λ we can maximize this marginal log-likelihood with respect to λ and β. The likelihood is nonlinear in the parameters and thus must be maximized numerically. The use of MLEs in spatial problems has been questioned by some practitioners since MLEs are generally biased for the (co)variance parameters. Consequently, *restricted maximum likelihood estimation* (REML) is often recommended. This leads to less bias in plug-in kriging variances.
If λ is known, the MLE of β is

$$\hat{\beta} = [\mathbf{X}\Sigma(\lambda)^{-1}\mathbf{X}]^{-1}\mathbf{X}'\Sigma(\lambda)^{-1}\mathbf{y}, \qquad (6)$$

the generalized least squares (GLS) estimate. In practice, one uses an estimate, say $\hat{\lambda}$, in place of λ producing:

$$\hat{\beta} = [\mathbf{X}\Sigma(\hat{\lambda})^{-1}\mathbf{X}]^{-1}\mathbf{X}'\Sigma(\hat{\lambda})^{-1}\mathbf{y}. \qquad (7)$$

Both estimation of the random effects (i.e., those which coincide with data locations), and prediction of "unobserved" random effects, is based on the Best Linear Unbiased Predictor (BLUP). One can derive the BLUP from several perspectives, including "distribution-free", Bayesian, and multivariate normal methods. All of these derivations either implicitly or explicitly assume that only first and second moment properties of the underlying spatial distribution are sufficient to describe the distribution.

For estimating a vector of random effects, say α_{pred}, which may include random effects corresponding to both sample locations and locations for which predictions are desired,

one must compute the quantities $\Omega = \text{cov}[\alpha_{\text{pred}}, \alpha; \lambda]$ and $\Sigma_{\text{pred}} = \text{var}[\alpha_{\text{pred}}; \lambda]$, which requires λ. The BLUP for known β and λ is

$$\hat{\alpha}_{\text{pred}} = \Omega\Sigma(\lambda)^{-1}(\mathbf{y} - \mathbf{X}\beta). \qquad (8)$$

When the components of the vector to be predicted are those random effects corresponding to data locations (i.e., $\alpha_{\text{pred}} = \alpha$), then $\Omega = \sigma_\alpha^2 \mathbf{R}_\theta$. In general, the prediction variance is

$$\text{var}(\hat{\alpha}_{\text{pred}} - \alpha_{\text{pred}}) = \Sigma_{\text{pred}} - \Omega\Sigma(\lambda)^{-1}\Omega'. \qquad (9)$$

Although the expressions for the predictor and its variance for known β and λ are convenient, these quantities are seldom known. In that case, one may plug β into (8), and it remains the BLUP; the prediction variance must be adjusted accordingly to account for the uncertainty in estimation of β. See the references for details. Accounting for unknown λ is much more difficult. In practice, the estimates obtained from MLE (or other approaches) are simply plugged into the known-λ expressions. This is the so-called "plug-in" predictor, or the estimated BLUP (EBLUP). Unfortunately, the variance computed from an analogous plug-in procedure is not, in fact, the correct variance of the EBLUP. In that case, the spatial prediction variance (9) underestimates the true variability in the predictions since it does not take into account the variability introduced by the estimation of the (co)variance parameters. Since the predictor depends on λ in a nonlinear fashion, accounting for uncertainty due to its estimation is problematic. Various approaches have been suggested to mitigate this concern (bootstrapping, empirical Bayesian, and Bayesian methods).

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Bibliography

Casella G. and George E.I. (1992). Explaining the Gibbs sampler. *The American Statistician* **46**, 167-174. [An easy-to-read explanation of one of the most popular MCMC approaches.]

Chib D.D., Cox L.H., and Ensor K.B. (1995). Understanding the Metropolis-Hastings algorithm. *The American Statistician* **49**, 327-335. [An accessible explanation of a powerful MCMC algorithm.]

Clayton D.G. (1995) Generalized linear mixed models. In *Markov Chain Monte Carlo in Practice* (Gilks W.R., Richardson S., and Spiegelhalter D.J., editors). London: Chapman and Hall. [An excellent overview of generalized linear mixed models from both frequentist and Bayesian perspectives.]

Cressie N.A.C, (1993). *Statistics for Spatial Data, Revised Edition*, New York: John Wiley and Sons.

[This book is the seminal reference on spatial statistics.]

Diggle P.J., Tawn J.A., and Moyeed, R.A. (1998). Model-based geostatistics (with discussion). *Applied Statistics* **47**, 299-350. [This paper provides the foundation for non-Gaussian spatial modeling.]

Gilks W.R., Richardson S., and Spiegelhalter D.J. (1995). *Markov Chain Monte Carlo in Practice*. London: Chapman and Hall. [One of the most practical compilations explaining MCMC.]

Higdon D. (1998) A process-convolution approach to modelling temperatures in the North Atlantic ocean. *Environmental and Ecological Statistics* **5**, 173-190. [This paper illustrates how one can model non-stationary spatial processes via a convolution approach.]

McCulloch C.E., and Searle S.R. (2001) *Generalized, Linear, and Mixed Models*, New York: John Wiley and Sons. [This text provides a nice unified framework of the modern view of linear models, linear mixed models, generalized linear models, and generalized linear mixed models.]

Robinson G.K. (1991). That BLUP is a good thing: The estimation of random effects. *Statistical Science* **6**, 15-51. [Classic paper describing best linear unbiased prediction in linear mixed models.]

Royle, J.A. and Berliner, L.M. (1999) A hierarchical approach to multivariate spatial modeling and prediction, *J. Agr. Biol. and Env. Statistics*, **4**(1):29-56. [Provides details on the hierarchical formulation of multivariate spatial models.]

Royle, J.A., Link, W.A., and Sauer, J.R. (2001) Statistical mapping of count survey data. In Predicting Species Occurrences: Issues of Scale and Accuracy, (Scott, J. M., P. J. Heglund, M. Morrison, M. Raphael, J. Haufler, B. Wall, editors). Island Press. Covello, CA. [Contains additional details on the BBS modeling example]

Stein, A., and Corsten, L.C.A. (1991) Universal kriging and cokriging as a regression procedure, *Biometrics*, **47** , 575-587. [Introduction to kriging ideas from a more traditional regression perspective.]

Ver Hoef, J.M. and Cressie, N. (1993) Multivariable spatial prediction, *Mathematical Geology*, **25**(2), 219-239. [Provides the traditional formulation of cokriging.]

Wikle C.K., Berliner L.M., and Cressie N. (1998) Hierarchical Bayesian space-time models, *Environmental and Ecological Statistics* **5**, 117-154. [This paper provides an extensive overview of hierarchical modeling of space-time dynamic processes.]

Biographical Sketches

Christopher K. Wikle obtained BS and MS degrees in atmospheric science from the University of Kansas in 1986 and 1989, respectively. From 1988 to 1991 he worked as an air pollution consultant, primarily studying potential environmental impacts of proposed power generation facilities. He then obtained an MS in statistics at Iowa State University in 1994 and a co-major PhD in both atmospheric science and statistics at Iowa State University in 1996. From 1996 to 1998 he was a visiting scientist in the Geophysical Statistics Project at the National Center for Atmospheric Research in Boulder, Colorado. He is currently Associate Professor of Statistics at the University of Missouri, Columbia. His research interests are in spatio-temporal models, hierarchical Bayesian methods, the introduction of physical information into stochastic models, statistical design of environmental monitoring networks, climate dynamics, turbulence, atmospheric waves, and the application of statistics to geophysical and environmental processes.

J. Andrew Royle obtained a BS degree in Fisheries and Wildlife Management from Michigan State University in 1990. He received Masters (1993) and PhD (1996) degrees in statistics from North Carolina State University. From 1996 to 1998 he was a visiting scientist in the Geophysical Statistics Project at the National Center for Atmospheric Research in Boulder, Colorado. Currently, he is a statistician in the Division of Migratory Bird Management with the U.S. Fish and Wildlife Service. His interests include

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