AN ABSTRACT OF THE DISSERTATION OF

Jill Ada Marie Anthony for the degree of Doctor of Philosophy in Wildlife Science presented on March 10, 2004.
Title: Wavelet Analysis: Linking Multi-scalar Pattern Detection to Ecological Monitoring.

Abstract approved: ______________________________
Lynne D. Houck

Wavelet analysis is an analytical and modeling tool for optimizing sampling efficiency and accuracy, particularly in the context of designing long-term, large-scale monitoring plans. As a pattern analysis method that accommodates and preserves non-stationarity, wavelet analysis provides novel visualization and analytical capabilities for increased insight into interactions between multi-scalar heterogeneous pattern and sampling design. Effective monitoring must involve sampling designs sufficiently detailed to detect ecologically significant patterns at multiple scales, yet logistically tractable and resource-efficient for sustained use. For this reason, methods that help optimize these objectives and contribute to the design of more efficient sampling prior to implementation are important for successful large-scale monitoring. The main objectives in this dissertation were: (1) to explore Complexity Theory as a framework for pattern analysis in ecological monitoring for conservation of species and habitat; (2) to examine the relative capabilities of semivariogram, Fourier analysis, and one-dimensional wavelet analysis to detect and classify spatio-temporal pattern in a comparison of stochastic processes, deterministic simulations, and empirical species range data for Western Meadowlarks; (3) to illustrate pattern detection and reconstruction capabilities of two-dimensional wavelet analysis in three bird species (Neotropical migrants) with varying degrees of heterogeneity (Field Sparrow, Brewer's Sparrow, and Red-eyed Vireo); and (4) to compare statistical and ecological inference and examine these approaches within the context of the statistical analyses in landscape ecology. The sampling properties and behavior of these spatial statistics are described and illustrated in a comparison of spatio-temporal patterns in species range data from the Breeding Bird Surveys. Both one- and two-dimensional wavelet analyses were better suited than semivariogram and Fourier analysis in separating signal from noise to identify and characterize ecological pattern in the Neotropical migrants. Wavelet analysis accommodates non-stationarity, compares multi-scalar pattern, localizes detected pattern to original data, provides flexibility in choice of analyzing filter, and retains the context of the pattern to view the system as a complex space-time volume. Monitoring within the framework of Complexity Theory for conservation of species and habitats will be increasingly important as we progress into the Twenty-first Century.

Wavelet Analysis:

Linking Multi-scalar Pattern Detection to Ecological Monitoring

by

Jill Ada Marie Anthony

A DISSERTATION

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APPROVED:

Major Professor, representing Wildlife Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Jill Ada Marie Anthony, Author

ACKNOWLEDGMENTS

What is life?
It is the flash of a firefly in the night.
It is the breath of a buffalo in the wintertime.
It is the little shadow which runs across the grass and loses itself in the sunset.
--Crowfoot's last words, 1890 (Blackfoot warrior and orator)

In finding my own path toward the completion of this doctorate, I have learned many profound lessons – about science, life, and the power of both attitude and passion. In my struggle to shape my own voice and identity as an emerging scholar, I have grown in my sense of self and in my sense of connectedness through relationships with others. All experiences have something to teach. Not all the lessons I've learned were wanted or appreciated; however, they have served to make me wiser and to deepen my appreciation for individuals and systems committed to support healthy living, learning, and relationships with others.

A dissertation is not written alone, although it may feel like isolation a good deal of the time. I'd like to mention a few people who helped me find my way through my dissertation journey.

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Thanks to my mother, Dorothea Anthony, and my partner, David Stephenson, for their emotional support throughout this long, long process. They persistently helped me in every way possible to keep my eye on this goal, no matter what hurdle lay along the path. These are incredible individuals whom I hold in the highest esteem. Who could ask for better friends in life than they have been to me?

How fortunate I am to have had all these wonderful and supportive companions along my journey.

I have liberated the albatross and now I am free.

CONTRIBUTION OF AUTHORS

Dr. G.A. Bradshaw was directly involved in design, interpretation, and early writing of Chapter 2; design and interpretation of Chapter 3; and editing Chapters 1 through 4. Because of her contribution to the research presented in this dissertation, she is a co-author on the manuscript submitted for publication resulting from Chapter 2 of this dissertation.

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DEDICATION

This dissertation is dedicated to
my mother, Dorothea B. Anthony, and my partner, David Stephenson.

I extend my deepest expression of love and appreciation
for the endless encouragement, support, and patience that you gave
and the sacrifices that you made during this doctoral program.

Thank you for bringing so much joy into my life.

Wavelet Analysis: Linking Multi-scalar Pattern Analysis to Ecological Monitoring

CHAPTER 1

INTRODUCTION

Given the exponential growth of human populations coupled with massive resource consumption and worldwide extinctions, the challenges facing conservation in the Twenty-first century are complex (Diamond 1984, Soule 1986, Western and Pearl 1989, Ehrlich 1997, Trauger 1999, Wilson 1999). Increased habitat fragmentation (Andren 1994), reduced biological or genetic diversity (Connor et al. 1979, Pratt and Cairns 1992), loss of endangered species (Pulliam and Babbitt 1997), effects of endocrine disruptors (Guillette et al. 1994) are just a few of the key conservation issues that operate on their own spatial and temporal scales. To mediate ecological integrity and sustainability, environmental scientists need to predict how species respond to changes in biotic and abiotic phenomena at multiple scales of space, time, and biological organization (Lubchenco et al. 1991, Kingsolver 1992, Spellerberg 1995). Long-term, large-scale monitoring programs are necessary to detect ecological pattern, to characterize its change over time, to measure current levels of variability, and to identify changes in variables that require conservation (Forman 1995, Spellerberg 1995, Suter 1995, Bradshaw et al. In Review). Conservation efforts that reduce ecosystem degradation and resource waste will allow ecosystem interactions to persist and evolve, maintaining the natural complexity and flexibility for continued use by present and future generations (Jackson et al. 1995).

An integrative approach is required to address the increasingly complex questions in conservation, because of the multivariate, multi-scalar, and multi-discipline nature of the problem. Collaboration among researchers from the applied sciences (e.g., ecology, biology, physiology, hydrology, agriculture) and from the social sciences promises better linkage between scientific perspectives and the spatial, temporal, and socio-political structure of decision-making (Lubchenco 1995, Bradshaw and Beckoff 2001). Interdisciplinary cooperation with computational physicists, mathematicians, signal processing engineers, public health specialists, and others would strengthen the approach to ecological monitoring as well. For several reasons, advanced statistics are crucial in meeting the growing need to protect species and habitats. First, ecological research is based on the ability to quantify and relate ecological pattern and phenomena (Pickett and Cadenasso 1995). Second, advanced methods (e.g., wavelet analysis, neural networks, Monte Carlo methods; Bradshaw and Spies 1992, Manly 1991, 1997, Haykin 1994) are necessary to quantify the complex spatial and temporal pattern that characterizes ecosystem complexity not captured adequately by classical methods used to quantify data structure (e.g., Morisita's Index, Ripley's K, semi-variance; Anthony 2004, Anthony and Bradshaw 2004, Anthony et al. 2004). The development of appropriate statistical methods for the study of complex ecosystems results in better design, implementation, and evaluation of monitoring strategies.

Statistical and Ecological Inference

Newly available statistical methods developed in atmospheric sciences, oceanography, and other disciplines must be adopted to improve monitoring and experimental design, analyses, and interpretation. Most importantly, closer statistical approximations of pattern in nature must be pursued to increase the accuracy of ecological inference (Bradshaw 1998, Buttenfield 2000). Statistics are only as good as their scope of inference. For example, inadequate data resolution for the scale in question and other limitations in experimental design reduce the ability to test scientific hypotheses and to verify spatially- and temporally-explicit models (Bradshaw 1998, Brugnach et al. Internal Review). These models, like those testing metapopulation theory, require field observations to evaluate computer model output (Soule 1986, Western and Pearl 1989, Hanski 1999). Often sampling properties are under-explored, such that degree of aggregation, sample size, missing values, autocorrelation of multiple individuals from the same group, interdependencies among individual observations over space and time, and other features are not taken into account. As a result, we limit our understanding of spatial, temporal, and organizational heterogeneity in ecological systems.

Wavelet Analysis

The research presented in this dissertation addresses these potential limitations and other issues that arise during pattern recognition and reconstruction with wavelet analysis in a large-scale, long-term avian monitoring program (Breeding Bird Survey; Sauer et al. 1999). One- and two-dimensional wavelet analyses detect, characterize, and quantify complex cross-scale and scale-specific patterns (Anthony 2004, Anthony and Bradshaw 2004, Anthony et al. 2004). These signal processing methods provide a means to investigate previously unexamined pattern in complex databases to answer questions we have not been able to address until now. Further, these methods offer a means to investigate patterns in the complex systems found in ecology, such as modeling prescribed wildfire boundaries for forest resource management/ecosystem restoration, evaluating the status of threatened salmonids relative to habitat quality within a watershed, or predicting the spread of invasive species.

For several reasons, wavelet analysis is well suited for multi-scale monitoring and other ecological endeavors than previously employed statistics (Anthony 2004, Anthony and Bradshaw 2004, Anthony et al. 2004). First, the assumptions for earlier statistic models often limit the accuracy of statistical inference or are not suited for complex datasets often encountered in ecology, whereas those for wavelets are compatible. For example, many ecologists have traditionally used Fourier analysis and semivariogram autocorrelation to describe the structure of ecological processes (e.g., species ranges; Bracewell 1978). However, both methods require stationarity and semivariogram is more successful at isolating single dominant patterns (Journel and Huijbregts 1978). These analyses operate under the assumption that ecological processes have a periodic pattern occurring uniformly across space and time, with a structure resembling a sine or cosine function. The description of a composite signal and the identification of an underlying pattern can be difficult when concurrent ecological processes actually vary in scale or temporal influence. This kind of variation cannot be accommodated by Fourier Transform nor semivariogram. By definition, these patterns are continuous functions, even though many ecological phenomena are discontinuous. However, semivariograms are useful in predicting the locations of static features, such as the location of mineral springs which are preferred habitat for Band-tailed Pigeons and determining the degree to which the variance in a regionalized variable depends on distance (Rossi et al. 1992). Fourier analysis is useful when data are stationary, equally spaced, and without missing values, which is present in some sound waves or it could be created in an experimental setting (Platt and Denman 1975).

Second, the flexibility of the kernel form of wavelet analysis, by its ability to tailor form to integrate individual features at one scale as a texture at multiple scales, is an advance in understanding ecological patterns as a multi-dimensional volume (as will be elaborated on below). The facility with which wavelets can visualize complex relationships such as a space-time volume captures a closer approximation of the way ecological relationships exist in nature: multi-scalar, nonlinear, and uncertain. Wavelet analysis captures a closer linkage to spatio-temporal dynamics. In this way, the research here encourages analytical methods like one- and two-dimensional wavelet analyses to be used in both a confirmatory capacity (i.e., confirming the presence of a feature from visual pattern detection of a perspective plot) and exploratory capacity (i.e., quantifying a feature not apparent in initial visual pattern detection, such as a seemingly non-existent cluster at the fourth level of scale). Wavelet analysis is also provides a complement to the shifting theoretical paradigms in ecology.

From Determinism to Complexity: An Epistemological Shift

Until relatively recently, deterministic models have provided the foundation for science and western society in general (Funtowicz and Ravetz 1990). The deterministic view assumes that knowledge is finite, given enough data, precision, accuracy, and correctness of theories. This perspective is called 'simple' (deterministic, linear) in contrast to the 'complex' view (integrated, nonlinear; *sensu* Strand 2002). In the simplest system, the whole is composed of as few parts as are needed for the system to function. The whole is a sum of the parts. A simple solar calculator is a non-ecological example. The desire may be to gather more information or data to build on the simple system, the building potential seems infinite, and building appears to predictably result in increasing returns. Many spatial and time series statistics would be applicable in a simple system (i.e., semivariogram; Journel and Huijbregts 1978).

Within the simple framework, 'complicated' represents a system composed of a large number of components that can be assembled or disassembled, but the whole is still a sum of all the parts (Cilliers 1998). A personal computer is non-ecological example of a complicated system. In a very complicated system, there is much more information than necessary for the system to function, but the system has reached the point of diminishing returns. The desire is for more information or data, even if there is no measurable increase in return. Fractal mathematics (Mandelbrot 1983) is a good example of a statistic suited for the complicated simple deterministic view.

Heisenberg's Uncertainty Principle states that in modeling time-frequency phenomena, we cannot be precise in the time domain and in the frequency domain simultaneously (Heisenberg 1927). Complexity Theory emerged as the progeny of the Uncertainty Principle and other ideas in quantum physics to shift the framework from certainty to uncertainty. This epistemological shift informs both the philosophy and implementation of science, allowing research the flexibility to be approached from either the simple or complex perspectives. The outcome in landscape ecology is that statistics, and quantification in general, are less fact than impressions of biophysical phenomena. In detecting and quantifying ecological pattern from data point to landscape, statistics morph from scientific confirmation and corroboration to glimpses into a multitude of possible states and conditions. Visually, our perception of spatial and temporal pattern in the simple view is grounded in the Dutch Realist paintings of Johannes Vermeer with crisp, photograph-like images of a Girl With a Pearl Earring (c. 1665) or A Street in Delft (c. 1658). The genius of a Vermeer is in the enthusiast's forgetting the brushstrokes all together with the precision of the image representing the object itself. In complexity, ecological pattern appears more like the French Impressionist brushstrokes of Claude Monet's Waterlilies (1903) or Japanese Bridge and Water-Lily Pond (1899). Even in Monet's painting, the intent of the image is discernable, even if it is composed of thousands of tiny strokes of paint. An observer can view a Monet with the image representation of the water lilies or the bridge in mind. Or the observer can decompose the image to focus on the brushstrokes. As science moves from the simple, deterministic perspective to the complex, uncertain model of the world, pattern analysis requires statistical methods that are accurate relative to the new model of the reciprocal relationship between pattern and process.

In the complex framework, the system is composed on a large number of interconnected components that interact with each other and with the environment in such a way that the components cannot be assembled and disassembled nor can the system be understood simply by analyzing its components (Cilliers 1998). The whole is greater than the sum of all the parts. The relationships among the components shift and change, often as a result of self-organization and often resulting in emergent properties. A computer with artificial intelligence is a non-ecological example of a complex system (e.g., an autonomous robot like SONY's dog-like AIBO or Honda's human-like ASIMO). In a complex system, no matter how much data or information you have, you will never know enough to fully understand the system. The desire is for more information or data, but there is never any measurable increase in return (e.g., The Butterfly Effect). The mathematical underpinning of quantitative methods must be complimentary to this boundless complexity. Wavelet analysis (Mallat 1988, 1989; Debauchies 1992) and neural networks (Haykin 1994) are statistical methods in landscape ecology that compliment Complexity Theory.

Wavelet analysis intrinsically trades off the time-frequency precision as this method copes with the limitations of Heisenberg's Uncertainty Principle in a data-dependent manner. Rather than being overwhelmed by the lack of structure, the mathematical basis of wavelet analysis transitions with the data from high resolution clarity to low resolution equivocality. The key to wavelet analysis' ability to address questions about complexity is the unique mathematical property of simultaneous precision in localizing the position of a feature in a signal and specificity about the frequency composition of that feature, achieving the greatest levels simultaneously possible under the Heisenberg Uncertainty Principle. During pattern analysis, the analyzing wavelets extract information about both what and where with the greatest joint resolution possible. Although the applicability of wavelet analysis in ecology was acknowledged about ten years ago (Bradshaw and Spies 1992), advancement in its practical application has been slow and fairly limited (Dale and Mah 1998, Bradshaw and Anthony 1999, Chen et al. 1999, Anthony and Bradshaw 2001, Csillag 2002, Anthony 2004, Anthony and Bradshaw 2004, Anthony et al. 2004). Much less is known about the ecological applications of two-dimensional wavelet analysis relative to one-dimensional wavelet analysis, such that it is much less well-documented (Anthony 2004). Wavelet analysis can examine multi-scalar pattern within and among scales by compacting and expanding the point of reference to match features in the data or the question of interest.

As the scientific framework shifts from the simple, deterministic model to the complex, uncertain model, data richness shifts from a paucity to a plethora of data. The trick is either discerning the right data for the scientific question of interest from the abundance of data or discerning that the right data does not exist or cannot exist. In a sense, the advent of the age of Complexity Theory in science has required/evoked an adjustment in how we relate to or think about ecology - our relationship to uncertainty, knowledge, and what knowledge constitutes. In this adjustment, landscape ecologists will have to develop ways to relate to pattern analysis in the new concept of biophysical sciences. In a complexity framework, an ecologist must come to terms with the reality that one can never know everything about the system, its patterns, or its processes. Given these guidelines, ecologists will have to strive to do the best they can, accept the uncertainty, and know nothing is definitive. How does this influence a conservationist's approach to sustainability? The emphasis in the design and implementation of data collection, management, and monitoring shifts to the means rather than the end.

This shift has several implications for wavelet analysis and the context of this dissertation. Wavelet analysis is a more sophisticated tool to look at the reciprocal relationship between pattern and process relative to several other times series and spatial statistics used in landscape ecology. Wavelet analysis provides a way to look at different aspects of the whole pattern and pieces of the pattern, because all the information is within the wavelet transform and retains the relationship among the constituents. Wavelet analysis has the flexibility to be useful in science performed under either the deterministic or the complexity framework, either ignoring uncertainty as a nuisance or embracing it as a means to inform ecological research design, implementation, and interpretation.

In adjusting landscape ecology and pattern analysis toward a Complexity approach, the statistics, tools, and techniques that existed before the shift must be evaluated for their applicability to the new goals to insure the best signal is detected and quantified. In terms of statistics, the gain and loss of data or information will make some methods more difficult to interpret and validate. Also, the shift requires the appreciation that precision is not always possible. Using the visualization example, the current deterministic view of science demands the Vermeer approach, but we are realizing that the best we can do is to create a Monet. In time, we will learn how to extract more information from the Complex perspective than the deterministic view. Other statistics will need to be compared and contrasted with wavelet analysis for their relative information loss. The ultimate goal is to learn how to appropriately detect ecosystem or landscape pattern, quantify it, and make decisions about conservation, management, and policy based on this information.

Advances in Ecological Monitoring

In many cases of long-term monitoring to date, study designs do not encompass variables on multiple levels of scale (Cohen et al. 1990). This deficit may have occurred because ecologists were not aware of multi-scalar connections or because these connections were ignored (given that technological advances at the time could not support these analyses). Thus, historical data sets are not in a format to promote linking sub-organismal effects (e.g., individual metabolic rate, mitochondrial DNA results, corticosterone levels) to landscape-level systems.

Traditional field sampling approaches have undergone considerable advances in study and experimental design to encompass multiple scales (Thompson and MacGarigal 2002, Torgersen 2002). Multiple phase and adaptive sampling provide the flexibility to identify even rare species' abundance with time-variant and heterogeneous distributions (Stohlgren et al. 1997, Thompson 1992, Ringold et al. 1996). Other monitoring efforts have adopted a hexagon sampling framework to facilitate computation and geometric concerns (Thompson 1992, Hunsaker et al. 1994).

Sophistication of data-capture technologies has reversed the data poor status to a level of abundant choices in data resolution with fairly exact locations and other data (e.g., global positioning systems [GPS], remote sensing, satellite imaging, remote cameras and microphones, automated electronic instrumentation for sampling in-stream properties; Goodchild et al. 1993, O'Neill et al. 1997). Better study design and advanced technologies have improved the efficiency and quality of longitudinal data collection and harnessed the newly introduced spatial and time series statistics for multiple scale analysis.

These analytical tools will generate new directions of research by distinguishing processes producing ecological patterns. A combination of data visualization and analysis is ideally suited for designing successful monitoring efforts within a cultural context. With pattern recognition, the influential factors and the scales on which they operate can be identified for implementation of a conservation, management, or restoration/recovery plan. By decompressing the data and reconstructing the original patterns, it is possible to suggest how to design monitoring programs to be efficient and cost-effective. Ultimately, these suggestions will be critical in designing long-term, large-scale ecosystem monitoring that is coordinated among multiple investigators for cooperative conservation efforts.

With the expanded scope of possibilities for describing and understanding ecological phenomena come new errors and uncertainties (Rastetter et al 1992, Costanza and Maxwell 1994, Heuvelink 1998). There is a lag time between computer-based capabilities of data collection and processing and simple human abilities to contextualize and effectively ascertain the meaning of such a wide array of results. Ideally, information would be collected at all scales simultaneously. Realistically, resource and logistical exigencies limit this sort of extensive field sampling. Compromises are necessary when large spatial extents or long time periods are desired. With a failure to meet statistical requirements of independence and number of samples (e.g., more than one watershed at the same latitude), questions of pseudo-replication arise (Hargrove and Pickering 1992). A consideration of design- versus model-based approaches becomes important to consider (Olsen and Schreuder 1997).

Large scale, long-term monitoring must weigh the costs and benefits of each sampling option to balance the inherent problems with the required compromises (Philippi et al. 1998). One example is how to manage image segmentation. The radiometric or geometric pixels of the encoded imagery do not correspond directly to the desired ecological unit of a tree of a bird, but contain a mixture of tree, soil, and other objects. Loss of spatial information requires an understanding of the object to pixel encoding process and several decoding steps to calculate bias introduced by sub-pixel heterogeneity and pixel aggregation errors (Rastetter et al 1994). A second example lies in understanding how to make inferences from one scale to another. This involves technical choices, such as sampling frame, sample unit, sample number, and sampling frequency (Bradshaw 1998). The efficacy of a monitoring program relies on the quality of conceptual models that describe the relationship of the sample to the desired scale of inference. Based on scaling relationships, information at one scale (e.g., woody debris at the stream reach scale) encodes information that describes patterns and processes at other scales (e.g., salmonid habitat quality at the basin scale). The development of conceptual and empirical models require extensive consideration of issues, such as the range in data resolution and the relationship between data resolution and the patterns and processes of interest. Many theoretical models are insufficiently articulated. A mechanistic, dynamic model provides the necessary context to define significant ecological change, often explicitly linking of process to an observed pattern. However, despite an increasing collection of spatially extensive data, the statistical power of large-scale monitoring is lessened by the absence of suitably detailed models to measure and test statistical significance to inform environmental decision-making.

Having considered exemplary elements of the spatial aspect of large-scale, long-term monitoring, the temporal element remains. Because time is not retrievable from spatial patterns alone, it is difficult to relate specific processes to the nested patterns in GIS snapshots, for instance (Allen and Hoekstra 1990, Cairns 1990, Peterson and Parker 1998). Until a long-term, large-scale monitoring program has been underway for some time, it is limited in the inference that can be made. The low frequency (e.g., long wavelength) patterns of slow processes (e.g., forest succession), subtle processes (e.g., 13-year El Nino), rare events (e.g., outbreak of the bubonic plague), and complex phenomena (e.g., trophic interactions) have not yet been captured in the short time series available (McClaren et al. 1995, Strayer et al. 1986). The detection of ecologically meaningful trends is difficult (Dayton et al. 1998). Change will only be detected if the time is appropriately long, the sampling frequency is appropriately spaced, the variables are appropriately selected to match the requirements for recording the event. Monitoring protocols must be carefully designed to focus on the pattern, process, or reciprocal relationship of interest, because it is not practical for any monitoring effort to encompass all aspects of a species and its habitat to date. It is doubtful that this is achievable in the future. Even satellite technologies have limitations in temporal sampling due to their set schedules for location, obscuring clouds, and unforeseen events. Thus, the temporal span of environmental data is orders of magnitude less than the available spatial extent. The absence of long-term data (the very low signal-to-noise ratio, in statistical terms) severely compromises the ability to identify trends. Many critical ecosystem questions are not yet supported with adequate time series and there is a question whether they will ever be due to financial and logistical constraints of conservation efforts. Without adequate funding and institutional commitment or some other persistent infrastructure, modeling based on short-term data is the only viable compromise for the time being. Even though this is the practical solution, caution is advised. Unsolved scaling questions, nonlinear components of pattern, interaction and cumulative effects and other unknown factors obfuscate meaningful inference of process from pattern (Karieva and Wennergren 1995). For instance, direct measurement is not possible for some elements of ecological studies (e.g., global species range). In monitoring and modeling, indirect or surrogate measures must suffice and they may not vary at the same spatial and temporal scales of the original ecological pattern or process. Thus, although technology and statistics in the Twenty-first century have advanced exponentially, accurate prediction is truly limited by critical gaps in our understanding of ecological dynamics and other facets.

Now, it is more apparent that the traditional species-specific approach to research, management, policy-making, and monitoring overlooks spatially- and temporally-explicit processes and their temporally dynamic character that influence every level of biological organization (Moloney et al. 1991, Bradshaw 1998). Integrating quantitative analysis, such as wavelets, in the sampling design and hypothesis-building phase of monitoring and experimental design of ecological strategies contribute to the integrated approach that environmental planning and management requires today. In this framework, sampling design, statistical tools, and modeling can be cross-checked and evaluated to ascertain that monitoring programs and other data techniques are appropriate for the processes they measure (Turner 1989). These approaches can: (1) identify the resources to protect, (2) distinguish the most effective level of protection, and (3) measure the success of these efforts in minimizing risks to human health and the environment. Realistic goals and well-planned conceptual and empirical models are the key to success.

Effective monitoring programs are extremely important in tracking change over long periods of time and space. The statistical methods presented here, used as a model-building tool, will improve indicator species research, monitoring programs, and risk assessment to better serve a hypothesis-testing framework in ecology. Contributions of biotic and abiotic multi-scale factors to ecological patterns and processes can be considered separately, while also considering spatial, temporal, and biological organization within the landscape. For example, conditions at the community level may substantially influence the prevalence of a specific factor via mediators at an individual level that previously appeared to be independent (Legendre and Fortin 1989). Further, if we can estimate and compare aggregations at separate biological levels, then we can target our monitoring or landscape management efforts toward the appropriate levels.

Objectives

This dissertation examined the methodology and application of four advanced spatial and times series statistics to ecological monitoring in landscape ecology. Within the framework of Complexity Theory, this study evaluated the relative abilities of semivariogram, Fourier analysis, one-dimensional-, and two-dimensional-wavelet analysis to detect and quantify multi-scale and scale-specific pattern in avian species distribution from the Breeding Bird Surveys. The four main objectives correspond to the following chapters:

(1) To explore Complexity Theory as a framework for pattern analysis in ecological monitoring for conservation of species and habitat.

(2) To examine the relative capabilities of semivariogram, Fourier analysis, and one-dimensional wavelet analysis to detect and classify spatio-temporal pattern in a comparison of stochastic processes, deterministic simulations, and empirical species range data for Western Meadowlarks.

(3) To illustrate pattern detection and reconstruction capabilities of two-dimensional wavelet analysis in three bird species with different degrees of heterogeneity (Field Sparrow, Brewer's Sparrow, and Red-eyed Vireo).

(4) To compare statistical and ecological inference and examine them within the context of these statistical analyses in avian landscape ecology.

Insights into spatial pattern in ecology with
Semivariogram, Fourier Analysis, and One-dimensional Wavelet Analysis

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Running Title: Methods in spatial ecology

ABSTRACT

One-dimensional wavelet analysis is a viable method for characterizing spatial and temporal pattern, discriminating types of pattern, and relating hierarchical phenomena across scales, thus facilitating the identification of their generative ecological processes. The wavelet transform preserves the relationship between scale and location in time series data, which is useful in describing multi-scale patterns. This paper describes the advantages of the derived function (the wavelet variance) in discriminating one-dimensional pattern. The resolution of wavelet variance is compared to semivariogram and Fourier power spectra to describe spatial or temporal data using a set of four simple, stochastic processes. To facilitate comparison, the expected value of the wavelet variance is derived explicitly in terms of the autocorrelation function. In this formalism, the wavelet variance does not show appreciable differences from the other two methods for the same scale of pattern identified in each case. However, in contrast to the semivariogram and similar to the power spectrum, the wavelet variance has the advantage of resolving periodic structure unambiguously, thereby facilitating the interpretation of multi-scale pattern. Further comparison indicates that the ability of both the wavelet variance and the power spectrum to resolve multi-scale pattern increases as the ratio of the magnitude of independent scales of pattern increases. Thus, pattern in data characterized by two or more scales is most easily identified when the ratio between their half-periods is large. One area in which the wavelet variance demonstrates a clear advantage over spectral analysis is in its flexibility in choice of basis. The form of the data deviates from a pure sinusoidal function to other morphologies (e.g., step functions). Fourier power spectral analysis introduces edge effects. Because the choice of an analyzing wavelet may be tailored to specific data morphology, the introduction of edge effects may be obviated by the use of the wavelet variance based on a given filter.

KEYWORDS

Autocorrelation, empirical, geostatistics, simulation, stochastic

INTRODUCTION

Ecological time series across large spatial and temporal scales are essential for resolving and understanding anthropogenic and natural sources of variability. Many ecological systems demonstrate changes in heterogeneity with scale (Allen and Starr 1982, Kolasa and Pickett 1991, Bradshaw and Spies 1992, Milne 1992, Wu and Qi 2000, Franklin and Mills 2003). As appreciation has increased for the existence and diversity of ecological phenomena, methods of pattern analysis were developed to characterize patterns in complex ecological data sets. In the 19th and early 20th centuries, the overall goal in spatial analyses was to separate non-random, relatively periodic or pseudo-periodic, heterogeneous distributions from background noise (Legendre et al. 1989). In these analyses, spatial homogeneity (uniformity) was assumed the null condition by convention. By the mid- and late 20th century, any departure from homogeneity and associations with biotic and abiotic components of the ecosystem were believed to indicate disturbance or deviation from a normative behavior or a state of equilibrium (Legendre et al. 1989). Currently, pattern analysis has evolved from its early beginnings of separating random from non-random signatures to quantifying and celebrating spatio-temporal variability (Legendre et al. 1989). Patterns generated by ecological processes vary not only as a function of scale, but also derive from contrasting features, such as alternating dense and sparse areas, patch types, patch size, patch shape, spacing, connectivity, anisotropy, and spatial arrangement (Grieg-Smith 1964, Usher 1975, Pielou 1977, Dale and MacIsaac 1989, Wiens and Milne 1989, Doak et al. 1992, Li and Reynolds 1995, Keitt 2000). Attention to non-random pattern has increased ecologists' awareness of the complexity and intricacies of spatial and temporal patterns.

Carefully constructed conceptual models that extend across multiple scales enhance our understanding of the reciprocal relationship between ecological patterns and processes (Jackson et al. 2000, Urban 2000). Differences in scale-heterogeneity relationships are useful in characterizing ecological systems and providing insight into processes that determine pattern at multiple scales (Watt 1947, Schneider and Piatt 1986, Cale et al. 1989, Turner 1989, Wiens and Milne 1989, Leps 1990, Menge and

Olsen 1990, Holling 1992, Levin 1992, Li and Reynolds 1995). Yet, differences in these relationships introduce some conceptual difficulties. For instance, the utility of many of these analyses is based on the assumption that observed spatial and temporal patterns are an expression of the sum, as well as interactions, of the processes driving the system (e.g., Horne and Schneider 1994). The concept of spatial and temporal dependence in biological systems exists implicitly in many ecological theories (e.g., competition, gap dynamics, predator-prey relations, species diversity; Levin and Kerster 1971, Pickett and White 1985, Legendre and Fortin 1989, Gilpin and Hanski 1991, Wiens et al. 1993, Pearson et al. 1995). However, the way in which iterative processes combine and interact is complex and therefore demands an equally sophisticated approach to the unraveling of the resultant patterns. The complexity of pattern results from the confounding factors of time, space, and interacting biotic and abiotic processes. This complexity requires analyses that both identify and resolve these relationships. Therefore, spatial methods must quantify pattern, discriminate types of pattern, and relate hierarchical phenomena across scales. Not only is the challenge to develop this methodology, but also to incorporate it into the analysis and theory of ecological processes. Although the direct relationship between pattern and process is difficult to define precisely (Shipley and Keddy 1987, Leps 1990), new methods and approaches increase the accuracy of these connections and generate new hypotheses to be tested about the reciprocal relationship between pattern and process.

Advances in computational and technological ability have facilitated the development of methods to quantify pattern and to provide insight into the underlying ecological processes (Platt and Denman 1975, Powell 1987, Dale and MacIsaac 1989, Moloney et al. 1991, Fortin et al. 2003). Landscape ecologists have applied a myriad of techniques to a relatively diverse set of problems in spatial analysis (Grieg-Smith 1964, Usher 1975, Ripley 1978, Ripley 1981, Mandelbrot 1982, Carpenter and Cheney 1983, Kenkel 1988, Dale and Blundon 1990, Cullinan and Thomas 1992, Milne 1992, Plotnick et al. 1993, McGarigal and Marks 1995, Plotnick et al. 1996, Larsen and Bliss 1998, Dale 2000, Schick and Urban 2000, Wu et al. 2000, Dale et al. 2002). Included among these techniques is a separate class of methods that use the autocorrelation function as the basis for the description of spatial structure (Rossi et al. 1992, Dale et al. 2002). While only the spatial domain will be discussed henceforth, space and time are largely interchangeable (i.e., dynamic spatial patterns determine temporal patterns). Autocorrelation function methods describe spatial structure by representing the data transect as a single realization of a stochastic process in which the spatial correlation is used to estimate statistical properties of the process over a range of scales. The advantage of a spatial stochastic approach over a deterministic-mechanistic approach is twofold: providing a continuous measure of pattern across scale within the limits of data resolution, and providing a statistical framework that can relate pattern to process and model to data with the quantification of pattern. From the prospective of ecological inference, the empirically derived autocorrelation function is a measure of independence of the biological variable from the spatially defined abiotic environment (e.g., marine biota, vegetation, soil microbes; Platt and Denman 1975, Powell 1987, Schick and Urban 2000, Franklin and Mills 2003).

Variography and spectral analysis are familiar techniques based on autocorrelation. These techniques have identified marine and terrestrial processes at various scales (e.g., seabird predator-prey spatial variance [Logerwell et al. 1998], vegetation community structure at stand levels [Renshaw and Ford 1984], and conifer forest structure at landscape levels [Cohen et al. 1990, Lundquist and Sommerfeld 2002]). Wavelet analysis is less common, but its use is increasing as awareness of the importance of pattern in linear features increases (Bradshaw and Spies 1992, Bradshaw and McIntosh 1994, Dale and Mah 1998, Saunders et al. 1998, Chen et al. 1999, Keitt 2000, Csillag and Kabos 2002) and as accessible software is developed (e.g., Splus, Mathematica, Matlab, Maple). All three methods have advantages and disadvantages, and the extent of their use is also a reflection of their preferred use by specific scientists. Selecting the appropriate method for an ecological question from the wide variety of analytical methods proposed can be difficult, especially when colleagues favor one approach over another and results from different methods can be conflicting. Thus, understanding the detection and quantification capabilities of a given method is critical in formulating an accurate interpretation of pattern analysis in spatial ecology.

In this paper, we provide an example of how to distinguish three alternative representations of spatial pattern analysis. We evaluate the ability of semivariogram, Fourier analysis, and one-dimensional wavelet analysis to detect and classify pattern in spatial ecology. We explore how the results of these spatial statistics can be compared using simulated data. Also, we incorporate these metrics into the analysis and interpretation of empirical ecological data. In the process, we clarify the questions for which each method excels in order to facilitate the selection of the appropriate method by ecologists. Our intention is for this comparison to provoke some reflection on the objectives and nature of pattern analysis, in particular the question of accuracy.

METHODS

OVERVIEW FOR COMPARISON OF THE THREE STATISTICS

We give a brief overview of their comparable metrics and then we calibrate semivariogram, Fourier, and wavelet analyses. Initially, one-dimensional wavelet analysis was prepared for comparison by calculating the wavelet variance from the wavelet transform. Then, all three mathematical expressions were redefined into common notation using the autocorrelation function. Finally, all three functions were translated to the frequency domain. These first steps are essential for comparing the properties of these three statistics.

Brief Review for Interpreting the Graphical Representations of the Three Statistics

The semivariogram represents spatial variability as a measure of the global average of structure in the data (Journel and Huijbregts 1978, Carr 2002). The similarity between all pair wise combinations of two points in the transect matrix is indicated as the average squared difference in the spatial correlation as a function of the distance between the points. The resulting vector has both a direction and distance value that characterize the increase or decrease in the curve. The semivariogram increases from a value near distance 0 along the transect (i.e., nugget) to its maximum value (i.e., sill) at a critical distance beyond which the graph remains relatively constant (i.e., range) or decreases. The lag is the distance along the transect. The nugget represents the inherent variability of the sample at a very small scale. The sill represents the sample variance among these spatially independent points. The range is the distance beyond which the points are no longer correlated (i.e., covariance becomes zero). Thus, the range indicates the distance along the transect after which the points are spatially independent, indicating the limit of the zone of influence of a single point in the sample. At the range, the curve becomes more or less constant or even decreases. The range indicates the characteristic scale over which the variable is correlated. Small ranges indicate data with values that change rapidly over space. A large range represents more spatial regularity. A relatively flat curve indicates a random pattern, lacking spatial dependencies.

Similar to the semivariogram, Fourier spectral analysis describes the global average of the structure in the data (Ripley 1978, Renshaw and Ford 1984, Legendre and Legendre 1998). The power spectrum partitions the variance of a signal into the contributions from different frequencies and determines the relative magnitude of each component. The periodogram is a graphical representation of power spectral analysis, representing the simultaneous least squares fit of a linear combination of sine and cosine functions to the original data. We did not specify a weighting statement to smooth the periodogram. Thus, the variability in the dataset was retained and the output was more comparable to the other time series methods. Spectral density or energy (magnitude of the function, amplitude) was plotted as a function of frequency. Peaks indicated either change in pattern at that scale, at dominant spatial or temporal scales, or at patch size.

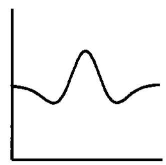
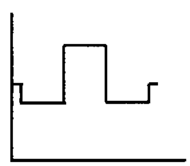
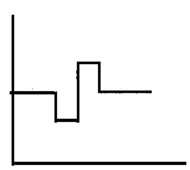
Because Fourier analysis assumes sine and cosine wave patterns, a large amplitude at a particular frequency indicates the characteristic scale of the data or the patch size. In periodograms, low frequencies represent long cycles or large scales and high frequencies are associated with short cycles or small scales. We plotted both axes on a logarithmic scale to observe small signals more easily and to observe small and large amplitude signals simultaneously. Cyclic patterns were detected clearly; however, there was a lot of variability with small spurious peaks. For the stochastic processes and deterministic simulations, we calculated scale with the inverse relationship between frequency and period (i.e., wavelength or period or scale = 1/frequency). On the log scale, each frequency has the same importance. For instance, a frequency of zero indicates an infinite cycle. A frequency of 0.5 indicates a cycle of two data points. For the empirical data, we calculated scale with a conversion to kilometers along the transect (i.e., wavelength or period or scale = [2pi/frequency]*5.57 km).

One-dimensional wavelet analysis represents spatial variability by mathematically approximating a data series with a linear combination of functions with specific resolution (i.e., scale) and location along the transect (Mallat 1989, Daubauchies 1992, Meyer 1993, Bruce and Gao 1994). Similar to the sine and cosine bases of Fourier analysis, wavelet analysis uses short waves as bases (i.e., analyzing wavelet, basis, filter). The shape, period, and frequency of the analyzing wavelets are flexible among analyses. The analyzing wavelet may be one of several functions fulfilling definable admissibility requirements (Table 2.1; Daubechies et al. 1986, Daubechies 1988, Mallat 1988, Daubechies 1992). The selection of an analyzing wavelet depends on the objectives of the study and physical structure of the data (e.g., width, smoothness, symmetry). For example, the Haar function has a step function configuration, which is well suited for edge and gradient detection (Gamage 1990, Bradshaw and Spies 1992). We will consider three analyzing wavelets in this paper: Mexican Hat, French Top Hat, and Haar (Figure 2.1).

The two main metrics of wavelet analysis are the wavelet transform and the wavelet variance. The one-dimensional wavelet transform decomposes the transect on a scale-by-scale basis, while retaining information about location. A specific feature contributing to the pattern can be traced directly back to the original data. The presence and intensity of small-scale patterns are related to large-scale features. The transform coefficients are plotted at the position of the corresponding wavelet function. The number of coefficients is related to the width of the wavelet function and the length of the transect. Thus, the relative importance of the coefficients is measured by comparing their magnitudes.

The wavelet transform for each scale is read by examining the graphical representation (e.g., grey-scale plot, multiresolution decomposition). In the grey-scale plot, the transform has a high value when data matches the wavelet filter in shape and

Table 2.1. Several exemplary filters demonstrate the flexibility in choice of the basis for one-dimensional wavelet analysis. It is possible to customize the basis for each analysis.

Analyzing Wavelets	**Simplified Shape**	**Data Features**	**Examples of Ecological Inference**
Mexican Hat	0 	Symmetrical, Rounded	Patches
Morlet	0 	Symmetrical, Rounded	Patches
French Top Hat	0 	Symmetrical, Squared	Patches
Haar	0 	Asymmetrical, Squared	Edges, Gradients
Daublet	0 	Asymmetrical, Rounded	Edges, Gradients
Symmlet	0 	Nearly Symmetrical, Rounded	Edges, Gradients
Coiflet	0 	Nearly Symmetrical, Rounded	Edges, Gradients

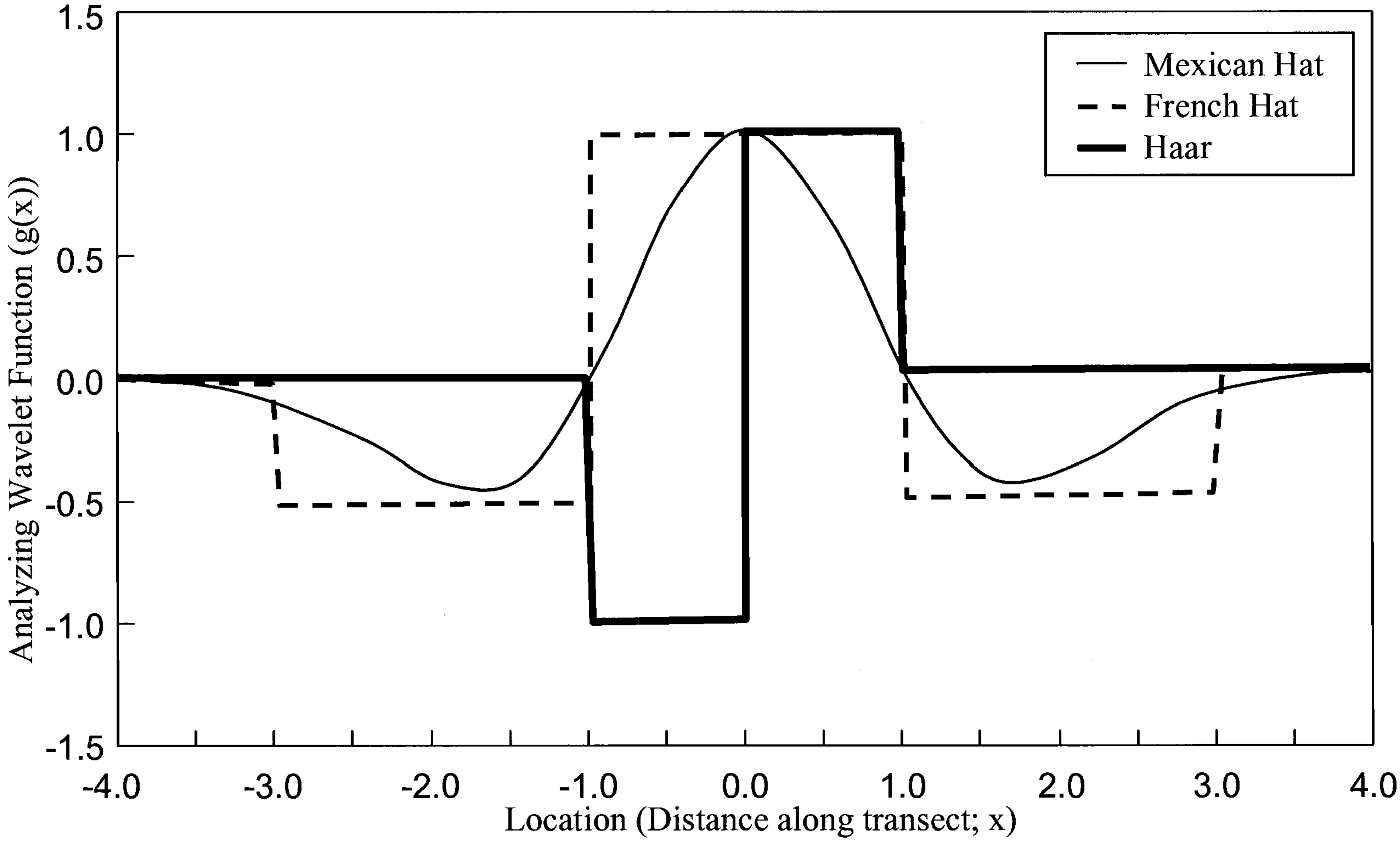

Mexican Hat
French Hat
Haar
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Analyzing Wavelet Function (g(x))
-4.0
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
4.0
Location (Distance along transect; x)

Figure 2.1.

dimension and a low value when they do not match (see Bradshaw and Spies 1992). The multiresolution decomposition of the signal is more detailed in its partition of energy, such that it is easier to relate a pattern to its influence at different scales (see Anthony and Bradshaw, Submitted).

The wavelet variance identifies the average spatial structure of data by measuring the energy contributed by features at each scale to the overall signal (Bradshaw and Spies 1992). This wavelet metric facilitates comparison between variables and among data sets, making this method comparable to the other statistical methods. Wavelet variance quantifies the patterns detected in the wavelet transform to describe dominant patterns in the signal (e.g., patch size, large gaps, diverse internal structure, nested pattern) at multiple scales.

Calculation of the Wavelet Variance from the Wavelet Transform

The first step in calibrating the three statistical methods is to translate their metrics into comparable forms. The wavelet variance is an expression of the wavelet transform. Wavelet variance quantifies the patterns detected in the wavelet transform to detect dominant scales within a data set. Consider a transect composed of n points at unit intervals. The wavelet transform of these data is analogous to series of convolutions of the data function $f(x_i)$, where x_i is location (i.e., distance along transect) with the analyzing wavelet function $g(x)$. In the discrete case, the wavelet transform is defined as:

$$\omega(a, x_j) = \frac{1}{a} \sum_{i=j-r_a}^{j+r_a} f(x_i) g\left(\frac{x_i - x_j}{a}\right) \qquad (1),$$

where r_a is defined to be the half-width of the analyzing wavelet beyond which the product is zero, x_j is the point at which $g(x)$ is centered, and a is the scale.

Interpretation of the wavelet transform requires visualization of the data to identify the scale and intensity of features in the data and their position along the transect. Effectively, the data are decomposed into discrete components of scale as a function of location along the record. To illustrate the wavelet transform, consider a simple pattern comprised of an alternating series of peaks and troughs at two scales, 4- and 20-meters (Figure 2.2a). The 4-meter peaks are clustered together to form a nested structure that is

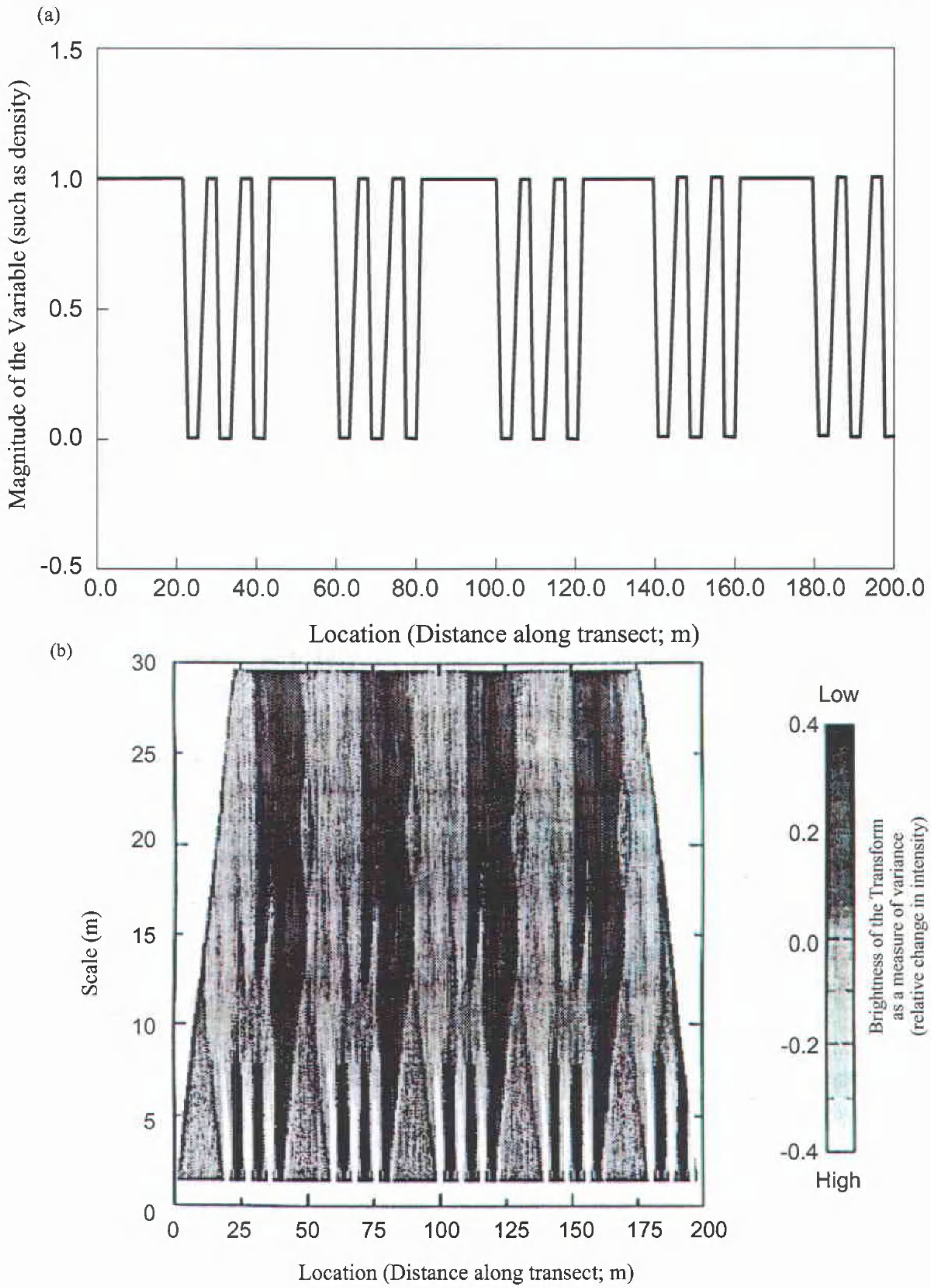

(a)
1.5
1.0
0.5
0.0
-0.5
Magnitude of the Variable (such as density)
0.0
20.0
40.0
60.0
80.0
100.0
120.0
140.0
160.0
180.0
200.0
Location (Distance along transect; m)
(b)
30
25
20
15
10
5
0
Scale (m)
0
25
50
75
100
125
150
175
200
Location (Distance along transect; m)
Low
0.4
0.2
0.0
-0.2
-0.4
High
Brightness of the Transform
as a measure of variance
(relative change in intensity)

Figure 2.2.

20-meters wide. The wavelet transform decomposes the data into both fine- and coarse-scale components that constitute the overall pattern (Figure 2.2b).

Derived from the wavelet transform, the wavelet variance facilitates comparison among multiple data sets by identifying the average spatial structure of the data. The wavelet variance is equal to the average value of the squared coefficients of the transform at each scale:

$$V(a) = \frac{1}{n - 2r_a} \sum_{j=1+r_a}^{n-r_a} \omega^2(a, x_j) \qquad (2).$$

To restrict the wavelet within the span of the data, j is limited in range between well-defined upper and lower bounds. This reduced dimensionality of the wavelet variance facilitates the analysis of pattern between multiple data sets. Although some location information is lost in the averaging process, calculation of the wavelet variance provides a summary of the information contained in the wavelet transform in a manner similar to Fourier power spectra. Peaks in the wavelet variance correspond to dominant scales of pattern in the signal. In contrast to power spectra, the wavelet variance is a function of a variable of time or space, rather than frequency.

Definition of the Three Methods in Terms of the Autocorrelation Function

Methods based on the autocorrelation function provide a theoretical framework for data analysis when f(x) is second-order stationary. Second-order stationarity implies that the mean and variance are constant across each transect and the covariance is a function of distance between points and not position (Journel and Huijbregts 1978). The empirically derived autocorrelation function provides a concise, statistical description of the spatial structure in the data. Both the semivariogram and Fourier power spectra may be expressed in terms of the autocorrelation function, $\rho(r_l)$, where r_l is the lag or distance between two points. Both the semivariogram and the spectral density function represent an average value across spatial scales.

The semivariogram is defined as the expected value of the differences between $Z(x+ r_l)$ and $Z(x)$, the values of the function at x and at r_l lag away from each x, respectively:

$$\gamma(h) = \mathrm{E}\left(\left(Z(x+r_1) - Z(x)\right)^2\right) \tag{3}$$

or, in explicit terms, of the auto-covariance function, $C(r_1)$:

$$\gamma(r_1) = C(0) - C(r_1) \tag{4}$$.

If $C(r_1)$ is normalized with the variance, C(O) [i.e., the sill; Journel and Huijbregts 1978], we obtain the correlogram as a function of $\rho(r_1)$:

$$\bar{\gamma}(r_1) = 1 - \rho(r_1) \tag{5}$$.

The normalized spectral density function in the discrete form for real-valued processes is:

$$h(s) = \frac{\sigma^2}{2\pi} \sum_{-\infty}^{+\infty} e^{-isr_1} \rho(r_1) ds \tag{6}$$.

Because the wavelet variance is composed of the squared coefficients of the wavelet transform, it is analogous to the power spectra, which is proportional to the squared modulus of the Fourier coefficients (Chatfield 1989). The expected value of the wavelet variance can be expressed in terms of the autocorrelation. Specifically, we wish to define the expected value of the wavelet variance, E(V(A)) in explicit terms of the autocorrelation function:

$$\mathrm{E}(V(a)) = \mathrm{E}\left(\omega^2(a, x_j)\right) \tag{7}$$.

For simplicity, consider the wavelet transform (Equation 1) for the given scale, a, and assume that $E(f(x)) = 0$. Then, writing $\omega(a) = \omega(x)$, the transform for the single scale, a, is given by:

$$\omega_a(x_j) = \frac{1}{a} \sum_{i=j-r_a}^{j+r_a} f(x_i) g\left(\frac{x_i - x_j}{a}\right) \tag{8}$$.

Substituting Equations 1 and 2 into Equation 8, we find the explicit expression for the expectation of $V(a)$:

$$\mathrm{E}(V(a)) = \frac{1}{a^2(n - 2r_a)} \sum_{j=1+r_a}^{n-r_a} \left\{ \sum_{i,k=j-r_a}^{j+r_a} g\left(\frac{x_i - x_j}{a}\right) g\left(\frac{x_k - x_j}{z}\right) F_{ik} \right\} \tag{9}$$,

where $F_{ik} = E(f(x_i)f(x_k))$. Because the wavelet functions g(x) are deterministic, only the expectation of the data function f(x) need be evaluated. Noting that the product of $f(x_i)f(x_k)$ is simply the autocovariance function $\sigma^2 \rho(x_i - x_k)$, and applying a change of variables, Equation 9 can be simplified to the form:

$$E(V(a)) = \frac{\sigma^2}{a^2} \sum_{1=-r_a}^{+r_a} \sum_{m=-r_a}^{+r_a} g_a(1) g_a(m) \rho(1-m) \quad (10).$$

Equation 10 represents an expression for the wavelet variance comparable to both the semivariogram and the spectral density function as defined in terms of the autocorrelation function (Journel and Huijbregts 1978, Chatfield 1989). Before comparing the responses of the three spatial methods to autocorrelation functions that correspond to a set of stochastic processes, we examined the range and magnitude of spatial information identified for a given specific scale by each technique. This analysis was performed most conveniently in the frequency domain.

Calibration of the Three Methods in the Frequency Domain

The calculation of the semivariogram and the wavelet variance may be interpreted as the result of a series of filtering processes applied to the data transect. In effect, the data are convolved with one of the three analyzing functions or wavelet functions. The equivalent of the analyzing function in the semivariogram is g(x) = -1 if x = -0.5, g(x) = 1 if x= 0.5, else g(x) = 0. The sums of squares of the convolved data are the non-centered variance (i.e., semivariogram or wavelet variance).

For ease of comparison, we computed these functions in the frequency domain, as demonstrated by the common use of Fourier transforms in data processing (Bracewell 1978). By transferring a time series into the frequency domain, spectral analysis can assess the periods embedded in the data. This representation of the analyzing function in the frequency domain is called the transfer function (Priestley 1981). The configuration of the transfer function will determine the proportion of the data intensity (i.e., the magnitude of the variable of interest) and period (i.e., the scale of pattern) retained in the analysis. A difference among the responses of each spatial autocorrelation method reflects a corresponding difference in the range and amount of spectral energy spanned by their respective transfer functions. To examine the frequencies (inversely related to scale) over which each transfer function extends, the wavelet transform of Equation 1 must first be defined in the frequency domain.

For the given scale, *a*, the wavelet transform can be written in the continuous form as:

$$\omega(x_j) = \frac{1}{a}\int_{-\infty}^{+\infty} f(x) g\left(\frac{x - x_j}{a}\right) dx \quad (11).$$

By the convolution and similarity theorems (Bracewell 1978), the Fourier transform of the wavelet transform is:

$$W_a(s) = aF(s)G(as) \quad (12).$$

where F(s) is the Fourier transform of the f(x) data function, G(as) is the Fourier transform of the analyzing wavelet of $1/a\{g(x/a)\}$, and $W_a(s)$ is the Fourier transform of the wavelet transform. Equation 12 simply states that the Fourier transform of the wavelet transform at scale *a* is equal to the product of the Fourier transforms of the data vector and the analyzing wavelet. This expression relates the frequency content of the wavelet transform to that of the individual wavelet and the data. By Rayleigh's theorem (Bracewell 1978) and using Equation 2, the wavelet variance, V(a), is represented in the frequency domain by:

$$V(a) \frac{1}{n - 2r_a} \int_{-\infty}^{+\infty} |F(s)|^2 |G(as)|^2 \, ds \quad (13).$$

Several features are noteworthy with respect to the transfer functions for each of the three wavelets for a scale of one (i.e., Mexican Hat, French Top Hat, Haar) and the semivariogram (Figure 2.3a). The amplitudes and locations of the dominant peaks differ slightly among the four transfer functions. Of the three analyzing wavelet functions, the Mexican Hat wavelet is the only transfer function with a single peak. Also, the rate at which the secondary peaks damp out differs among the French Top Hat wavelet, Haar wavelet, and semivariogram functions. These observations indicate that the bandwidth (i.e., the frequencies or similarly the scales over which the function ranges for a

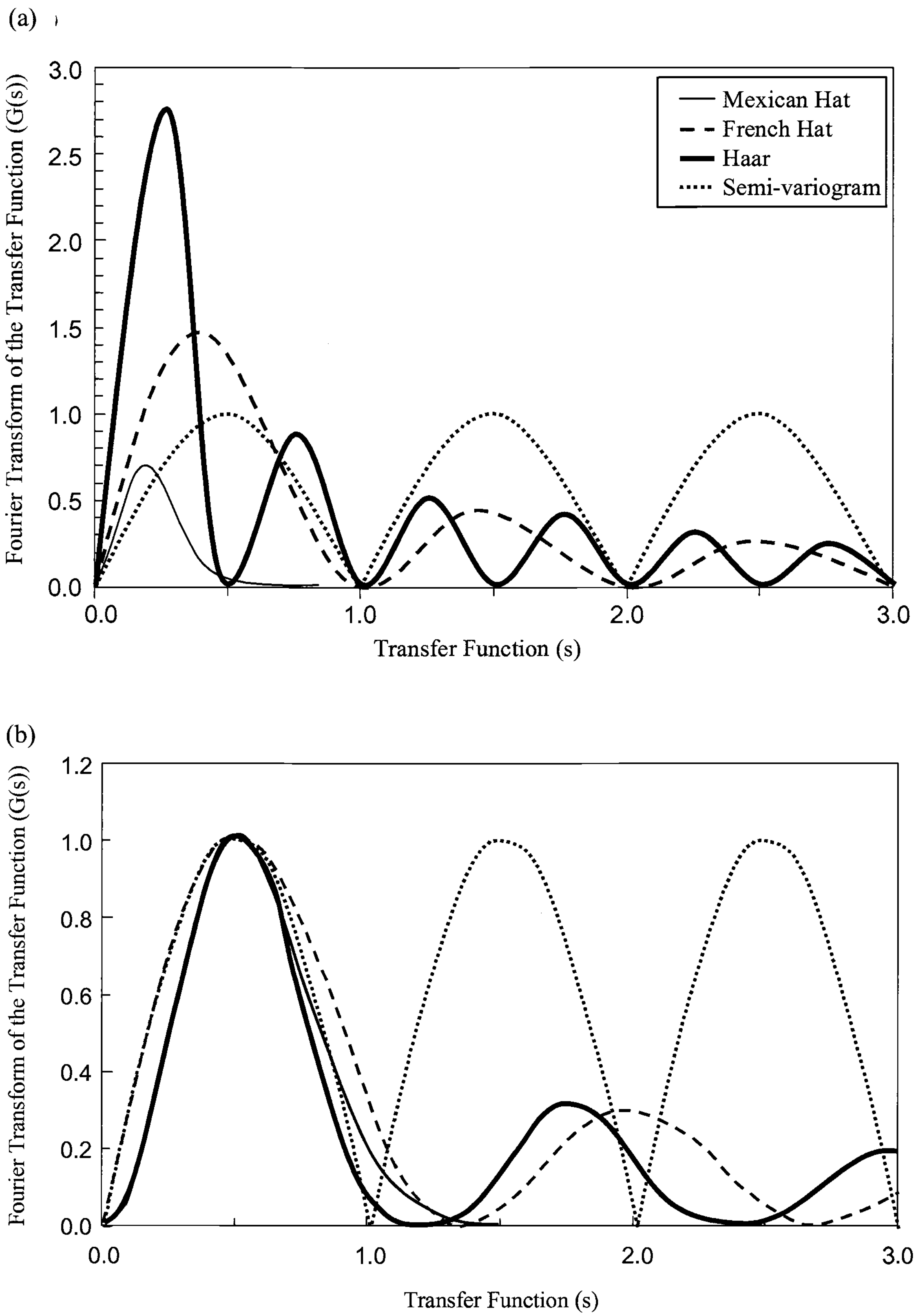

(a)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Fourier Transform of the Transfer Function (G(s))
Mexican Hat
French Hat
Haar
Semi-variogram
0.0
1.0
2.0
3.0
Transfer Function (s)
(b)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Fourier Transform of the Transfer Function (G(s))
0.0
1.0
2.0
3.0
Transfer Function (s)

Figure 2.3.

specified scale) and magnitude of energy passed by each transfer function differs as a function of frequency.

Based on these observations alone, one might conclude that the capabilities of the various methods might not be equivalent when applied to a given data set. However, because the absolute scaling and magnitude of the functions are somewhat arbitrary, some of the differences may be artificial. For this reason, the locations and magnitudes of the dominant peaks of the three wavelet variances were calibrated to the semivariogram in the frequency domain to isolate function morphology alone. This calibration ensures that each of the four functions pass approximately the same energy at the dominant bandwidth frequency. While the calibration procedure has minimized differences among the functions with regard to the location of the dominant peak in the transfer function, the various contributions from secondary peaks is still distinct (Figure 2.3b). In particular, the magnitude of the semivariogram transfer function does not diminish with increasing frequency as do the wavelet functions. Rather, the transfer function of the semivariogram is composed of integral peaks of the same amplitude and form.

The transfer function changes as a function of increasing scale, a. As a increases, the peak becomes narrower and shifts to the left, excluding the high frequency components (Figure 2.4). While the rate of exclusion decreases more rapidly as a increases (Figure 2.4), the bandwidth remains constant when plotted on a logarithmic scale (Mallat 1989). This implies that, at coarser scales of resolution, fewer and fewer fine-scale features are included in the transform and, hence, the wavelet variance. A corresponding data-smoothing process occurs in the spatial domain with increasing scale. Conversely, information contained in large-scale features is carried through to finer scales as well. While fine-scale patterns in multi-scale data dominate coarser features (relative to the transect length), the corresponding wavelet variance is more strongly influenced by the signature of fine-grained features.

COMPARISON OF THE THREE STATISTICS

Once the semivariogram, Fourier, and one-dimensional wavelet statistics were in comparable forms, we evaluated their abilities to detect and classify pattern in spatial

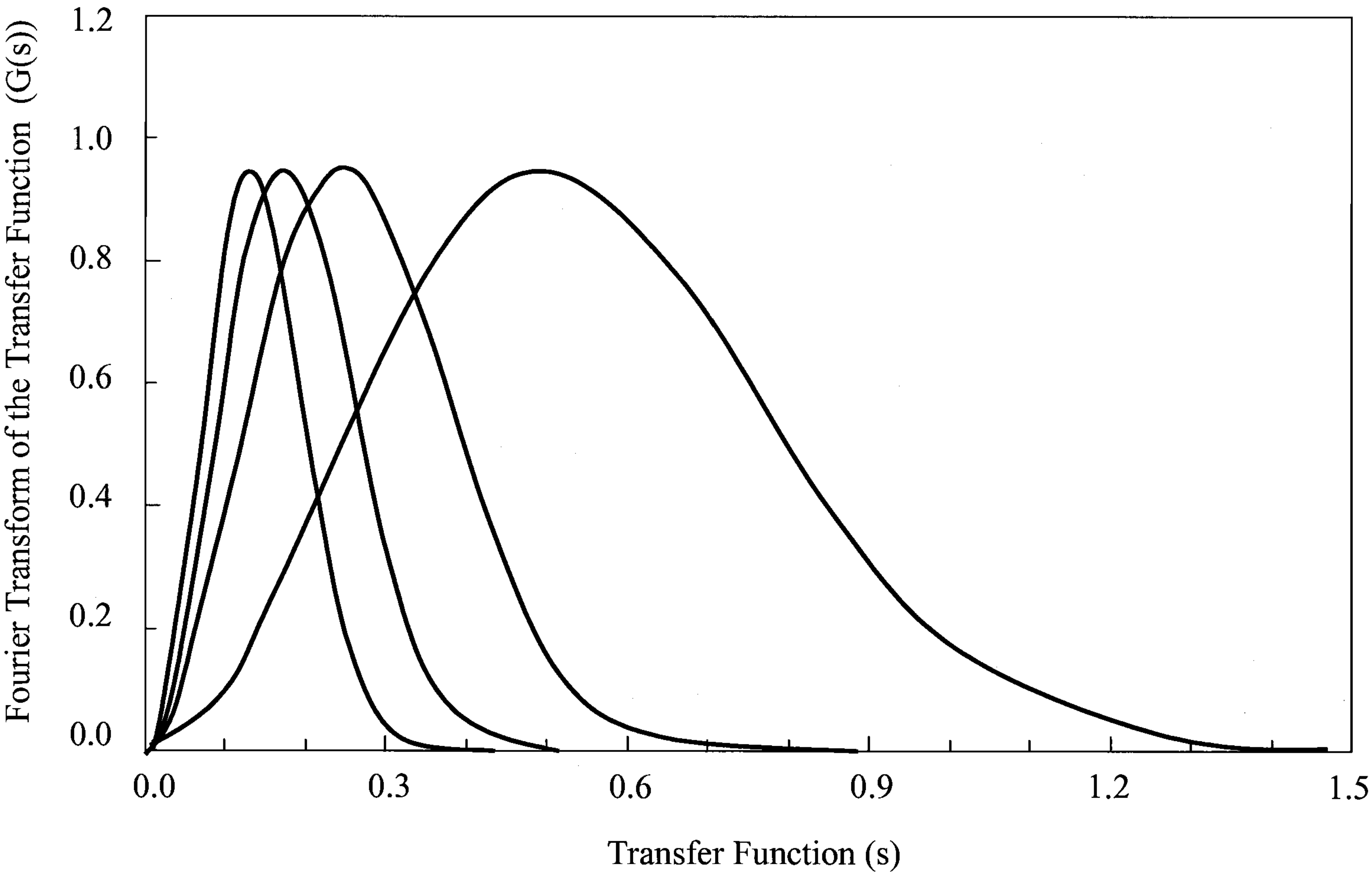

1.2
1.0
0.8
0.6
0.4
0.2
0.0
Fourier Transform of the Transfer Function (G(s))
0.0
0.3
0.6
0.9
1.2
1.5
Transfer Function (s)

Figure 2.4.

ecology. First, we examined their relative abilities to detect pattern by calculating their responses to autocorrelation functions that correspond to a set of four simple, stochastic processes. Second, we designed three deterministic simulations to highlight their differences in analyzing multi-scalar pattern. Finally, we applied these statistics to empirical data to select the appropriate method to detect the internal structure of a heterogeneous transect from the Breeding Bird Survey (BBS; Robbins et al. 1986, Sauer et al. 1999).

For ease of comparison, we restricted spatial pattern to one dimension, referring to point data along a transect in one direction (e.g., north to south, east to west), and displaying aggregations with high density and gaps with low or zero density. A gap is any part of the transect at least one-meter wide where the measure of percent opening is positive. Non-stationarity occurs when the pattern in this alteration of patches and gaps is not constant along the transect (i.e., the mean varies with distance along the transect). Data were analyzed with PV-Wave 6.1 (Visual Numerics Inc., Boulder, CO) and S-plus 2000 (Insightful Corp., Seattle, WA).

A. Four Stochastic Processes Based on the Autocorrelation Function

The autocorrelation functions of four stochastic processes (additive moving average, non-additive moving average, auto-regressive order one [AR(l)], and auto-regressive harmonic) were used to examine the difference in response among the three spatial statistics for a parameter generating randomly placed 5-meter patches along each transect. These specific models were chosen based on their semblance to physical and ecological processes. All four stochastic processes conformed to first-and second-order stationarity. Five cases for the three time series methods were explored: semivariogram, Fourier analysis, Mexican Hat wavelet, French Top Hat wavelet, and Haar wavelet analysis. As the wavelet variance is more comparable to the output for semivariogram and Fourier analysis, we present only this wavelet metric in this section. In addition, we addressed the relative flexibility in the choice of data filter (i.e., basis) in wavelet analysis by using the best filter for each analysis.

The additive and non-additive moving average models were adopted from Moloney et al. (1991). The additive moving average model works best for data with successive events that are additive and accumulate in magnitude over space (e.g., vegetative growth). Where patches overlap, the density is the sum of the contributions of the separate patches. In contrast, the presence of a patch in the non-additive moving average model allows overlap of successive patches, but the value of overlapping patches does not exceed unity. That is, magnitude of patches does not increase with overlap. This model is appropriate for presence/absence vegetation cover studies. An AR(l) or Markov process is the extension of moving average of infinite order (Chatfield 1989). This model describes empirical processes, such as conifer cone distribution (Dale et al. 1993). Finally, an auto-regressive harmonic autocorrelation function was included to assess the effects of varying degrees of periodicity on the transform response (Priestly 1981). Often, ecological data contain repeating structure, and the objective of many analyses is to quantify the scale of the repeating pattern (e.g., Tucker et al. 1986, Cohen et al. 1990). An auto-regressive harmonic model is simply the sum of the products of two AR(1) functions with two trigonometric functions. The time series resembles a stationary, pseudo- periodic process (Priestley 1981).

B. Simulated Data Analysis: Three Cases of Non-uniform and Data Feature Morphology

Having compared the relative ability of the statistics to detect simple stochastic processes, we extended the comparison to three simulations with deterministic patterns of increasing complexity. The three simulated transects facilitate comparison among the spatial statistics due to their non-random pattern. Thus, the relative ability of each statistic to detect pattern is more easily recognized in simulated data than in random or empirical datasets. We evaluated the effects of these differences as they related to multi-scale, non-uniform data (i.e., pattern varies along the transect) and data feature morphology (e.g., asymmetrical structure, progression of scalar components).

The comparison among statistics was simplified to reflect the findings in the stochastic processes portion of the study. Semivariogram analysis was excluded from further consideration due to its limitations in detecting multi-scalar pattern. Henceforth, we compared the relative abilities of spectral and wavelet analyses in detecting pattern. As the wavelet variance is more comparable to the output for Fourier analysis, we only presented the wavelet metric in this section. For each remaining wavelet analysis, we only used the appropriate filter for the pattern (i.e., Haar or Mexican Hat). The French Top Hat wavelet filter was excluded from further analyses, as this filter is no longer appropriate for the datasets.

The first simulation was a simple, non-uniform pattern in which the period changed along the transect but the mean and variance were constant (Figure 2.5a). This deterministic data transect consisted of a cosine function with a period of ten in the first half of the transect followed by a cosine function with a period of thirty. Thus, the ratio between the two scales of pattern was 1:3. To facilitate comparison, the Mexican Hat wavelet basis was chosen to detect the rounded, symmetrical data features (Figure 2.5b) in a similar manner to Fourier spectral analysis (Figure 2.5c).

The second simulation expanded the first with a more complicated, non-uniform pattern: the mean and variance remained constant within each transect, but varied among multiple transects (Figure 2.6a). This simulation consisted of a data set of five transects that incrementally increased the ratios between the scales of pattern (i.e., half-period) in the first and second halves of the transects sequentially from one to five. That is, the first transect had a ratio of one between the first and second halves of the transect and were composed of a cosine function of the same period of 10 meters. The second transect had a ratio of two, which corresponds to a period of 10 meters in the first half of the transect and 20 meters in the second half. The third transect was the same as our first simulation with 10- and 30-meter periods. The ratios of the first half to the second increased incrementally to five in the fifth transect. The Mexican Hat filter was chosen for wavelet analysis to detect the rounded features (Figure 2.6b) in a similar manner to Fourier analysis (Figure 2.6c).

The third simulation resembled the first illustrative pattern (Figure 2.5a) with the simple, non-uniform distribution in the form of a cosine function with two scales in a 1:3 ratio (i.e., period ten followed by period thirty). Similar to the first two simulations, the mean and variance did not vary within the transect. To highlight the influence of feature morphology within data on pattern detection, the rounded, symmetrical peaks were replaced by square, symmetrical peaks with distinct edges (Figure 2.7a).

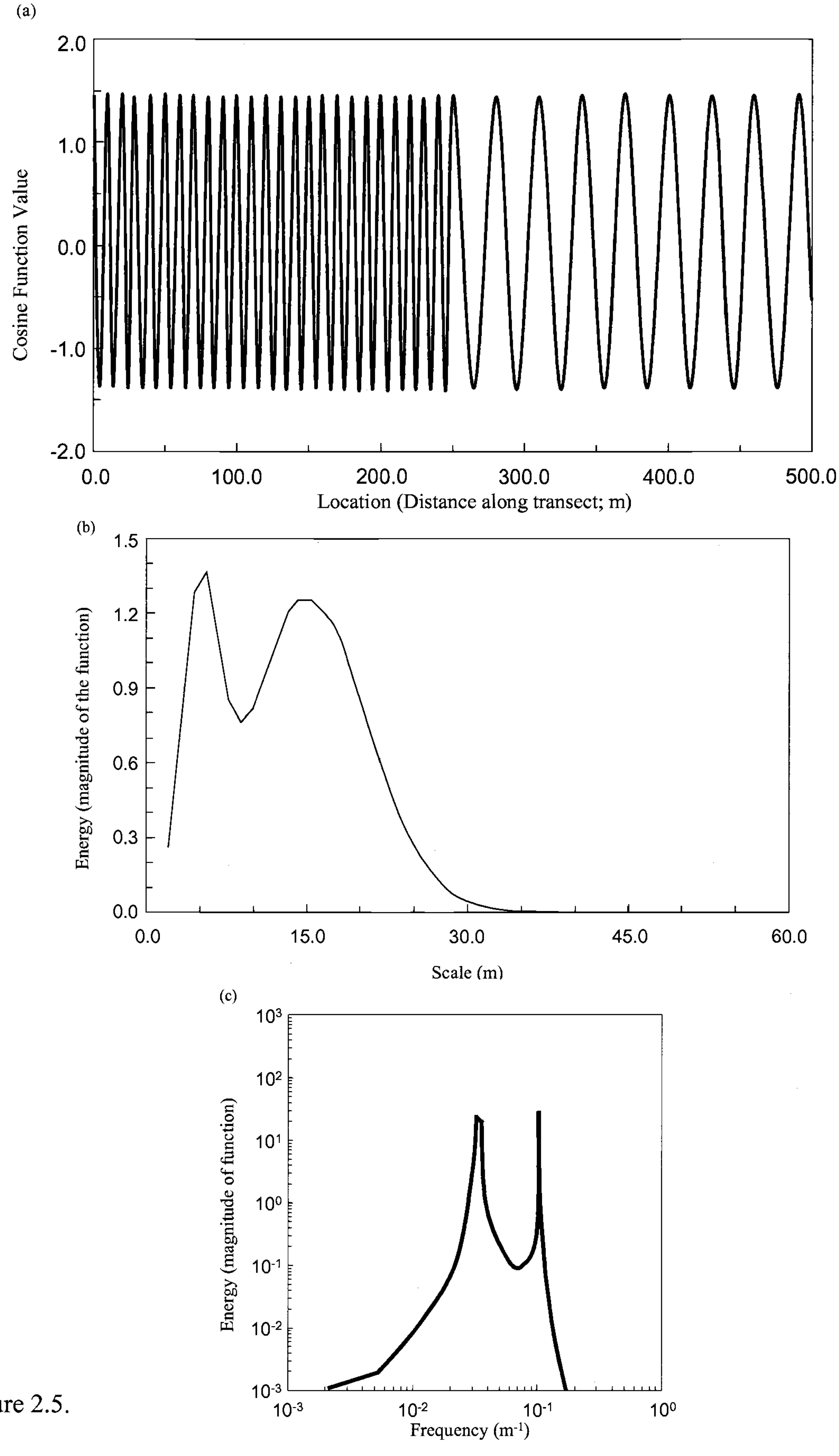

(a)
2.0
1.0
0.0
-1.0
-2.0
Cosine Function Value
0.0
100.0
200.0
300.0
400.0
500.0
Location (Distance along transect; m)
(b)
1.5
1.2
0.9
0.6
0.3
0.0
Energy (magnitude of the function)
0.0
15.0
30.0
45.0
60.0
Scale (m)
(c)
10^3
10^2
10^1
10^0
10^{-1}
10^{-2}
10^{-3}
Energy (magnitude of function)
10^{-3}
10^{-2}
10^{-1}
10^0
Frequency (m^{-1})

Figure 2.5.

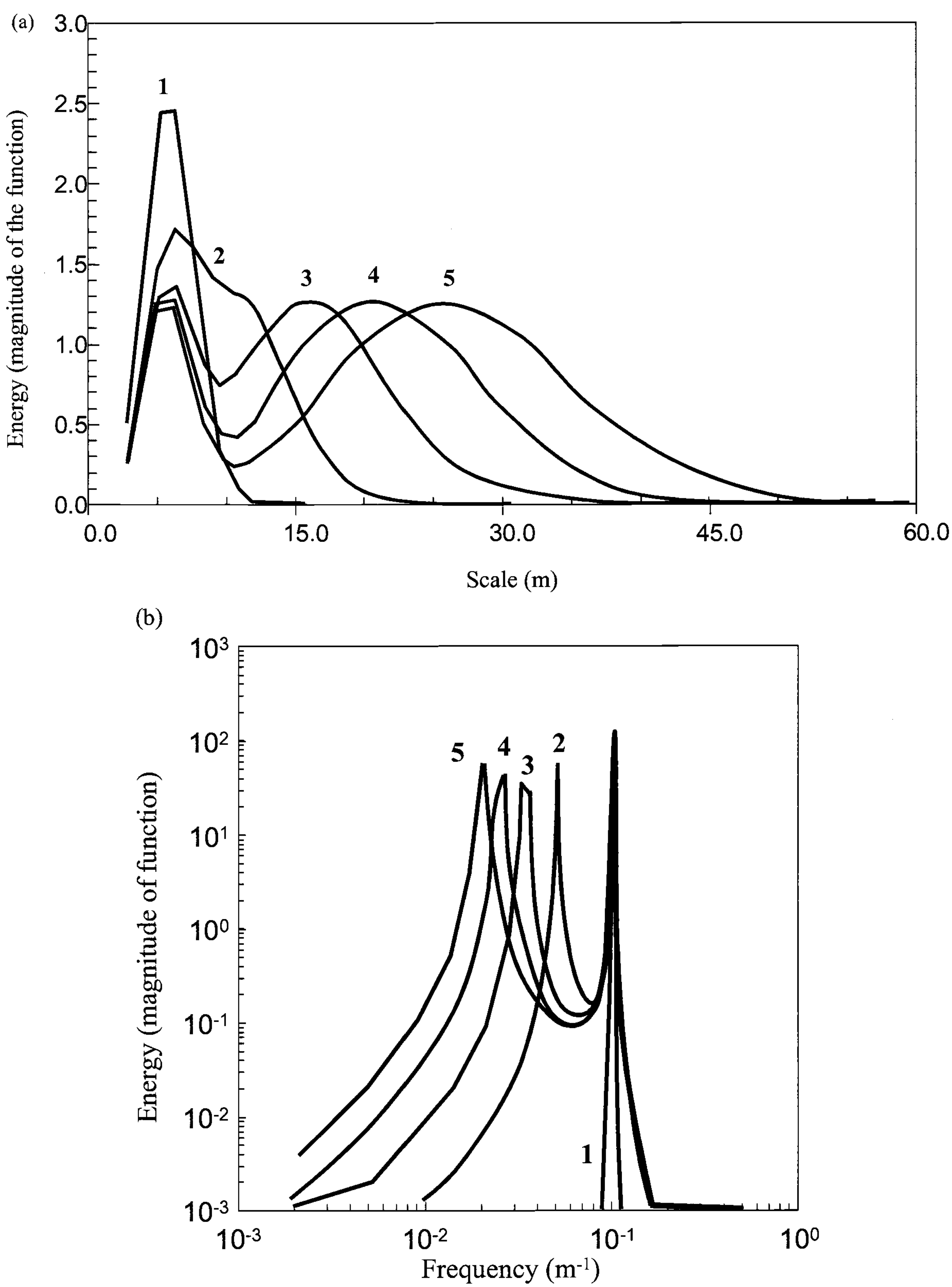

(a)
Energy (magnitude of the function)
Scale (m)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
15.0
30.0
45.0
60.0
1
2
3
4
5
(b)
Energy (magnitude of function)
Frequency (m^{-1})
10^3
10^2
10^1
10^0
10^{-1}
10^{-2}
10^{-3}
10^{-3}
10^{-2}
10^{-1}
10^0
5
4
3
2
1

Figure 2.6.

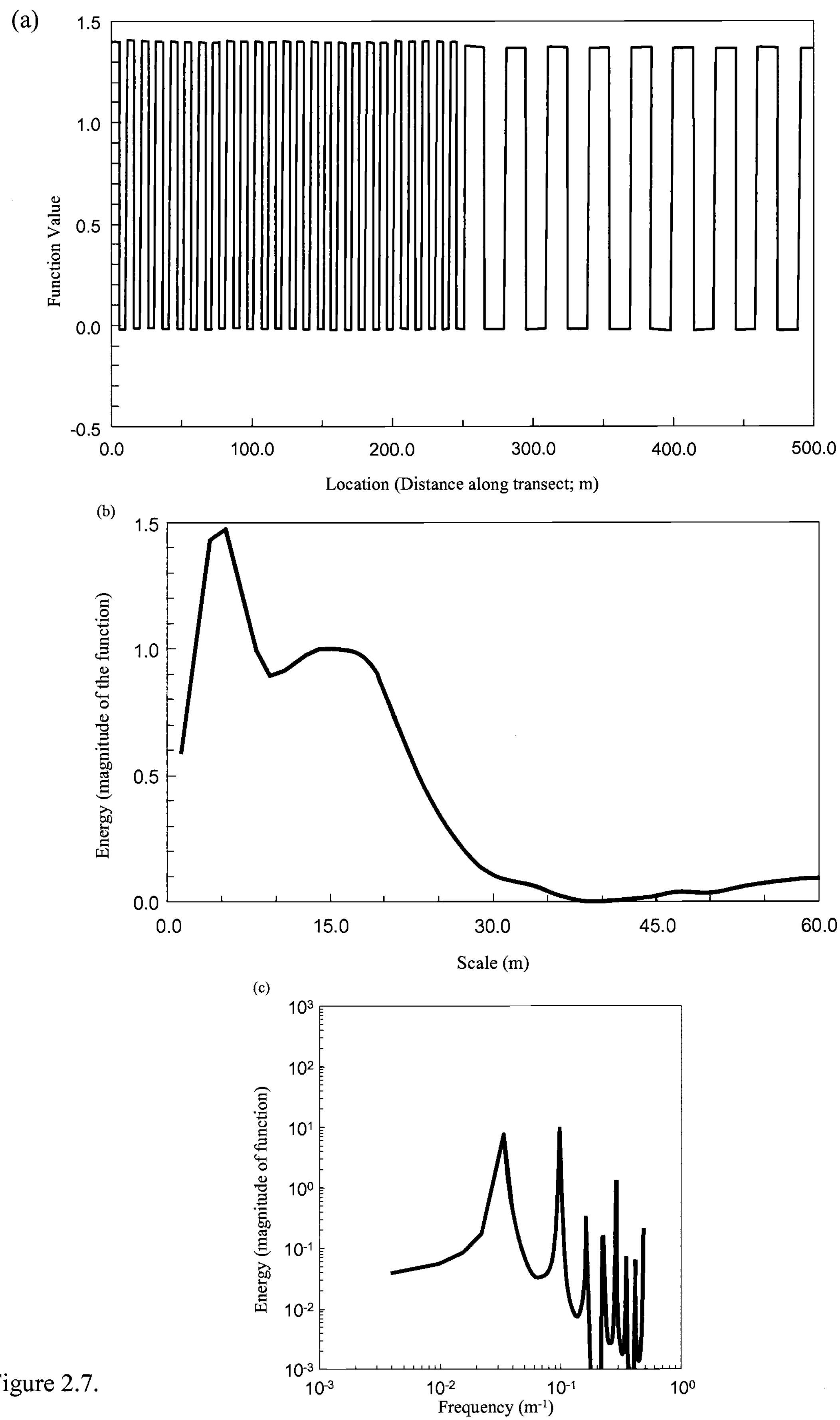

(a)
1.5
1.0
0.5
0.0
-0.5
Function Value
0.0
100.0
200.0
300.0
400.0
500.0
Location (Distance along transect; m)
(b)
1.5
1.0
0.5
0.0
Energy (magnitude of the function)
0.0
15.0
30.0
45.0
60.0
Scale (m)
(c)
10^3
10^2
10^1
10^0
10^{-1}
10^{-2}
10^{-3}
Energy (magnitude of function)
10^{-3}
10^{-2}
10^{-1}
10^0
Frequency (m^{-1})

Figure 2.7.

This change in feature shape accentuated the utility of choice in the analyzing wavelet basis depending on known characteristics of the data and the research questions. To better detect the squared data features, the Haar wavelet basis was selected in place of the Mexican Hat to compare wavelet (Figure 2.7b) and Fourier analyses (Figure 2.7c).

C. Empirical Data Analysis: A Case Study of the Western Meadowlark

After examining the merits and limitations of these methods in detecting pattern in the simple stochastic processes and increasingly complicated deterministic simulations, we conclude the comparisons with multi-scalar, non-uniform, empirical data from the North American Breeding Bird Survey (BBS). The mean and variance varies along each transect. Once again, we limited this comparison to power spectrum and wavelet analysis because we found that semivariograms do not distinguish multi-scalar structure from single-scale repeating structure. As the wavelet variance is more comparable to the output for Fourier analysis than is the wavelet transform, we presented only this wavelet metric. Also, we limited the wavelet analysis to the appropriate filter for the empirical dataset, the Mexican Hat.

Analyzing the four stochastic processes and the three deterministic simulations provided the background to select the appropriate method for ecological analysis. These analyses demonstrated how well these three statistics perceived random pattern modeled by the stochastic processes and known patterns in the deterministic simulations. Pattern in empirical data is even more difficult to visualize and quantify, due to multiple scales and variation of the mean and variance along the transect. In this section, we focused on the similarities and differences between visual and statistical pattern recognition. In the visual description of heterogeneity, we characterized the patterns at large, intermediate, and small scales. Internal structure was grouped together into one category in the small scale, because smaller groupings of individual peaks and gaps are difficult to differentiate visually.

The empirical data consisted of one transect with complex heterogeneous internal structure with mixed density patches (some very large) and mixed intensity gaps. The Western Meadowlark (*Sturnella neglecta*) is a short-distance migrant that nests on the ground in grassland habitats. The BBS was coordinated by the United States Geological

Survey Patuxent Wildlife Research Center and the Canadian Wildlife Service National Wildlife Research Center. Bird distribution along the survey transects was recorded in early or mid-June, with some desert transects run as early as May. Counts from 1966 through 1999 were compared to calculate density (i.e., total number of birds per tenth of a decimal degree latitude and longitude square). The transect extended west to east across the United States and Canada from -124.4 to -73.7 decimal degrees longitude and north to south 37.0 to 39.0 decimal degrees latitude (Figure 2.8). One degree of latitude is approximately 111 kilometers. The distance of one degree longitude varies with latitude. At 45 degrees latitude, one degree longitude is approximately 55.7 kilometers. Thus, the transect was approximately 222 kilometers in width and 2,824 kilometers in length. We combined BBS counts over the distance of one decimal degree of latitude on either side of the transect every 0.1 decimal degree of longitude, obtaining greater than 100 data points along the transect. Combining several BBS surveys in a two degree latitude band characterized bird distribution better than only including the few transects that lined up with the center decimal degree longitude. Essentially, each point represented an area. Structure at smaller scales was rounded to the nearest 0.1 decimal degree and multiple measurements at one location were averaged into one value. Missing values were converted to zeros, rather than interpolated, to retain the pattern originally observed in the data. Land cover generalizations were obtained from the National Atlas of the United States, provided by the United States Department of the Interior. The appropriate analyzing wavelet basis for these BBS data was a nearly orthogonal v-spline approximating the Mexican Hat with modified properties (e.g., compressed peak).

Having completed these analyses, we could more clearly summarize the advantages and disadvantages of the three statistics, as well as the questions best suited for each.

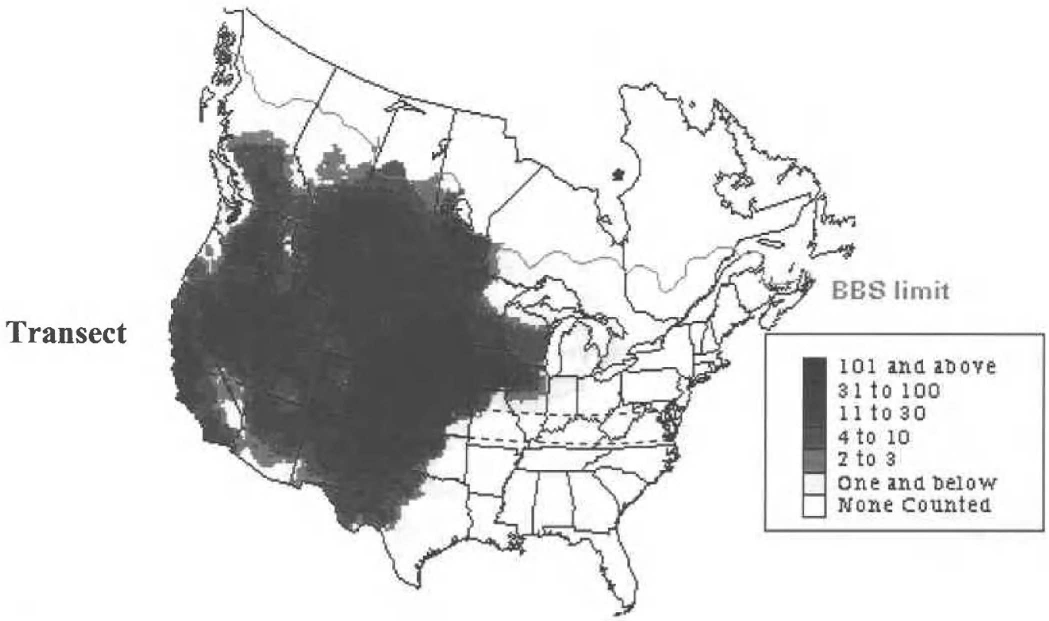

Transect
BBS limit
101 and above
31 to 100
11 to 30
4 to 10
2 to 3
One and below
None Counted

Figure 2.8.

RESULTS

COMPARISON OF SEMIVARIOGRAM, FOURIER ANALYSIS, AND ONE-DIMENSIONAL WAVELET ANALYSIS

A. Four Stochastic Processes Based on the Autocorrelation Function

We examined the relative ability to detect pattern in a set of four stochastic processes among semivariogram, Fourier, and one-dimensional wavelet statistics (i.e., Mexican Hat, French Top Hat, Haar). All five cases of spatial statistics detected the repeating 5-meter patch in the additive moving average models (Figures 2.9a and 2.9b). Spectral analysis (Figure 2.9b), Mexican Hat wavelet (Figure 2.9a), and Haar wavelet (Figure 2.9a) were most accurate with their detection of 5-meters as the characteristic scale (Table 2.2). Our results for the power spectrum analysis of the additive moving average model resemble those of Moloney et al. (1991). The French Top Hat wavelet slightly underestimated patch size at 3-meters (Figure 2.9a). The semivariogram range detected the first peak closer to 6-meters than 5-meters (Figure 2.9a).

The responses for non-additive moving average models were similar to the additive moving average models for the repeating 5-meter patch (Figures 2.9c and 2.9d). The patch formation may not be extensive enough to differentiate these models. The patch size may be small and the probability of patch overlap low such that the plant density measurement of the additive moving average model resembles the 'patch-no patch' assignment of the non-additive moving average model.

Patch size was adequate to demonstrate differences among spatial statistics in detecting pattern (Figures 2.9c and 2.9d). The power spectrum (Figure 2.9d), Haar wavelet (Figure 2.9c), and Mexican Hat wavelet (Figure 2.9c) similarly detected the 5-meter patches in both the additive and non-additive moving average models (Table 2.2). This similarity is expected when a one-dimensional patch has a small size, distinct boundaries, and a symmetrical shape. The semivariogram detected a patch at 5.4 meters, which is a reasonable approximation of the 5-meter patch (Figure 2.9c). The French Top Hat wavelet slightly underestimated the patch at 4.4 meters (Figure 2.9c). The three wavelet analyses detected a single pattern for the additive moving average and a second

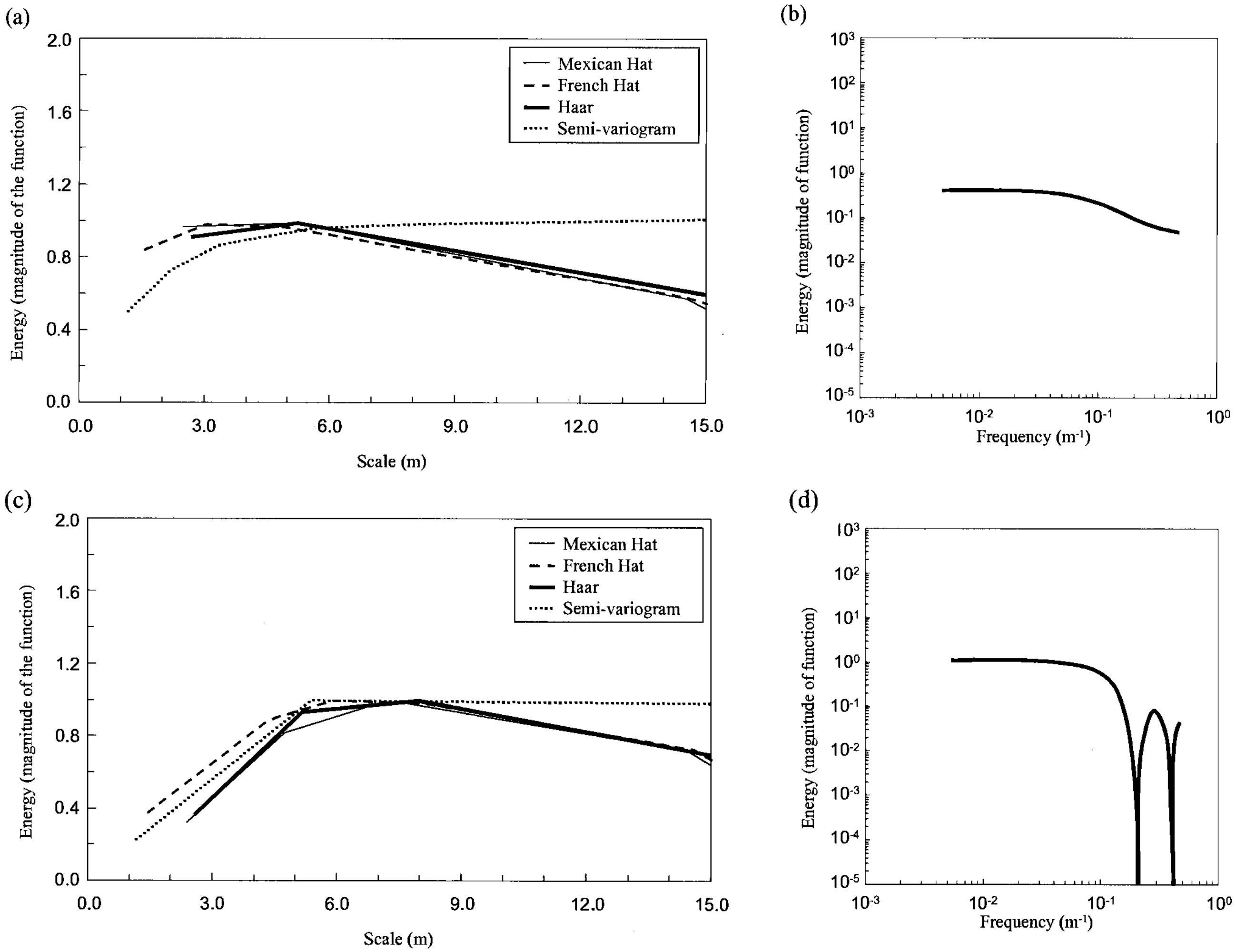
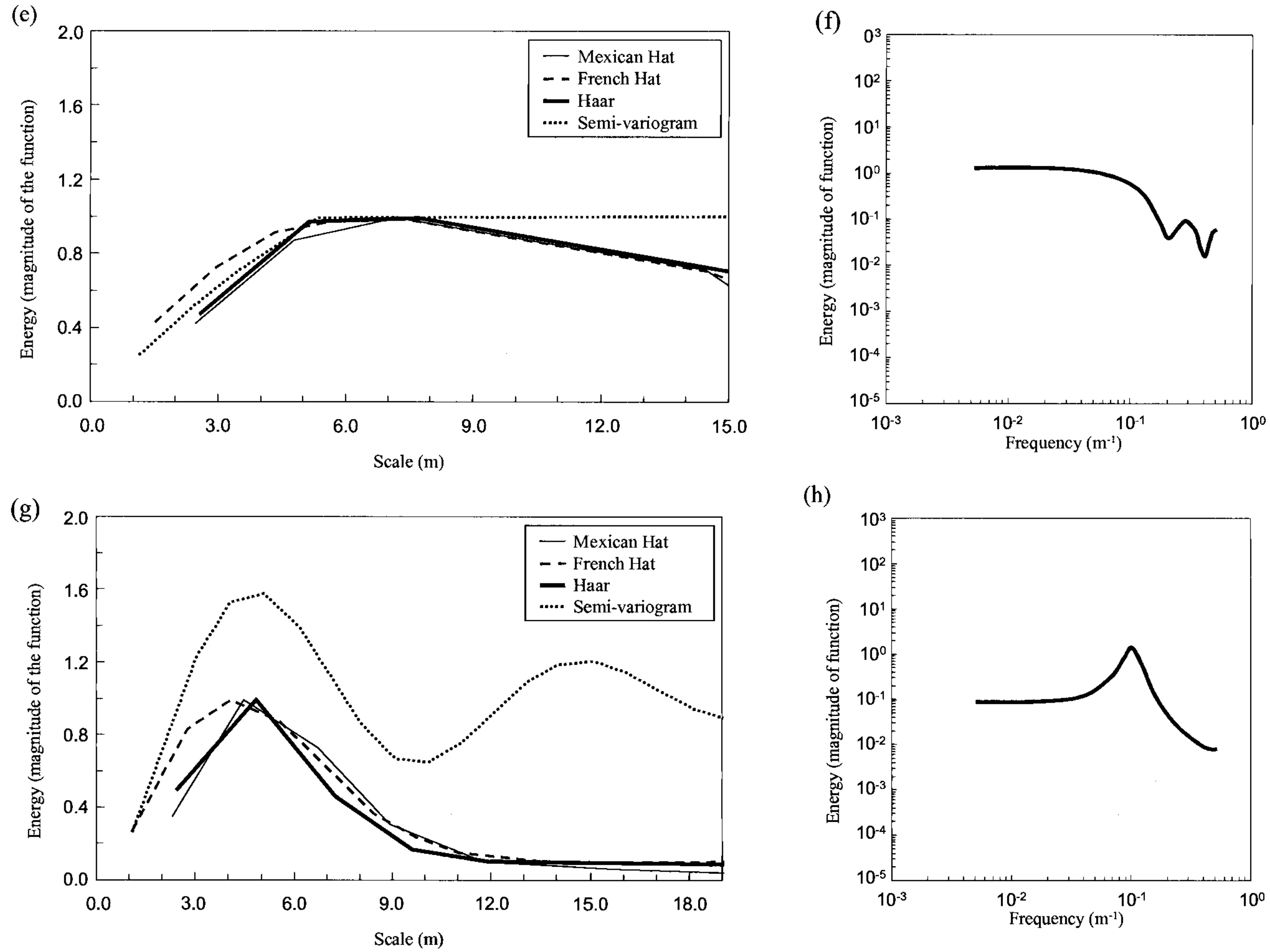

(a)
Mexican Hat
French Hat
Haar
Semi-variogram
Energy (magnitude of the function)
Scale (m)
(b)
Energy (magnitude of function)
Frequency (m-1)
(c)
Mexican Hat
French Hat
Haar
Semi-variogram
Energy (magnitude of the function)
Scale (m)
(d)
Energy (magnitude of function)
Frequency (m-1)

Figure 2.9a-d.



(e)
Energy (magnitude of the function)
Scale (m)
Mexican Hat
French Hat
Haar
Semi-variogram
(f)
Energy (magnitude of function)
Frequency (m^{-1})
(g)
Energy (magnitude of the function)
Scale (m)
Mexican Hat
French Hat
Haar
Semi-variogram
(h)
Energy (magnitude of function)
Frequency (m^{-1})

Figure 2.9e-h.

Table 2.2. Summary of the capabilities of one-dimensional wavelet variance, semi-variogram, and Fourier power spectra in (a) Four Stochastic Processes, (b) Three Simulated Datasets, and (c) One Empirical Dataset. The number in parentheses is the actual scale value read from the output, and the number outside the parentheses is the final scale to one significant figure.

(a) Four Stochastic Processes

Statistic, measure	Additive Moving Average	Non-additive Moving Average	Auto-regressive Order One	Auto-regressive Harmonic
	5 m patch	5 m patch	5 m patch	5 m patch
Semi-variogram, range	6 (5.7)	5 (5.0)	5 (5.0)	5 (5.0) 15 (15.0)
Fourier Power Spectrum, period (1/f)	5 (5.0)	5 (5.0)	5 (5.0)	5 m half-period; 10 m period
One-dimensional Wavelet Analysis: Mexican Hat, wavelet variance	5 (5.1)	5 (4.5) 7 (6.9)	5 (4.5) 7 (6.6)	5 (4.5)
One-dimensional Wavelet Analysis: Haar, wavelet variance	5 (5.1)	5 (5.0) 7 (7.1)	5 (4.8) 7 (7.2)	5 (4.7)
One-dimensional Wavelet Analysis: French Top Hat, wavelet variance	3 (2.6)	5 (5.3) 7 (7.1)	5 (5.0) 7 (7.0)	3 (2.8) 4 (4.1) 6 (5.5)

Table 2.2. Continued

(b) Simulated Data

Statistic, measure	Simple, Non-uniform	More Complicated, Non-uniform					Data Feature Morphology
	10 m period/ 30 m period, cosine	10 m period/ 10 m period, cosine	10 m period/ 20 m period, cosine	10 m period/ 30 m period, cosine	10 m period/ 40 m period, cosine	10 m period/ 50 m period, cosine	10 m period/ 30 m period, cosine with square edges
Fourier Power Spectrum, period (1/f)	10 (10.0) 30 (30.3)	10 (10.0)	10 (10.0) 20 (20.0)	10 (10.0) 30 (30.3)	10 (10.0) 40 (40.0)	10 (10.0) 50 (50.0)	2 (2.0) 2 (2.4) 3 (2.7) 3 (3.3) 5 (4.8) 6 (5.9) 10 (10.0) 30 (30.3)
One-dimensional Wavelet Analysis: Mexican Hat,	5 (4.5) 5 (5.4) 15 (14.8)	5 (4.5) 5 (5.4)	5 (4.5) 5 (5.4) 10 (9.5)	5 (4.5) 5 (5.4) 15 (14.8)	5 (4.5) 5 (5.4) 20 (20.0)	5 (4.5) 5 (5.4) 25 (25.0)	---
One-dimensional Wavelet Analysis: Haar,	---	---	---	---	---	---	5 (4.5) 5 (5.4) 15 (14.8)

Table 2.2. Continued

(c) Empirical Data

Statistic, measure	Heterogeneity: mixed density clusters, mixed intensity gaps, conversion = 5.559 km — Detected Patch/Scale	Frequency
Fourier Power Spectrum, period ([2Π/f]*5.559)	80.652 94.885 106.89 126.74 153.14 211.23 311.29	0.433071 0.368110 0.326772 0.275591 0.228078 0.165354 0.112205
One-dimensional Wavelet Analysis: Mexican Hat, wavelet variance	44.472 88.944 177.89 355.78 705.99 1,411.98	----

pattern between 6 and 8 meters for the non-additive moving average model (Figures 2.9a and 2.9c).

Viewed as a spherical model (Journel and Huijbregts 1977) with a patch parameter of 5 meters, the response of the semivariogram to the AR(1) or Markov process model showed 5.3 meters (Figure 2.9e). The power spectrum had an inflection point around 5 meters, although accurate detection is more difficult with this method (Figure 2.9f). The three analyzing wavelets differed slightly (Table 2.2), with the Haar and Mexican Hat closely approximating 5 meters and the French Top Hat showing a scale of dominance around 4.3 meters (Figure 2.9e). The three wavelet analyses detected a second pattern for the AR(1) model between 6 and 8 meters.

In an auto-regressive harmonic process with period parameter of 10 meters, the dominant spatial feature dimension will equal the half-period (i.e., the 5-meter patch size). Both the Haar and Mexican Hat wavelets demonstrated a distinct peak centered close to 5 meters (Figure 2.9g), while the French Top Hat indicated a more diffuse peak centered around 4 meters. The power spectrum showed a peak at ten meters (the full period) with a half-period at 5 meters (Figure 2.9h). The responses of these functions matched our expectations based on the statistics' previous ability to detect the 5-meter patch (Table 2.2).

The noticeable deviation in the auto-regressive harmonic process model was the semivariogram (Figure 2.9g). In addition to a distinct peak at 5 meters, a second peak was centered at 15 meters. When we extended the scale beyond 20 meters to include higher scales, the semivariogram demonstrated a repeating peak structure at 10-meter intervals (Bradshaw, unpublished data). The bimodal curve was not unexpected (Figure 2.9g), as the autocorrelation function for a sinusoidal function is similar in form (Chatfield 1989).

Similarly, the difference in behavior between the semivariogram and the wavelet variance was reflected in their respective transfer functions. Recall that unlike the analyzing wavelets, the semivariogram transfer function did not damp with frequency but occurred at integral values (Figure 2.3b). As a result, hierarchical or multi-scale structure was difficult to distinguish from single-scale repeating structure with semivariogram analysis. In contrast, the wavelet variance and the power spectra appeared to resolve the difference between repeating, single-scale and multi-scale structure unambiguously (i.e., discerning repeating structure as a single pattern). This illustrative pattern was simple compared to patterns in complex simulations or empirical data. Interpretation of the semivariogram becomes more challenging when the data contain measurement error coupled with aperiodic and periodic components of pattern (Cohen et al. 1990).

The wavelet variance and power spectrum appeared to distinguish single-scale, repeating structure from multi-scale patterns more clearly than did the semivariogram. Wavelet analysis differs from Fourier spectral analysis in two ways: (1) due to the localization property, wavelet analysis does not require stationarity and (2) a specific basis may be assigned for each wavelet analysis (in addition to trigonometric bases; e.g., Fourier analysis). This flexibility in basis increases the pool of usable data and hypotheses available for testing. The Haar and Mexican Hat wavelet filters appeared to detect the 5-meter patch better than the French Top Hat (Table 2.2). We continued to examine the effects of these differences in the following section, as the effects relate to multi-scale, non-uniform data, and data feature morphology.

B. Simulated Data Analysis: Three Cases of Non-uniform and Data Feature Morphology

We examined the relative ability of semivariogram, Fourier, and one-dimensional wavelet statistics to detect pattern in three simulations of increasing complexity.

The first simulation was a simple, deterministic, non-uniform pattern concatenating one cosine function in the first half with a second cosine function in the latter half of the transect. This data structure maintains a constant mean and variance despite the non-uniform pattern (i.e., the period changing across the transect; Figure 2.5a). Somewhat surprisingly, the Fourier power spectrum and the Mexican Hat wavelet analysis were comparable in their abilities to identify two distinguishable peaks that correspond to the two scales of pattern and to detect the 1:3 ratio for the periods (Table 2.2). Due to the rounded shape of the functions, the power spectrum identified the two scales of pattern precisely at 10m and 30m (Figure 2.5c). Wavelet analysis detected the 5m and 15m half-periods (Figure 2.5b, Table 2.2).

The second simulation was a more complicated expansion of the simple, deterministic non-uniform pattern of the first simulation. The dataset consisted of five transects, with the ratios between first and second halves increasing from one to five (Figure 2.6a). Thus, the mean and variance were constant within any transect, but varied among all five transects. Fourier and wavelet analyses were comparably able to detect the two scales per transect and to identify the ratios for all five variations (Table 2.2). To some degree, the resolution capabilities of both the Fourier power spectrum and the wavelet analysis improved as the ratio between the two scales of pattern increase (i.e., half-period; Figures 2.6b and 2.6c; Table 2.2). Yet, the third transect was identical to the first simulation, and the patterns with greater and lesser ratios had very similar detection.

The third simulation addressed data feature morphology (e.g., asymmetrical structure, progression of scalar components) as variation of filter (i.e., basis) to highlight the relative flexibility of these two methods. The ratio between the half-periods for this transect was the same as for the first simulation (i.e., 1:3), but the peaks were square and the edges were distinct (Figure 2.7a). This non-uniform data structure had a constant mean and variance.

Fourier and wavelet analyses were not comparable in their abilities to detect the two scales and to identify the ratios between halves (Table 2.2). Fourier power spectra were limited to trigonometric functions as their basis. The two dominant scales and the ratio between the two sequential patterns were difficult to distinguish amid the extraneous information and energy at finer scales. Fourier analysis identified the two scales of periodic structure in the data as before. But, some of the eight peaks reflected real pattern while others were spurious (Figure 2.7c). The power spectrum perceived the square edges of the peaks in the data as high frequency components of the signal. Rather than clarifying the pattern, Fourier added noise to the signal and became more difficult to interpret.

Wavelet analysis is only limited by the researcher's ability to define the basis best suited for the data structure and hypothesis/question. For example, wavelet analysis decomposes the data into a progression of scalar components (e.g., Mexican Hat for rounded symmetric features, French Top Hat for squared symmetric features, Haar for asymmetric features and edges). Thus, the Haar filter was used to detect the squared waves and distinct edges of this pattern, as opposed to the Mexican Hat filter used for the first simulation. The Haar wavelet variance identified the two dominant scales of pattern and the 1:3 ratio in the half-periods (i.e., 5m and 15m; Figure 2.7b, Table 2.2). If the central objective of such a study is to distinguish dominant scales of pattern, the wavelet variance would be the appropriate choice. Often, this high flexibility in basis and non-stationarity in data recommend wavelet analysis over Fourier analysis, but method selection clearly depends on data morphology and study objective.

C. Empirical Data Analysis: A Case Study of the Western Meadowlark

In the previous two sections, illustrative stochastic and deterministic signals with known patch sizes at one and two scales provided a means to compare the detection abilities of these statistics under known conditions. Now, we shift the investigation to address their different abilities in detecting patterns in empirical data. Patch size and the number of scales are unknown, thus the comparison is extended to include visual pattern detection historically used by ecologists to 'eyeball' pattern in their data. In the empirical dataset, we describe the observed distribution of Western Meadowlarks in a transect across the United States. Then, we note the similarities and differences between visual perception of pattern from the distribution plots versus statistical perception of pattern by Fourier and wavelet analysis. Finally, we compare the characterization of this pattern by the spatial statistics.

Visual pattern recognition is the traditional means for ecologists to interpret animal population trends. The heterogeneous distribution of Western Meadowlarks along the transect was patchy with mixed density clusters and mixed intensity gaps (Figures 2.8 and 2.10). Most birds were located in the western half of the transect. At this latitude, Western Meadowlarks ranged from the Pacific coast of northern California (0 km) to eastern Kentucky-southwestern Ohio (2,306 km). However, relatively few birds were distributed east of Kansas (1,643.2 km).

On the largest scale, this heterogeneous pattern was discontinuous with irregular patches, several high peaks, and one very high spike (Figure 2.10, Table 2.3a). The peaks and gaps in Western Meadowlark distribution created a bimodal pattern. Land cover patterns influenced the distribution and extent of clusters along the transect. The grassland-cropland mosaic in the Great Plains of Kansas and eastern Colorado supported the largest cluster of Western Meadowlarks (Figure 2.11). This series ranged from the highest density of birds in the center to very low densities on the eastern tail of distribution. The savannah-cropland-pasture-woodland-forest mosaic in California and the shrubland-grassland-forest-sparsely vegetated mosaic in Nevada supported the smaller cluster of Western Meadowlarks. The gap that separated these clusters extended from eastern Nevada across the state of Utah. The habitat in this region was similar to that in Nevada with an increase in forested land and BBS routes cover this region. Thus, this area may simply be uninhabited and available for range expansion. Western Meadowlarks were largely absent or in extremely low densities in the largest gap that spanned from the irrigated cropland-grassland-pasture of eastern Kansas to the Atlantic Ocean. Land cover to the east became more forested, especially with deciduous broadleaf forests in western Missouri. Also, eastward range expansion was limited by competition with the Eastern Meadowlarks (*Sturnella magna*), with high concentrations in eastern Kansas, Missouri, and toward the Atlantic coast.

Distribution features at the large scale were separated into distinct features associated with land cover on the intermediate scale. Western Meadowlark distribution became more clearly quadrimodal with the division of the clusters from the bimodal pattern at the largest scale (Figure 2.10, Table 2.3a). The larger cluster was separated in two by a small gap after the highest peak. The land cover within this gap was mostly composed of cropland/grassland mosaic in western Kansas with an increase in irrigated cropland and pasture compared to the surrounding area (Figure 2.11). Upon closer, examination, this gap was created by an absence of survey transects at this longitude. Previously, it was unclear whether the gap is a true feature or sampling error. This gap

Table 2.3. Noteworthy features in Western meadowlark distribution from the visual pattern recognition (i.e., qualitative interpretation of the distribution plot in Figure 10) for the (a) large and (b) intermediate scales. The smallest scale is the sampling resolution at every 5.559 km.

(a) Large Scale

Perceived Relative Importance of Feature[1]	Feature	Location along transect (km)	Length (km)	Geographical Location	Generalized Land Cover
Low to Moderate	Peaks	555.90	0 - 555.90	eastward from the coastal zone in northern California	Pacific Ocean to savannah-cropland-pasture-woodland-forest mosaic in California; shrubland-grassland-forest-sparsely vegetated mosaic in Nevada
Moderate	Gap	311.30	550.34 - 867.20	eastward from eastern Nevada across Utah	increasing shrubland mixed with dryland and forests
Very Low to Very High	Peaks	778.26	872.80 - 1,645.5	eastward from western Colorado to eastern Kansas	forest to savanna to grassland and grassland-cropland mosaic with and mixed irrigated cropland/pasture/dryland in the Great Plains
High	Gap	1,178.5	1,645.5 - 2,824.0	eastward from eastern Kansas to the Atlantic Ocean	irrigated cropland-grassland-pasture transitioning into increased forest (especially deciduous broadleaf)

[1] Peaks: Very high > 7,000 birds; high = 5,000 – 6,999 birds; moderate = 1,500 – 4,999 birds; low = 20 – 1,499; very low < 20

Table 2.3. Continued

(b) Intermediate Scale

Perceived Relative Importance of Feature[1]	Feature	Location along transect (km)	Length (km)	Geographical Location	Generalized Land Cover
Low	Gap	44.472	0 - 44.472	eastward from the coastal zone in northern California	Pacific Ocean to savanna and forest
Low to Moderate	Peaks	316.86	44.472 - 361.33	eastward further into eastern California	grassy regions of the Pacific coastal zone in between major highways to cropland, savanna, national forests and Yosemite National Park across drier shrubland/grassland
Low	Gap	83.385	361.33 - 444.72	eastward from eastern California to western Nevada	sparse vegetation within the shrubland/grassland around Nellis Air Force Base and Death Valley National Park
Low	Peaks	111.18	444.72 - 555.90	eastward further into western Nevada	shrubland with grassland, towns close to Desert National Park with Wildlife Refuge near Death Valley National Park
Moderate	Gap	311.30	555.90 - 867.20	eastward from eastern Nevada across Utah	increasing shrubland mixed with dryland and forests; many desert National Parks
Very Low to Very High	Peaks	416.93	867.20 - 1,284.1	eastward from western Colorado to western Kansas	many National Forests, Fort Carson Military Reservation, and Comanche National Grassland in western Colorado to primarily grassland and savanna in eastern Colorado to grasslands and grassland/cropland mosaic in western Kansas
Low	Gap	44.472	1,284.1 - 1,328.6	eastward within western Kansas	cropland/grassland mosaic with increased irrigated cropland/ pasture
Low to High	Peaks	316.86	1,328.6 - 1,645.5	eastward from western Kansas to eastern Kansas	grassland/cropland mosaic including Great Plains National Grassland with grassland, savanna, and mixed irrigated cropland/pasture/dryland
High	Gap	1,178.5	1,645.5 - 2,824.0	eastward from eastern Kansas to the Atlantic Ocean	irrigated cropland-grassland-pasture transitioning into increased forest (especially deciduous broadleaf)

[1] Peaks: Very high > 7,000 birds; high = 5,000 – 6,999 birds; moderate = 1,500 – 4,999 birds; low = 20 – 1,499; very low < 20

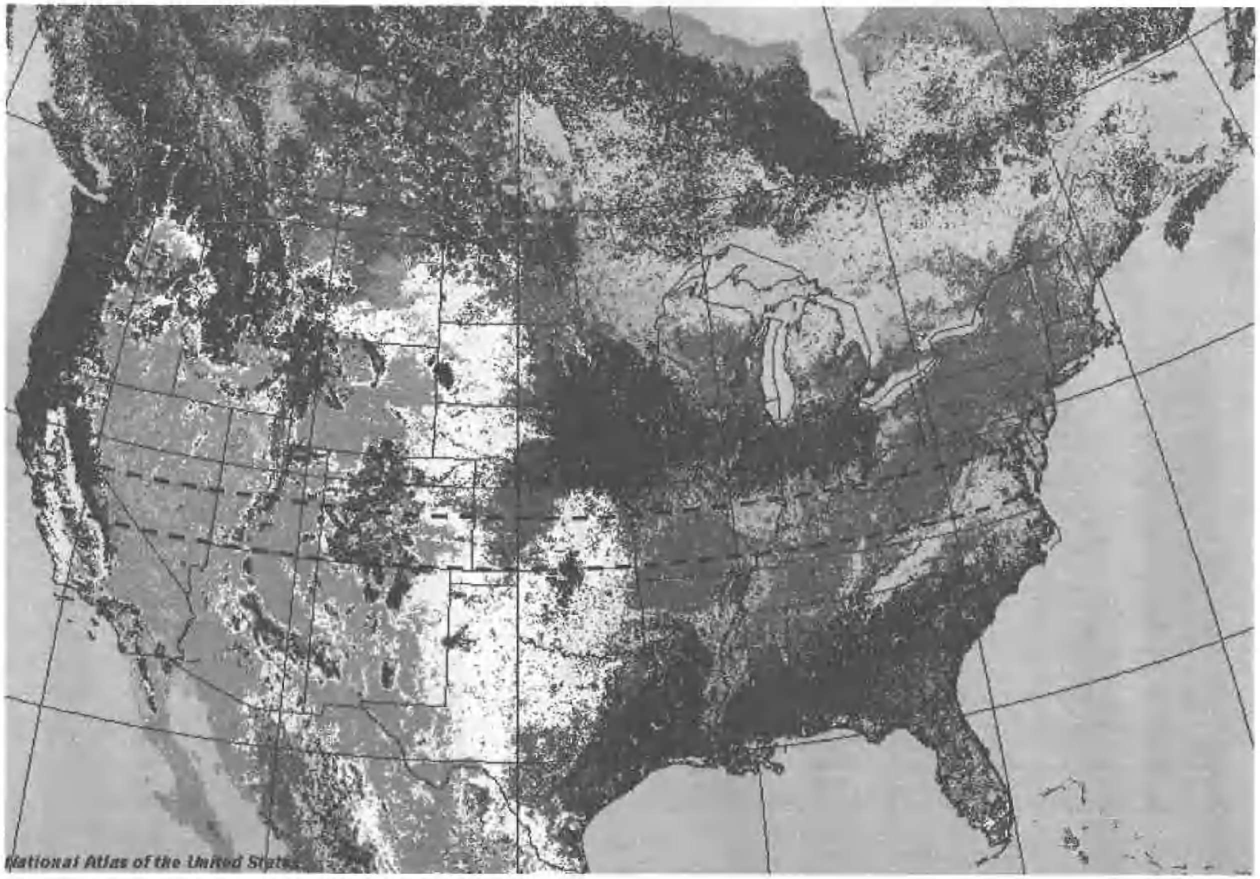


Figure 2.11.

did not appear as important at the large scale, because of the high peaks on either side. However, at the intermediate scale, this gap divided the eastern patch, with more consistent bird densities from the western patch with more inconsistent bird distribution. Possibly, higher densities of birds around the National Grassland on the eastern side were the core area for this cluster and the peaks on the western side represented dispersal.

The cluster to the east in the Great Plains of Kansas consistently supported high and moderate densities of birds (Figure 2.10). The dominant grassland/cropland mosaic land cover supported the highest densities with relatively high numbers in grassland, savanna, and mixed irrigated cropland/pasture/dryland (Figure 2.11). The cluster to the west spanned from the grasslands of western Kansas to the forests of western Colorado (Figures 2.10 and 2.11). The grasslands supported the highest concentration of Western Meadowlarks and the highest peak in the sample was in a region dominated by grasslands and grassland/cropland mosaic. At this latitude, eastern Colorado transitioned into primarily grassland and savanna, which maintained high and moderate densities of birds. Western Meadowlarks decreased with the increase of forests with moderate peaks in regions around national forests and Fort Carson Military Reservation. Overall, birds in this cluster gradually and irregularly increased to the highest peak (Figure 2.10).

A moderate gap that spanned Utah separated the two clusters in the east from the two in the west (Figure 2.10, Table 2.3a). The landscape changed from primarily forest in western Colorado to primarily shrubland in eastern Utah, which did not support Western Meadowlarks (Figure 2.11). Increasing shrubland mixed with dryland and forests deterred Western Meadowlark range expansion from either direction. Western Meadowlarks may not have dispersed into this region due to the hot, dry climate and intermittent human use and its associated water. At this latitude, Utah has many desert National Parks, whereas Colorado has many National Forests and Comanche National Grassland. The shrubland with grassland in the small cluster in western Nevada supported low densities of birds in areas near towns and the Desert National Park with Wildlife Refuge. This cluster was composed of small, distinct peaks separated by small gaps (Figure 2.10). The sparse vegetation within the shrubland/grassland around Nellis Air Force Base and Death Valley National Park created the gap separating sub-clusters in eastern California-western Nevada. The low to moderate cluster to the west spanned from the drier shrubland/grassland across national forests and Yosemite National Park, savanna, cropland, and in between major highways to the grassy regions of the Pacific coastal zone (Figures 2.10 and 2.11). The transition from savanna and forest to the Pacific Ocean resulted in a small gap in Western Meadowlark distribution at the western end of the transect. Finally, the largest gap in Western Meadowlark distribution at this latitude extended from the eastern Kansas to the Atlantic Ocean.

Distribution patterns at the intermediate scale were further divided to every peak and gap at the smallest scale (i.e., 5.559 km). Bird densities along the transect were irregular, varying greatly from very low with one bird recorded to very high with 13,394 birds (Figure 2.10). The single very high peak was located in western Kansas (1,281.1 km). Most peaks represented 20 to 1,500 birds, but many peaks were larger (1,501 to 5,000 birds) or smaller (< 20 birds). Only six peaks were greater than 5,000 birds.

Visual pattern recognition was useful in qualitatively distinguishing pattern at the three general levels of scale. However, any attempt to assess relative influence of features contributing to these patterns was limited. Spatial statistics provide a quantitative means to distinguish multiple levels of scale. Each statistical method detected different aspects of the pattern. Wavelet analysis also distinguished the relative contributions of features to the pattern overall and at each scale.

Fourier analysis quantified the multi-scalar pattern and indicated the relative contribution of the features at each scale. Seven dominant scales of periodic structure were detected in the distribution of western meadowlarks (Figure 2.12a, Table 2.2c). All seven scales were less than 312 km long. This spectral analysis perceived these repeating trigonometric functions (in order of importance): 106.89 km, 311.29 km, 80.652 km, 126.74 km, 153.14 km, 94.885 km, and 212.23 km. The Fourier coefficients oscillated within the narrow spectral range of 58 and 66 (Figure 2.12b). The strongest influence came from 106.89 km, 311.29 km, and 80.652 km. These spectra appear to

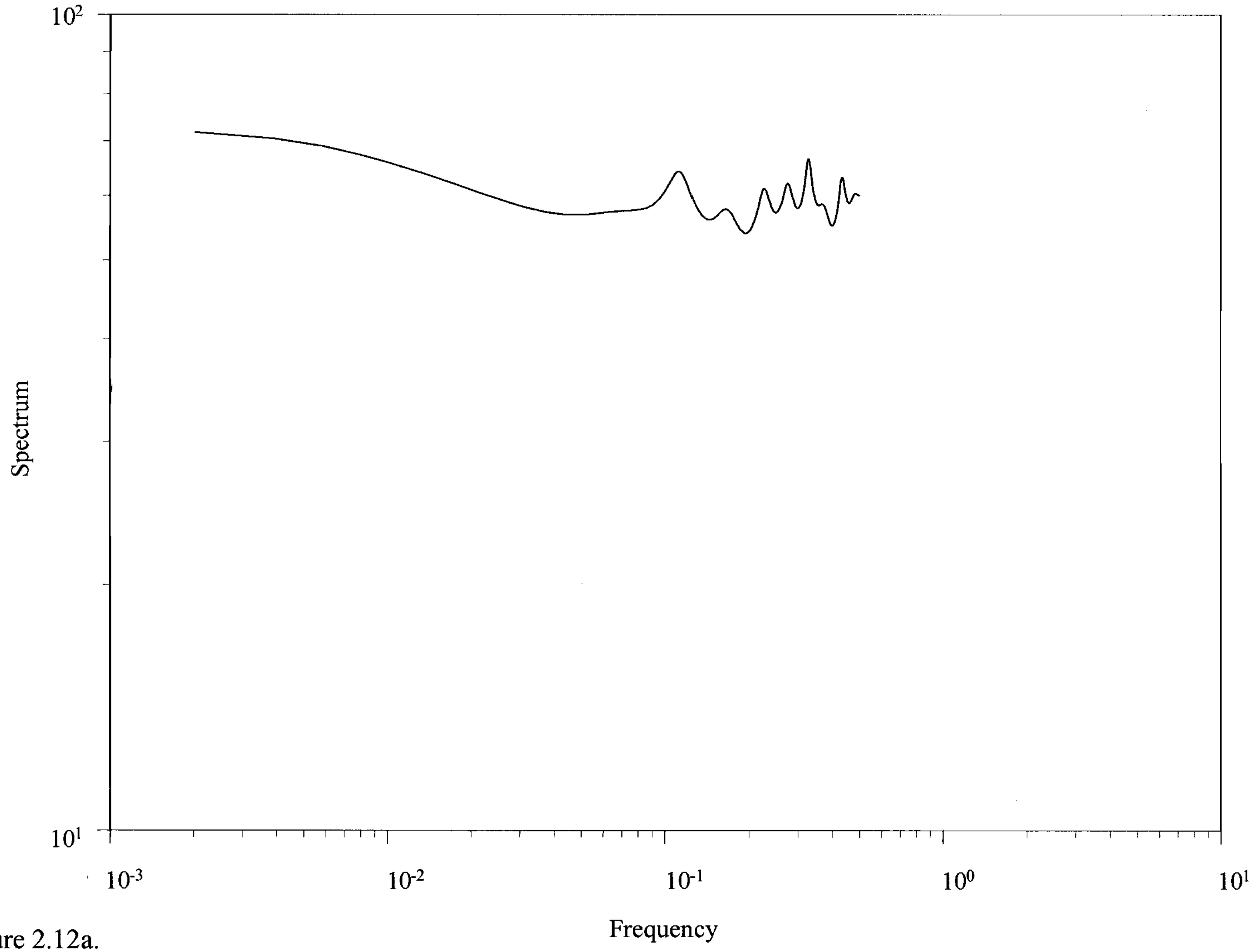
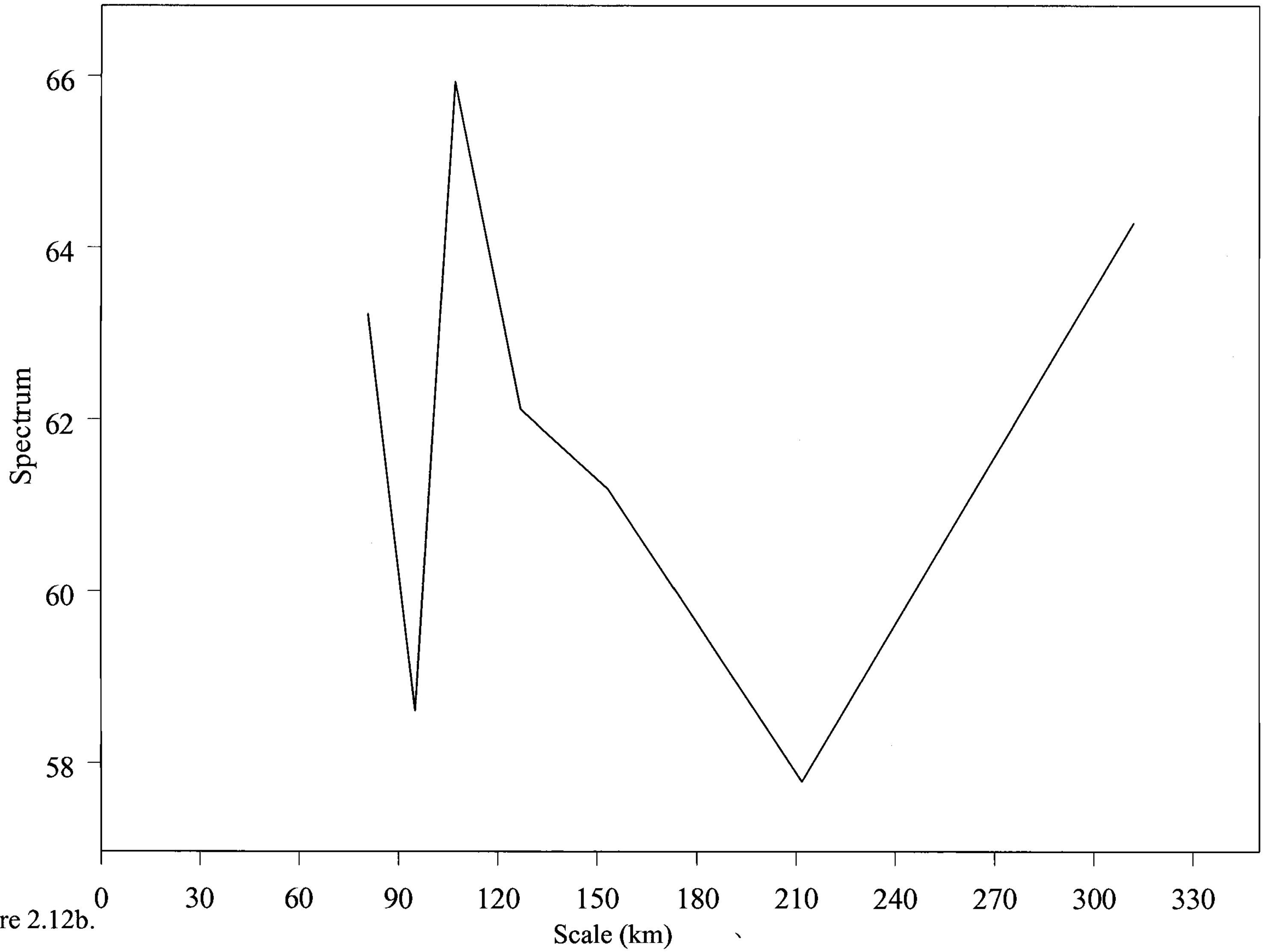


Figure 2.12a.



66
64
62
60
58
Spectrum
0
30
60
90
120
150
180
210
240
270
300
330
Scale (km)

Figure 2.12b.

correspond to features detected visually. The last four spectra were weaker. Fourier analysis is susceptible to spurious peaks irrelevant to the analysis. The patch at 212.23 km appeared to lack any ecological context. Both 94.885 km and 153.14 km provided additional information about smaller sections of the 311.29 km interval, but contributed little else. The 111.18 km peak in Nevada and the small 83.385 km gap to its west are possibly contributing to the strong contributions of 106.89 and 80.652 to the spectral analysis. Fourier did quantify some of the internal structure of the data in a way that was partially compatible with visual pattern recognition. The results appeared to be an adequate, but non-ideal approximation of the data. Fourier analysis did not provide further insight into the relative contributions of features to the overall pattern.

The pattern at the largest dominant scale (311.29 km) spanned the first series of peaks along the transect (Figure 2.10). This repeating interval accurately captured the moderate 311.30 km gap spanning the drylands of Utah that appeared on both the visual large and intermediate scales (Table 2.3). The adjacent second gap in bird distribution was in a region of sparse vegetation mixed with some shrubland and grassland. Fourier analysis detected accurately the boundary between the first cluster and the second gap. The limitations of this method resulted in the subsequent interval extending beyond the gap through the second cluster and into the third gap. This scale was close to detecting the first cluster and the last cluster on the visual intermediate scale (both 316.86 km), but it did not match the other visual patterns. The first cluster of Western Meadowlarks on the visual intermediate scale spanned from the grassland regions near the Pacific Ocean between the highways, cropland, savanna, Yosemite National Park, and across national forests to drier shrubland with some grassland in western Nevada. The last cluster contained low to high peaks in the region of the Great Plains National Grassland.

Patterns were detected according to the shape of the waveform filter, with peaks at the beginning and a last peak at the end. Features were identified by clusters of peaks. Gaps were a means to delineate clusters of peaks. For instance, the small gap (44.472 km) at the beginning of the transect was skipped over. Thus, the first cluster on the large scale spanned 316.86 km, rather than 361.86 km had the pattern started at the origin. Fourier analysis appeared to detect the first series of peaks at the beginning of the transect and repeat the interval of this pattern in a waveform to the end. Thus, patterns at the beginning of the transect were characterized better than those that were large or later.

None of the dominant scales were greater than 312 km (Table 2.2c). Several explanations are possible. Perhaps there were no larger dominant scales in these data or the large patterns may not have been cyclic. One may predict a dominant scale encompassing the entire transect or the large cluster in the center of the transect. However, this pattern is not continuous from the beginning of the transect due to the large gap to the west. Most likely, larger patterns were described in terms of smaller scales.

Wavelet analysis depicted multi-scalar, mixed pattern heterogeneity in Western Meadowlark distribution across the mid-United States. The wavelet transform detected six dominant scales in Western Meadowlark distribution (Table 2.3c). The greatest contribution came from scale 6 with patch size 1,411.98 km, followed by 44.472 km, 88.944 km, 355.78 km, 177.89 km, and 705.99 km. Most of the energy of the wavelet transform is in the details of scale one (D1; 62%). Scale two (D2) follows with 16% of the total energy. The smoothed crystal at S6 has half the energy at D2 and the each scale diminishes to the least contribution at scale 5 (D5).

The wavelet variance graphically depicts this dispersion of energy in the signal and indicates the relative contribution of the features at each scale to the overall pattern (Figure 2.13). Overall, the nested pattern of the wavelet variance reflected a very high peak spanning the coarser scales, low amplitude at the intermediate scales, and a moderate peak at the finer scales. This signal reflects large peaks and clusters of small peaks, some moderate and large gaps, and a diverse internal structure. The wavelet variance demonstrated a gradually decreasing trend from a higher peak at Scale 1 to a high, consistent pattern among the intermediate scales 3 through 5 and a steep increase to a very high peak at scale 6, representing low frequency clusters. All of these wavelet variances are high relative to other Western Meadowlark transects across North America (See Anthony 2004). Thus, the pattern was dominated by features at the largest scale as well as at the smallest scale. The density was irregular with the amplitude of

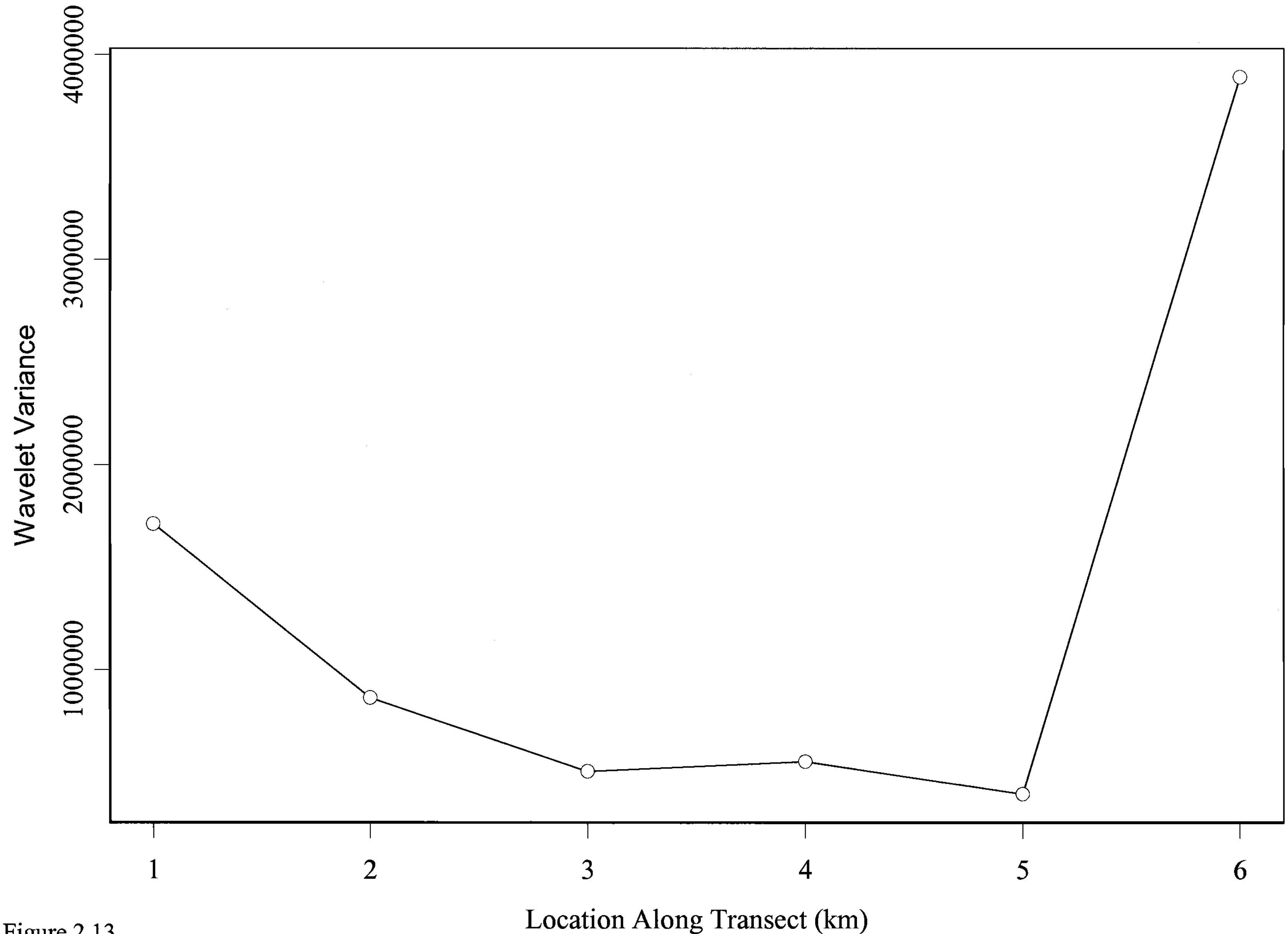

4000000
3000000
2000000
1000000
Wavelet Variance
1
2
3
4
5
6
Location Along Transect (km)

Figure 2.13.

peaks and gaps varying widely. Yet, the wavelet variances are distributed relatively evenly across scales three through five, representing moderate intensity gaps of varying lengths. Additional wavelet metrics are available to identify the exact location of these features (See Anthony 2004).

Wavelet analysis confirmed some of the pattern perceived by the human eye. The strongest signal was from scale 6 with patch size 1,411.98 km. The closest feature to this magnitude is the long gap on the eastern end of the transect (1,178.5 km). The 44.472 km gaps in the intermediate scale are easily located on the western end of the transect, before any birds are detected, and in between the clusters with the highest peaks in the center. The signal at the 88.944 km scale is moderately strong, suggesting the influence of the second gap (83.385 km). The 355.78 km patch size relates to the combined first gap and first cluster in the west (i.e., 44.472 + 316.86 = 361.33 km), the moderate gap in Utah (311.30 km), the final large cluster of high peaks, and perhaps the nearby broad cluster of peaks (416.93 km) on the intermediate visual scale. On the large scale, this scale may be picking up the 311.30 km gap. The 705.99 km patch size is picking up the wide cluster of peaks on the large scale (778.26 km).

Wavelet and Fourier analyses detected a similar number of scales (Table 2.3c), but some of Fourier's scales did not appear relevant to this analysis as they did not relate directly back to observable pattern in the data. The wavelet scales spanned about half the transect, whereas the Fourier scales were skewed toward higher frequency signals. Wavelet detected the gap at the beginning of the transect and incorporated it into its detection of the larger 361.33 km feature. Fourier appeared to skip over this gap and concentrate on the first cluster of peaks, and other features of similar width.

DISCUSSION

We compared the resolution capabilities of semivariogram, Fourier power spectrum analysis, and wavelet analysis (i.e., wavelet transform, wavelet variance). Semivariogram and Fourier analysis are well known for pattern detection based on the autocorrelation function. To facilitate comparison, we re-derived the wavelet variance in terms of the autocorrelation function and its calibration to the semivariogram in the frequency domain to remove arbitrary differences. In this formalism, the wavelet variance did not show appreciable differences from the other two methods for the same scale of pattern. Yet, in contrast to the semivariogram and the power spectrum, wavelet analysis has the advantage of resolving periodic structure unambiguously, thereby facilitating the identification and interpretation of multi-scale pattern in empirical data.

We demonstrated that one-dimensional wavelet analysis is effective in characterizing spatial and temporal structure in multi-scale ecological phenomena. The wavelet transform quantifies spatial structure (e.g., scale, intensity, location along the transect) by decomposing the overall pattern into its fine- and coarse-scale components. The wavelet transform acts as a local filter that does not need to be defined *a priori*, relates the magnitude of the signal to its location along the transect, and allows flexibility in choice of analyzing wavelet to match data parameters and study objectives (Bradshaw and Spies 1992). The wavelet variance determines the dominant mean scales in the data. By telescoping spatial information to quantify the contribution of each scale component to the entire transect, the wavelet variance facilitates comparison among data sets.

COMPARISON OF THE METHODS OF THE THREE STATISTICS

First, we consider several of the more important strengths, limitations, and assumptions of the three statistics. Next, we discuss the salient results from our comparison of these methods from analysis of the stochastic, deterministic, and empirical datasets. Then, we compare the pattern detection among all three statistics. After comparing observed and expected results, we conclude with a clarification of the questions answered by these statistics and those asked by ecologists.

Strengths, Limitations, and Assumptions of the Three Statistics

Semivariograms are descriptive statistics in ecology that represent spatial variability geographically within a dataset. This method excels in the description of an average structural dimension, especially when signals are choppy. Its capabilities in the detection of local features deviating from the mean are limited (Cohen et al. 1990). Semivariograms lose the detail to describe local features deviating from the mean, which is important in determining internal structure. Interpretation becomes difficult when data have multi-scalar structure. For the most part, semivariograms are limited to stationary data on a single scale (i.e., The Hole Effect in mining statistics can detect nested structures, but otherwise semivariograms cannot). Semivariograms are useful and estimation is unbiased when all variables have a constant mean. At the same time, however, the estimation of covariates is biased. Table 2.4 summarizes the analytical capabilities of semivariograms and the other statistics. In a semivariogram, peaks indicate the dominant scales, but oversimplify data characterized by sharp spikes.

Both semivariogram and Fourier analysis measure spatial correlation as a function of the distance between two points. Both methods use a weighted iterative function to predict data based on the values of neighboring data. Semivariograms do not model the actual position of the data, but rather model spatial correlation as a function of separation distance. The functions used to calculate semivariogram and Fourier power spectra are stationary and extend to infinity. Thus, these functions operate under the false assumption that ecological processes have a periodic pattern occurring uniformly across space and time. The description of a composite signal and the identification of the underlying pattern can be difficult when countercurrent ecological processes actually vary in scale or temporal influence. Table 2.5 presents exemplary studies implementing each method in ecology and biology. For instance, semivariogram detects relationships between spatial pattern in vegetation and environmental factors (e.g., soil).

Fourier power spectra and wavelet analysis are more similar in using linear combinations of sines and cosines to represent a transect. A theorem in mathematics states that any continuous function can be represented as an infinite sum of linear combinations of sine and cosine functions, expanded and compressed to match the inherent character of the collection of points and related by proximity. The pattern-specific wavelet filter provides more versatility in describing dominant patterns at multiple scales than does the trigonometric filter used by Fourier analysis. Fourier analysis is most useful in detecting cyclic, linear functions. Wavelet analysis is a viable alternative in detecting pattern previously overlooked by semivariogram analysis and Fourier power spectra. Wavelet analysis offers an elegant way to analyze complex

Table 2.4. Summary of the capabilities of one-dimensional wavelet analysis, semi-variogram, and Fourier power spectra in characterizing pattern in complex data sets, with examples of ecological inference. A plus sign (+) represents strength in the spatial method in encompassing the indicated type of data, a minus sign (-) represents weakness, and a tilda sign (~) represents moderate capability. Information specific to a specific analyzing wavelet is indicated by the first letter: Mexican Hat by an M, French Top Hat by an F, Haar by an H, Daublet by a D, Symmlet by an S, and Coiflet by a C.

One-dimensional Wavelet Analysis	Semi-variogram	Fourier Power Spectrum	Type of Data	Examples of Ecological Inference
+	-	~	Multiple scales	Relates pattern to process at multiple scales (e.g., spatial pattern of forest canopies and understory vegetation); heterogeneity
+	+	+	Fine-scale patterns	Relates pattern to process at one scale (e.g., vegetation community structure at stand level)
+	+	~	Coarse-scale patterns	Relates pattern to process at one scale (e.g., conifer forest structure at landscape level)
+	-	-	Non-stationarity	Differentiates mean and variance changing along the transect (e.g., gradients)
+	-	-	Non-uniformity	Differentiates period changing along the transect
+	-	-	Flexibility in choice of basis	Tailored to the pattern (e.g., edge detection in satellite imagery)
+	-	-	Presence/Absence	Detects pattern (e.g., presence/ absence vegetation cover studies)
$+_{\text{M, F}}$	-	+	Patches	Distinguishes symmetric features, average patch size
$+_{\text{H, D, S, C}}$	-	-	Sharp contrast/Step function	Detects asymmetric features, edges, and gradients (e.g., ecotone boundary, road, management area)
+	-	+	Repeating, cyclic pattern	Distinguishes regular pattern (e.g., stripes, diurnal temperature change)
+	-	~	Periodic, non-cyclic pattern	Distinguishes successive, additive events (e.g., vegetative growth)

Table 2.5. Examples of published studies in ecology using semi-variogram, Fourier power spectra, and one-dimensional wavelet analysis.

Statistic	Ecological Topic	Feature	Reference
Semi-variogram	Distribution	Whiptail lizard	Ver Hoef, J.M., Cressie, N., Fisher, R.N., and Case, T.J. 2001. Uncertainty and spatial linear models for ecological data. Pages 214 – 237 in Hunsaker, C.T., Goodchild, M.F.. Friedl, M.A., and Case, T.J. (eds.), Spatial Uncertainty in Ecology: Implications for Remote Sensing and GIS Applications. Springer-Verlag, New York.
Semi-variogram	Predicting population patterns	Moose	Ver Hoef, J.M. 2001. Predicting finite populations from spatially correlated data. 2000 Proceedings of the Section on Statistics and the Environment of the American Statistical Association, pgs. 93-98.
Semi-variogram	Relating spatial pattern to environmental factor	Hardwood forest, soil characteristics	Palmer, M.W. 1990. Spatial scale and patterns of species-environment relationships in hardwood forests of the North Carolina piedmont. Coenoses. 5: 79-87.
Semi-variogram	Description of spatial structure at large scales	Forest soil, Lake water chemistry, Air temperature, Precipitation	Oliver, M.A. and R. Webster. 1986. Combining nested and linear sampling for determining the scale and form of spatial variation of regionalized variables. Geographical Analysis 18: 227-242.
Semi-variogram	Distribution (presence/absence)	Vascular plants in high arctic sedge meadows	Young, C.G. 1994. Spatial distribution of vascular plants in high arctic sedge meadow communities. M.Sc. Thesis. Edmonton, Canada: University of Alberta.
Semi-variogram	Description of spatial pattern in an exploited landscape in relation to conservation, with emphasis on edges, core area, fragment shape	Birds in Old-growth forests	Cullinan, V.I. and J.M. Thomas. 1993. A comparison of quantitative methods for examining landscape pattern and scale. Landscape Ecology 7: 211-227.
Semi-variogram	continuous-valued data such as digitized spectral imagery		Cohen, W.B., T.A. Spies, and G.A. Bradshaw, 1990, "Semi- variograms of digital imagery for analysis o f canopy structure . Remote Sensing o f the Environment. Vol 34. pp. 167 -178.
Fourier Analysis	Predator – prey spatial associations	Seabird	Logerwell E.A., R.P. Hewitt, and D.A. Demer. 1998. Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. Ecography. 21:2:212-223.
Fourier Analysis	assess scales of spatial pattern in vegetation		Usher 1975

Table 2.5. Continued

Statistic	Ecological Topic	Feature	Reference
Fourier Analysis	assess scales of spatial pattern in vegetation		Ripley 1978
Fourier Analysis	assess scales of spatial pattern in vegetation		Grieg-Smith 1983
Fourier Analysis	identify scales of patchiness in distribution		Turner et al 1991
Fourier Analysis	extinction rates in community ecology and paleoecology		run searches on "self-organized criticality" or "1/f noise" with extinction
Fourier Analysis	time series analysis of ecosystem processes		Falter, Atkinson, and Langdon. 2001. Production-respiration relationships at different timescales within the Biosphere 2 coral reef biome. Limnol. Oceanogr. 46(7) 3653-3660.
Fourier Analysis		long-term acorn production by xeric oaks in Florida	Warren Abrahamson of Bucknell University; "Long-term patterns of acorn production for five oak species in xeric Florida uplands" has been accepted for publication in Ecology
Fourier Analysis	remote sensing with an imaging spectrometer (AVIRIS)	Plant absorption features, LAI, biomass, leaf water content, canopy structure, species assemblages, etc	Refs at www.cstars.ucdavis.edu
Fourier Analysis	animal behavior through time, treating the frequency of occurrence of a particular behavior as a frequency of a wave		Desportes, J.-P., N. B. Metcalfe, F. Cezilly, G. Lauvergeon, and C. Kervella. 1989. Test of the sequential randomness of vigilant behaviour using spectral analysis. Animal Behaviour 38:771-777. Desportes, J.-P., N. B. Metcalfe, B. Brun, and F. Cézilly. 1990. Vigilant behaviour: predictability or randomness? spectral analysis of series of scan durations and their relationship with inter-scan intervals. Ethology 85:43-50. Desportes, J. P., N. B. Metcalfe, J. W. Popp, R. M. Meyer, A. Gallo, and F. Cézilly. 1993. Relationship between scan and interscan durations in three avian species. Canadian Journal of Zoology 71:1466-1469.

Table 2.5. Continued

Statistic	Ecological Topic	Feature	Reference
Fourier Analysis	characterize periodic behaviour in both temporal and spatial data		Platt & Denman 1975
Fourier Analysis	characterize periodic behaviour in both temporal and spatial data		Ford & Renshaw 1984
Fourier Analysis	characterize periodic behaviour in both temporal and spatial data		Kenkel, N. C. 1988. Spectral analysis of hummock-hollow pattern in a weakly minerotrophic mire. Vegetatio 78: 45-52.
Wavelet Analysis	examine canopy structure	forest	Bradshaw, G. A. and Spies, T. A. 1992. Characterizing canopy gap structure in forests using wavelet analysis. J. Ecol. 80: 205-215.
Wavelet Analysis	microclimatic patterns		Saunders et al. 1998
Wavelet Analysis	understory plant diversity		Brosofske et al 1999a
Wavelet Analysis	understory plant diversity		Chen et al. 1999
Wavelet Analysis			Cipra, 1990
Wavelet Analysis			Ranchin, T. and Wald, L. 1993. The wavelet transform for the analysis of remotely sensed images' INT.J. Remote Sensing ,1993. vol. 14, No.3, 615-619.
Wavelet Analysis			Bradshaw, G. A. and McIntosh, B. A. 1994. Detecting climate- induced patterns using wavelet analysis. Environ. Poll 83: 135- 142.
Wavelet Analysis			Dale, M. R. T. and Mah, M. 1998. The use of wavelets for spatial astern analysis in ecology. J. Veg. Sci. 9: 805-814.
Wavelet Analysis			Thompson, J. N. 1994. The Coevolutionary Process. The University of Chicago Press, Chicago. Emerging synthesis of evolutionary and ecological theory strongly emphasizes the importance of regional landscape mosaics the organization of biological diversity - species that evolve quite different coevolutionary specializations in different parts of their geographic 'Allie. The spatial structure of landscapes is a key component that determines the context in which coevolutionary specialization occurs
Wavelet Analysis			Hochberg, M. E. and van Baalen, M. 1998. Antagonistic coevolution over productivity gradients. Am Nat. 152: 620-634. Emerging synthesis of evolutionary and ecological theory strongly emphasizes the importance of regional landscape mosaics the organization of biological diversity - Recent theoretic- work has supported the idea that coevolutionary relationships can vary along gradients, and in some cases, the direction of the interaction may even reverse
Wavelet Analysis			Gastafson, E. J. 1998. Quantifying landscape spatial pattern: What is the state of the art? Ecosystems 1: 143-156.

signals, particularly the ecological relationships represented by non-linear, chaotic, or fractal behavior.

Fourier analysis is more similar to wavelet analysis, but semivariogram and wavelet analysis do share several features. Semivariogram is similar to one-dimensional wavelet analysis in detecting orientation, the patch size of the edge, and the steepness of the edge. Semivariogram is part of kriging for prediction and wavelet analysis has prediction, image analysis, and image reconstruction capabilities (1/acf=sv). Two differences between these methods are: (1) semivariogram requires the original data, whereas wavelet analysis uses interpolated data, and (2) semivariogram can use regular gridded data or not, whereas wavelet analysis can only interpolate regular gridded data.

Wavelet analysis uses mathematical functions to capture multi-scale temporal and spatial patterns in complex data sets with clustered points. Wavelet analysis accommodates and preserves non-stationarity in large spatial and temporal data sets, providing a continuous measure of pattern across scale (within the limits of data resolution). The empirically derived autocorrelation function can serve as a measure of the independence of the biological variable from the spatially defined abiotic environment. Thus, the statistical properties of wavelet analysis decompose a one-dimensional signal with uniform or non-uniform structure to detect pattern in the data, classify the pattern by intensity and regularity, and relate hierarchical phenomena across scales.

One disadvantage of wavelet analysis is a lack of integrated measures of significance. However, bootstrapping and Monte Carlo (Manly 1991) are viable means to evaluate precision. For example, calculate the wavelet variance for 1,000 randomizations of the data. The wavelet variance for the original data is considered statistically significant at $\alpha = 0.05$, if it exceeds 95% of those calculated for the randomizations. Other limitations of one-dimensional wavelet analysis include the requirement for large sample sizes (i.e., greater than 100 points per transect) and an intolerance for missing observations (i.e., a missing value must be assigned a zero value). Data must be collected with sufficient resolution and extent to capture the patterns and processes of interest. The scope of the analysis is only as large as the sampling resolution (e.g., 11 x 2,824 kilometers in the BBS data). Despite these limitations, we believe one-dimensional wavelet analysis represents an advance in statistical methodology available to ecologists.

A. Four Stochastic Processes Based on the Autocorrelation Function

The three methods of pattern analysis were compared for their relative ability to detect pattern by calculating their responses to autocorrelation functions that correspond to a set of simple, stochastic processes. These four stochastic processes were chosen for their similarity to physical and ecological processes. The additive moving average model is useful for data with successive events that are additive and accumulate in magnitude over space (e.g., vegetative growth). The non-additive moving average model allows for overlap among successive patches without losing individual patch size (e.g., presence/absence of vegetation cover or disturbance). The AR(l) model or Markov process extends the moving average to describe empirical processes (e.g., conifer cone distribution). The auto-regressive harmonic model assesses the effects of varying degrees of periodicity (e.g., repeating pattern).

Through the analysis of four one-dimensional stochastic models, we developed a framework for identifying dominant scales in the pattern. Semivariogram closely approximated the scale of pattern in the simple systems, but it did not perform well with the repeating, single-scale structure of the auto-regressive harmonic. The pattern calculated for these data was comprised of a measurement error coupled with aperiodic and periodic components of pattern (Cohen et al. 1990). Thus, semivariogram would not be expected to characterize accurately the periodic, multi-scalar pattern of vegetation data. Spectral analysis performed well under all four stochastic processes. Overall, the wavelet variance did not differ greatly from the Fourier analysis. When data are characterized by a repeating, single-scale structure, the wavelet variance and the Fourier power spectrum provide relatively unambiguous results. The French Top Hat wavelet basis did not identify any of the stochastic processes very accurately. However, the Mexican Hat and Haar wavelet bases yielded consistent insight into the scales of these patterns. Thus, the relative flexibility in the wavelet basis allows for the best filter to be used for each analysis.

B. Simulated Data Analysis: Three Cases of Non-uniform and Data Feature Morphology

With the insight into how well the Fourier and wavelet analyses detected pattern in four single-scale patterns, we examined their ability to detect multi-scalar pattern in three deterministic simulations. First, a simple non-uniform pattern with constant mean and variance. Then, a more complicated series of five non-uniform patterns with constant mean and variance along each transect, but with incrementally increasing ratios between the scale in the first half and in the second half. Finally, a pattern identical to the first simulation but with a variation in the data feature morphology – the peaks are square and have edges. All three patterns are multi-scalar with two scales.

The deterministic models challenged the statistics to detect the known pattern of these three different non-uniform multi-scalar transects, each demonstrating two scales. Non-uniformity denotes data exhibiting a trend or a changing pattern along the length of the sample (i.e., period changes along the transect). Semivariogram and power spectra have limited tolerance of non-uniformity. These statistics assume first- and second-order stationarity (Priestley 1977, Journel and Huijbregts 1978), such that the mean and variance must be constant all along the transect (even when the pattern is non-uniform overall). Whereas, the localization property in the wavelet transform and wavelet variance dismisses any requirement for stationarity (Mallat 1988). One of the main strengths of the wavelet transform is the detection of non-uniform and hierarchical structure in the data (Argoul et al. 1989, Bradshaw and Spies 1992).

Both Fourier and Mexican Hat wavelet analyses detected the two scales in all three simulations. In the first and second simulations, Fourier analysis even quantified the two scales of periodic structure correctly (Figures 2.5 and 2.6, Table 2.2). However, in the third simulation, the power spectrum perceived the square edges of the peaks as high frequency components of the signal and energy at finer scales (Figure 2.7, Table 2.2). Fourier's ability to distinguish the signal from the noise was diminished, as was its ability to identify the ratio between the halves. Fourier power spectra are limited to trigonometric functions as their basis. In contrast, the Haar wavelet detected and quantified the two dominant scales of pattern equally well in all three simulations. If the main object of a study was to distinguish dominant scales of pattern, the Fourier has enough limitations that the wavelet variance would be a better choice in the present example.

This flexibility in the choice of the wavelet basis is an important advancement over the limited use of trigonometric functions as bases in semivariogram and Fourier analysis. Thus, the function defining the basis for wavelet analysis may be tailored to specific data feature morphology, not just the rounded edges of the Mexican Hat or the squared edges of the Haar and the French Top Hat (Table 2.1). This flexibility in choice of the analyzing wavelet as the basis offers wavelet variance a distinct advantage over spectral analysis. This advantage is seen particularly when the data morphology is non-sinusoid (e.g., edge detection in satellite imagery, presence/absence vegetation data). Selection of the analyzing wavelet depends on the physical structure of the data and the objectives of the study. Simulation examples indicate that Fourier power spectra can introduce high frequency responses as the form of the data features deviates from a pure sinusoidal function. As a result, the interpretation of power spectra given similar data feature morphology may prove ambiguous when the data are characterized by pattern at the same scale of the 'edge effects'.

C. Empirical Data Analysis: A Case Study of the Western Meadowlark

The heterogeneous distribution of the Western Meadowlark was unknown until we explored the multi-scalar pattern with Fourier and wavelet analyses. Semivariogram was excluded from this analysis based on its poor performance in the simpler stochastic processes analyses. Of the seven scales detected by Fourier analysis, one peak was spurious and the status of two others was uncertain. There is no way to 'ground-truth' the scales with the data to be certain whether there are seven, six, or four dominant scales in these data.

COMPARISON OF STATISTICAL AND ECOLOGICAL APPLICATIONS

Before we can isolate relationships between heterogeneity, biotic and abiotic components of the ecosystem, and multi-scale phenomena responsible for ecological patterns, we must understand the capabilities of the available analytical methods. Do the questions the statistics answer match the ecological questions we're asking? By evaluating the ability of these three spatial statistics to detect and classify pattern in ecology, we will learn more about how much influence the assumptions and limitations have on the interpretation of real data.

Once we can characterize the internal structure of a species range, we can begin to tease out the factors that determine the distribution and abundance of plants and animals in space and time. - ecological monitoring (ex. endangered plants, selecting reserve). Populations have characteristics important in monitoring, the most basic of which are population size, dispersion (the distribution of individuals in space), population density, natality and mortality, and age-class or size-class distribution. Individuals with narrow tolerance for a few factors would be good indicator species. If you know the distribution and important scales, you can collect data at their appropriate level to address assumptions. The precision (e.g., how many samples need to be taken, how many quadrats, how large, etc) of absolute estimates of population density depends on several factors, including temporal and spatial patterns of dispersion, the method of sampling, and observer bias. Also, important is the frequency of sampling. Time series analysis and the statistical analysis of periodicity provide some guidance. The simplest variables that could be used for monitoring are number of species, species composition, and proportional abundance of species

An increased awareness of the importance of the spatial and temporal context of ecosystem phenomena has motivated interest in methods of pattern analysis. Pattern is comprised of several components, broadly grouped as the presence of single or multi-scale pattern, contrast (i.e., relative amplitudes of the data), non-uniformity, and data feature morphology (e.g., asymmetrical steps, symmetrical patches). Our results show that an appropriate choice of method for pattern analysis will depend on one or more data attributes, as well as the properties of the data (e.g., sample size, transect length, range of scales). Each method will provide a slightly different perspective, depending on the type of data and study objectives involved. Clarity and accuracy of interpretation of an analysis of ecological data in the spatial domain will depend ultimately on these factors and will determine the method or sets of methods employed.

In this manuscript, we have limited our interpretation of the wavelet metrics to those relevant for comparison among methods (i.e., wavelet transform, wavelet variance), even though additional metrics are available. Yet, in essence, the differences among methods in detecting pattern in empirical data are somewhat irrelevant. Being able to use visual and statistical 'lenses' with different capabilities to describe pattern becomes a strength rather than a weakness. The researcher amasses insight into the assumptions and limitations of the statistics, the answer to his/her question, and the assumptions and limits of the ecological question itself, and. Agreement among two or more methods lends more credence to the detected pattern, but none of the information can be easily dismissed as invalid. The 'true' internal structure in empirical ecological data, such as Breeding Bird Survey distributions, is neither known nor confirmable. Within the constraints of that measure, the pattern exists. Applying multiple 'lenses' to the data strengthens the researcher's familiarity with the nature of the data as well as the detectable pattern in the data. Shifting perspective better informs both the decision-making based on the questions posed and the generation of new questions.

CONCLUSIONS

In this comparison of semivariogram, Fourier analysis, and wavelet analysis in terms of the autocorrelation function and empirical data, our results support the superiority of wavelet analysis in identifying and characterizing ecological pattern. One-dimensional wavelet analysis is useful in separating signal from noise. The empirically derived autocorrelation function segregates biotic and abiotic components of pattern to better relate the model to data and pattern to process. With additional information on potential processes acting on Western Meadowlarks (e.g., topography, weather, human activities), wavelet analysis could be extended to evaluate potential processes generating the measured patterns. One-dimensional wavelet analysis needs to be further developed in an ecological context, such as a comparison among different types of patterns or different species. Future research should consider the development of pattern-specific data filters and the extension of probability statistics to define confidence intervals and other means to test hypotheses using wavelet analysis. Another extension of these spatial statistics is to examine increased complexity in the internal structure of pattern at different scales in two-dimensional wavelet analysis.

All of these statistical tools are useful in detecting and quantifying ecological pattern in pursuit of understanding their generative processes. Because of the differences between the ecological questions asked and the statistical questions answered, several methods should be employed to gain a richer understanding of multi-scalar pattern. It is not known *a priori* which method will be most useful in the analysis of pattern. Each analysis has the potential to yield insight into the nature of a wide variety of spatially determined ecological processes. An educated selection of a suite of complementary statistics best suited for the question of interest and the data at hand is the best approach to uncovering ecological pattern.

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Two-dimensional Wavelet Analysis for Quantifying Spatial Data and Designing Monitoring Programs in Ecology

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ABSTRACT

Large-scale monitoring presents considerable challenges for the detection and quantification of ecological phenomena over large spatial areas and long time spans. Effective monitoring must involve sampling designs sufficiently detailed to detect ecologically significant patterns at multiple scales, yet be logistically tractable and resource-efficient for sustained execution. For these reasons, methods that help optimize these objectives and contribute to the design of more efficient sampling prior to implementation are important for successful large-scale monitoring. We present an approach that uses two-dimensional wavelet analysis in tandem with simulation modeling to select optimal sampling designs for large-scale spatio-temporal ecological phenomena. While wavelet analysis shares many properties in common with other methods of pattern analysis, it has some unique visualization and analytic capabilities that provide insight into understanding the interactions between multi-scalar pattern (heterogeneity) and sampling design. Wavelet analysis is presented as an analytic and modeling tool for optimizing sampling efficiency and accuracy in the context of designing large-scale species monitoring plans. These properties are described and illustrated using species range data from the Breeding Bird Survey (BBS) with several levels and types of spatio-temporal range patterns.

KEYWORDS

Breeding Bird Survey, Field Sparrow (*Spizella pusilla*), Pattern Detection, Pattern Reconstruction, Red-eyed Vireo (*Vireo olivaceous*), Semivariogram

INTRODUCTION

Landscape ecologists use spatial statistics to characterize biotic and abiotic patterns to understand the dynamics of ecological processes across multiple scales. The utility of these analyses is based on the assumption that observed spatial patterns are an expression of the sum and interactions of the processes driving the system. In this reciprocal relationship, ecological processes infer pattern and ecological pattern reflects processes. In theory, spatial analyses are tools to identify ecological pattern and to suggest the process that created the pattern. In practice, ascertaining a one-to-one mapping between ecological pattern and process is difficult. Multiple and interacting processes can create a spectrum of patterns. Conversely, similar patterns can derive from different processes. These concerns underlie the difficulties in designing landscape analyses that conform to the statistical rigor apparently accessible at finer scales (Wiens 1976, Hunsaker et al. 1994, Hurlburt 1984, Turner et al. 1989, Wiens 1989, Risser 1990). Data are collected in diverse settings, studies, and applications outside the traditional scope of statistical inference. Given the demand that ecological sampling be rigorous, understanding how to interpret pattern has become increasingly important in ecology.

Historically, most ecological studies either focused on the spatial domain or the temporal domain, holding one or the other regionalized variable constant (Wiens 1989). In large part, this was due to limitations in time and resources for data collection. More recently, a number of long-term, large-extent data sets are available that contain adequate spatial and temporal coverage for performing statistical analyses in both domains (Thompson 1992, Hunsaker et al. 1994, Rosenzweig 1995, Ringold et al. 1996, Stohlgren et al. 1997, Dhamala et al. 2001). Further, much of field-based data is augmented by the use of remote sensing, Geographic Information System (GIS), Landsat Thematic Mapper (TM), Advanced Very High Resolution Radiometer (AVHRR), and satellite imagery (Iverson et al. 1989, Tueller 1989, Roughgarden et al. 1991, Ehrlinger and Field 1993, Goodchild et al. 1993, Miller 1994, Campbell and Hofer 1995, Rey-Benayas and Pope 1995, O'Neill et al. 1997, Quattrochi and Goodchild 1997, Wu et al. 1997). Simultaneous interpretation of pattern in spatial and temporal domains leads to closer approximations of the way ecological relationships exist in nature. This knowledge will strengthen our understanding of ecology and will aid in selecting sampling resolutions with appropriate scale in future studies. In some ways, ecology has shifted from the problem of a paucity of data to a plethora of information. The challenge is how to make sense of the multi-scalar information.

A new generation of spatial and time series statistics can be employed to describe and quantify ecological pattern. A few examples are Fourier spectral analysis (Usher

1975, Ripley 1978, Grieg-Smith 1983, Renshaw and Ford 1984, Legendre and Fortin 1989, Turner et al. 1991, Cillinan and Thomas 1992, Gardner 1998), lacunarity (Mandelbrot 1983, Pietgen and Saupe 1988, Allain and Cloitre 1991, Plotnick et al. 1993, Plotnick et al. 1996, Zeng et al. 1996, Wu et al. 1997, Larsen and Bliss 1998, Dale 2000), fractals (Mandelbrot 1983, Milne 1992), fragstats (McGarigal and Marks 1995), and wombling (Fortin 1994). Yet, the assumptions of these statistics can limit the accuracy of ecological inference. For instance, Fourier spectral analysis and standard semivariogram-kriging operate under the assumption that data occur uniformly across space and time with a periodic structure resembling a sine or cosine function (see Anthony et al. 2004). These methods cannot accommodate the non-uniform and multi-scalar nature of most ecological pattern. Thus, by considering the boundaries of inference of a statistic prior to implementation, our ecological inference in interpreting pattern will be more accurate and our future research more informed.

Wavelet analysis and other statistics are employed to optimize the signal to noise ratio, representing an image with the most clarity and parsimony. Wavelet analysis is superior in its ability to decompose data with non-stationary properties (e.g., the mean changes with location) and complexity at multiple scales. Thus, as an advance over semivariogram and Fourier analysis, wavelet analysis assumes data are non-uniform and multi-scalar with both periodic and aperiodic components (see Anthony et al. 2004). Wavelet analysis is an image processing tool with increasing applications in ecology (Bradshaw and Spies 1992, Bradshaw and McIntosh 1994, Dale and Mah 1998, see Anthony et al. 2004). Wavelets have been applied to imagery segmentation in electrical engineering (Kubota and Huntsberger 1998); earthquakes, wind, and ocean movement in atmospheric sciences (Gurley and Kareem 1999); mammography and brain imaging in medical research (DeVore et al. 1996, Hilton et al. 1996, Kolaczyk 1996, Sartene et al. 1996); fingerprint identification in Federal Bureau of Investigation (FBI) crime scene investigation (Bradley et al. 1993, Bradley and Brislawn 1994); iris recognition in security systems (Daugman 2001); and remote sensing (Ranchin and Wald 1993). The shared goal of these applications is to reconstruct an object or image from indirect, incomplete, or noisy observations in their data.

Often in ecology, we are trying to either confirm and quantify pattern we can already see (confirmatory analysis) or detect pattern that we may not usually identify (exploratory analysis). The mathematical functions of wavelet analysis point out aspects of pattern that we may have unintentionally overlooked with our limited baud rate and inherent observer bias. In spatial ecology, both the signal and the noise are relevant. The peaks exist relative to the valleys. By integrating the location and relative magnitudes of peaks, we can define the edges and boundaries of species range across multiple scales. Wavelet analysis is particularly useful in detecting and quantifying the internal structure of ecological data. This method integrates information about the dominant and average patterns in a system across scales to describe hierarchical phenomena and to link spatial and temporal patterns to system function. In landscape ecology, wavelet analysis identifies features in biogeographical distribution (e.g., patches, peaks, edges) and integrates this information at different scales.

Wavelet analysis is an analytical and modeling tool for optimizing sampling efficiency and accuracy, such as in the context of designing large-scale monitoring plans. Effective monitoring must involve sampling designs sufficiently detailed to detect ecologically significant patterns at multiple scales, yet logistically tractable and resource-efficient for sustained execution. For this reason, methods that help optimize these objectives and contribute to the design of more efficient sampling prior to implementation are important for successful large-scale monitoring. Two-dimensional wavelet analysis in tandem with simulation modeling is useful in selecting optimal sampling designs for large-scale spatio-temporal ecological phenomena.

In this manuscript, we evaluate the ability of two-dimensional wavelet analysis to detect and classify pattern in long-term, large-scale ecological analyses, such as the Breeding Bird Survey (BBS). Specifically, we illustrate how to compare the changes in the boundaries and internal structure of the geographical range of two Neotropical bird species. Namely, we compare the different spatio-temporal patterns of Field Sparrows (*Spizella pusilla*) and Red-eyed Vireos (*Vireo olivaceous*) in North America. We compare the pattern detection capabilities of two-dimensional wavelet analysis with that of standard semivariogram. We discuss possible approaches to statistical analyses following pattern detection. Ultimately, we suggest a means to incorporate the pattern reconstruction capabilities of two-dimensional wavelet analysis in the design of field experiments and monitoring programs to encompass multi-scalar data. It is crucial that data resolution is appropriate for the scale for ecological inference.

METHODS

This section contains a brief summary of the natural history of the two Neotropical migrants and of the Breeding Bird Survey before comparing pattern recognition in two-dimensional wavelet analysis and standard semivariogram.

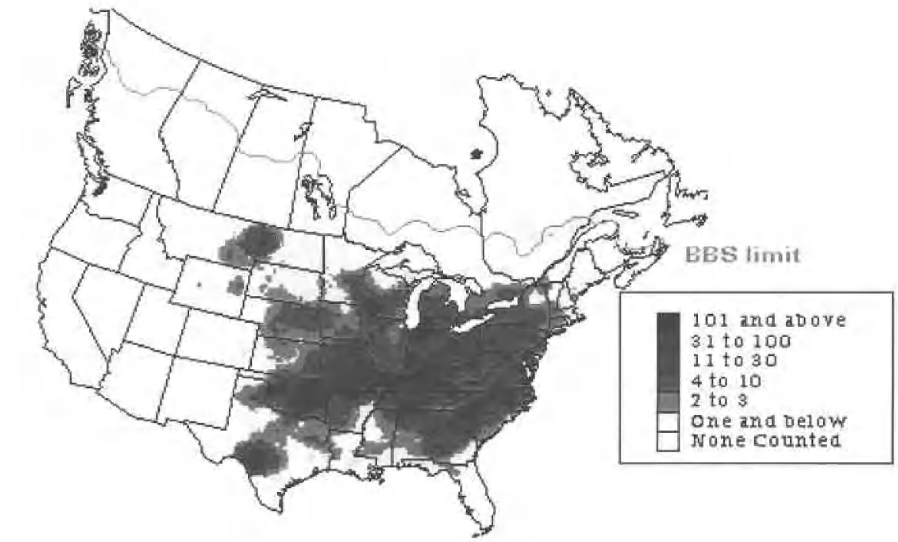
Case Studies of Neotropical Migrants

We illustrate pattern detection by examining heterogeneity in the distribution of two neotropical migrant birds in North America. The low heterogeneity of Field Sparrows was compared to the high heterogeneity of Red-eyed Vireos. Field Sparrows breed in successional-scrub habitats, mostly in the Eastern and Mid-western States (Figure 3.1a). Distribution varied with numbers ranging from 0 to 30 birds in each transect. Field Sparrows lay three to five eggs in open-cups on the ground (Gough et al. 1998). This species has demonstrated a declining trend since the BBS monitoring program began in 1966 (Sauer et al. 1999).

In comparison with the relatively stable main cluster of Field Sparrows, Red-eyed Vireos had a more complicated pattern. Red-eyed Vireos are relatively abundant in woodland habitats throughout the Eastern, Mid-western, and Northern reaches of the BBS (Figure 3.1b). Distribution varied more than for Field Sparrows, with numbers ranging from 0 to 100 birds in each transect. Red-eyed Vireos lay two to four eggs in an open-cup nest in the mid-story canopy (Gough et al. 1998). This species has demonstrated an increasing trend since the BBS monitoring program began in 1966 (Sauer et al. 1999).

Breeding Bird Survey

We examined the spatio-temporal patterns in North American songbird distribution and abundance from the long-term, large-scale Breeding Bird Survey (Sauer et al. 1999). For over thirty years, the BBS has surveyed an extensive set of routes in the a)


BBS limit
101 and above
31 to 100
11 to 30
4 to 10
2 to 3
One and below
None Counted

b)

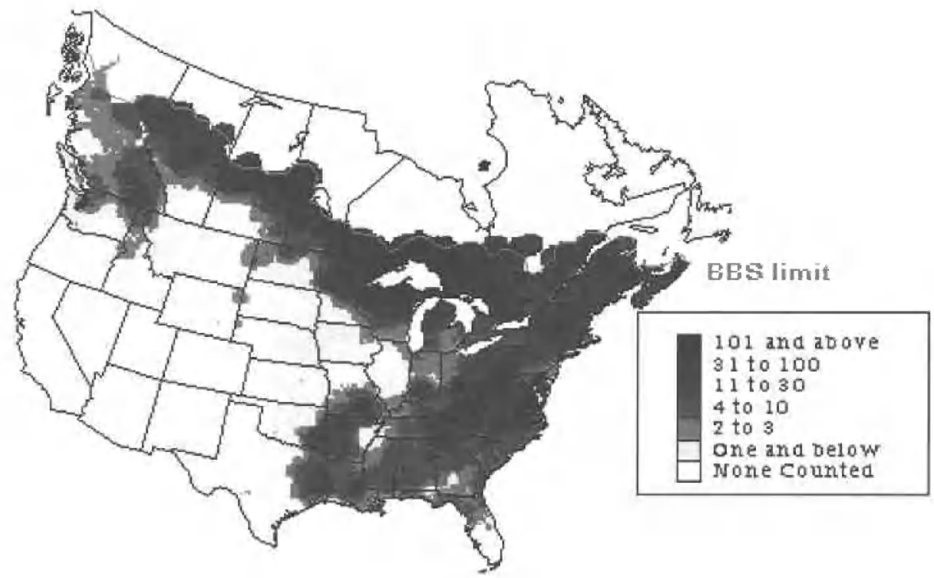

BBS limit
101 and above
31 to 100
11 to 30
4 to 10
2 to 3
One and below
None Counted

Figure 3.1.

United States and southern Canada to determine the species ranges of breeding birds (Sauer et al. 1997). The BBS is coordinated by the United States Geological Survey Patuxent Wildlife Research Center and the Canadian Wildlife Service National Wildlife Research Center. Bird distribution along the survey routes was recorded in early or mid-June, during the peak of the songbird breeding season, with some desert transects run as early as May (Sauer et al. 1997).

BBS distribution maps display patterns in abundance and distribution over time. This BBS data set has four variables: a route identifier, latitude, longitude, and number of birds within a species detected for each year. BBS transects extended across the United States and Canada (Figure 3.2a). Each route is 24.5-miles long with 50 stops (inter-stop interval = 0.5-miles). In a three-minute point count, observers record all birds heard or seen within 0.25-mile of the stop. For each species, all counts from 1966 through 1995 were used to calculate density (i.e., total number of birds per tenth of a decimal degree latitude and longitude square). Counts were weighted by number of surveys to resolve some of the variability. Two-dimensional wavelet analysis requires a square or rectangular grid. Thus, North America was extended to form a rectangle: 22.60 to 69.05 decimal degrees latitude from south to north and –176.6 to – 44.82 decimal degrees longitude from west to east (Figure 3.2b). As the surveys do not span the entire North American area, we interpolated data in between surveys. Missing values were converted to zero, irrespective of whether there was available habitat or ocean. For some analyses, the number of birds detected per year was compiled over six 5-year intervals to reduce the sampling differences (i.e., non-random nature of the sample, irregular spacing of the counts, observer bias).

The number of scales available for consideration was limited by data resolution. In this case, the data resolution ranges from 135 to 6000 km^2. We could have interpolated to a finer grid, but we wanted to retain the original data. One degree of latitude is approximately 111 kilometers and one tenth of a degree is 11.1 kilometers. The distance of one-degree longitude varies with latitude. We calculated the distance of each degree longitude at 45 degrees latitude, such that one-degree longitude is approximately 55.7 kilometers and one tenth of a degree is 5.57 kilometers. Thus, the grid was

Figure 3.2a.

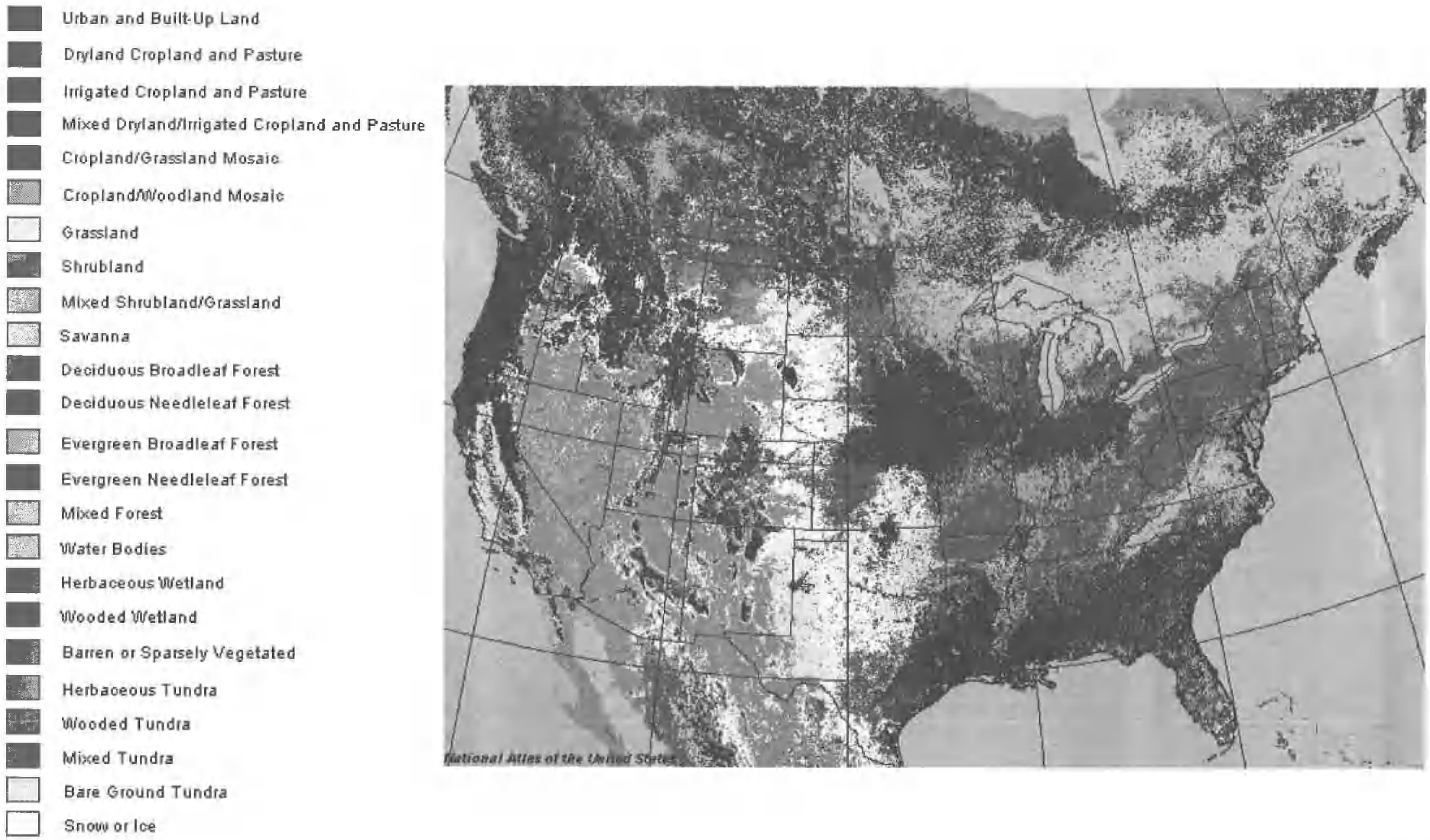

Urban and Built-Up Land
Dryland Cropland and Pasture
Irrigated Cropland and Pasture
Mixed Dryland/Irrigated Cropland and Pasture
Cropland/Grassland Mosaic
Cropland/Woodland Mosaic
Grassland
Shrubland
Mixed Shrubland/Grassland
Savanna
Deciduous Broadleaf Forest
Deciduous Needleleaf Forest
Evergreen Broadleaf Forest
Evergreen Needleleaf Forest
Mixed Forest
Water Bodies
Herbaceous Wetland
Wooded Wetland
Barren or Sparsely Vegetated
Herbaceous Tundra
Wooded Tundra
Mixed Tundra
Bare Ground Tundra
Snow or Ice
National Atlas of the United States

Figure 3.2b.

approximately 2,034 kilometers in width and 7,308 kilometers in length. Supplemental land cover generalizations were obtained from the National Atlas of the United States, provided by the United States Department of the Interior (Figure 3.2b).

Comparison of Wavelet Analysis and Semivariograms in Two-Dimensions

Data analysis in two dimensions is an advancement over one dimension. As opposed to quantifying how energy is spatially distributed at multiple scales along a horizontal or vertical transect, two-dimensional analysis quantifies how energy is partitioned in the horizontal, vertical, and diagonal directions at different resolutions. In this section, we review how to read the graphical representations for two-dimensional wavelet analysis and standard semivariogram before comparing the pattern detection capabilities of these statistics.

Two-dimensional wavelet analysis is novel in its ability to detect and quantify the boundaries and the internal structure of a species geographical range at multiple scales. Wavelet analysis integrates information about the dominant and average patterns in a system across scales to describe hierarchical phenomena and link spatial and temporal patterns to system function. Wavelets identify individual features that exist at one scale and contribute to the whole as a texture at another scale, or scaling up. Wavelet analysis discriminates different types of pattern and locates these patterns within the original map. This capability enables us to determine the exact geographic position of a detected pattern and to interpret the individual pattern in its own biotic and abiotic context. In the process, wavelet analysis characterizes the degree of heterogeneity in the data. Examples of high heterogeneity are patterns with more steep gradients and high to low peaks. Homogeneity occurs when pattern is evenly spaced across time.

Two-dimensional wavelet analysis represents spatial variability in complex data sets (e.g., images, maps) by using linear combinations of mathematical functions to approximate the signal in horizontal, vertical, and diagonal directions (Daubechies 1992, Bruce and Gao 1996). A wavelet basis is chosen according to the nature of the data and the questions of interest. A contracted, high frequency form of the basis is used for temporal analysis and a dilated, low frequency form is used for frequency analysis. The original signal is completely specified by wavelet coefficients that represent how well the data match the analyzing wavelet. Two-dimensional wavelets quantify how energy is spatially distributed at each scale and how it is partitioned in the horizontal, vertical, and diagonal directions at different resolutions (Meyer and Ryan 1993). The magnitude of components in the signal can be directly related to their position along the transect and information about the location of the pattern is retained as scale is increased. Thus, individual events and sets of events may be related to higher order pattern, thereby elucidating the exact hierarchical structure. Wavelet analysis provides a continuous measure of spatial and temporal pattern across scale within the limits of data resolution.

Wavelet analysis has three main advantages over other spatial statistics (especially semivariograms): (1) data can be non-stationary (i.e., the mean and variance can vary with location); (2) wavelets can detect and quantify pattern at multiple scales; and (3) the flexibility in the selection of the wavelet basis (see Anthony et al. 2004). Additionally, wavelets include a measure of independence among data points (see Anthony et al. 2004). Examining pattern in the internal structure of Neotropical bird distribution from BBS data requires all four of these strengths, so we will examine each one in more detail.

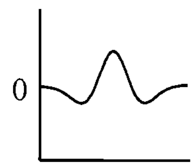
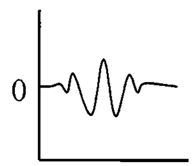
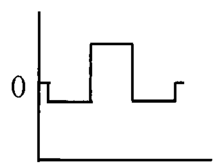
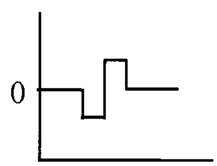
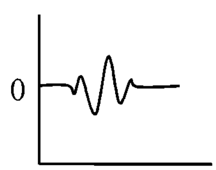
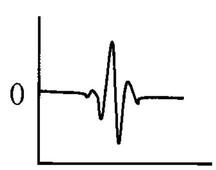
First, wavelet analysis is able to clarify the structure of pattern in data with non-stationary properties (i.e., statistically variant over time or space). Many ecological patterns are a combination of periodic and aperiodic components and their frequency behavior evolves over time. Wavelet analysis provides insight into the frequency structure of stationary and non-stationary data, separating signal from the noise. A wavelet function does oscillate around zero, like the sine and cosine waves of Fourier analysis, but the oscillations dampen down to zero and the function is localized in space and time. Thus, wavelets are good building block functions for a variety of signals, including those with non-smooth features and those that change over time and space. Two-dimensional wavelet analysis further detects pattern previously overlooked by quantifying how energy is positioned in the horizontal, vertical, and a combination of the two in the diagonal direction at different spatial resolutions.

Second, wavelet analysis excels at providing insight into complexity of pattern at multiple scales. Wavelet analysis evaluates a signal or image on a scale-by-scale basis, maintaining information about location while separating pattern into separate spatial components. The coarse and fine resolution components capture the high and low frequency features of the pattern and both the features at each scale can be related back to their location in the original data. Not only is pattern detected and quantified, but it can also be located and connected to other factors in the environment to better understand the processes creating the ecological pattern.

Third, wavelet analysis may be executed with several different basis functions, each one examining the data for different data morphologies. The wavelet basis is composed of the mother wavelet to characterize the detail and high frequency portions of the signal and the father wavelet to represent the smooth and low frequency components (Mallat 1988, 1989; Daubauchies 1992; Meyer 1993, Meyer and Ryan 1993). The wavelet basis determines the type of pattern detected (e.g., patches, edges, boundaries), such that each basis provides a different perspective of the data (Table 3.1). Flexibility in choosing a particular filter allows the researcher to tailor the analysis to suit a given objective. For example, the step morphology of the Haar wavelet will identify steep gradients or edges in the data that may correspond to such phenomena as ecotones or boundaries. Other wavelet filters, such as the French Top Hat, are best suited to quantify patch structures. Choice of filter can help minimize spurious noise at the higher frequencies as well. For example, the 'squared' edges of presence-absence data can be misread by Fourier methods as high frequency signal, whereas use of the Haar filter in wavelet analysis matches the data morphology and gives an accurate representation of the signal (see Anthony et al. 2004). If one of the standard wavelet bases does not meet your needs, you can construct your own form.

Selection of the best wavelet basis depends on the structure of the data (e.g., curved or square peaks), the question of interest or goals of the analysis (e.g., patches, edges, boundaries), and factors in computation (e.g., symmetry, orthogonality). Gather information about the internal structure of the data from the perspective plots and background knowledge of the bird's demographic patterns. Isolate the types of pattern

Table 3.1. Several exemplary filters demonstrate the flexibility in choice of the basis for two-dimensional wavelet analysis. It is possible to customize the basis for each analysis.

Analyzing Wavelets	**Simplified Shape**	**Data Features**	**Examples of Ecological Inference**
Mexican Hat		Symmetrical, Rounded	Patches
Morlet		Symmetrical, Rounded	Patches
French Top Hat		Symmetrical, Squared	Patches
Haar		Asymmetrical, Squared	Edges, Gradients
Daublet		Asymmetrical, Rounded	Edges, Gradients
Symmlet		Nearly Symmetrical, Rounded	Edges, Gradients
Coiflet		Nearly Symmetrical, Rounded	Edges, Gradients

in the data you would like to quantify to address your hypotheses. Finally, make an informed decision about the best wavelet basis function and its properties with the information you've collected to form your desired outcome with the main basis features (i.e., smoothness, temporal and spatial localization, frequency localization, ability to represent local polynomial functions, orthogonality, and symmetry; Bruce and Gao 1996).

The best wavelet basis depends on the choices about how to balance these main basis features with the nature of the data and objectives of the research. The wavelet basis function must be appropriately smooth to efficiently represent the unknown underlying pattern. The number of derivatives that exist for a wavelet function is one indication of smoothness. The Haar wavelet is discontinuous, so it is not differentiable nor is it smooth. But this choice is acceptable when the researcher is characterizing boundaries and edges. The d4 wavelet is continuous, but it is not differentiable either, whereas the d12 wavelet is twice differentiable with two derivatives. Support width influences both smoothness and temporal/spatial localization. Wider support widths produce smoother wavelets. More compact wavelet bases (e.g., Haar) better localize features in space and time. A high number of vanishing moments allows the wavelet basis to better represent higher degree polynomial signals, as well as a smoother approximation of the pattern. Generally, smoother wavelets have better frequency localization properties. Thus, the Haar basis has poor ability to localize features in frequency, which is not a problem when boundaries and edges are the objective. For an accurately representation of unknown pattern, wavelet coefficients must not drift relative to the original signal. Symmetrical wavelet bases avoid phase shifts. Biorthogonal wavelets are either symmetric or anti-symmetric; symmlets (e.g., s4, s12) and coiflets (e.g., c6, c12) are nearly symmetrical; daublets (e.g., d4, d12) are highly assymetrical, and all orthogonal wavelets (except the Haar) are assymetircal due to their compact support widths. Finally, orthogonality of the mother and father wavelets is a central feature for some applications of wavelet analysis. The vspline biorthogonal wavelets are nearly orthogonal and can be used like the Mexican Hat. As is true for any statistical program, it is possible to haphazardly select a wavelet basis without considering these options, but not understanding the analysis makes inference more difficult or inaccurate at the least. Haar was the appropriate analyzing wavelet basis for these BBS data, to better detect species range boundaries.

Finally, the empirically derived autocorrelation function can serve as a measure of independence among data points. These four main advantages are relevant for both one-dimensional and two-dimensional wavelet analyses, even though the representation of the data differ. In one-dimension, a signal is a series of numbers that represent the measurements of some recording device in time or space (e.g., bird counts along a transect, bird song, air temperature). In two-dimensions, an image is a representation of the measurements of a recording device in time or space (e.g., map of bird counts, pixels in a photograph) with x, y, and z coordinates for each data point on a grid. In the following paragraphs, we will consider the anatomy of wavelet analysis to examine how each metric illuminates our understanding of pattern and its interpretation in an ecological context.

Two-dimensional wavelet analysis has three main metrics: (1) the Wavelet Transform describes spatial structure by identifying the amplitude and location of pattern at multiple scales; (2) the Box-and-Whisker plot further elucidates multiscale complexity by displaying the internal structure of the pattern and highlighting the degree of heterogeneity; and (3) the Wavelet Variance identifies the dominant patterns in scale. As supplemental constituents of wavelet analysis, perspective plots and contour maps clarify the basic context of the original data to better interpret the statistical analyses. So, first one becomes familiar with the data and looks for visible pattern with the perspective plots and contour maps for the entire study period and for smaller time intervals. Then, the wavelet transform defines the magnitude and location of each pattern at each scale. Next, the box-and-whiskers plot provides another view of the wavelet coefficient's distribution among scales and directions, providing some insight into the issue of signal versus noise. Finally, both visible and previously undetected patterns are confirmed with the wavelet variance.

Perspective plots facilitate examination of data for visual clues to the inherent geographical and temporal variation in the data (i.e., pattern visible without a statistical lens, Figure 3.3a). Visual observations of the magnitudes and locations of peaks, valleys, and gaps provide a sense of the overall pattern in distribution. An overview of the species pattern during long-term monitoring is gained by examining a perspective plot of the original BBS data over the entire study period. Examining the pattern in Field Sparrow and Red-eyed Vireo distribution in a series of smaller intervals clarifies the temporal aspect of the magnitude and locations of shifting boundaries (i.e., translation in space). We examined six five-year intervals for change in pattern for these species.

Contour maps provide a view of bird distribution from the top (Figure 3.3b1). This vantage gives an indication of the expansion and contraction of the species range, demonstrating which areas a bird more consistently uses over the entire study period. A black diamond denotes a high peak in a small area (i.e., a steep peak); an open shape denotes a broadly based peak; and a ring in a contour means a broadly based high peak. The shaded oval covers the region where birds are always present. Perimeter maps are contour maps with an outline of the perimeter of the species range for each of several time intervals to represent change in habitat use over time (Figure 3.3b2). The central area of overlap is the center portion shared by all the perimeters and represents stability in habitat use over time. Locating regions within the central area of overlap occupied by birds over the entire study period identifies persistent habitat. These metrics provide familiarity with the nature of the data, and facilitate recognition and interpretation of pattern produced with the more advanced wavelet metrics.

The wavelet transform is the core output for wavelet analysis, depicting location, directionality, and coarse to fine scale resolution (Figures 3.3c1 and 3.3c2). Data are evaluated by a selected wavelet basis function and assigned a coefficient to represent how close the match in shape and dimension (Figure 3.4). When the analyzing wavelet encounters a feature in the data with a similar shape and dimension, the absolute value of the assigned wavelet coefficient is high. Thus, the signal is transformed into a series of coefficients with discrete energies. As scale increases, the size of the filter doubles but the shape remains the same. To distinguish the North-South, East-West, and diagonal components, the orientation of the filter is turned accordingly, with the

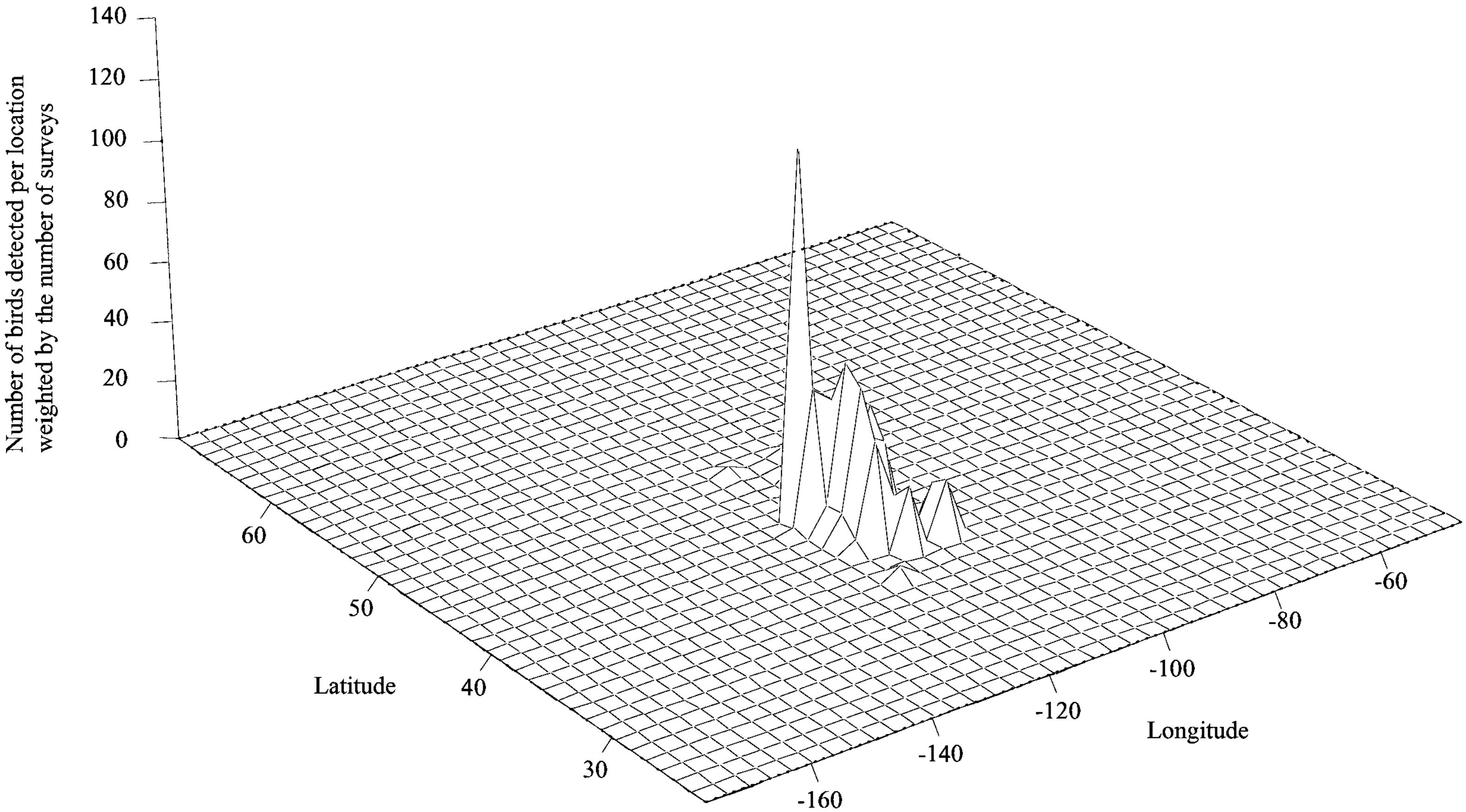

140
120
100
80
60
40
20
0
Number of birds detected per location weighted by the number of surveys
60
50
40
30
Latitude
-160
-140
-120
-100
-80
-60
Longitude

Figure 3.3a.

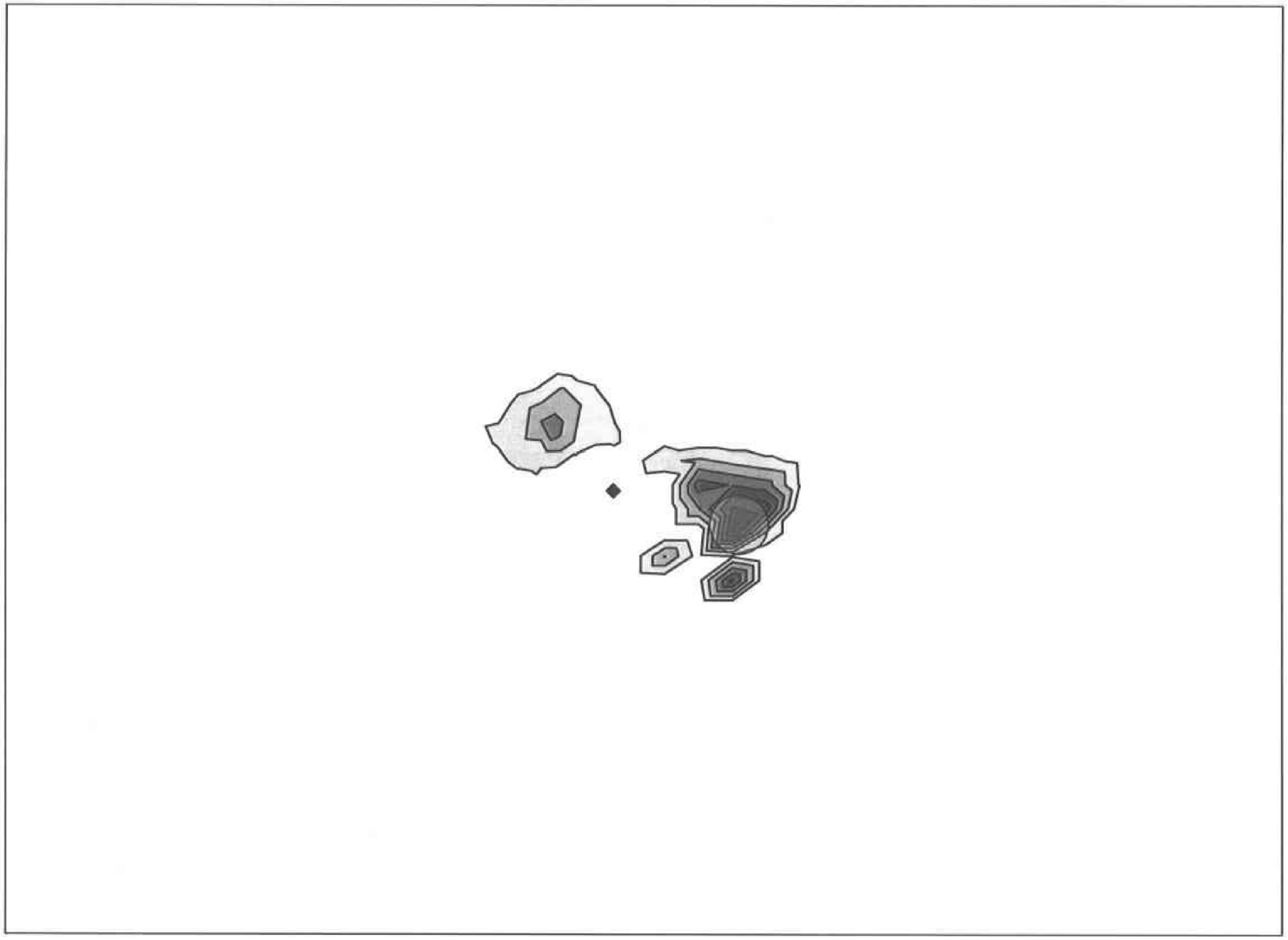


Figure 3.3b1.

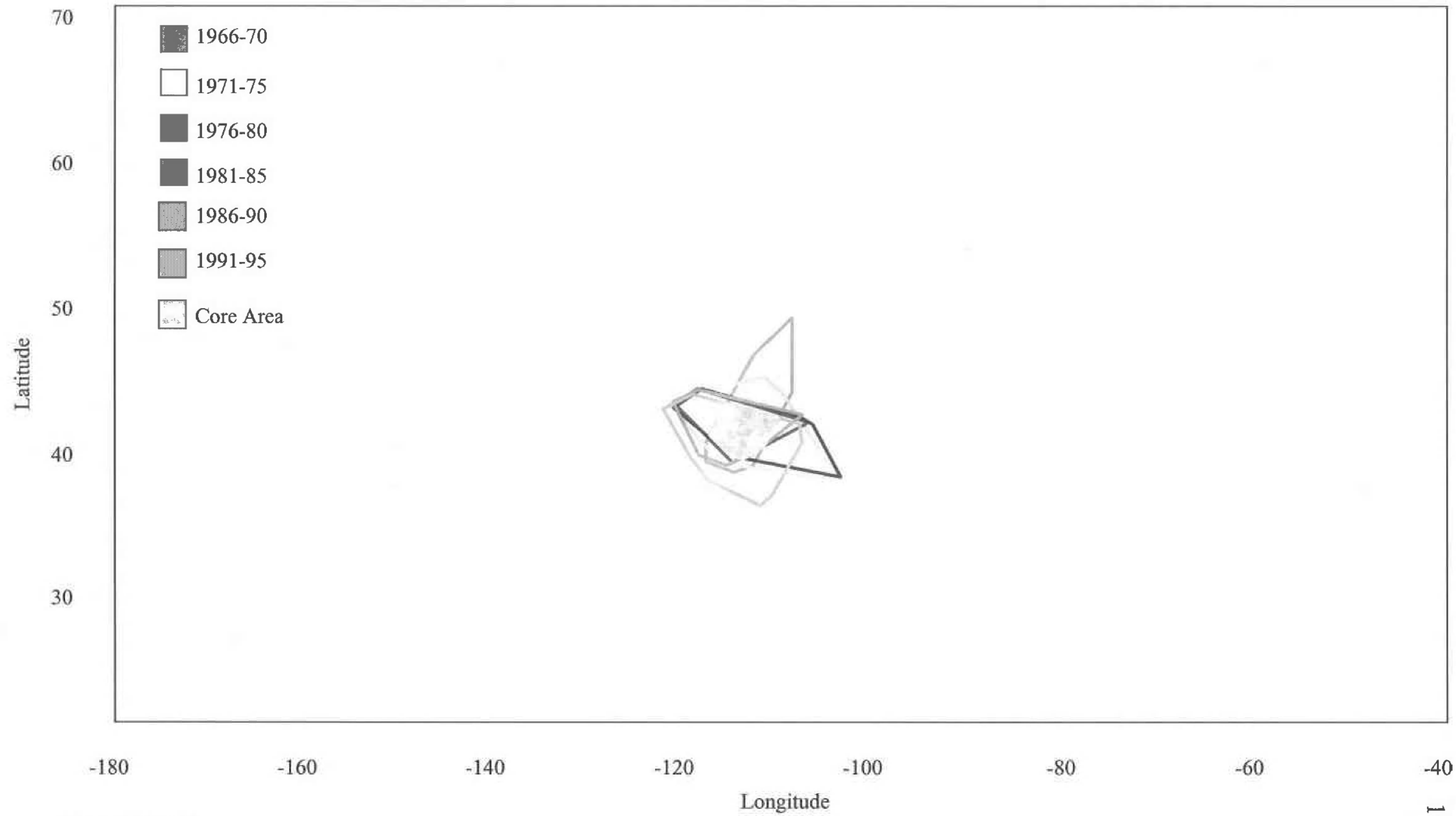

70
60
50
40
30
Latitude
1966-70
1971-75
1976-80
1981-85
1986-90
1991-95
Core Area
-180
-160
-140
-120
-100
-80
-60
-40
Longitude

Figure 3.3b2.

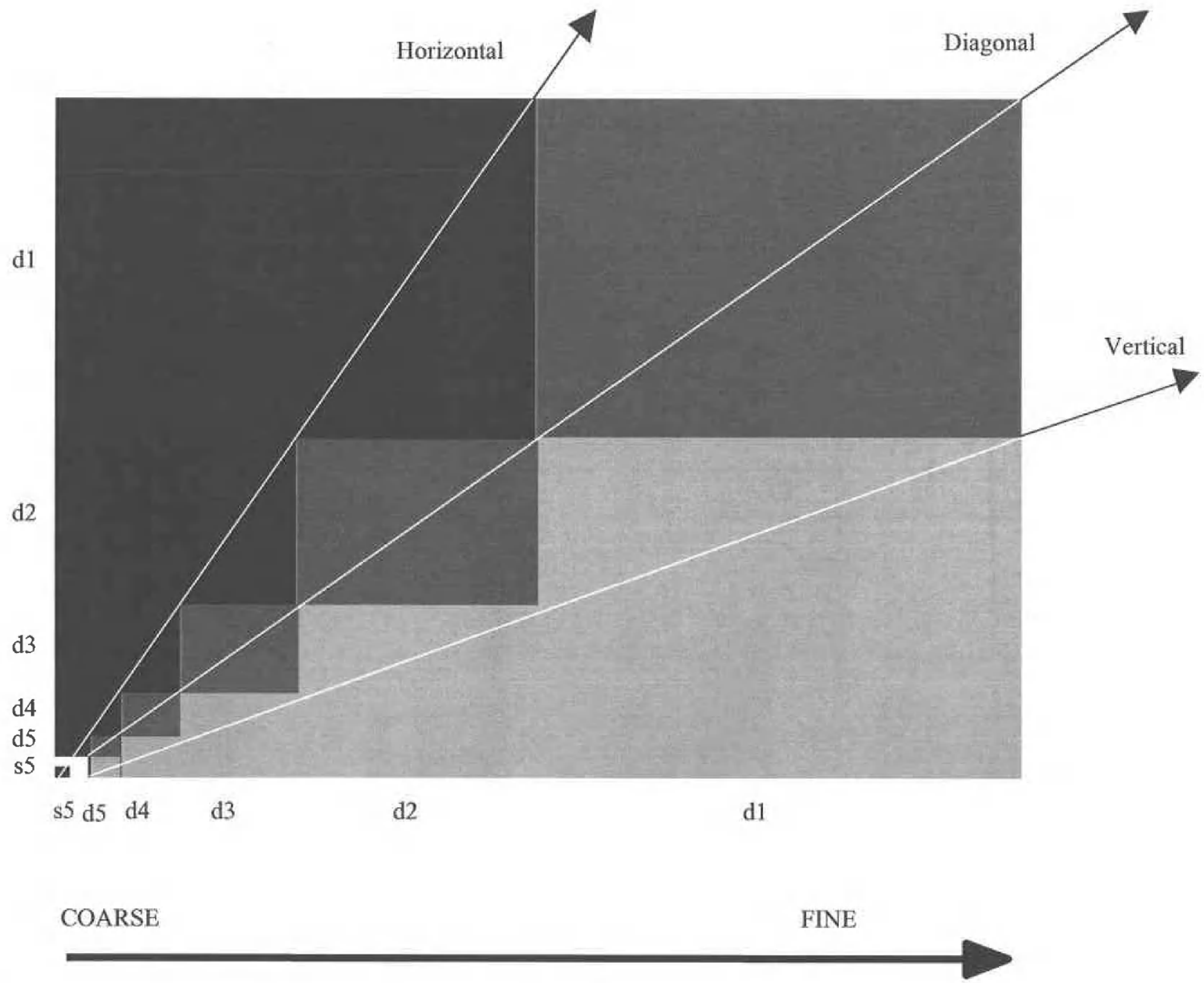

Horizontal
Diagonal
Vertical
d1
d2
d3
d4
d5
s5
s5 d5 d4 d3 d2 d1
COARSE
FINE

Figure 3.3c1.

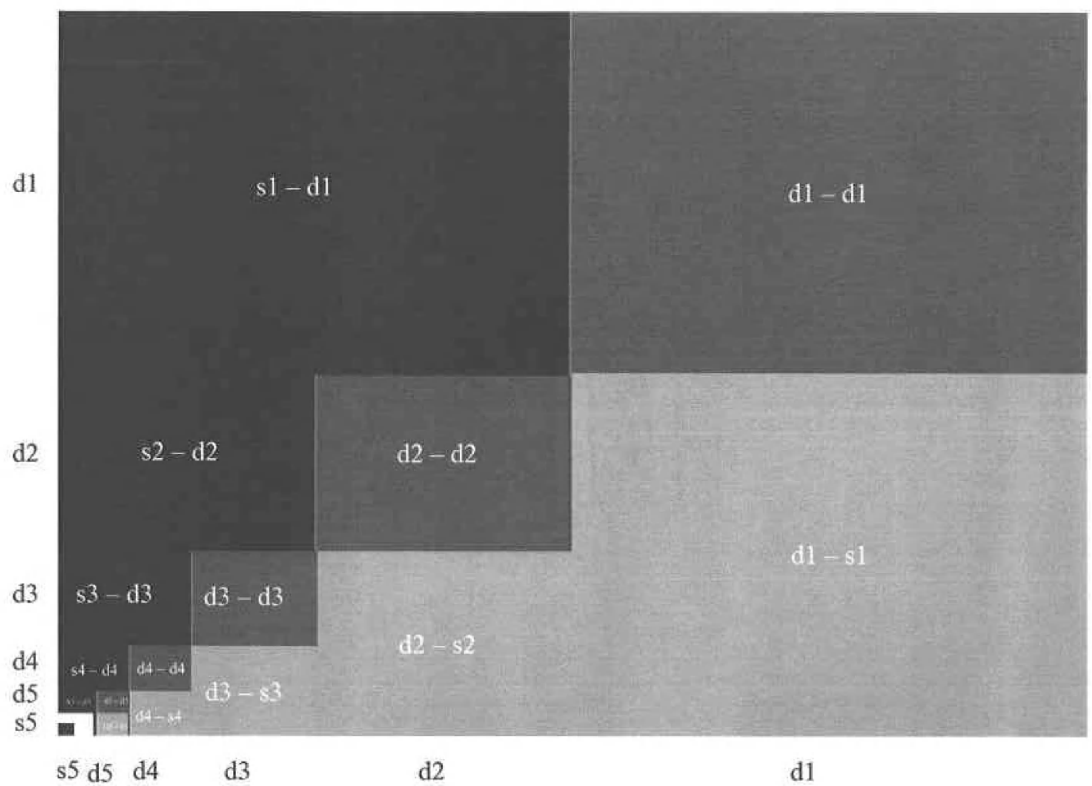

d1
d2
d3
d4
d5
s5
s1 – d1
d1 – d1
s2 – d2
d2 – d2
s3 – d3
d3 – d3
s4 – d4
d4 – d4
d1 – s1
d2 – s2
d3 – s3
d4 – s4
s5
d5
d4
d3
d2
d1

Figure 3.3c2.

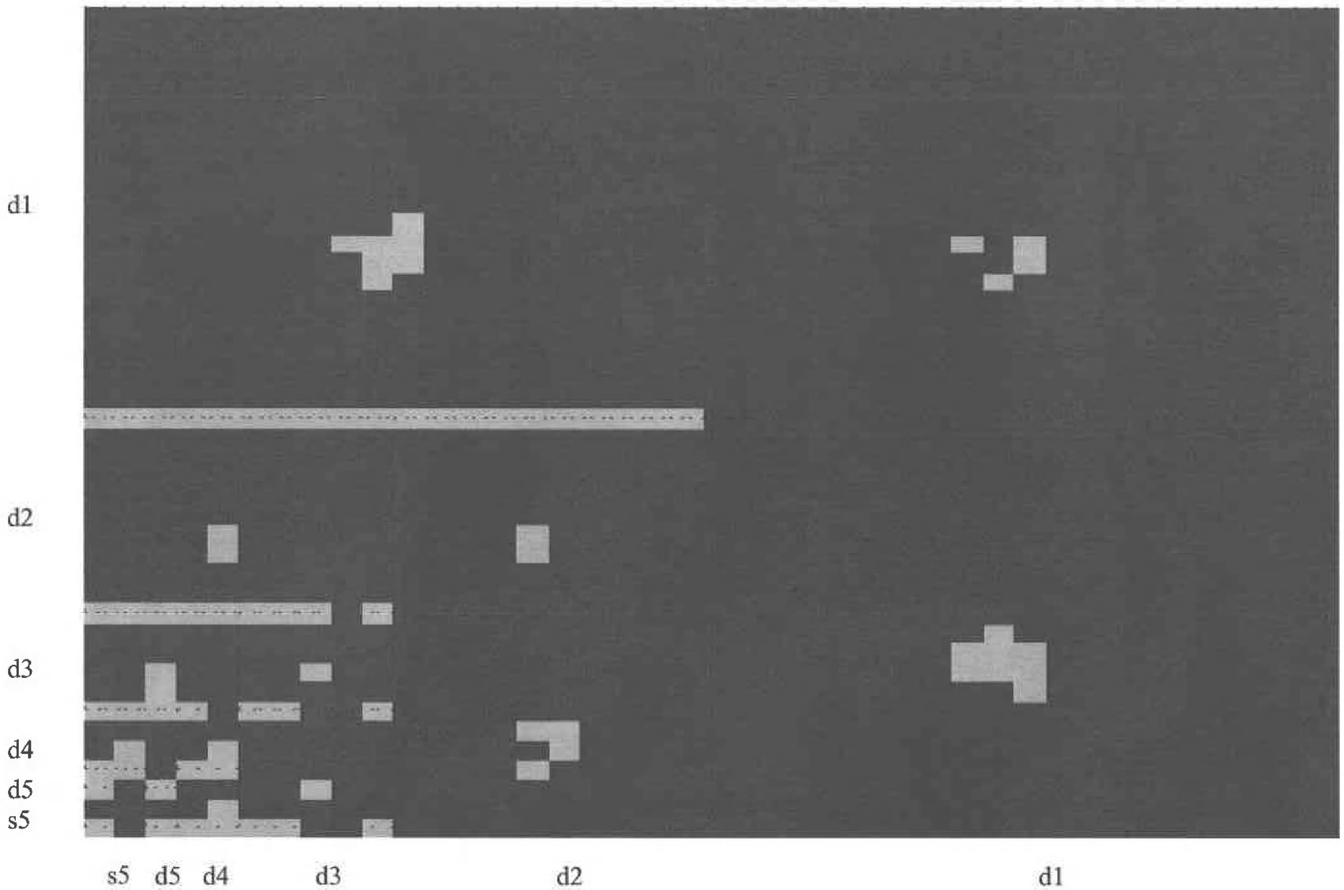


Figure 3.3c3.

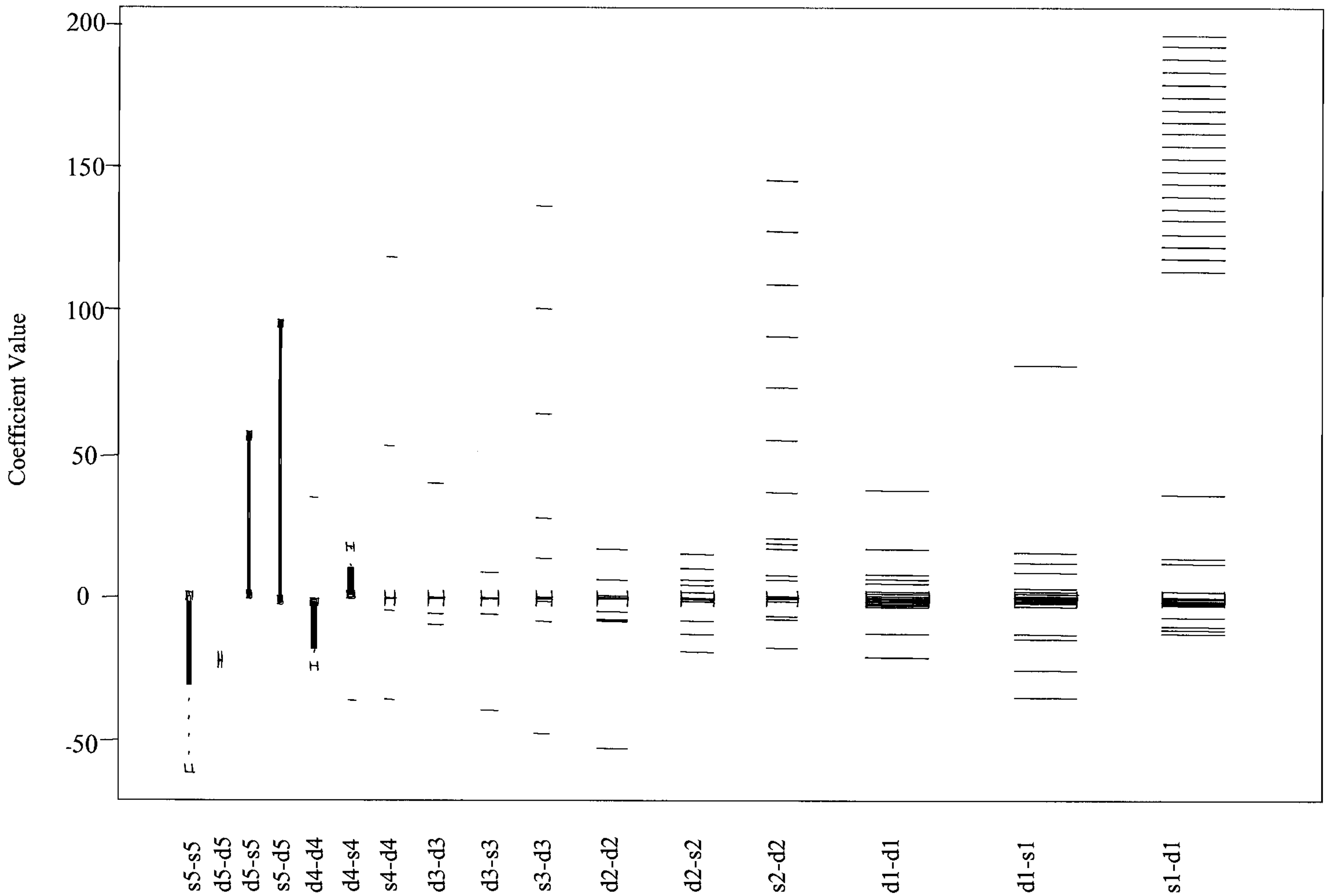
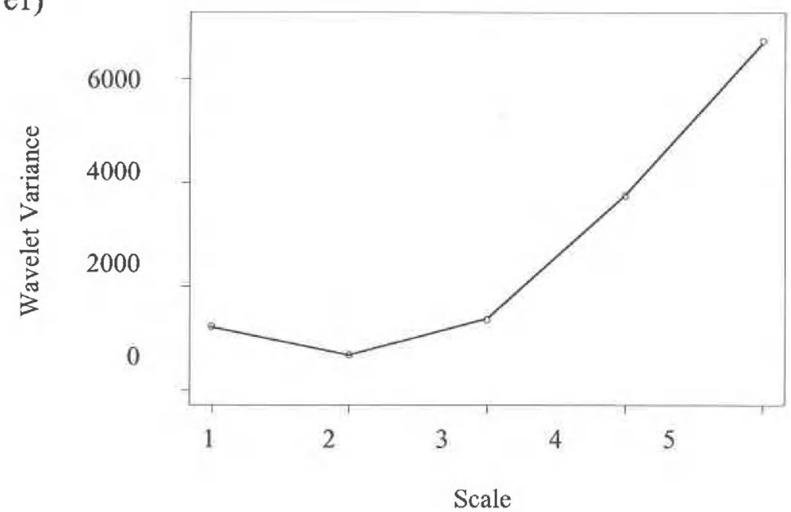


Figure 3.3d. Wavelet Crystal

e1)



e2)

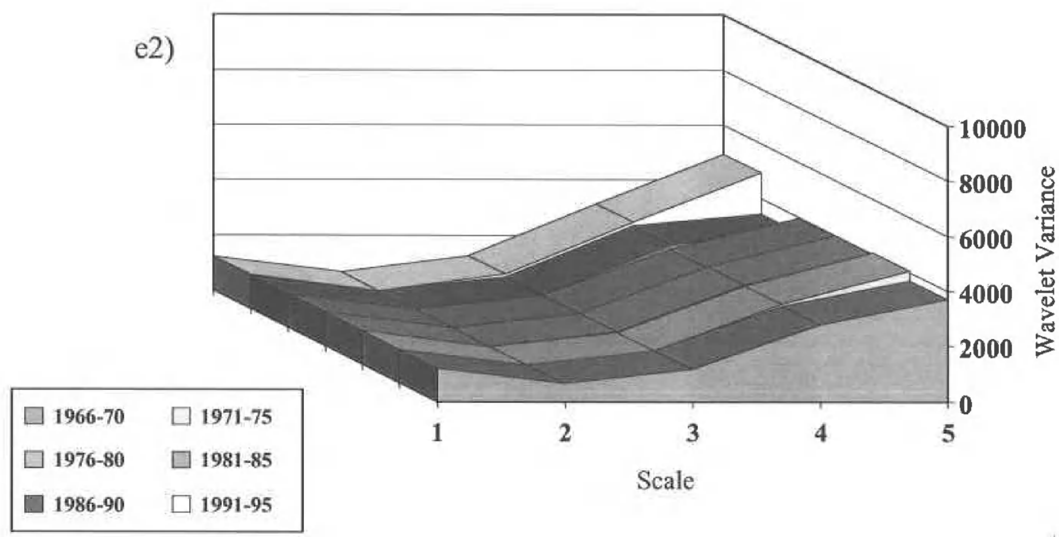


Figure 3.3e1 and 3.3e2.

Haar Wavelet

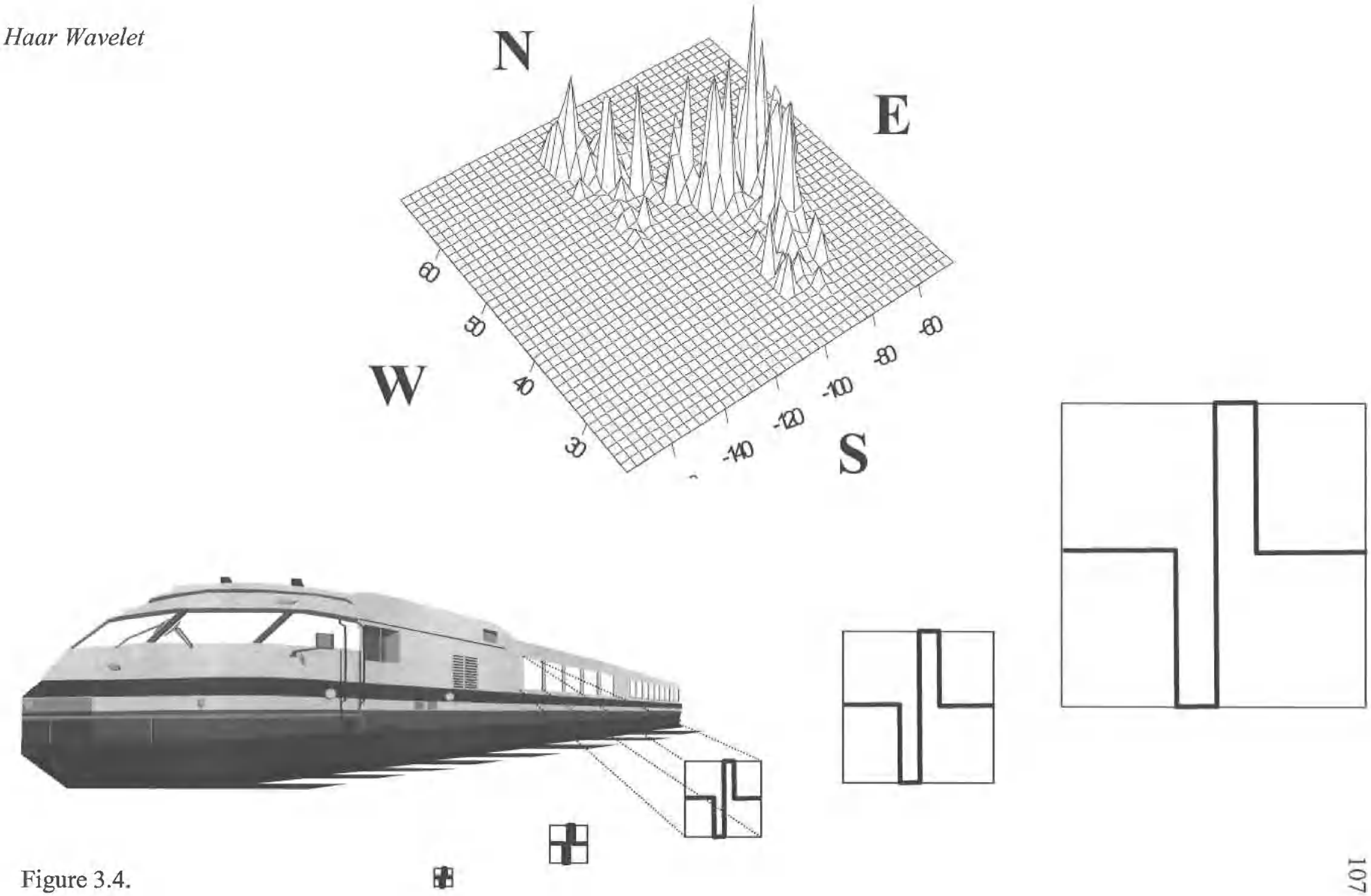


Figure 3.4.

diagonal component incorporating both the horizontal and vertical functions in its' shape. The coefficients are organized into crystals according to their scale and orientation in the survey. Thus, this metric quantifies spatial structure as a function of scale and position. The wavelet transform identifies multi-scale shifts in amplitude and location. The wavelet transform allows one to track the edges and map their location on the species range, and to determine patch size. Wavelet analysis is a two-dimensional function that retains information about location as it advances across scales. Two-dimensional wavelet transform is defined as:

$$W(a,b) = \frac{1}{a}\int_0^n \int_0^n f(x,y) g\left(\frac{x-b}{a}\frac{y-c}{a}\right) dxdy \qquad (1),$$

where a is the range of scales, b is the location in the image in the horizontal direction, c is the location in the image in the vertical direction, n is the length of the transect, x is the distance along the transect, and g is the wavelet filter (e.g., Haar).

To visualize the wavelet transform, imagine a train moving along the tracks of the perspective plot (Figure 3.4). The window is the shape of the analyzing wavelet of your choice (i.e., Haar in Figure 3.4). The train will move along the data sequentially in the directions of North-South, East-West, and Diagonal (i.e., Northeast-Southwest, Northwest-Southeast). As the train moves down the track and encounters features in the data, each section the size of the wavelet basis is assigned a coefficient based on its similarity to the shape and dimension of the filter. As scale increases, the size of the window or basis is doubled but the shape remains the same. The wavelet transform is a collection of these coefficients at each scale.

The two-dimensional wavelet transform representation of the image or map summarizes the location of multi-scale pattern, shifts in amplitude and location with scale, spatial stationarity for the specified time period, pattern directionality (i.e., North-South, East-West, Northeast-Southwest, and Northwest-Southeast), and pattern resolution (i.e., coarse to fine; Figure 3.3c1). Each subsection or crystal of the wavelet transform (e.g., s1-d1) contains the collection of coefficients for that scale in that direction (Figure 3.3c2). The width of the crystal corresponds to the number of observations it contains (i.e., scale), such that the larger-sized crystals represent the finer or smaller scales.

Features in the original data are positioned in their precise location within a crystal. The darkness of the pixels relates the magnitude of that coefficient within the crystal. Large coefficients tend to correspond to important features, such as boundaries. For example, a larger peak with notable influence on the overall pattern could be detected with larger coefficients at higher scales. If we examined the wavelet transforms for these data in subsequent time intervals, we could detect the increase or decrease in the peak with larger or smaller coefficients at these scales or others. Thus, the wavelet transform allows one to map the size and location of specific features (e.g., edges) and track their change in location as scales increase. Patch expansion can be represented by an increase in the number of clustered coefficients at higher scales. In an ecological framework, the exact size and location of the species range or patch originally detected in the perspective plots or contour maps can be confirmed and quantified.

As the main metric, information contained in the other wavelet constituents is summarized in the wavelet transform. By viewing the data in a number of ways, the most information about the pattern is extracted from the data. Each metric provides a unique view of the data that contributes to the big picture. Or the metrics can be reorganized for a new interpretation, such as the perspective plots being useful as one thirty-year plot and as six five-year plots. Similarly, the wavelet transform can be re-plotted to depict only the top 5% contributing wavelet coefficients (resembling Figure 3.3c2). This plot can be interpreted as a whole by considering the three outermost crystals and moving in toward the s5-d5 crystal or by scale in the three directions. Next, we will explore the viewpoints of the box-and-whisker plots and the wavelet variance.

Box-and-whiskers or boxplots summarize the distribution of the coefficients, providing a means to examine the texture of the pattern within and among scales (Figure 3.3d). The boxplot depicts: (1) the internal structure [i.e., amplitude and scale of specific patterns], (2) overall degree of heterogeneity [i.e., homogeneous to very heterogeneous], (3) relative multi-scale complexity [i.e., simple, moderate, complex], and (4) specific information about how energy is distributed across scales and directions. The boxplot is a way to determine whether the internal structure was derived from a primary coefficient contributing a majority of the pattern or whether the influence was distributed over many patches. Thus, boxplots expand on information from the wavelet variance (i.e., sum of squares of coefficients; Bruce and Gao 1996). Where the wavelet transform provides information about location, directionality, and scale and the wavelet variance collapses this information into one number per scale to depict the relative influence of each scale to the overall pattern, boxplots display how the energy is distributed within each scale. The additional insight of wavelet analysis into the complexity of the pattern can be examined to see more information than was visible with the naked eye.

Boxplots depict the wavelet transform coefficients side-by-side and grouped by crystal. The boxes indicate the interquartile range; the middle white strip is the median; and the width of the box is proportional to the square root of the number of observations in the crystal. Within a scale, the boxplot has the same number of coefficients. The dynamic range tends to decrease from coarse to fine scales. An individual box-and-whisker represents a wavelet transform crystal and each whisker is a coefficient. The strength of the signal is the value of the coefficient squared. Recall the coefficient represents how well the data match the analyzing wavelet. Densely packed wavelet coefficients with low values suggest few features stand out (i.e., homogeneity). Whereas, densely packed coefficients with high values represent high heterogeneity with more peaks and edges. Loosely packed wavelet coefficients with a large dynamic range of high to low values lie on the spectrum of intermediate heterogeneity.

The wavelet variance displays the number of scales, the dominant scales, and the relative values of the wavelet coefficients at each scale for comparison among scales and among data sets (Figure 3.3e1). By collapsing the information of the wavelet transform (as well as the boxplot) into one number per scale, the wavelet variance provides a measure of the contribution of energy of each scale component to the overall pattern in the image. In this way, wavelet variance can be used to identify dominant patterns in a manner similar to the semivariogram and Fourier spectrum to discriminate and quantify spatial pattern. The overall pattern of the wavelet variance plot provides insight into the overall pattern of the data and generates questions for the other metrics, such as Is the majority of the dominant scale the result of one primary coefficient or is the influence distributed over several patches? The examination of six five-year intervals provides a sense of the relative multiscale stability in pattern over time and space (Figure 3.3e2). These plots show shifting densities and boundaries over time. Wavelet variance plots in the three directions summarize anisotropy or different pattern in North-South, East-West, and Diagonal. The wavelet variance is the sum of squared wavelet coefficients at each scale. The equation for two-dimensional wavelet variance is defined as:

$$v^2(a) = \frac{1}{|A|}\int_A W^2(a,b)db \qquad (2),$$

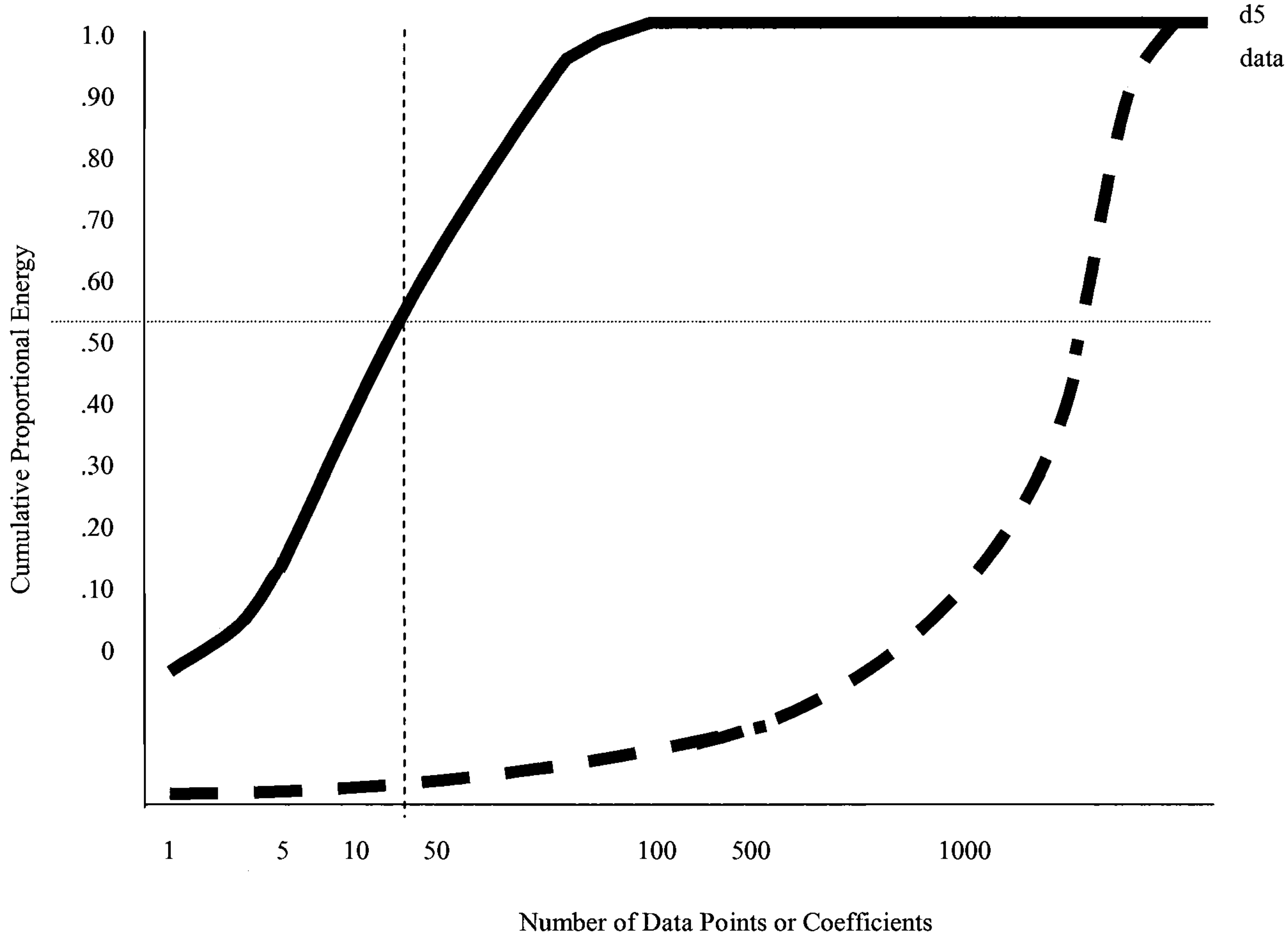
where a is the range of scales, n is the length of the transect, b is the distance along the transect, $|A|$ is the area of the image, and the integral is over the image area. The scale of the patch, height of the patch, and number of patches determine the magnitude of the wavelet variance.

Interpretation of the shape of the wavelet variance plot provides additional information about pattern. The peaks of the overall plot can be compared (e.g., bird A has peaks eight times those of bird B). A high wavelet variance represents high energy at that scale. High contrast and density of events in the image can be the result of high bird counts, high peaks, more peaks, or a number of low or high intensity gaps. A low wavelet variance represents low energy at that scale. Low contrast and density of events in the image can result from several small peaks, small clusters, large gaps, or lack of distinct structure. The wavelet variance provides a smoother view of the pattern texture to compliment the more detailed, rougher view of the wavelet transform and box-and-whisker plots.

Thus far, we have discussed wavelet analysis in terms of pattern recognition applied to the internal structure of species geographical range. Another application of this time series statistic is pattern reconstruction, which is useful in designing efficient sampling protocols for species or habitat conservation. With its data compression properties, two-dimensional wavelet analysis is well suited to evaluate and fine-tune the sampling design of monitoring programs. Based on pilot data, pattern can be reconstructed with fewer data and monitored for change over time and space.

By selecting the best wavelet basis adapted to the data or truncating coefficients below a threshold, the data is sparsely represented in the wavelet approximation (Bruce and Gao 1996). The energy contained in the signal or image is compacted into a relatively small number of wavelet coefficients. This sparse coding makes wavelets a good tool for representing the information contained in the data with fewer points (e.g., 50% of the data points to create the same pattern as 100% of the data). The FBI uses wavelet data compression to speed up fingerprint identification (Bradley et al. 1993, Bradley and Brislawn 1994). Digital images of fingerprints at 589,824 bytes are reconstructed in 45,621 bytes with two-dimensional wavelet analysis. The same technology is being developed to recognize human eye iris patterns for unique identifiers in security systems (Daugman 2001). Data compression can be applied to conservation ecology to develop more data and cost efficient field experiments, management efforts, and monitoring programs.

The image reconstruction plot shows the concentration of energy to illustrate how the wavelet transform compacts a greater proportion of the energy into fewer coefficients than the original data (Figure 3.5). The untransformed original data (dashed line) contributes 100% of the energy in more than 1,000 data points, whereas the wavelet transform compacts the same energy in about 75 coefficients (note, in this case, one data point is equivalent to one wavelet coefficient on scale 1). If the reconstruction of 95% of the energy were adequate, then closer to 60 coefficients would be required. But, 80% of the energy of the signal is represented in less than 50 coefficients. Surprisingly, more than 60% of the energy in the image is due to the contributions of only ten coefficients out of over 1,000 total. The signal to noise ratio would provide further insight into the decision whether increasing the number of data points would increase the precision of the reconstruction. The wavelet transform would identify where these coefficients are located in the image to inform the researcher about how to adjust the sampling design. If the slope of the wavelet transform line is greater



Cumulative Proportional Energy
1.0
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
d5
data
1
5
10
50
100
500
1000
Number of Data Points or Coefficients

Figure 3.5.

than that for the energy line, then wavelet analysis compacts a greater proportion of energy into fewer coefficients than the original data. Lines that are close together require more points to reconstruct the image than those far apart. Pattern reconstruction is one more useful tool for two-dimensional wavelet analysis to quantify ecological pattern.

S*tandard semivariogram* is another spatial statistic for pattern detection in ecological data. This statistic provides an alternate view of bird distribution to compliment and provide comparison for pattern detection in wavelet analysis. The semivariogram is a graphical representation of spatial variability that excels in the description of an average structural dimension (Journel and Huijbregts 1978, Bradshaw and Spies 1992, Carr 2002). Linearly related to the autocorrelation function, semivariogram is a measure of spatial correlation as a function of the distance between two points (rather than the actual position). The semivariogram is taking the mean of the sum of the squared differences between two point pairs. The equation for the semivariogram is defined as

$$\gamma(d) = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}(y_i - y_j)^2}{2n_d} \qquad (3),$$

where $\gamma(d)$ is the measure of similarity between all combinations of two points in a matrix and produces the average squared difference. The resulting vector relates distance and direction values that model the spatial correlation as a function of separation distance, rather than modeling the actual position of the data points. A weighted iterative function predicts data based on neighboring values. The functions used to calculate the semivariogram are stationary and extend to infinity. Thus, semivariogram is best at defining the single most characteristic scale, rather than multiple scales. Semivariograms are best at identifying the smallest scale, as the first scale isolated in the graphic.

As mentioned above, semivariogram has a directional component similar that in wavelet analysis. The North-South component corresponds to 0 degrees in the semivariogram and horizontal in wavelet analysis. As the filter moves along the plane in an East-West direction, the analyzing wavelet calculates the vertical edge. The East-

West component is 90 degrees in the semivariogram and vertical in wavelet analysis. The filter moves along the vertical plane in a North-South direction to calculate the horizontal edge. Finally, the Northwest-Southeast and Northeast-Southwest component is 45 degrees in the semivariogram and diagonal in wavelet analysis. The filter moves along the diagonal plane in a Northwest-Southeast direction to calculate the diagonal edge.

The anatomy of the semivariogram includes the nugget, sill, range, and lag. The semivariogram increases from a value near distance 0 along the transect (i.e., nugget) to its maximum value (i.e., sill) at a critical distance beyond which the graph remains relatively constant (i.e., range) or decreases. The lag is the number of data points between the two values under consideration. The nugget represents the inherent random error in the sample at a very small scale. A large nugget may indicate the inadequate minimum data resolution for the spatial structure (i.e., pattern may exist at smaller scales than the minimum between-sample distance). The sill marks the end of the zone of influence of a single sample, representing the sample variance. The height of the sill indicates the steepness of the edge of the patch. The range is the distance along the transect at the sill. Beyond the range, the samples are no longer correlated and are independent (i.e., covariance becomes zero). Thus, the range is the limit of the zone of influence of a single point in the sample. After the sill, the curve becomes more or less constant or even decreases. The peak at the range represents points that are very different from one another and the following shelf represents similarity. The range provides the location of the dominant pattern, the average patch size, or average distance between patches. Small ranges indicate data with values that change rapidly over space. A large range represents more spatial regularity.

The spherical form of the semivariogram is typical with the characteristic scale being identified as the distance at which the semivariance levels off (i.e., the range; Figure 3.6). Interpretation of the Gaussian and exponential forms are similar with the characteristic scale identified by the location of the sill. The linear form has an unlimited capacity for dispersion. A plot that does not rise but oscillates around the sample variance has a sample interval greater than the range. In this case, the

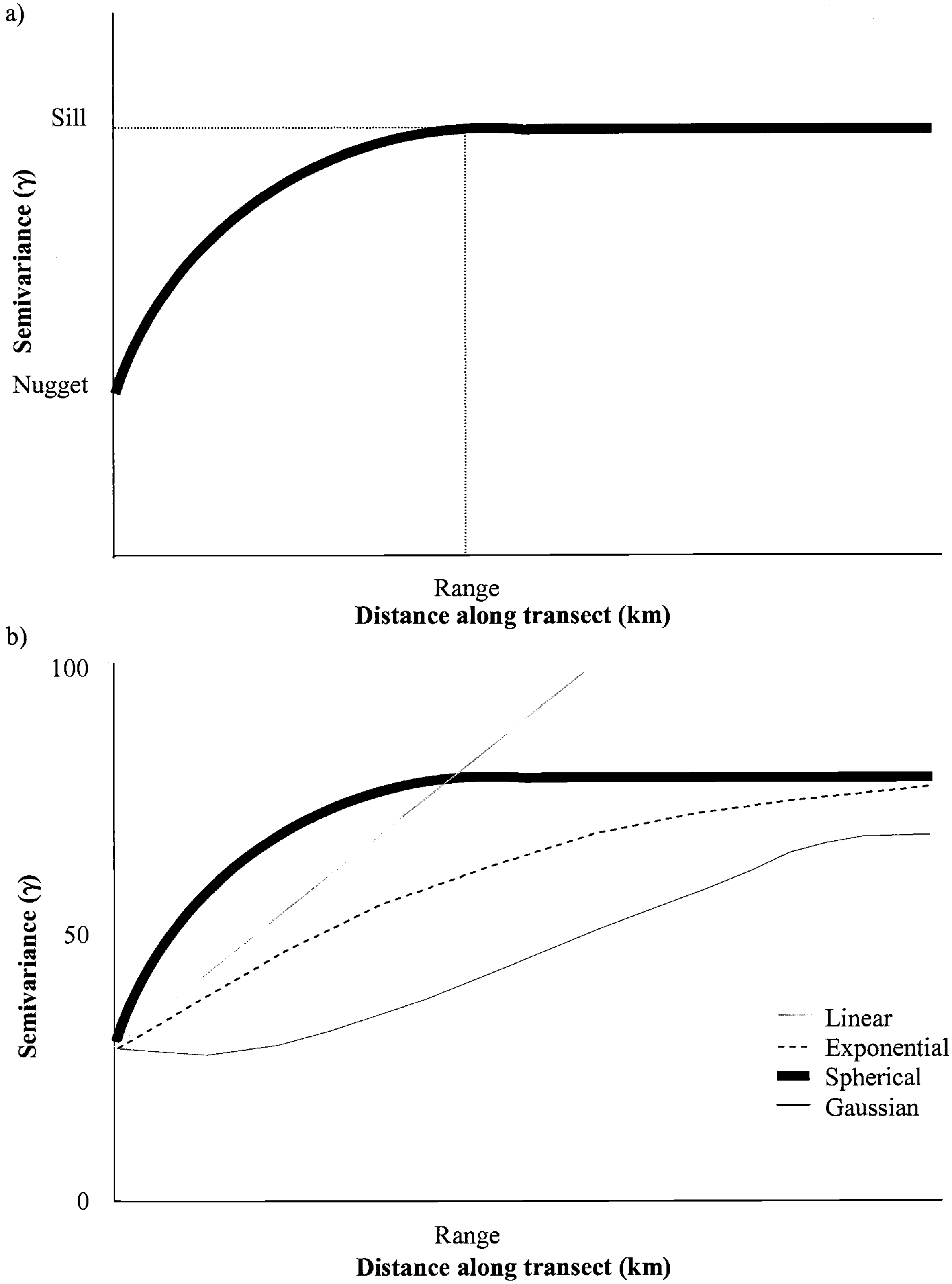

a)
Sill
Nugget
Semivariance (γ)
Range
Distance along transect (km)
b)
100
50
0
Semivariance (γ)
Linear
Exponential
Spherical
Gaussian
Range
Distance along transect (km)

Figure 3.6.

semivariance is equal to the sample variance. A relatively flat curve indicates random pattern, lacking spatial dependencies. The curve may oscillate.

Data were analyzed with S-plus 2000 (Insightful Corp., Seattle, WA).

RESULTS

In this section, we explore the pattern detection capabilities of two-dimensional wavelet analysis by illustrating the differences in heterogeneity between two Neotropical migrant birds. The low heterogeneity of Field Sparrows is characterized by a smaller area, lower bird density, lower peaks, fewer peaks, and moderate change over time. The high heterogeneity of Red-eyed Vireos is characterized by larger species range, high bird density, higher peaks, more peaks, greater diversity of peak height, and more change over time. Briefly, we examine the pattern reconstruction capabilities of two-dimensional wavelet analysis. Finally, we examine the pattern detection capability of standard semivariogram and compare it to wavelet analysis.

Two-dimensional Wavelet Analysis' Ability to Detect and Classify Complex Pattern

Case Study of the Field Sparrow

The internal structure of the distribution of Field Sparrows in North America exemplifies relatively low heterogeneity. The summer distribution of this ground-nesting Neotropical migrant spanned the successional-scrub habitats in the Eastern and Midwestern United States (Figure 3.1a). Regions with the highest concentrations appeared to occur mainly in Deciduous broadleaf forest, grasslands, and mixed dryland/irrigated cropland/pasture (Figures 3.1a and 3.2b). Yet, even these densities were low compared to those for Red-eyed Vireos. Field Sparrows were not detected on the West Coast. The BBS identified this as a declining population (Sauer et al. 1999).

Perspective plots --- Field Sparrows were clustered in a moderate, localized region of the BBS study area that extended approximately half way across the United Sates (Figure 3.7a). Over the thirty-year interval, their density was relatively low, with a maximum peak of 30 birds. The species range was choppy with numerous peaks that varied in height but were all relatively small. Most peaks were low with some higher peaks interspersed and several very low peaks along the edges. Most of the birds were

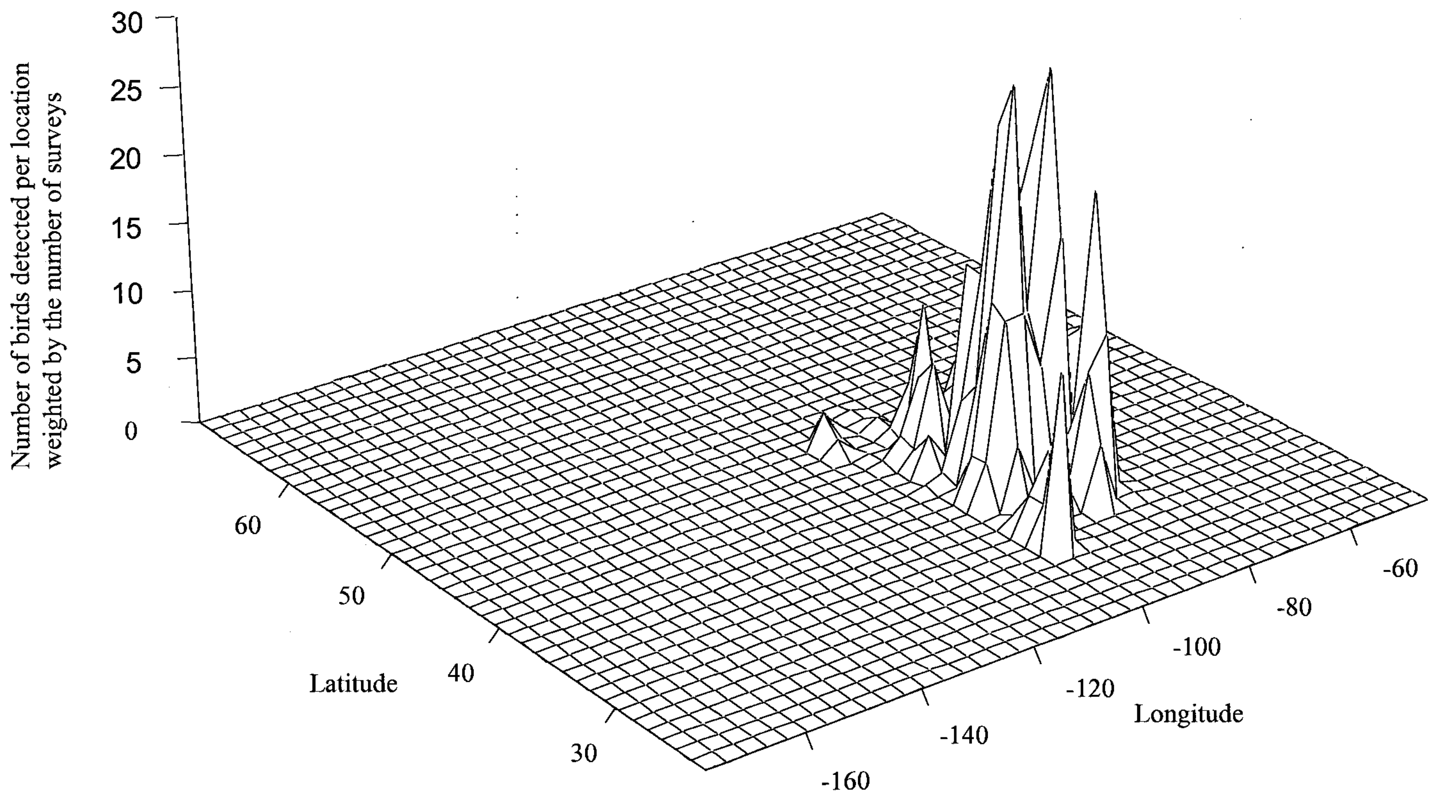

30
25
20
15
10
5
0
Number of birds detected per location
weighted by the number of surveys
60
50
40
30
Latitude
-60
-80
-100
-120
-140
-160
Longitude

Figure 3.7a.

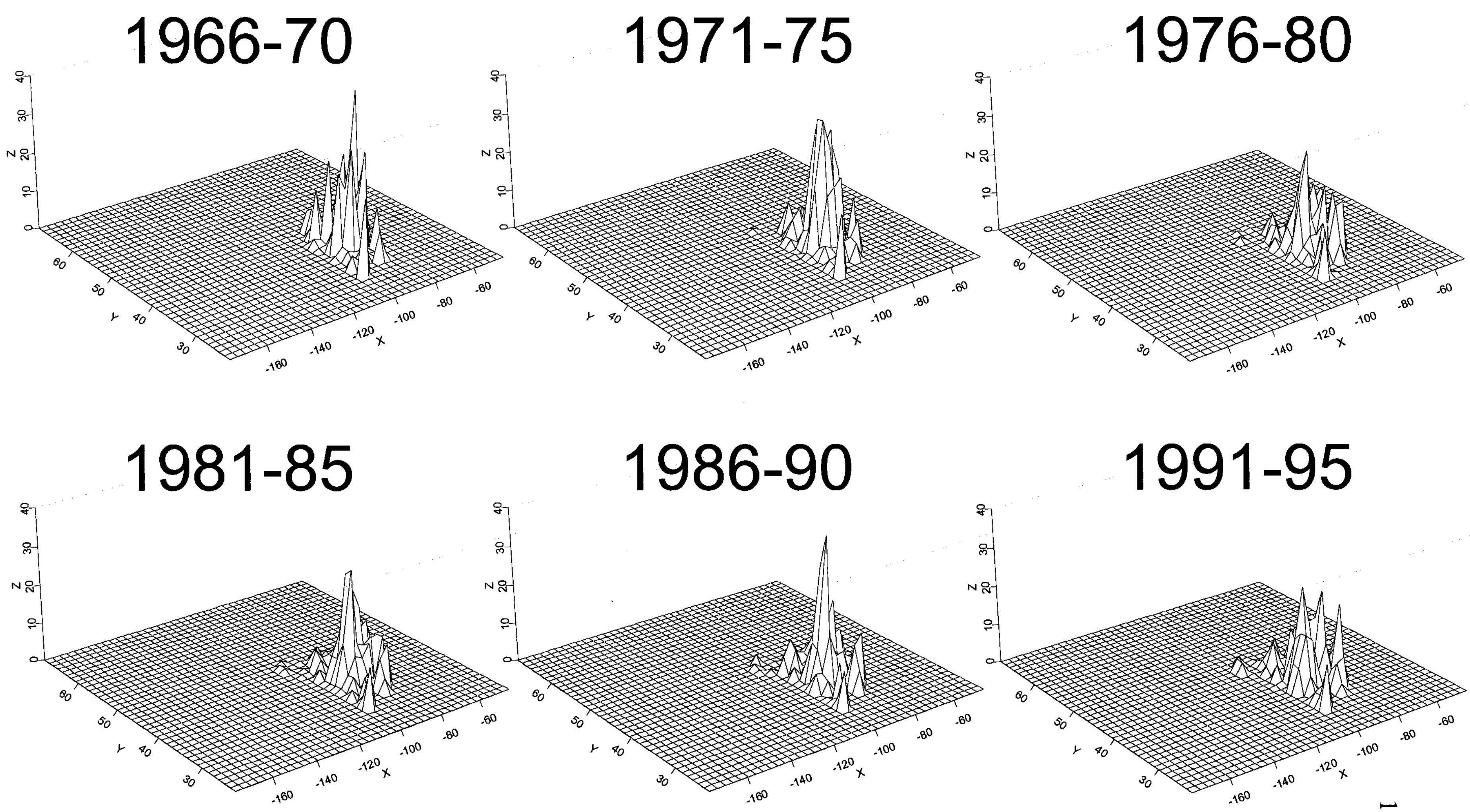

1966-70
1971-75
1976-80
1981-85
1986-90
1991-95
Z
0
10
20
30
40
Y
30
40
50
60
X
-160
-140
-120
-100
-80
-60

Figure 3.7b.

located in one cluster in the center of the species range.

The morphology of Field Sparrow distribution demonstrated a strong, fairly consistent core that filled in over time while dispersal northwest increased (Figures 3.1a, 3.7a, and 3.7b). The location of the centroid and edges were relatively stable. A prominent feature of the core was one large patch of birds off-center to the east. The gradient in abundance at the northern boundary appeared gradual, with a diagonal element in the northwest. The southern edge had a relatively non-uniform, moderately steep transition into the centroid area. The eastern edge was a sharp transition from intermediate peaks to the Atlantic Ocean coastline.

Although the basic morphology was relatively stable, the magnitude of the peaks did fluctuate over time. For instance, 30 birds was the highest peak for Field Sparrows, a low density for the Red-eyed Vireo case study. This highest peak was observed during the 1966-70 interval in the center, west of the one large patch of birds, but only persisted for that interval. This peak diminished over time, with many of these birds moving slightly to the west and others moving northward. From 1971-75 through 1980-85, the base built up and the population distribution extended slightly to the northwest. In 1986-90, the center peak had increased dramatically and the patch extended northward again. By 1991-95, the highest peak had decreased and the birds had spread evenly to the surrounding area, strengthening the northwest species range expansion.

Contour maps --- Classification as a declining species was more apparent in the contour maps than in the perspective plots (Figure 3.8a). A consistent core attracted birds or summer distribution, but the morphology of habitat use around this core varied among the five-year intervals. Field Sparrows were always present to the east of the shaded oval, but the pattern habitat use differed. In contrast to the perspective plots, the edges did not appear stable over time.

Field Sparrows had a relatively stable species perimeter over time (Figure 3.8b). Despite the changes in the perspective plots over time, the extent of the species range appeared to maintain its position at 30 to 45 degrees latitude and -75 to -100 degrees longitude. The shape of the perimeter remained relatively similar over time. The perimeter expanded from 1966-70 to 1971-75, remained relatively consistent until a

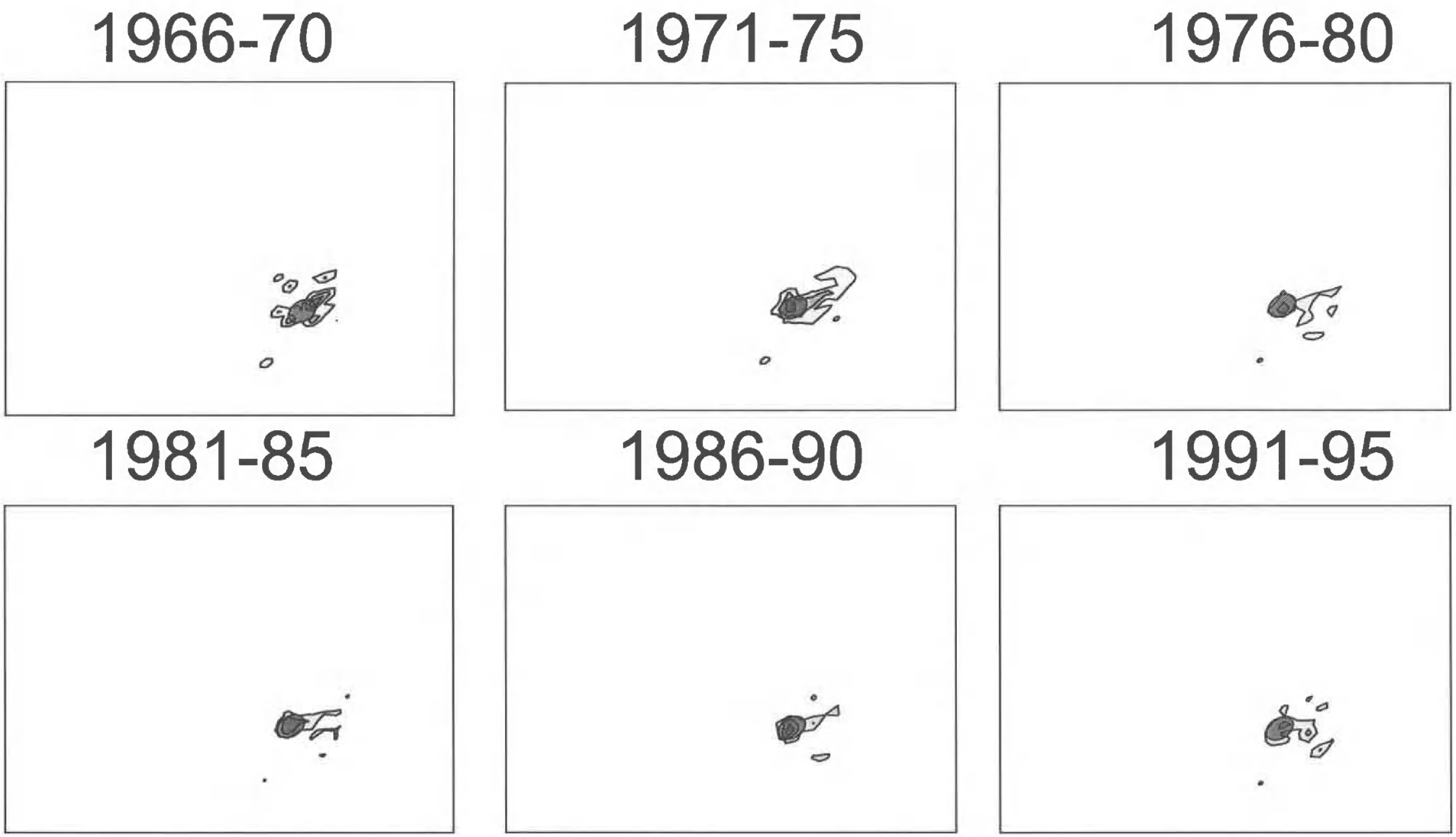
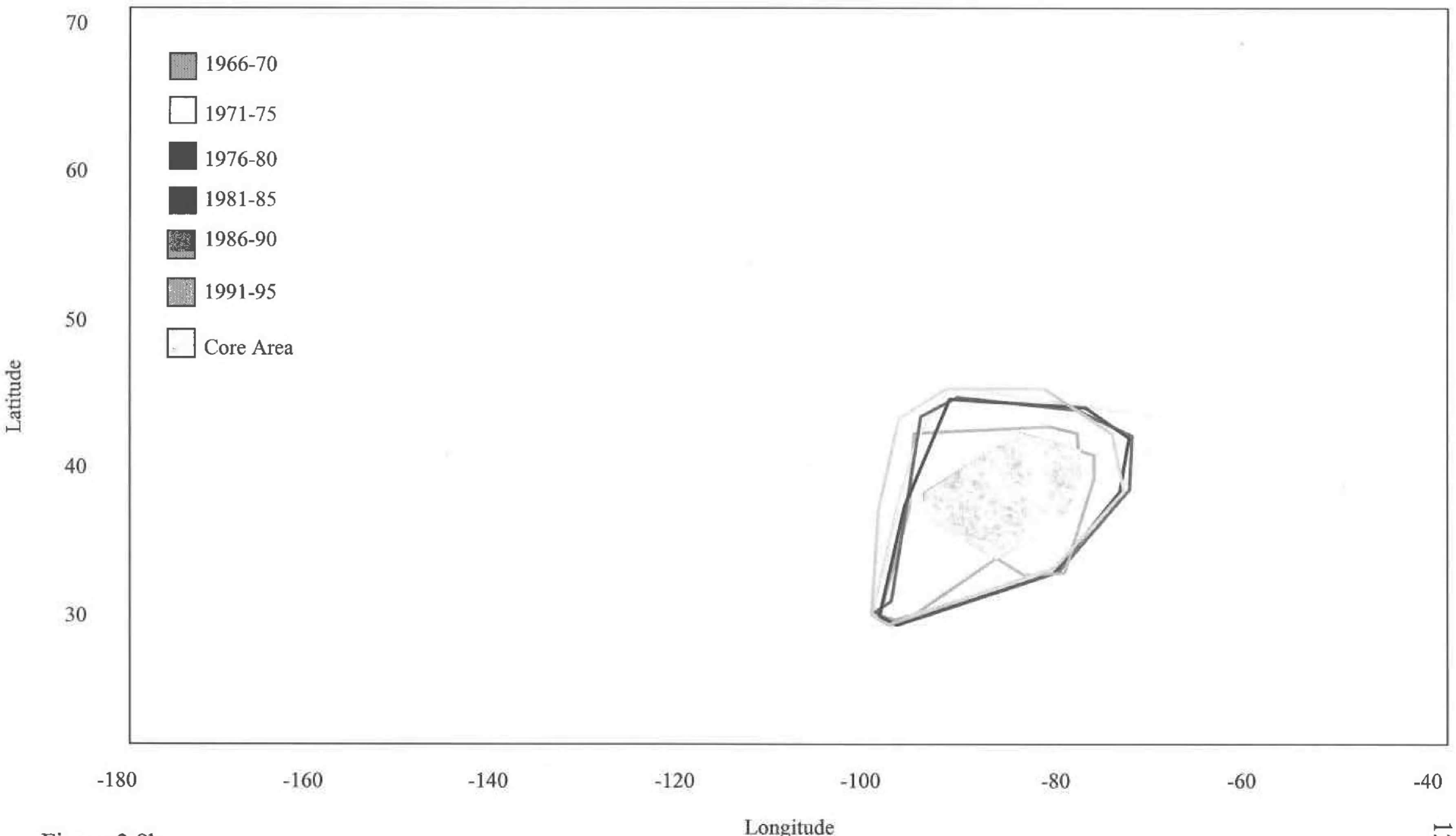


Figure 3.8a.



70
60
50
40
30
Latitude
1966-70
1971-75
1976-80
1981-85
1986-90
1991-95
Core Area
-180
-160
-140
-120
-100
-80
-60
-40
Longitude

Figure 3.8b.

large contraction in 1986-90, which was restored in 1991-95. The central area of overlap maintained a position at latitude 35 to 40 degrees and longitude -90 to -90 degrees.

Thus, according to visual pattern detection, Field Sparrows had a relatively consistent pattern in their species range over time. The main wavelet metrics confirmed and clarified the pattern further.

Wavelet Transform --- Low heterogeneity in Field Sparrow distribution was emphasized by the remarkable lack of pattern displayed in the wavelet transform for the entire thirty-year study period (Figure 3.9). The wavelet transform identified 5 scales of pattern in the Field Sparrow distribution, but the characteristics that represent low heterogeneity (e.g., low bird density, low peaks, small area) produced a very low energy signal. The strength of the energy in each feature was too low to stand out from the surrounding lack of birds. But, the energy of Field Sparrow distribution did show up at the largest scale. The dark pixels in the lower left corner of the wavelet transform represented the strong influence of the coarsest scale to the overall signal. This dark region represented scale 5 in all three directions (i.e., crystals s5-d5 for North-South, d5-s5 for East-West, and d5-d5 for the diagonal component).

To clarify how the wavelet transform identified five scales from a seemingly homogeneous distribution, we plotted the dominant features contributing the top 5% of the energy to the overall signal (Figure 3.10). The location of the centroid was confirmed in this view of the wavelet transform, as it appears in many crystals. All three directions contributed to the top 5% of the energy at all five scales.

To examine directionality over the thirty-year period, we magnified the wavelet transform crystals at Scale 1 because they are close to the original data (Figure 3.11). The Haar analyzing wavelet focuses on defining boundaries and edges, so it is possible to delineate species range and calculate its size from this view of the wavelet transform. The darker pixels indicate the strong edges of the species range and the light pixels beyond the dark represent either range expansion in that direction or temporary dispersal. The directional pattern observed in the perspective plots was confirmed as well. For instance, Field Sparrow dispersal northwest was apparent in the darker pixels

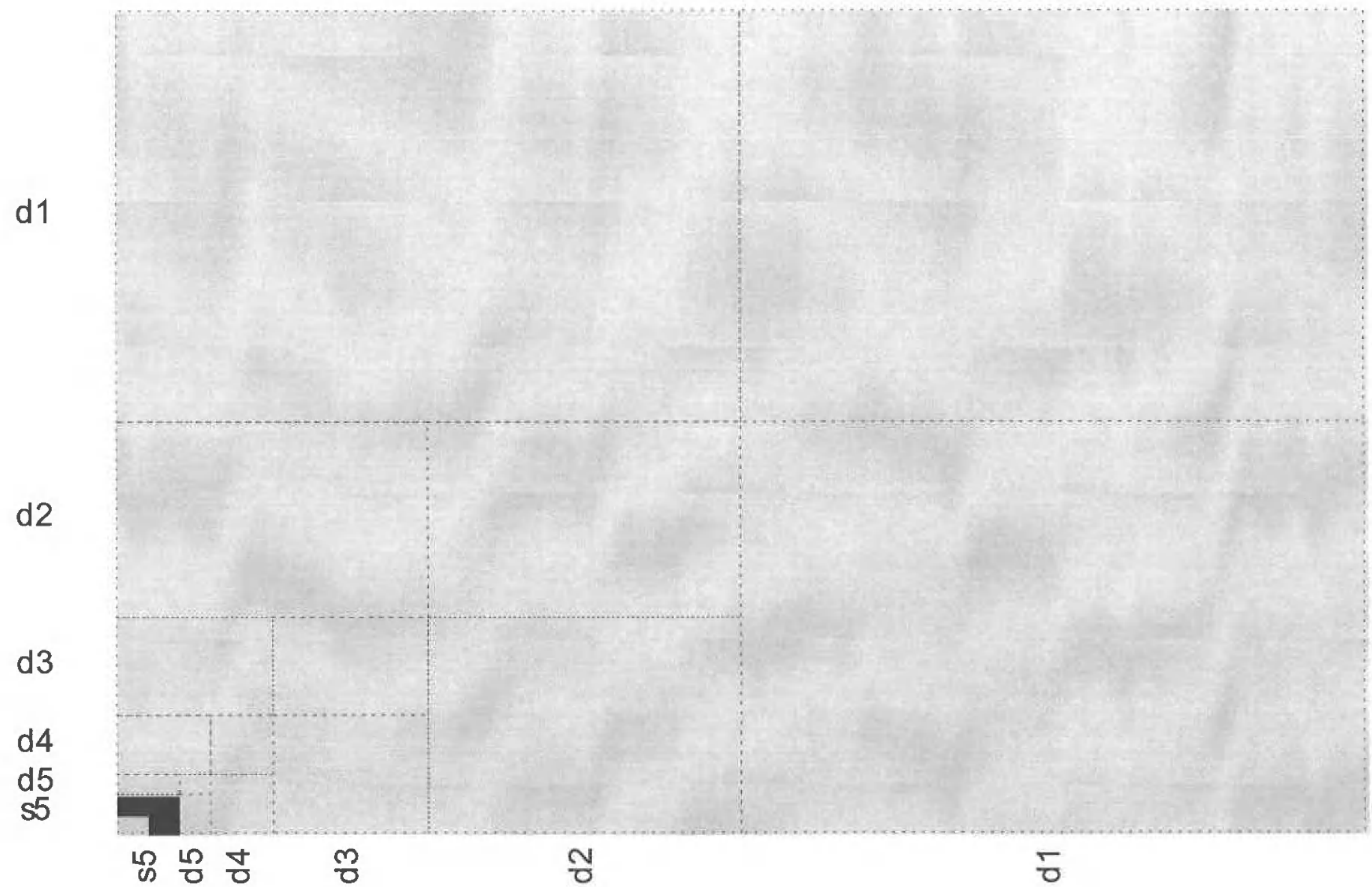


Figure 3.9.

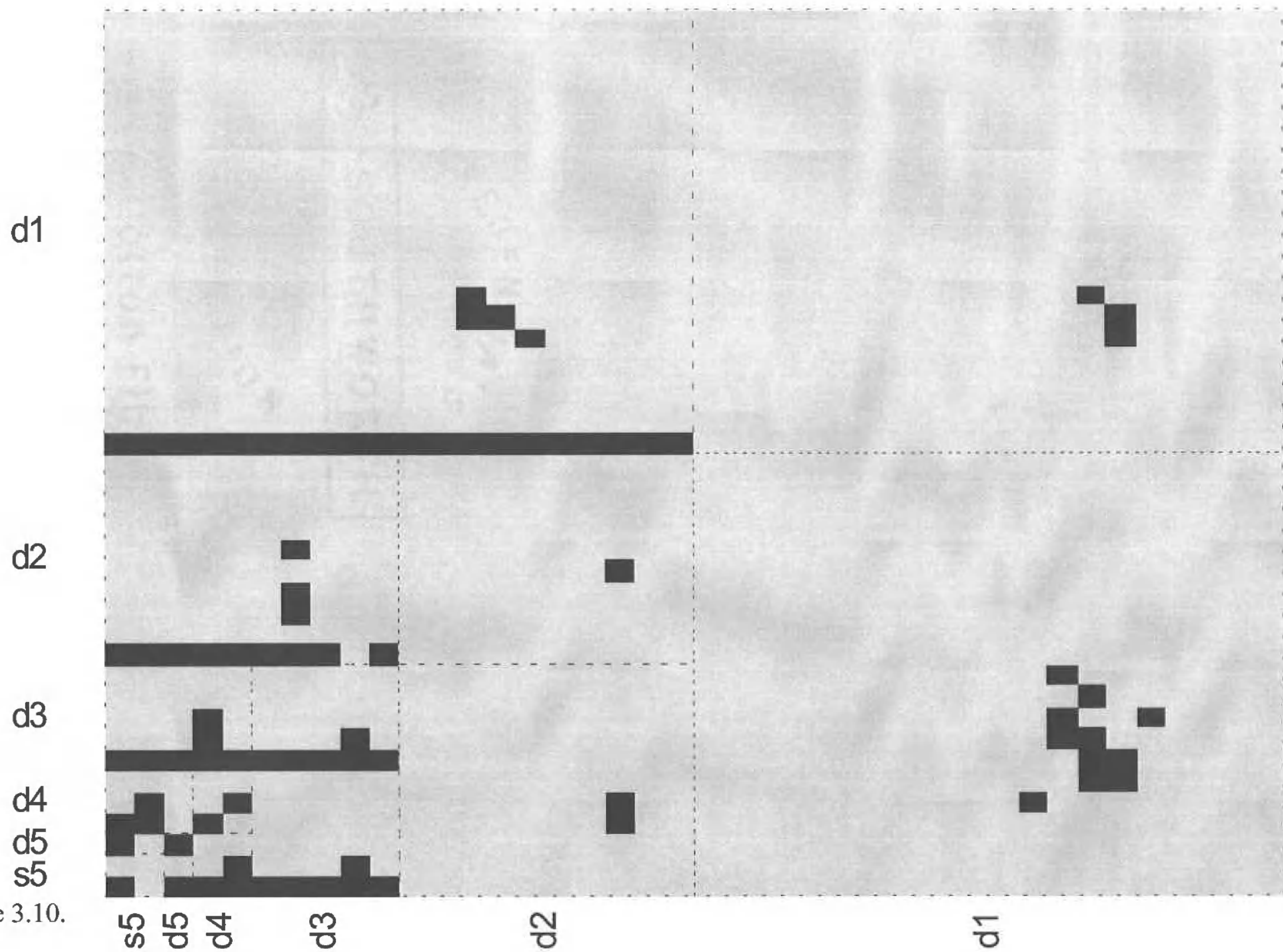


Figure 3.10.

a) North-South

b) East-West

c) Diagonal

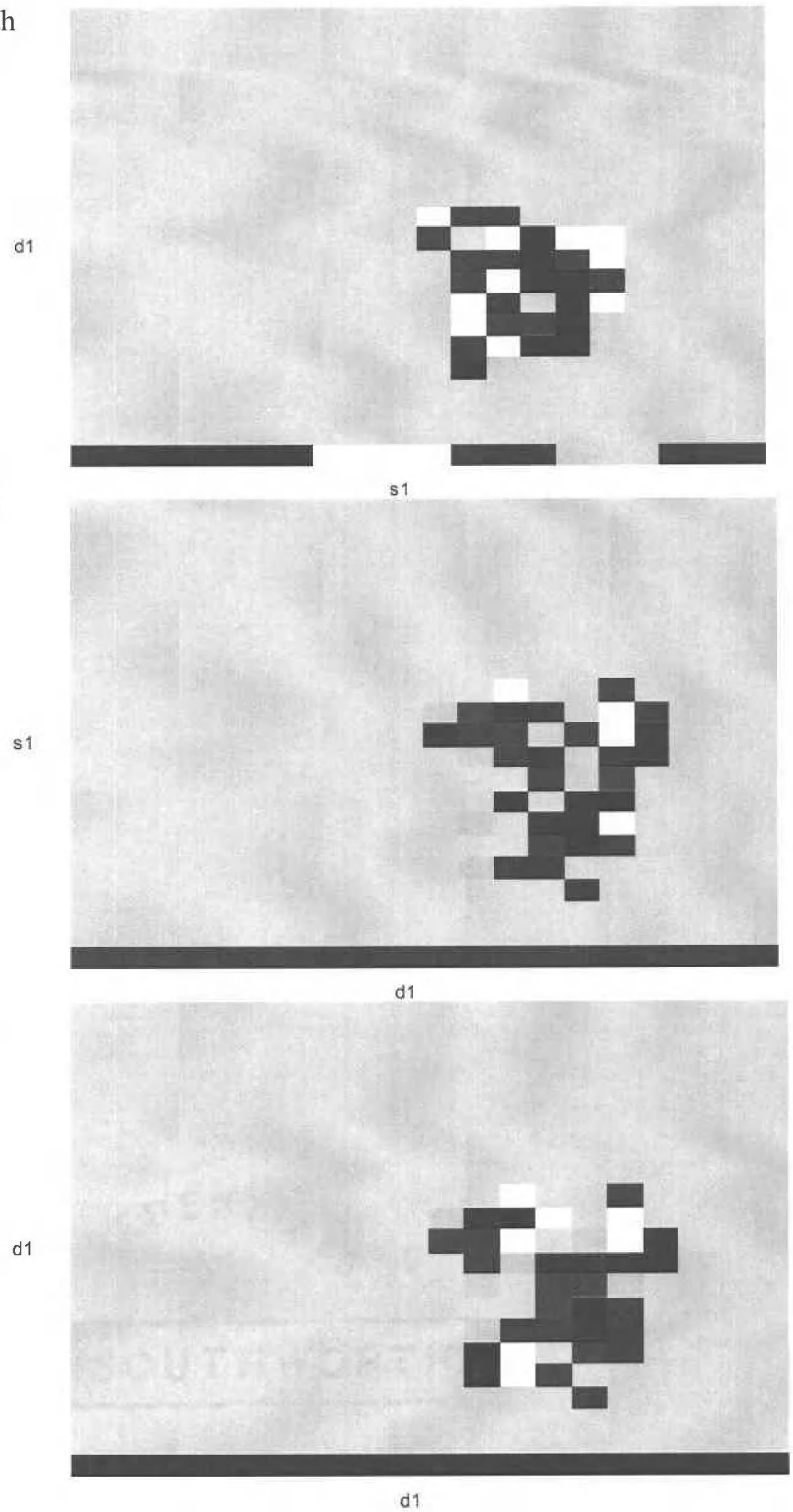


Figure 3.11.

to the North (Figure 3.11a), to the West (Figure 3.11b), and Northwest-Southeast (Figure 3.11c). The steep transition of the southern edge into the centroid was highlighted in the North-South view (Figure 3.11a). The sharp transition into the eastern edge of Field Sparrow distribution was apparent in the East-West component (Figure 3.11b).

Box and whiskers --- The Field Sparrow boxplot showed a relatively simple pattern with localized complexity, as there was less change over space and time, more stationarity (Figure 3.12). Low heterogeneity was represented by the ample white space, relatively fewer negative crystals, intermediate space in the tails, tightly packed crystals giving height to the center bar, and relatively less steep edges (as indicated by fewer bars on either side of the center bars). The definition of a peak was clearer and there were few distinguishable peaks.

The pattern was fairly consistent in scale and direction (Figure 3.12). Because the Haar analyzing wavelet detects edges and boundaries, a high absolute value of a coefficient represents more edge and a low value is less edge. The boxplot for the relatively stable, low-density population of Field Sparrows had few coefficients and most have a low absolute value. Many low coefficients reflected a texture that is relatively less edgy. More may be happening in the intermediate scales, based on the crystals in the tails of the North-South component.

Crystals were more widely dispersed in the North-South component and more tightly packed at each scale. Specifically, the dynamic range of the tails for the North-South boxplots (e.g., s1-d1) decreased from scale 1 to scale 4. This finding agreed with the prior wavelet metrics. Yet, information was unevenly distributed across scales. The North-South crystal at scale 1 (e.g., s1-d1) contributed almost 80% of the energy to the wavelet from many large peaks. Actually, all North-South components for all five scales contributed over 95% of the energy overall. The crystals contributed the following energy to the overall signal: almost 80% for s1-d1, a little over 10% for s2-d2, about 5% for s3-d3, around 3% for s4-d4, and 1% or less for s5-d5 and all others. The long tail on the North-South component at scale 5 indicated a large contribution from several large coefficients and the long tail on the North-South component at

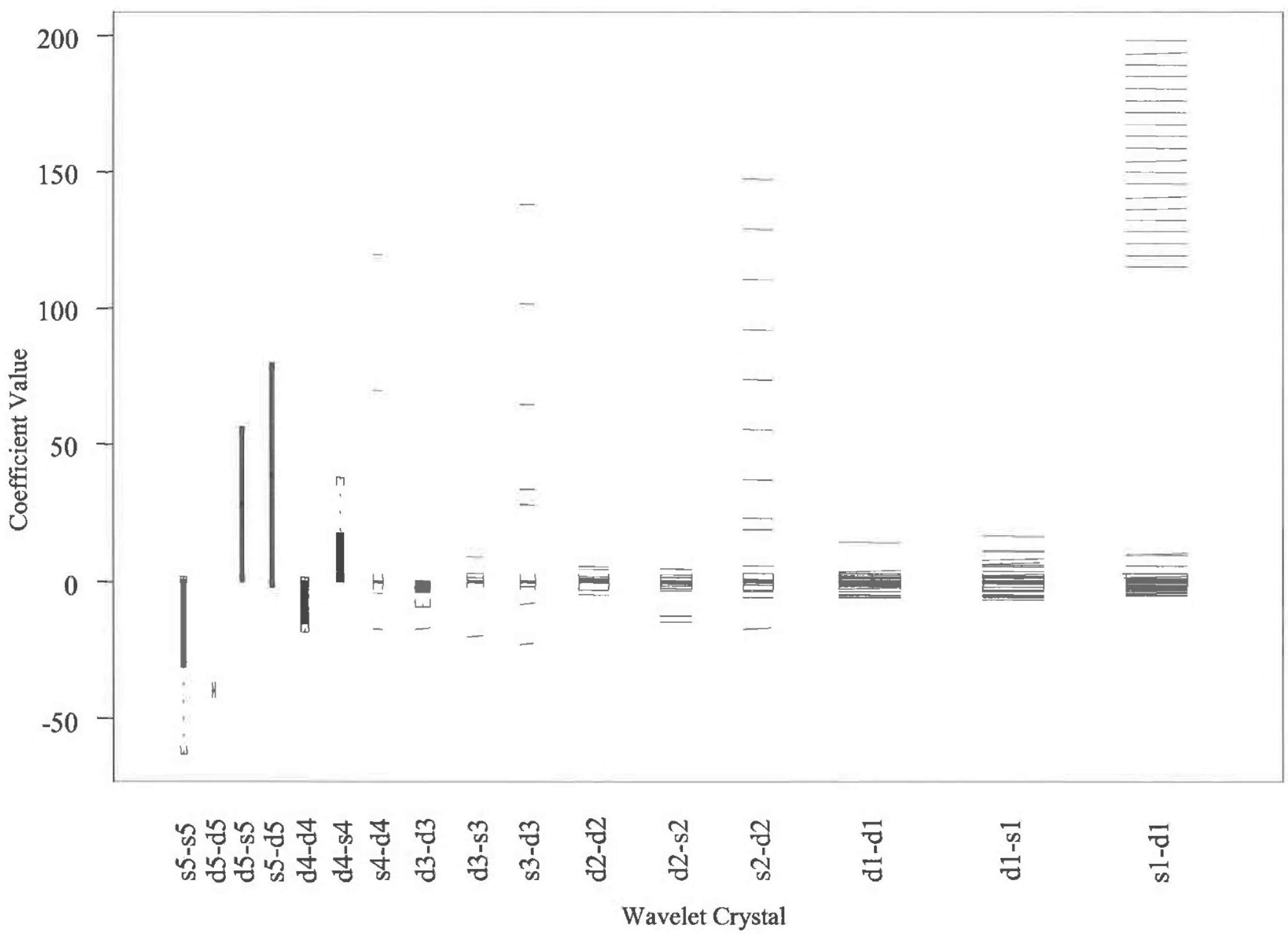

Coefficient Value
200
150
100
50
0
-50
s5-s5
d5-d5
d5-s5
s5-d5
d4-d4
d4-s4
s4-d4
d3-d3
d3-s3
s3-d3
d2-d2
d2-s2
s2-d2
d1-d1
d1-s1
s1-d1
Wavelet Crystal

Figure 3.12.

scale 2 demonstrated a large contribution from a few coefficients. The mid-eastern orientation was indicated by the high-density bars of 'no pattern' in each East-West direction.

Wavelet Variance --- The relatively low numbers, low peaks, and few peaks lead to heterogeneity that approaches homogeneity. The overall wavelet variance demonstrated very low heterogeneity at fine scales 1 through 3, and low heterogeneity at coarse scales 4 and 5 (Figure 3.13a). Although the heterogeneity remained relatively low throughout the scales, the wavelet variance doubled from scales 1 to 4 and tripled at scale 5. The overall trend in the wavelet variance was similar over the six five-year intervals (Figure 3.13b). Any differences became more pronounced as scale increased.

Each component contributes to the overall wavelet variance (Figure 3.14). In terms of scale, the pattern of the overall wavelet variance was visible in all three components. The overall patterns were fairly similar within each component. Scales 1 through 3 demonstrated the least heterogeneity and scales 4 and 5 demonstrated the most heterogeneity. Most of the heterogeneity at scales 1 through 3 was generated by the pattern in the North-South component (i.e., horizontal edge). All three components contributed to the patterns at scales 4 and 5, however, North-South contributed about two times as much energy as East-West (i.e., vertical edge) and about four times as much energy as Diagonal (i.e., diagonal edge).

In terms of direction (i.e., component), most of the overall wavelet variance was derived from the North-South component (i.e., the horizontal edges; Figure 3.14). The horizontal edge was dominant at all five scales, especially scales 4 and 5. The gradient was sharper (i.e., steeper edges) west to east than south to north. The contribution of the North-South component was dominant, the contribution of the East-West component was moderate, and the contribution of the Diagonal component was low. Thus, heterogeneity in distribution primarily varied from west to east. The vertical edge (i.e., East-West component) contributed about twice the energy of the diagonal component, such that the heterogeneity west to east was greater than the relatively homogeneous diagonal edge (i.e., Northwest-Southeast, Northeast-Southwest).

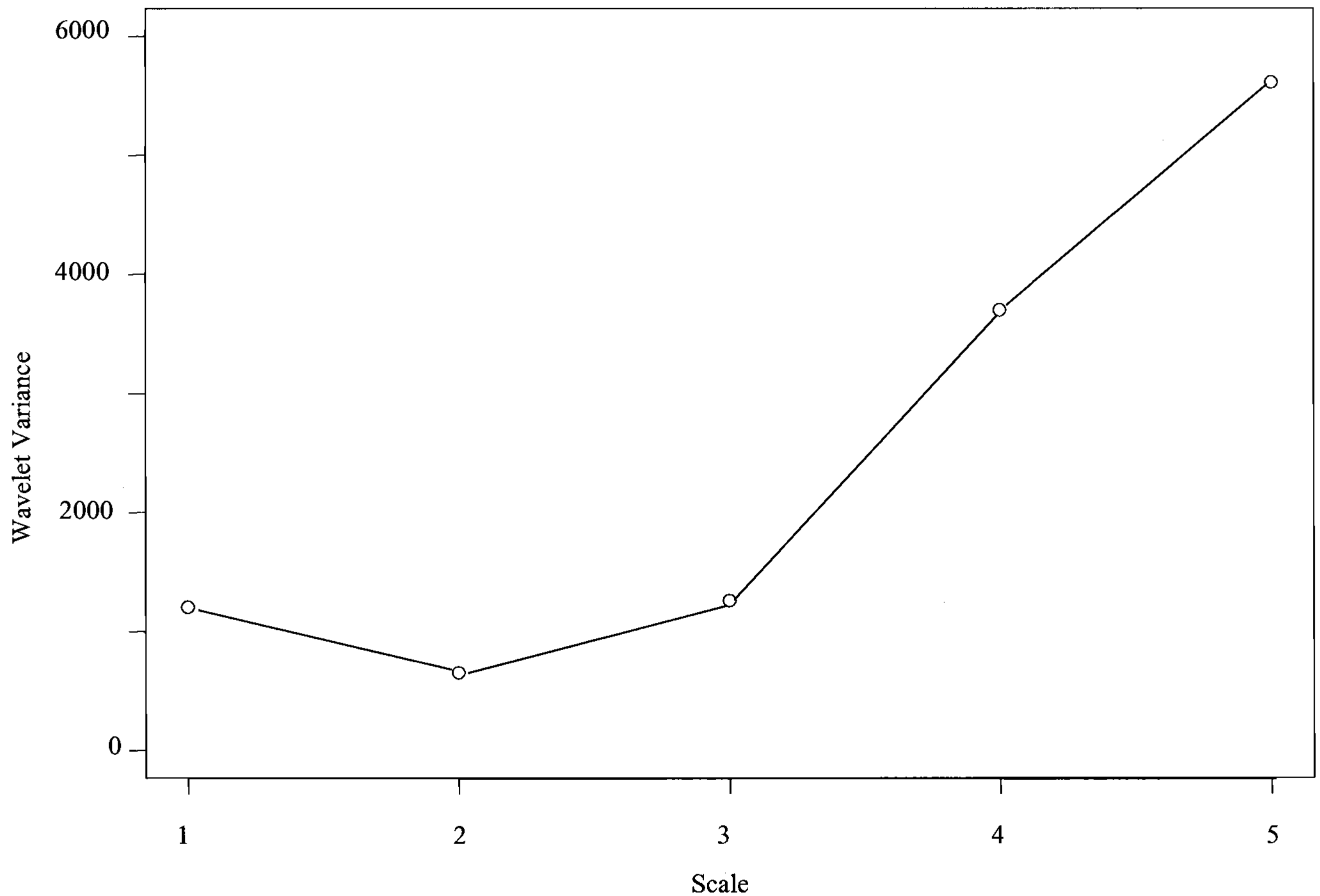


Figure 3.13a.

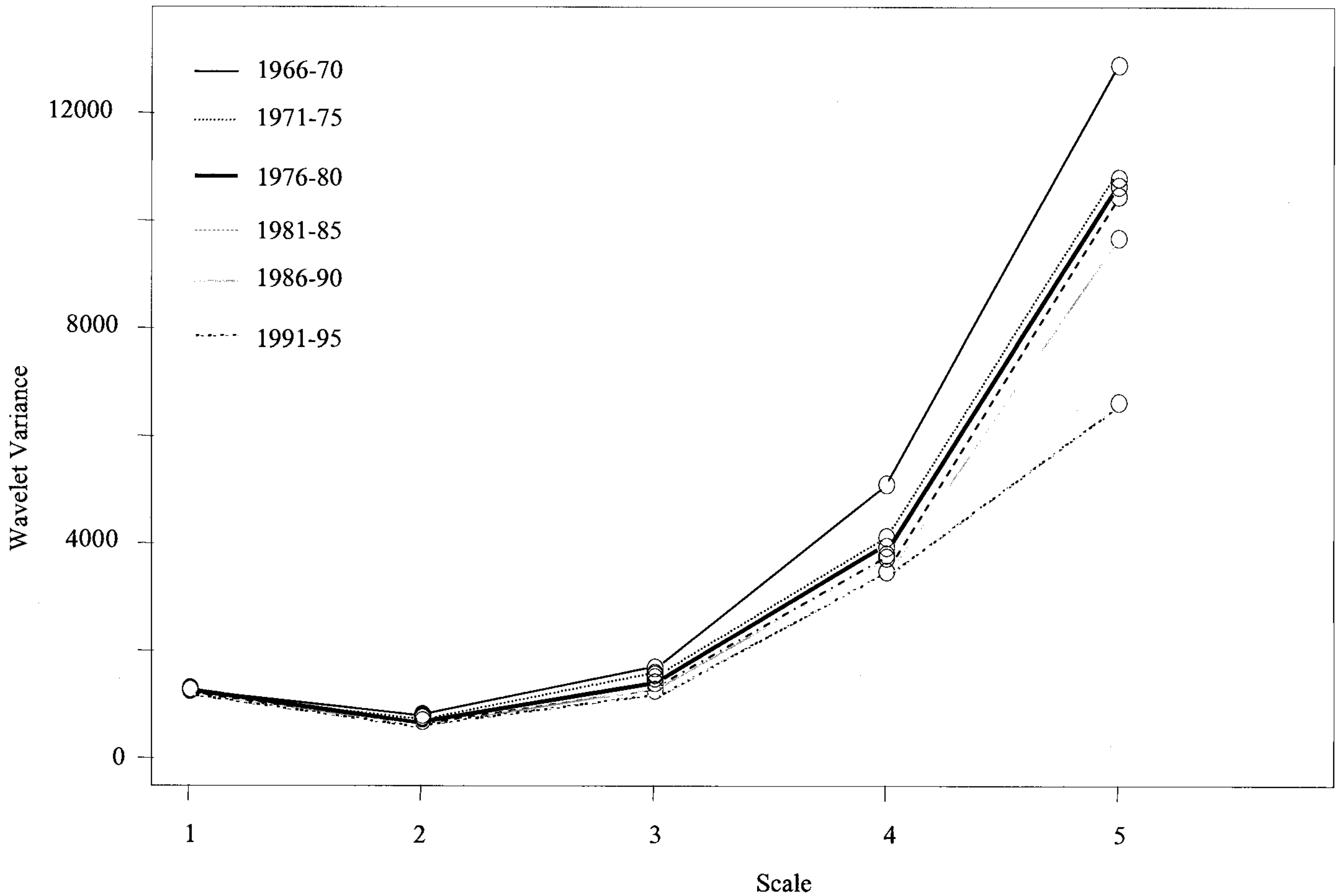
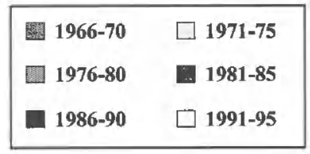
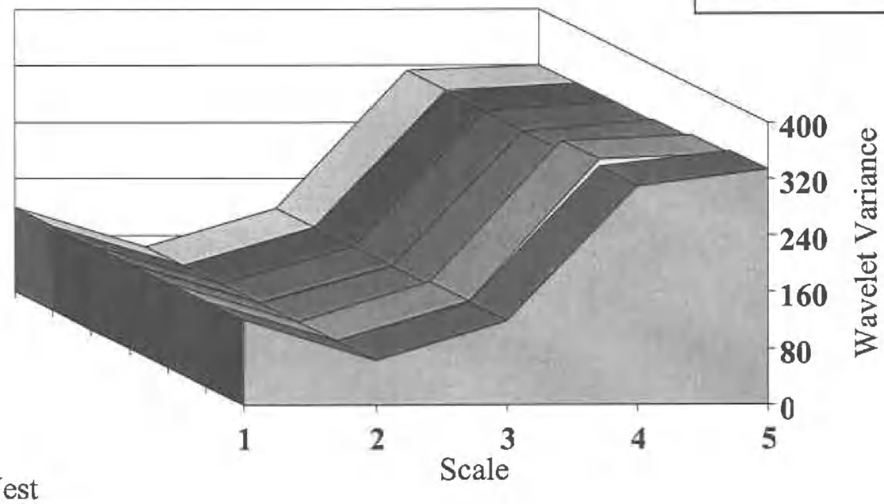

1966-70
1971-75
1976-80
1981-85
1986-90
1991-95
12000
8000
4000
0
Wavelet Variance
1
2
3
4
5
Scale

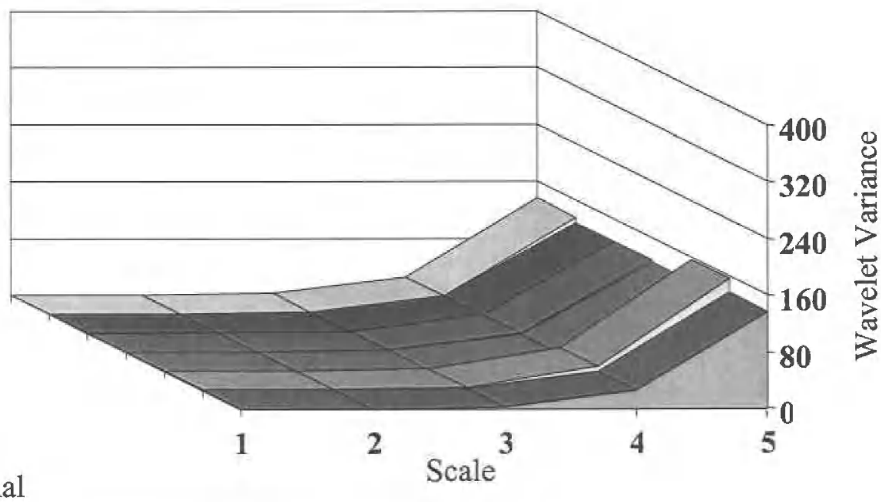
Figure 3.13b.



1) North-South



2) East-West



3) Diagonal

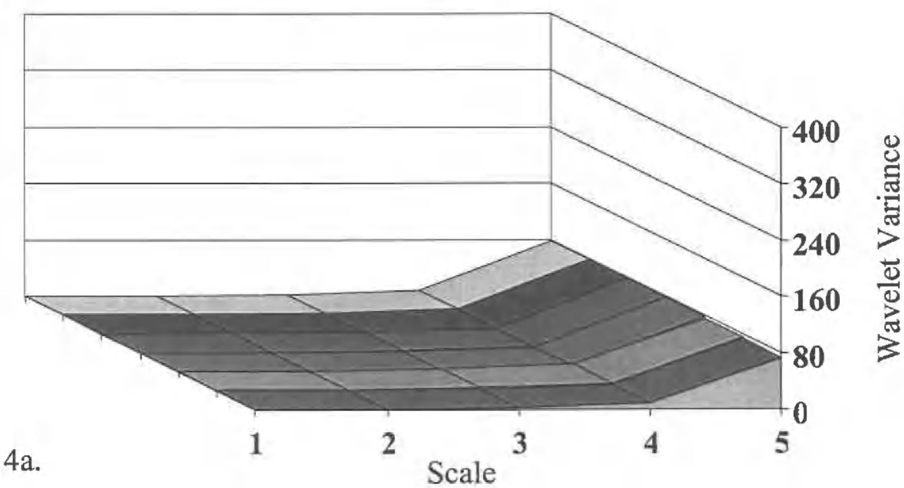
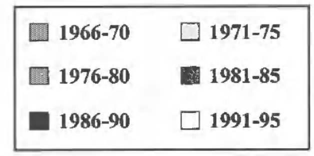
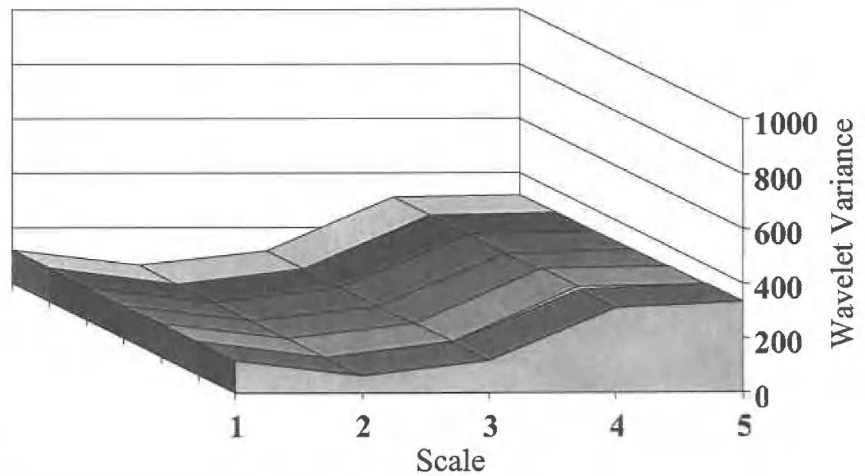


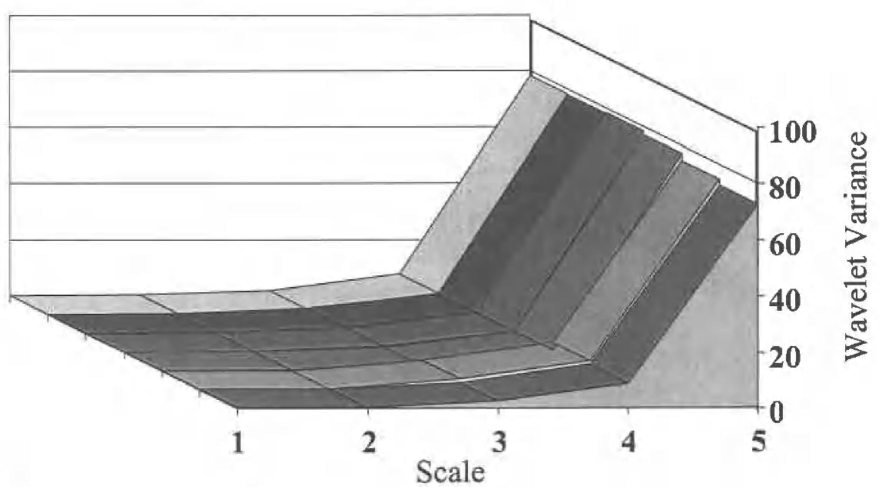
Figure 3.14a.



1) North-South



2) East-West



3) Diagonal

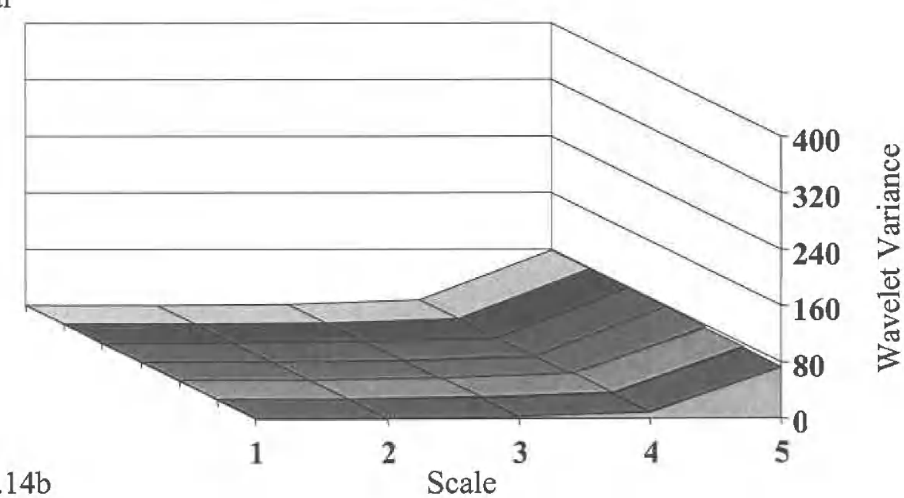


Figure 3.14b

The Field Sparrow population was relatively stable over time. The scalar and directional patterns remained relatively similar among the five-year intervals (Figure 3.14). The main species range remained relatively constant in size, shape, and patchiness over time, apparently remaining in the same geographical position. The heterogeneity was greater at larger scales than at smaller scales, more similar to the scale at which we perceive these data. The steepest North-South gradient at scale 5 was in 1966-70 and the shallowest gradient was in 1991-95. The strongest East-West edge at scale 5 was in 1971-75 and the least edge was in 1976-80. The steepest gradient at scale 5 diagonally was in 1991-95 and the shallowest was in 1966-70.

Case Study of the Red-eyed Vireo

In comparison with the relatively stable main cluster of Field Sparrows, Red-eyed Vireos had a more complicated pattern. The internal structure of the distribution of Red-eyed Vireos in North America represented relatively high heterogeneity. The summer distribution of this mid-story canopy nesting Neotropical migrant spanned the entire BBS area, except the Southwest United States (Figure 3.1b). The highest concentrations were dispersed along the East Coast and the Midwestern border with Canada. According to their preference for woodland habitat, the highest concentrations were in regions with land cover dominated by Deciduous broadleaf forest, mixed forest, Evergreen needle leaf forest, cropland/woodland mosaic, and mixed dry land/irrigated cropland/pasture (Figures 3.1b and 3.2b).

Perspective Plots --- Red-eyed Vireos had multiple clusters and multiple steep peaks that expanded, contracted, or moved in a general diagonal direction (Figure 3.15a). Over the thirty-year interval, their density was relatively high, with a maximum peak of 100 birds (Figures 3.1b and 3.15a). The species range of Red-eyed Vireos was about twice that of the Field Sparrow. Most peaks were high and intermediate with several low peaks along the edges. Gradients in abundance were distributed throughout the study area (Figure 3.15a).

The distribution of Red-eyed Vireos had a more dynamic morphology than that of the Field Sparrows, with a more pronounced gradient in abundance and extent in the overall species range (Figure 3.15b). In examining the distribution over time, the North

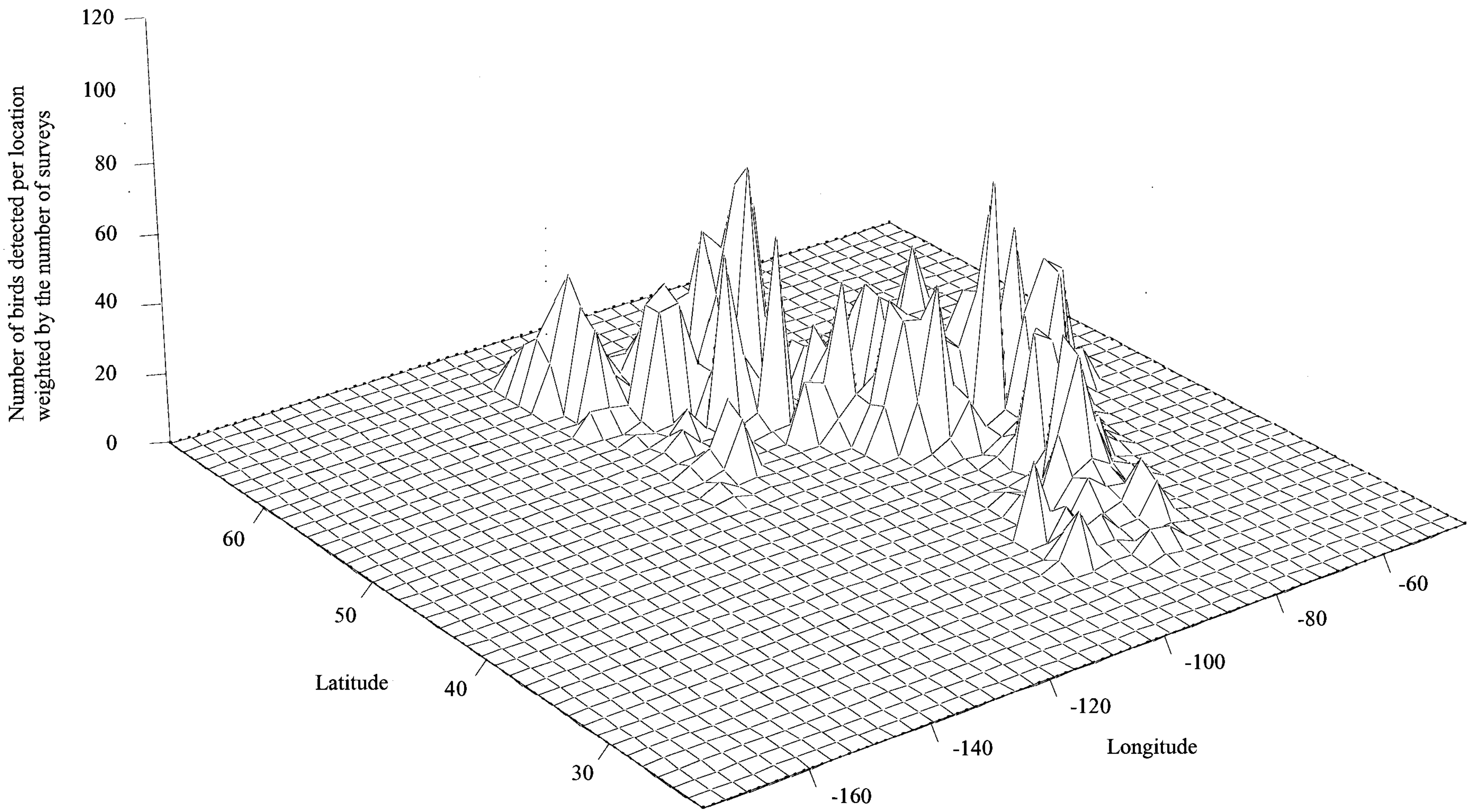

Number of birds detected per location
weighted by the number of surveys
0
20
40
60
80
100
120
Latitude
60
50
40
30
Longitude
-160
-140
-120
-100
-80
-60

Figure 3.15a.

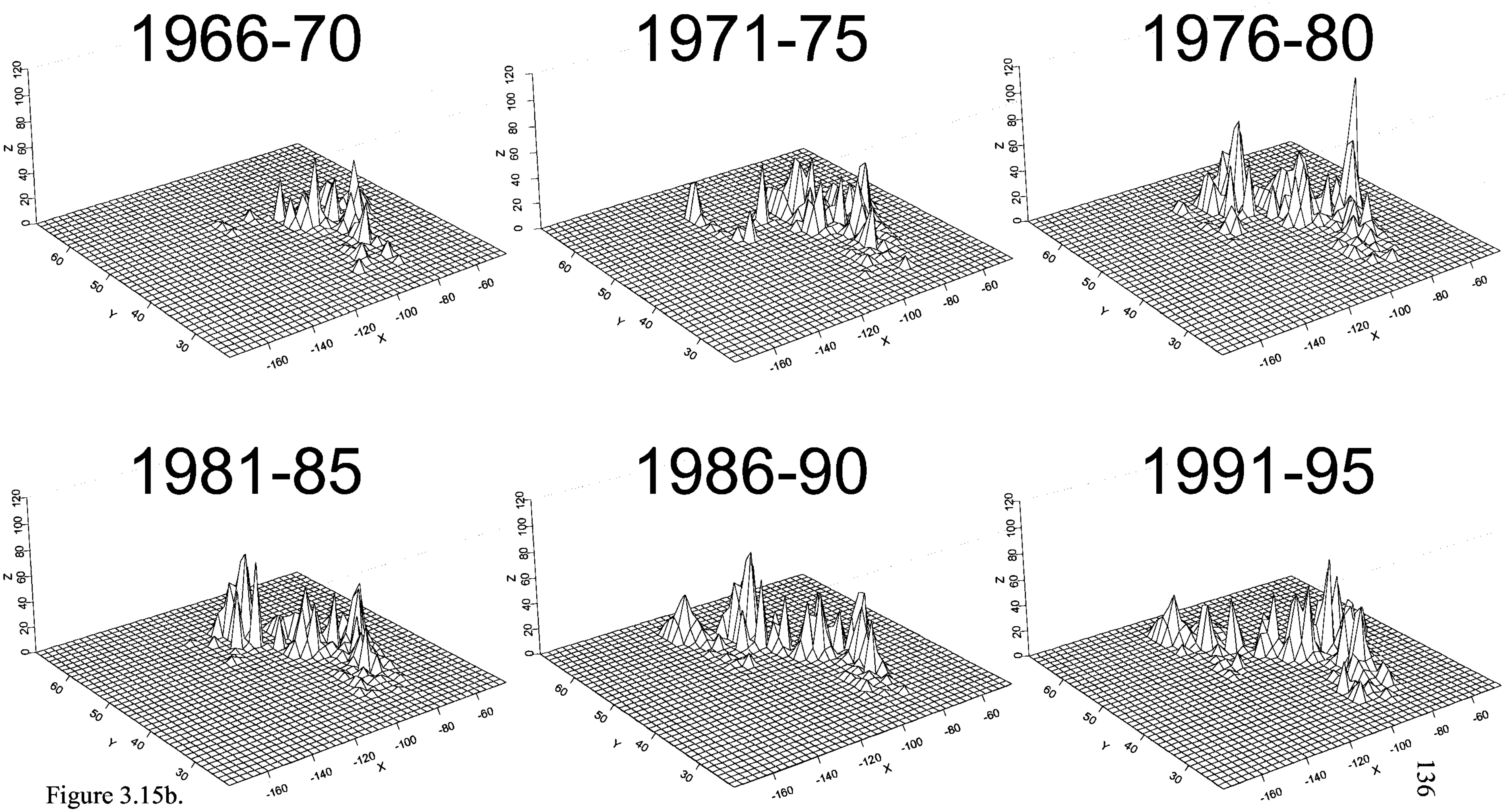

1966-70
1971-75
1976-80
1981-85
1986-90
1991-95
Z
0 20 40 60 80 100 120
Y
30 40 50 60
X
-160 -140 -120 -100 -80 -60

Figure 3.15b.

American Red-eyed Vireo population had a consistent core in the northern Midwestern United States with increasing dispersal in all directions. The distribution demonstrated an overall increase in patch size over time with a dispersion of peaks that change size over time.

The density of Red-eyed Vireos was relatively high with a maximum of 100 in the 5-year intervals (Figure 3.15b). The smallest distribution occurred in 1966-70 with the main patch in the north mid-western United States and small peaks represented range expansion in all directions. In 1971-75, the base of the main patch increased and the species range expanded in all directions. In 1976-80, the population distribution extended and one of the original peaks increased to the highest peak. In 1981-85, the species range contracted in the same basic shape and the highest peak decreased. The distribution was patchier by 1986-90. In 1991-95, the patches broke up into smaller sizes. The internal structure of the species range was dynamic with 86-90 more similar to 91-95 than the others are similar to one another. Many patches changed shape and size over time and appeared to bud off to adjacent patches. The moderate, narrow, steep peak at 50-100 was a consistent feature.

The northern and eastern boundaries of Red-eyed Vireo distribution had steep gradients in abundance (Figures 3.1b and 3.15a). The southern and western edges had relatively gradual transitions.

Contour Maps --- Increasing trend and heterogeneity was apparent in the contour plots (Figure 3.16a). The shaded oval of persistent habitat use for Red-eyed Vireos was located around the New York, New Hampshire, and Vermont. Range expansion took place in all directions with the most movement to the northwest and the least to the east. The internal structure was composed of many patches that expand, contract, and move over time, appearing to bud off to adjacent patches. Other than the highest consistent main peak in the shaded oval, the locations of the highest peaks varied over time.

Perimeter maps depicted complex spatial structure over time and space (Figure 3.16b). In comparison with the one main stationary patch in the Field Sparrow, the central area of overlap for the Red-eyed Vireo was composed of multiple patches with a more expansive extent and a NW directional trend. The spatial extent of the central

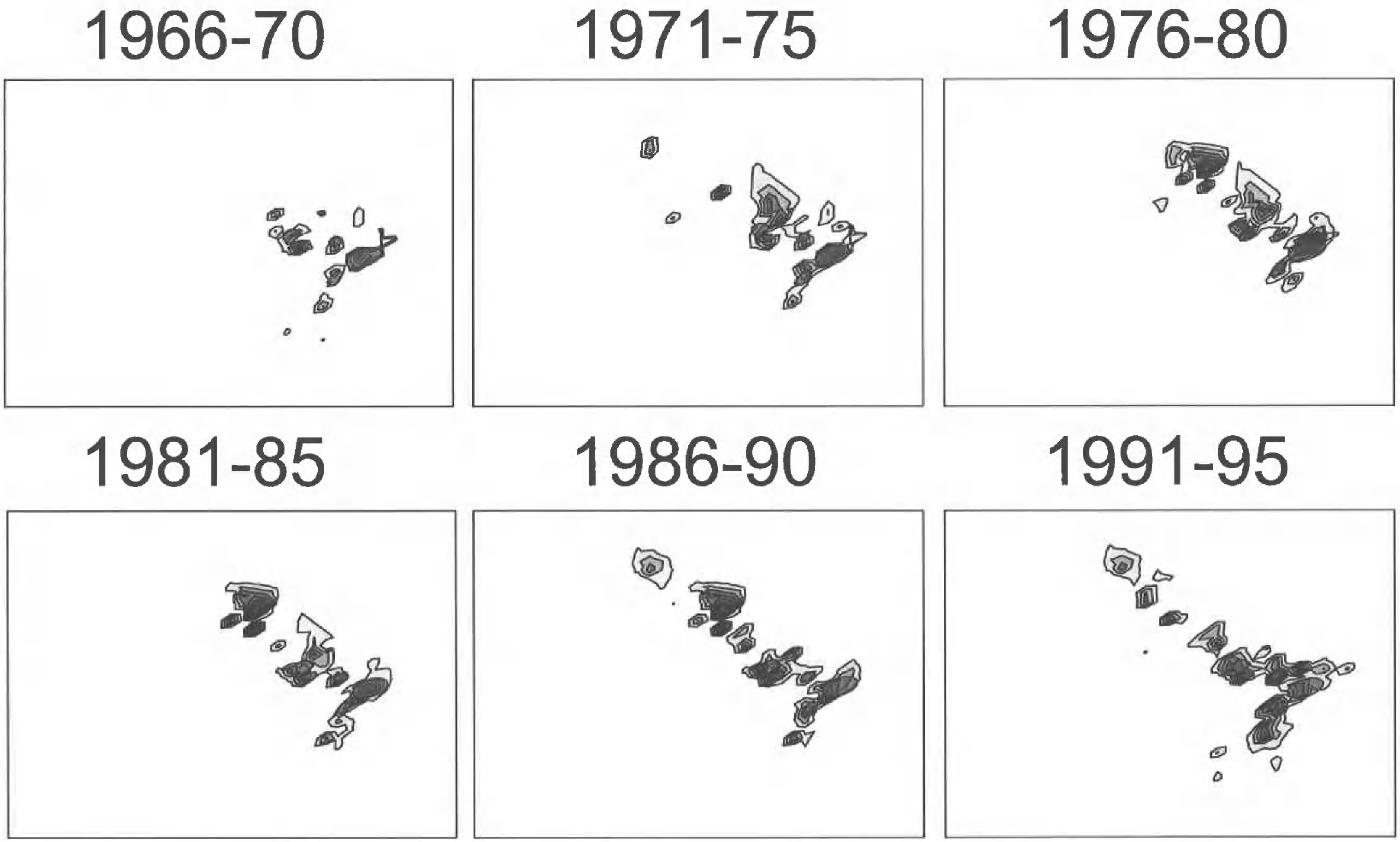


Figure 3.16a.

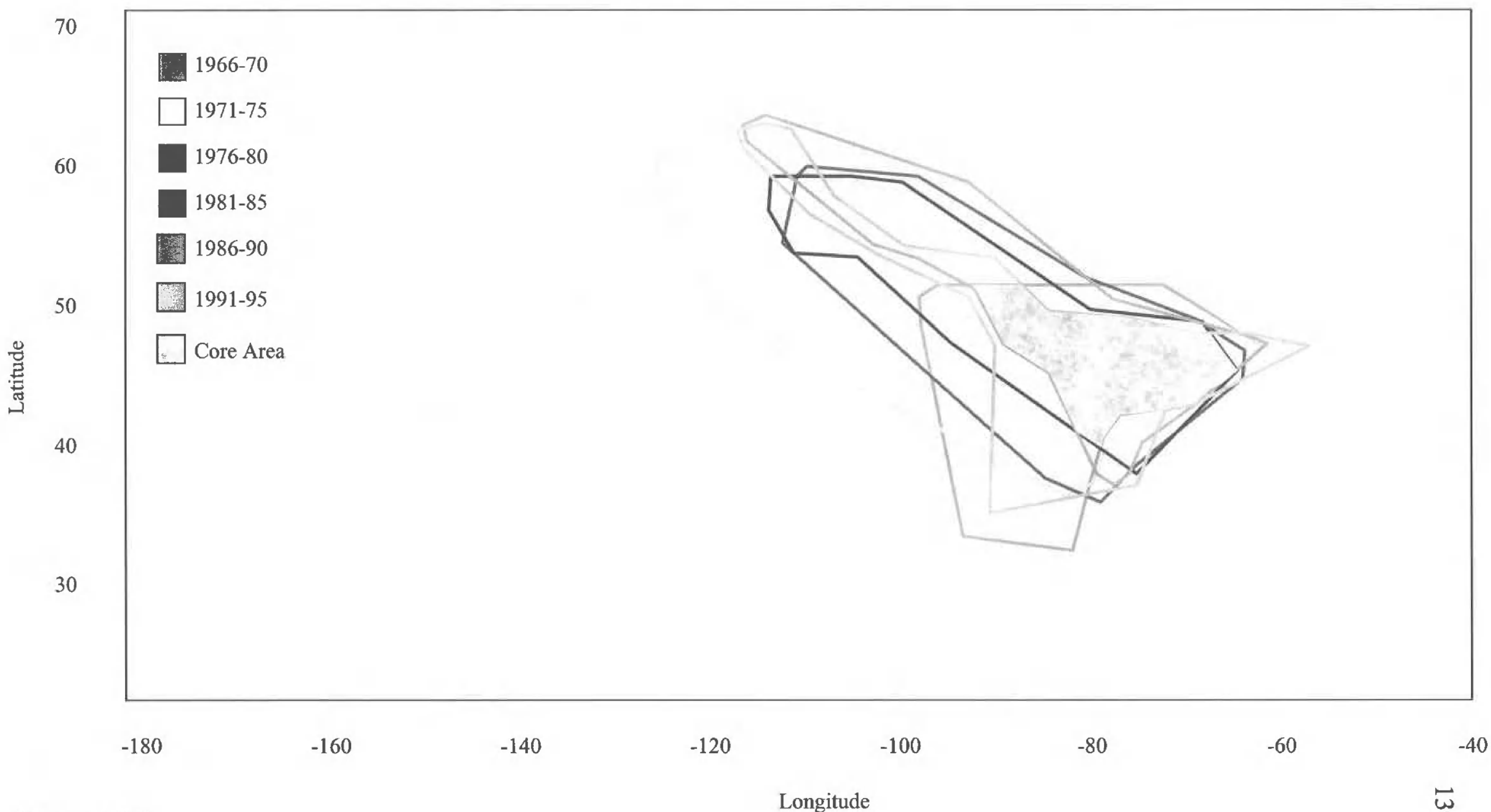

1966-70
1971-75
1976-80
1981-85
1986-90
1991-95
Core Area
70
60
50
40
30
Latitude
-180
-160
-140
-120
-100
-80
-60
-40
Longitude

Figure 3.16b.

area of overlap was greater and the perimeters changed shape and size over time. The extent of species range was dynamic over time. Over the entire time period, the species perimeters extended from latitude 35 to 60 and longitude –100 to –125, almost doubling in expanse in a NW direction. The extent of species range appeared to remain relatively constant in latitude (~ 35 to 60, except ~30 to ~50 in 1966-70) and eastern longitude (~ -60 to -65) over time. The changes occurred in the other directions with the greatest change to the west. The western longitude varied from –100 in 1966-70, -115 in 1976-80, -125 in 1971-75, 1986-90, and 1991-95. The central area of overlap appeared to extend from 35 to 50 latitude and –65 to –95 longitude.

Wavelet Transform --- In contrast to the low heterogeneity in Field Sparrow distribution, the high heterogeneity of the Red-eyed Vireo was dramatically apparent in the wavelet transform for the entire thirty-year study period (Figure 3.17). Pattern was abundant in all five identified scales. Darker pixels demonstrated a stronger influence of the energy of that coefficient to the overall heterogeneity. Because the Haar analyzing wavelet specializes in identifying edges and boundaries, the darker coefficients represented steep changes in abundance. The patterns at each scale were strong and demonstrate heterogeneity. The interspersed light and dark coefficients characterized the many patches that make up the species range. The Haar picked up many edges through the Red-eyed Vireo distribution.

The top 5% contributors of energy to the signal simplified this pattern (Figure 3.18). Prominent features occurred in every direction at every scale. This concurred with the observation that many patches change shape and size over time and appeared to bud off into adjacent patches. This dynamic nature of Red-eyed Vireo summer distribution was ideal for Haar to detect the shifting boundaries over a large space and multiple scales. The shaded oval of persistent habitat use around the New York, New Hampshire, and Vermont was apparent at each scale. The crystal for scale 2 in the East-West direction (i.e., d2-s2) showed several strong signals in a tight cluster.

Directionality was more apparent in the magnified wavelet transform crystals at scale 1 (Figure 3.19). The patchy internal structure was highlighted with the location of the dark and light coefficients in all three directions. These pixels indicated the edges

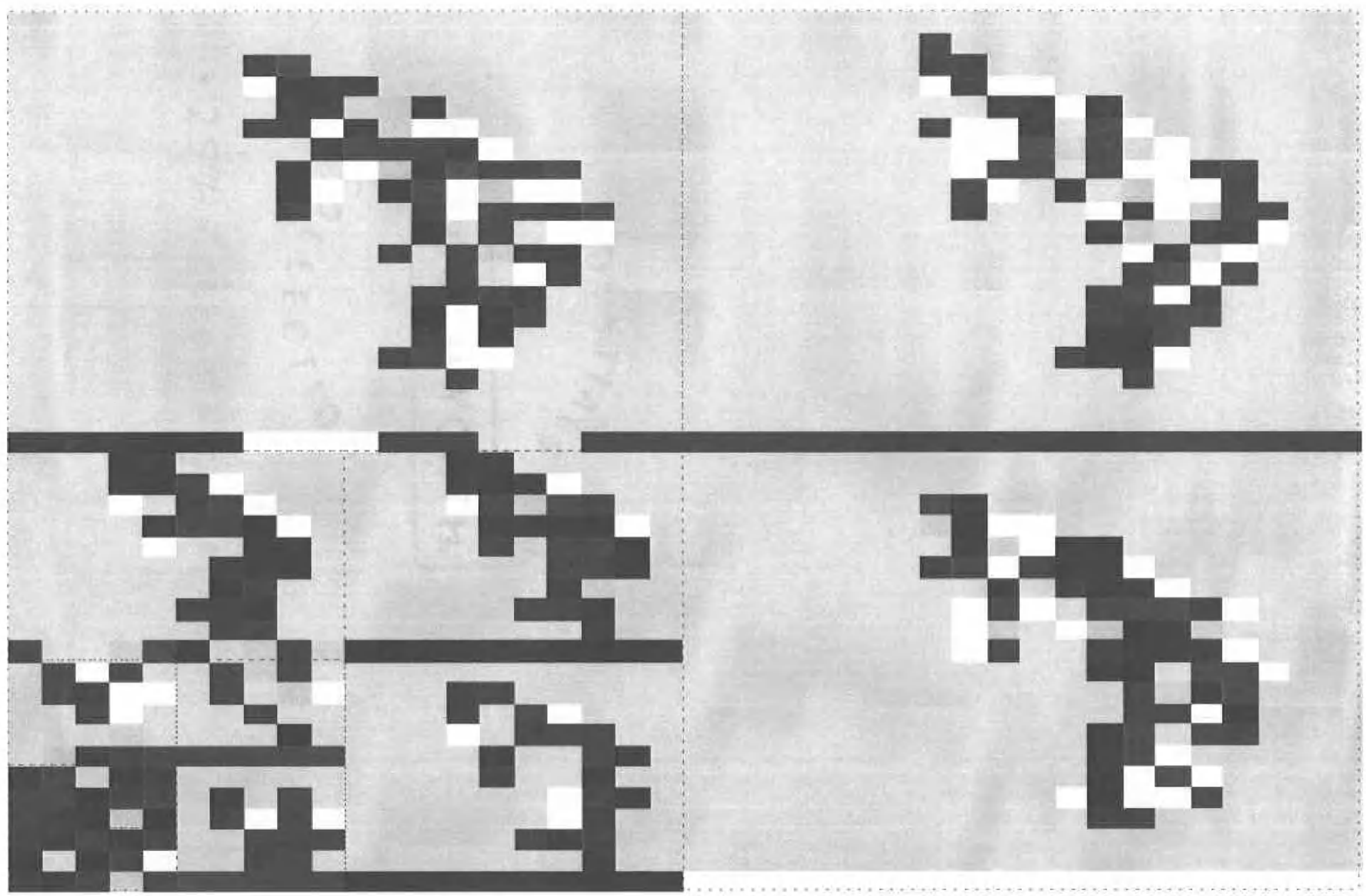


Figure 3.17.

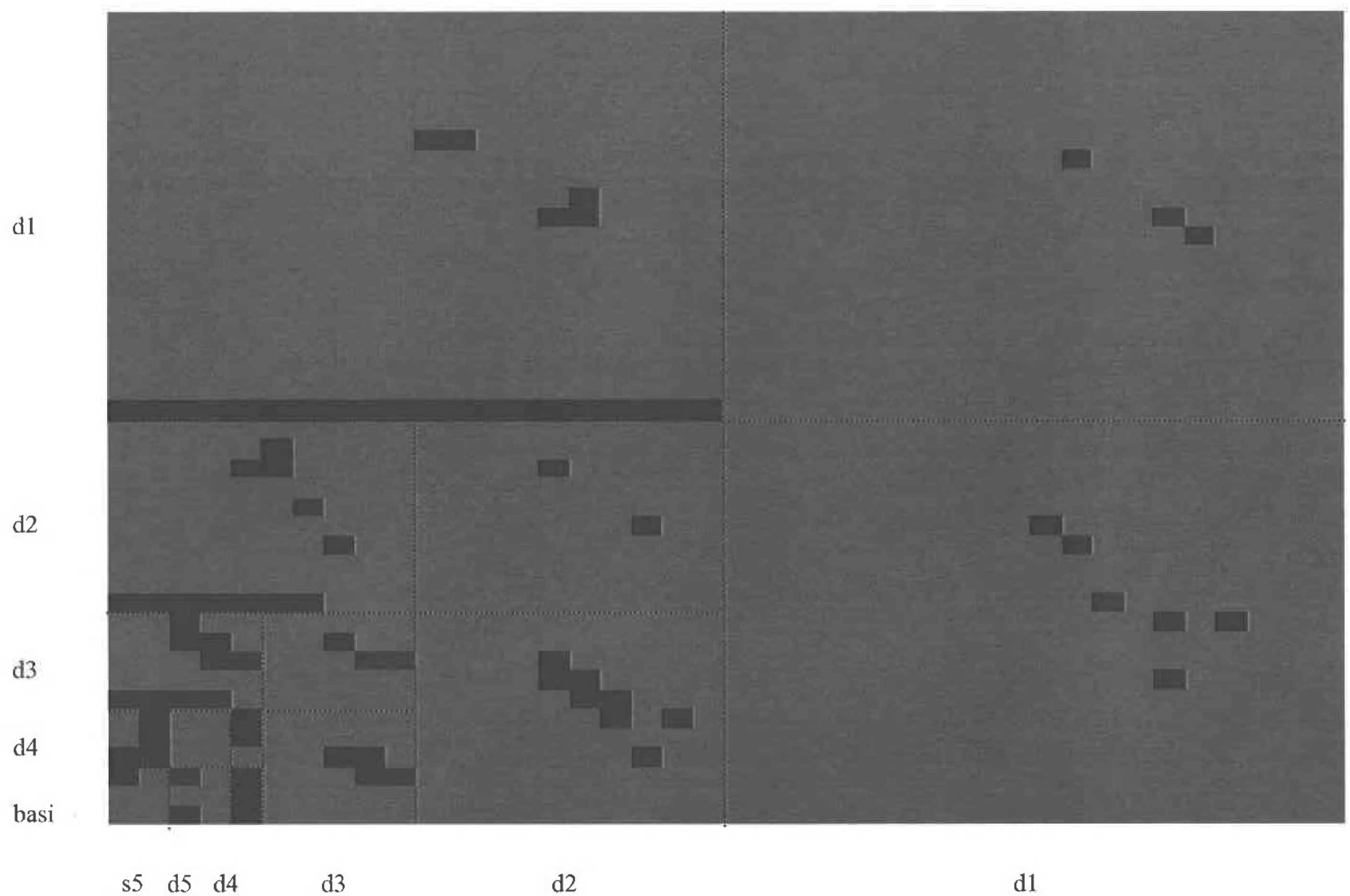
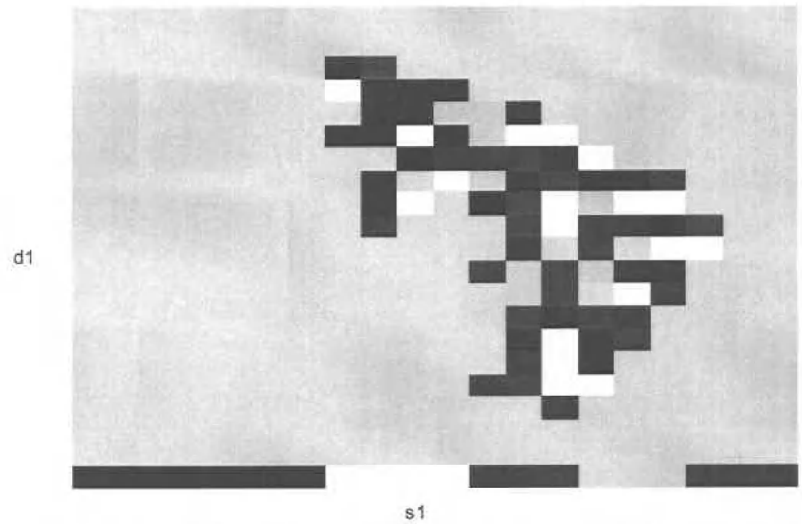
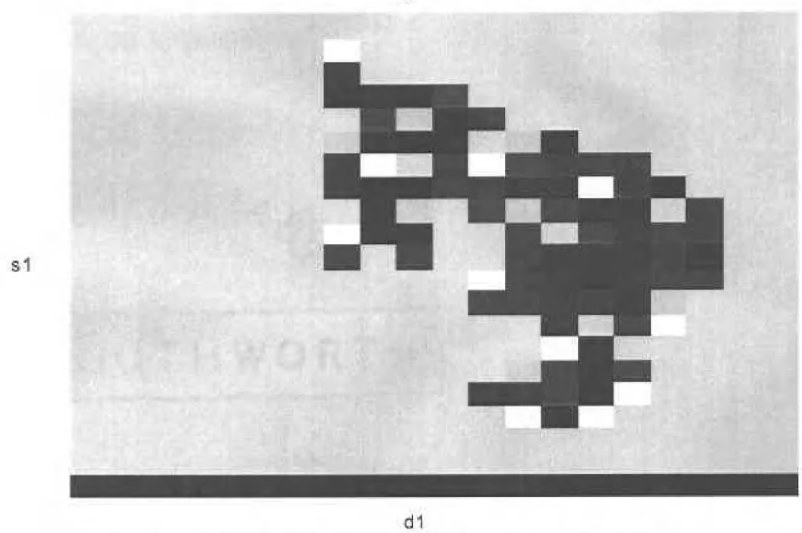


Figure 3.18.

a) North-South



b) East-West



c) Diagonal

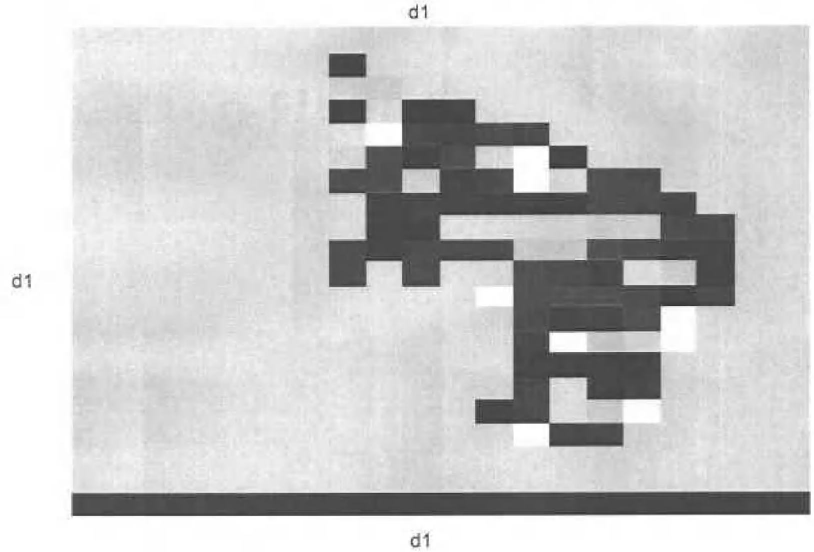


Figure 3.19.

on each side of the clusters of birds. The steep gradients at the northern boundary of the species range were especially apparent in the North-South component (Figure 3.19a). The eastern boundary was very dark on the East-West component (Figure 3.19b). The relatively gradual gradients in the South and West were apparent in contrast. The Northwest-South east orientation of Red-eyed Vireo distribution was apparent in the Diagonal component (Figure 3.19c). The contour maps indicated the most movement in the range expansion were in the northwest and the wavelet transform confirmed this with high coefficients in the North and Northwest directions (Figures 3.19a and 3.19c). The least expansion took place in the east, which one could assign to the strong dark pixel boundary in the East-West component (Figure 3.19b).

Box-and-whiskers --- The boxplot for Red-eyed Vireos showed multi-scalar complexity with expansion and contraction across space and time in many directions (Figure 3.20). The internal structure was more complex with many more peaks and edges than that for the Field Sparrow. High heterogeneity was represented by the reduced white space within an individual box and whisker, relatively more large absolute value of crystals, more space in the tails, and relatively steep edges (as indicated by more bars on either side of the center bars). High heterogeneity and increased roughness was characterized by more even distribution of information within scales and across scales. Even so, the North-South crystal at scale 1 (e.g., s1-d1) contributed around 70% of the energy to the wavelet from many large peaks (Figure 3.20). Actually, all North-South components for all five scales contributed over 95% of the energy overall. The crystals contributed the following energy to the overall signal: around 70% for s1-d1, a little over 10% for s2-d2, about 8% for s3-d3, around 3% for s4-d4, around 3% for s5-d5, and 2% or less for all others.

The boxplot for the relatively unstable, high-density population of Red-eyed Vireos had many coefficients. Most had a moderate absolute value and many had a high absolute value. This reflects an edgy texture in the distribution. Like the Field Sparrow, the wavelet crystals were tightly packed around zero at each scale. Also, the wavelet crystals were more widely dispersed in the North-South component. Specifically, the dynamic range of the tails decreased, albeit more gradually, from

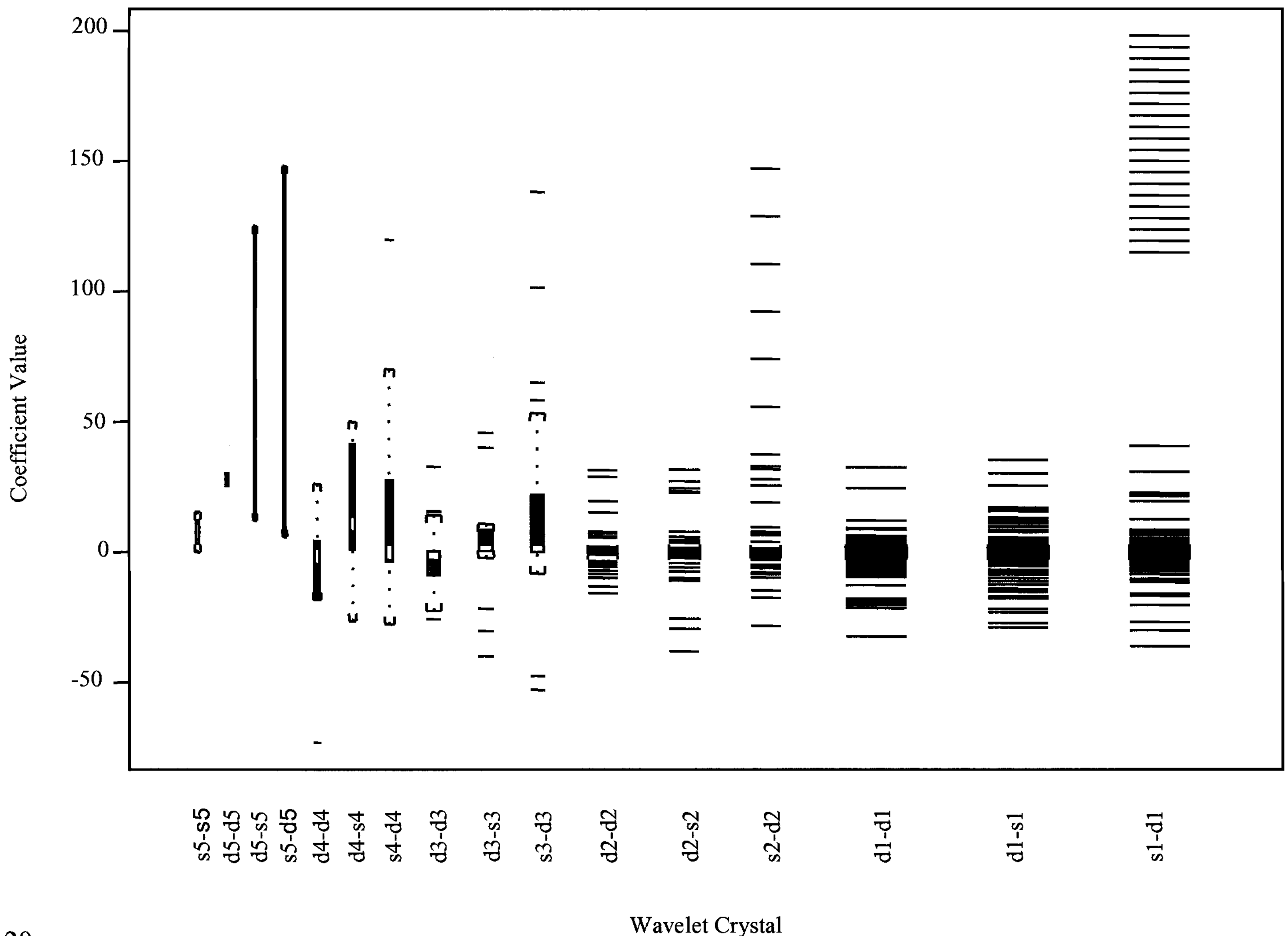

Coefficient Value
200
150
100
50
0
-50
s5-s5
d5-d5
d5-s5
s5-d5
d4-d4
d4-s4
s4-d4
d3-d3
d3-s3
s3-d3
d2-d2
d2-s2
s2-d2
d1-d1
d1-s1
s1-d1
Wavelet Crystal

Figure 3.20.

scale 1 to scale 4 and increased at scale 5 (i.e., s1-d1, s2-d2, s3-d3, s4-d4, s5-d5). Unlike the Field Sparrow, the coefficients around zero were more loosely dispersed to represent more peaks with a variety of edges.

Wavelet Variance --- The relatively high numbers, high peaks, and more peaks lead to higher heterogeneity in Red-eyed Vireos. The overall wavelet variance demonstrated very low heterogeneity at fine scales 1 through 3, low heterogeneity at coarse scale 4, yet high heterogeneity at scale 5 (Figure 3.21a). Although the heterogeneity remained relatively similar throughout scales 1 through 3, the wavelet variance increased twofold from scales 1 to 4 and tenfold to scale 5 (Figure 3.13a). The overall trend in the wavelet variance was similar over the six five-year intervals (Figure 3.13b). The differences became more pronounced as scale increased. The pattern for the Red-eyed Vireo was more complex across scales than that of the Field Sparrow (Figures 3.13a, 3.13b, and 3.21a). Surprisingly, both birds had similar patterns at scales 1 through 3, despite their different internal structures. The higher amplitudes of the peaks and the patchiness contributed to the difference in scales 4 and 5.

The pattern of contribution of each component to the overall wavelet variance varied in the Red-eyed Vireo (Figure 3.22). In terms of scale, the pattern of the overall wavelet variance was visible in all three components. The overall patterns were different within each component. Scales 1 through 3 demonstrated the least heterogeneity. Scales 4 displayed increased heterogeneity in all three components, yet the patterns are similar among intervals. The most heterogeneity occurred in scale 5. Most of the heterogeneity at scales 1 through 3 was generated by the pattern in the North-South component (i.e., horizontal edge). All three components contributed to the patterns at scales 4 and 5.

In terms of direction (i.e., component), most of the overall wavelet variance was derived from the North-South component (i.e., horizontal edges; Figure 3.22). The horizontal edge was dominant at all five scales, especially scales 4 and 5. The contribution of the North-South component was dominant, the contribution of the East-West component was moderate, and the Diagonal component provided little influence.

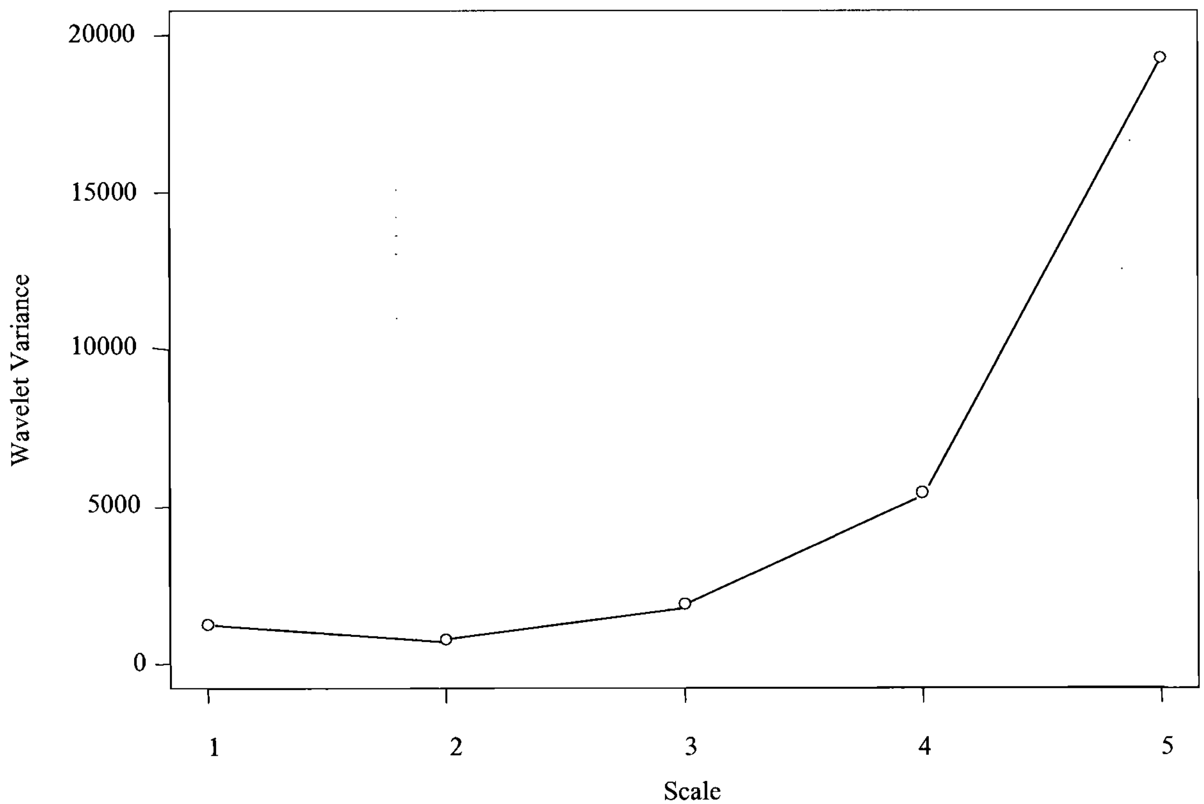
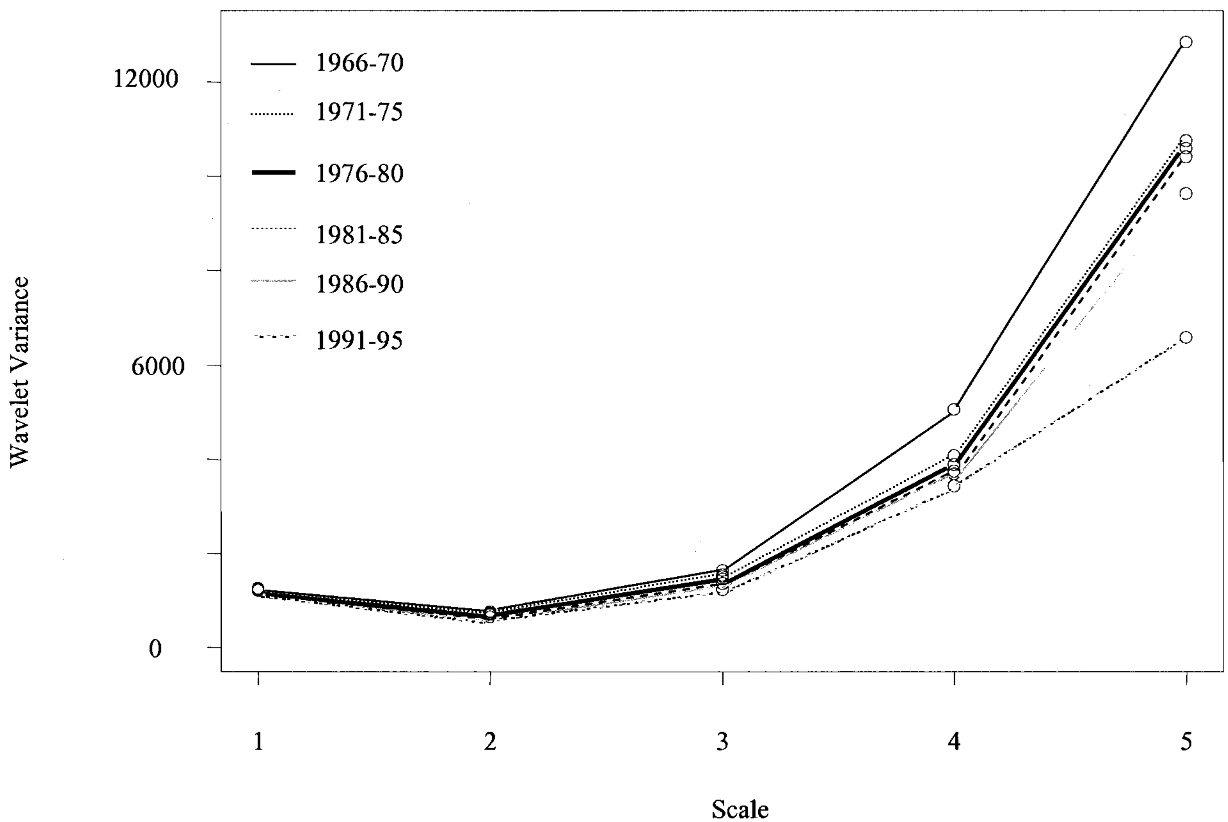


Figure 3.21a.



1966-70
1971-75
1976-80
1981-85
1986-90
1991-95
12000
6000
0
Wavelet Variance
1
2
3
4
5
Scale

Figure 3.21b.

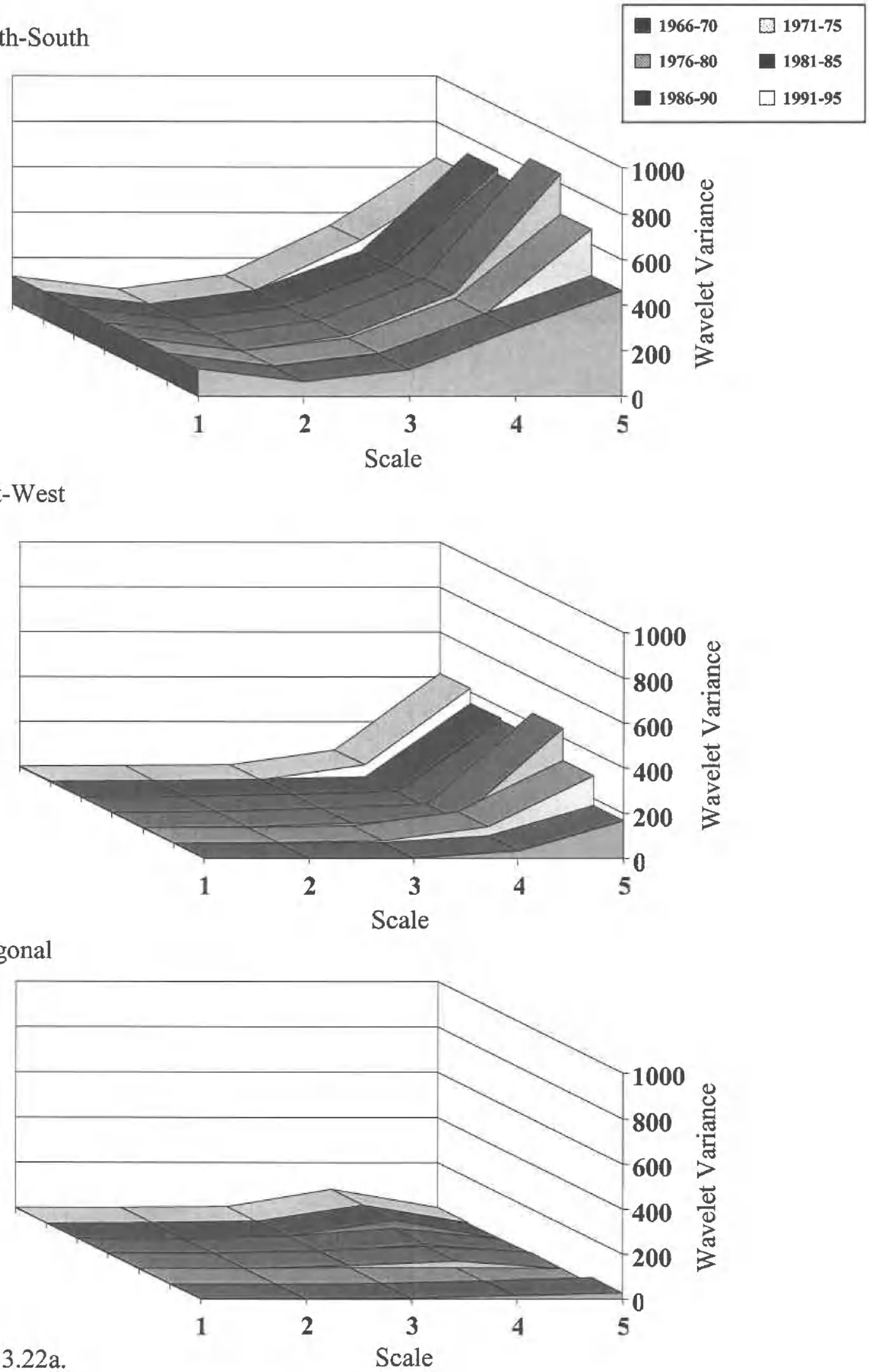
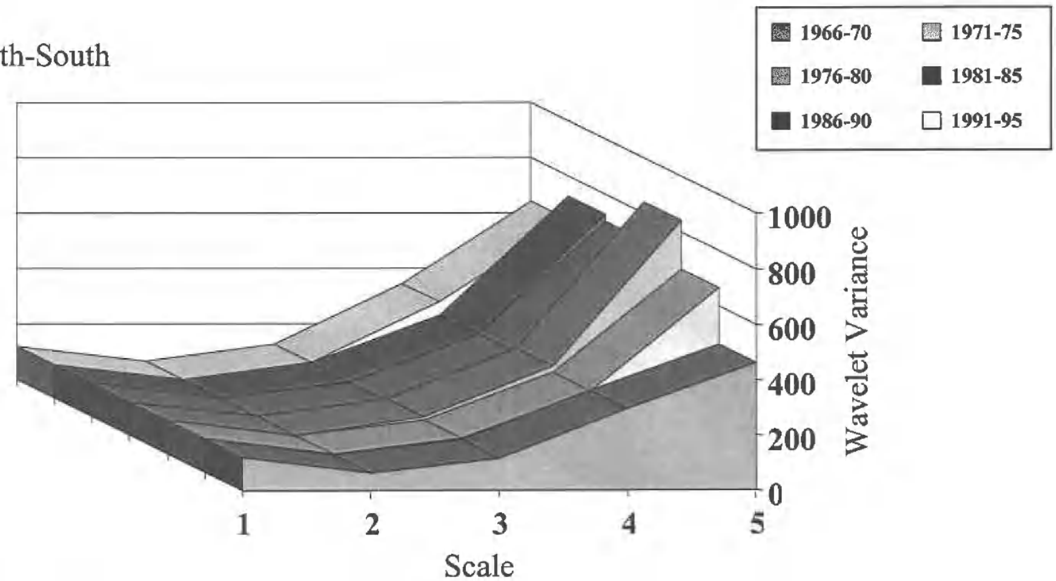
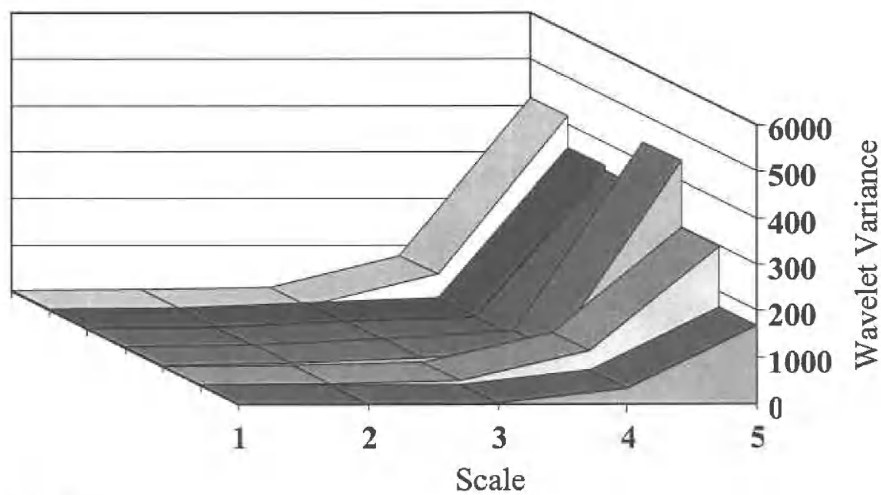

1) North-South
1966-70
1971-75
1976-80
1981-85
1986-90
1991-95
1000
800
600
400
200
0
Wavelet Variance
1
2
3
4
5
Scale
2) East-West
1000
800
600
400
200
0
Wavelet Variance
1
2
3
4
5
Scale
3) Diagonal
1000
800
600
400
200
0
Wavelet Variance
1
2
3
4
5
Scale

Figure 3.22a.

1) North-South



2) East-West



3) Diagonal

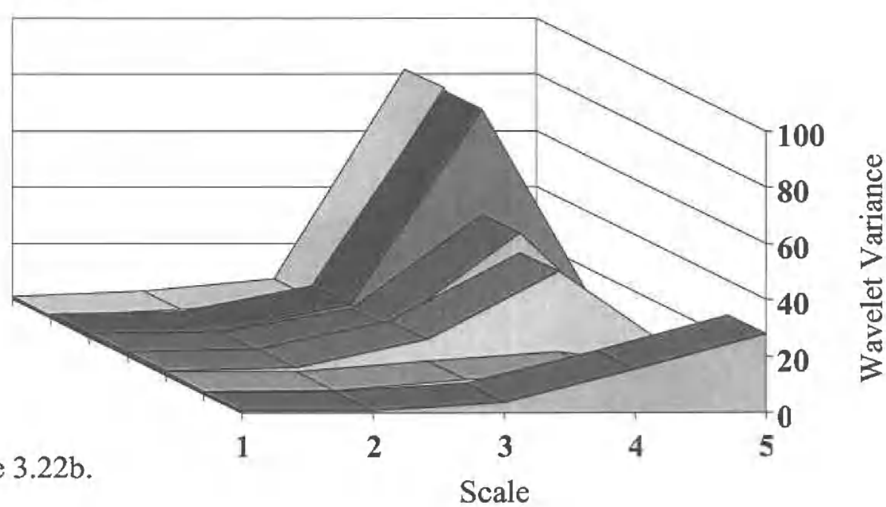


Figure 3.22b.

The contribution from the North-South component was two to four times that from the East-West component and up to ten times that of the diagonal component.

The Red-eyed Vireo population was relatively complex over time. The scalar and directional patterns were relatively similar among the five-year intervals at scales 1 through 3 and differed at scales 4 and 5 (Figure 3.22). The main species range varied in size, shape, and patchiness over time. The heterogeneity was greater at larger scales than at smaller scales. The steepest North-South gradient at scale 5 was in 1976-80 and the shallowest gradient was in 1966-70 (Figure 3.22a). The 1976-80 interval had more birds, the highest peak, and the most high peaks in a pattern that has the most variation along the North-South edge (Figure 3.22a). Whereas, the 1966-70 interval had fewer birds, few peaks, and less steep peaks in a pattern with the least variation along the North-South edge. Likewise, the strongest East-West edge at scale 5 was in 1976-80 and the least edge was in 1966-70 (Figure 3.22b). The steepest gradient at scale 5 diagonally was in 1966-70 and the shallowest was in 1986-90 (Figure 3.22c).

Comparison of Pattern Detected in the Case Studies by Wavelet Analysis

Visual pattern recognition with perspective plots, contour maps, and perimeter maps may have identified the differences between the low heterogeneity in the Field Sparrow and the high heterogeneity in the Red-eyed Vireo. Not only did wavelet analysis confirm these differences, but it detected specific pattern on multiple scales, quantified it, located this pattern back in the original data, and characterized the features that contributed to the overall pattern. The example graphics at the beginning of the chapter used to explain the wavelet metrics were the plots for the Brewer's Sparrow over the same time and space. The summer distribution of Brewer's Sparrows was on the West Coast of the United States (Figure 3.23). With visual pattern recognition (e.g., perspective plot), the order of increasing complexity appeared to be Brewer's Sparrow, Field Sparrow, then Red-eyed Vireo (Figures 3.3, 3.7, and 3.15). Brewer's Sparrow appeared to have low density with low peaks with one low spike. Field Sparrows had a moderate density with more peaks and a larger species range. Red-eyed Vireos had a high density with a large number of peaks that changed over time. The pattern appeared to go from simple to simple with localized complexity to high multi-scalar complexity.

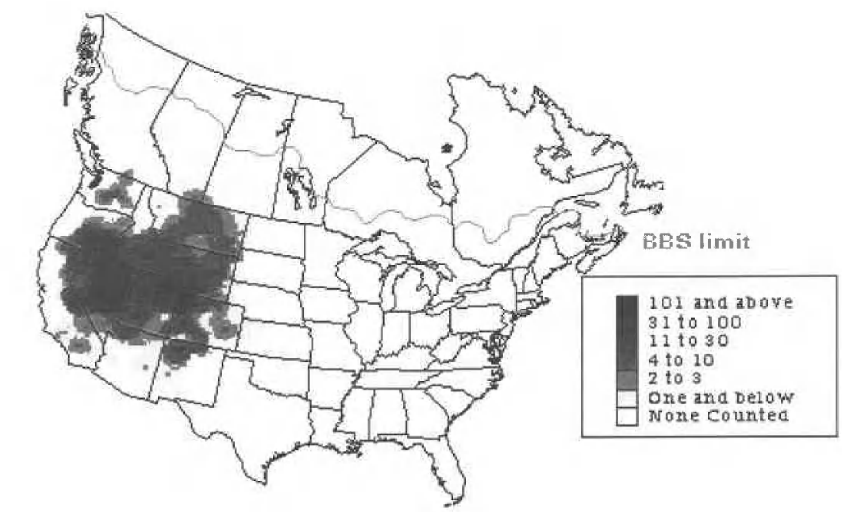

BBS limit
101 and above
31 to 100
11 to 30
4 to 10
2 to 3
One and below
None Counted

Figure 3.23.

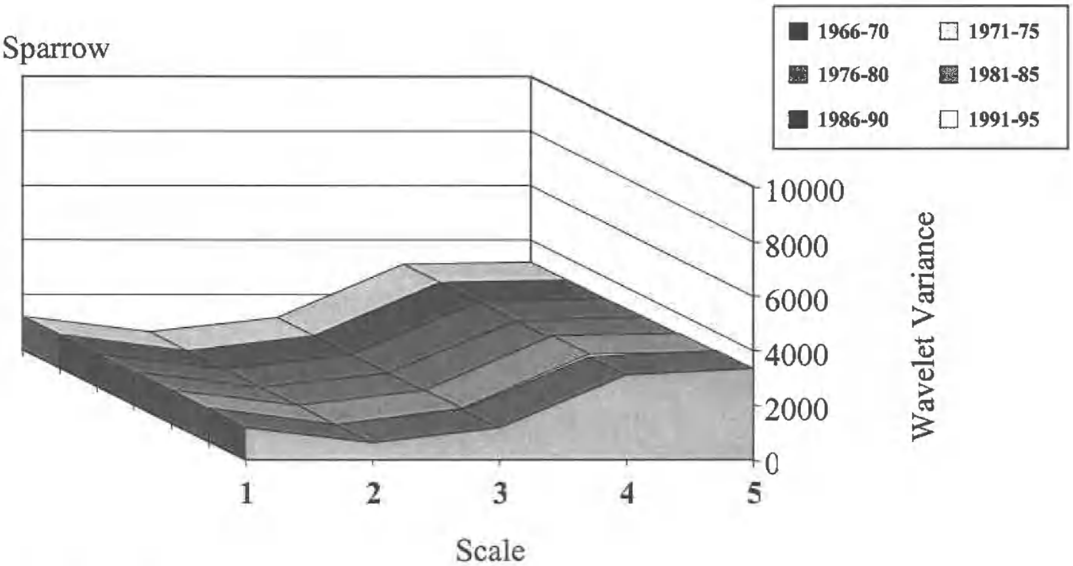
However, with two-dimensional wavelet analysis to confirm and quantify pattern, the order of increasing complexity was actually Field Sparrow, Brewer's Sparrow, then Red-eyed Vireo (Figure 3.24). The differences were most apparent in the diagonal component, in which the Field Sparrow is relatively stable and the Brewer's Sparrow and Red-eyed Vireo show temporal variability (Figure 3.24c). All three species had a stronger pattern in the North-South (Figure 3.24a). But, there was more temporality in the East-West component, even the Field Sparrow showed a little change over time (Figure 3.24b). Figure 3.25 summarized the relationship between stability and temporal dispersion and stability.

In addition to pattern detection, two-dimensional wavelet analysis was well suited for pattern reconstruction. This capability was useful in designing efficient sampling designs for monitoring efforts, management, and field experimentation.

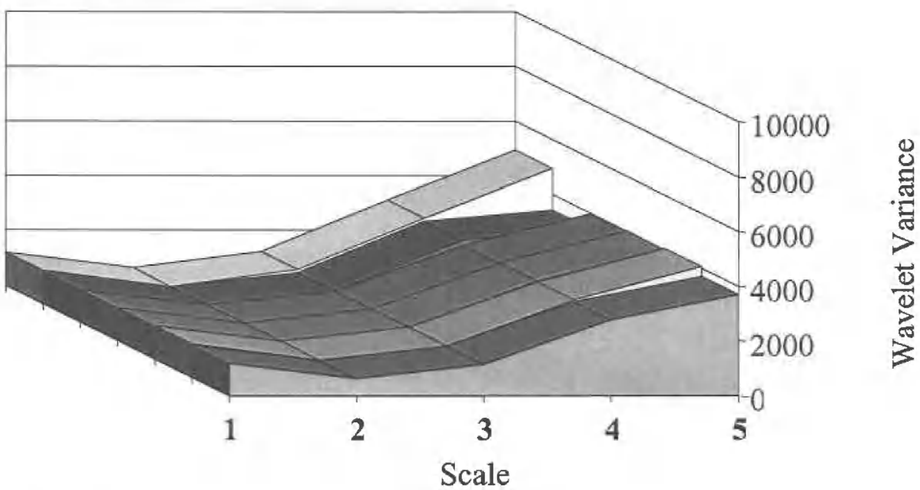
Pattern Reconstruction with Two-dimensional Wavelet Analysis

In evaluating the Neotropical birds for a basic pattern reconstruction, the wavelet basis and the data lines were close together and had similar slopes (Figure 3.26). In both data sets, the untransformed original data contributed 100% of the energy in 508 points. The objective of this reconstruction was to recreate the basic shape and features of the edges, rather than to regenerate a detailed view. For the Field Sparrow, the Haar wavelet basis compacted the energy of the original data in 240 coefficients. If reconstruction at 95% were adequate, we would only need about 60 coefficients. As desired accuracy decreased, so did the number of coefficients. Only around 35 coefficients were required for 90% accuracy, 25 for 80%, 20 for 70%, 17 for 60%, and 13 for 50% of the energy. For the Red-eyed Vireo, only 130 coefficients were required for 100% reconstruction, 30 for 95%, 25 for 90%, 20 for 80%, 17 for 70%, 13 for 60%, and 10 for 50% of the energy. Try several models to find the balance of accuracy and efficiency. The reconstruction can be adjusted to increase the accuracy. After selecting the desired accuracy, a reconstructed wavelet transform can be plotted and the coefficients located in the original data. For each bird, scale 1 in all three directions was chosen as an example to compare the reconstructed wavelets (Figures 3.27 and 3.28) to the original data (Figures 3.11 and 3.19) due to their similarity in perspective.

Field Sparrow



Brewer's Sparrow



Red-eyed Vireo

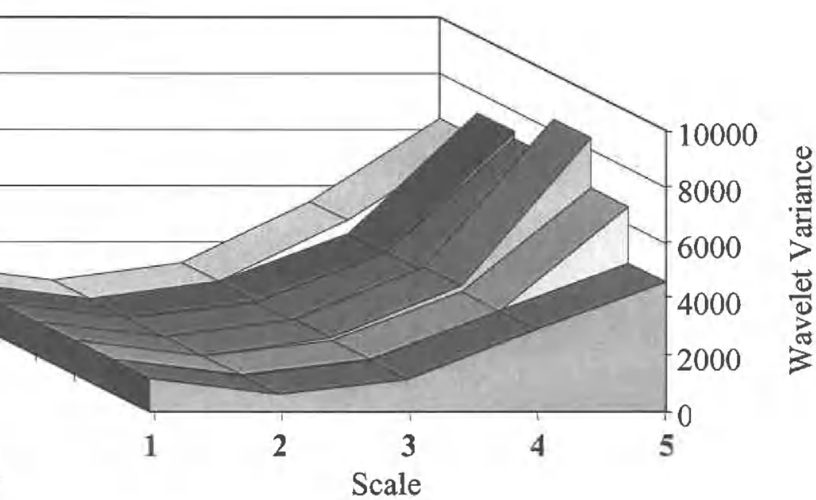
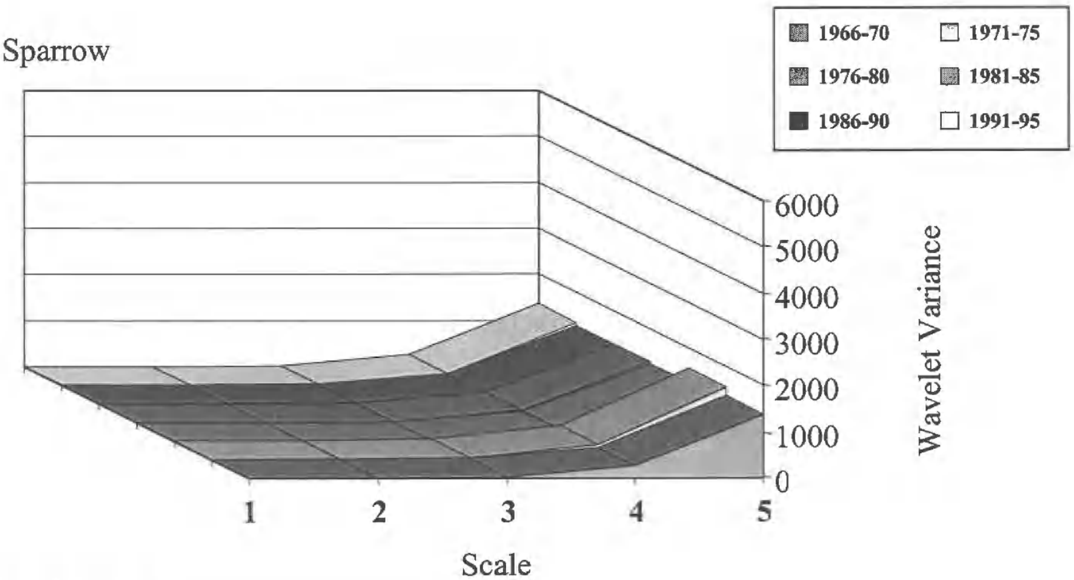
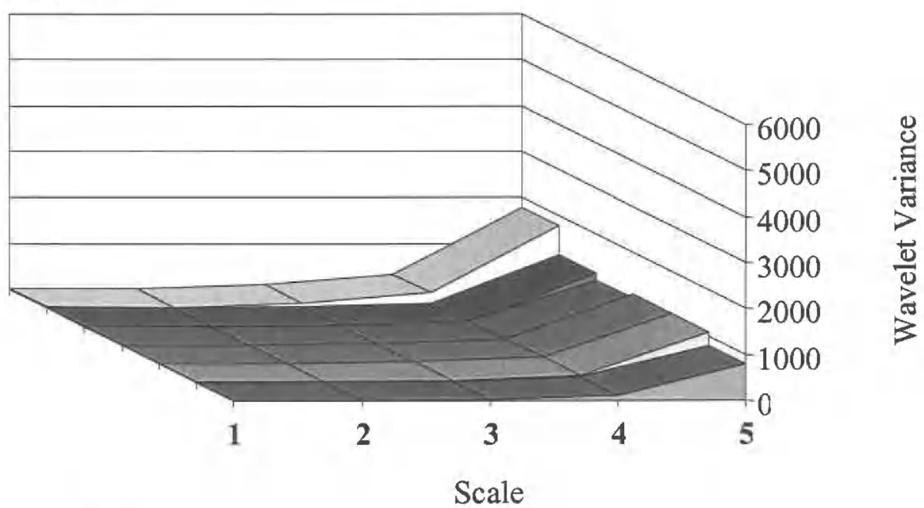


Figure 3.24a.

Field Sparrow



Brewer's Sparrow



Red-eyed Vireo

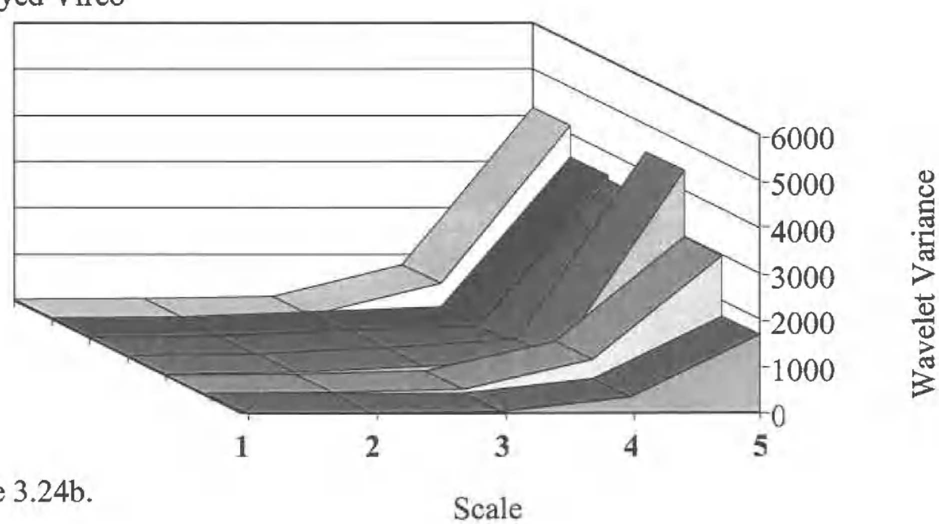
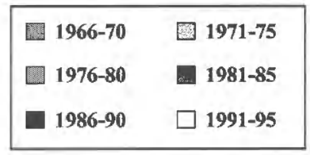
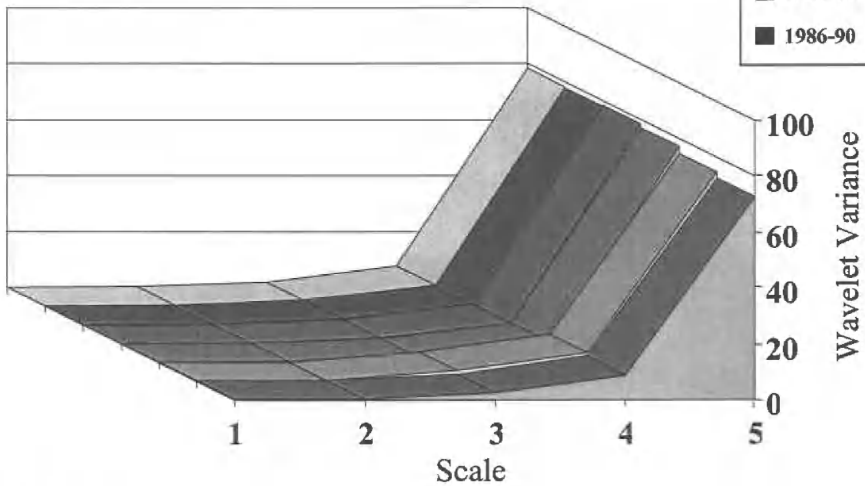


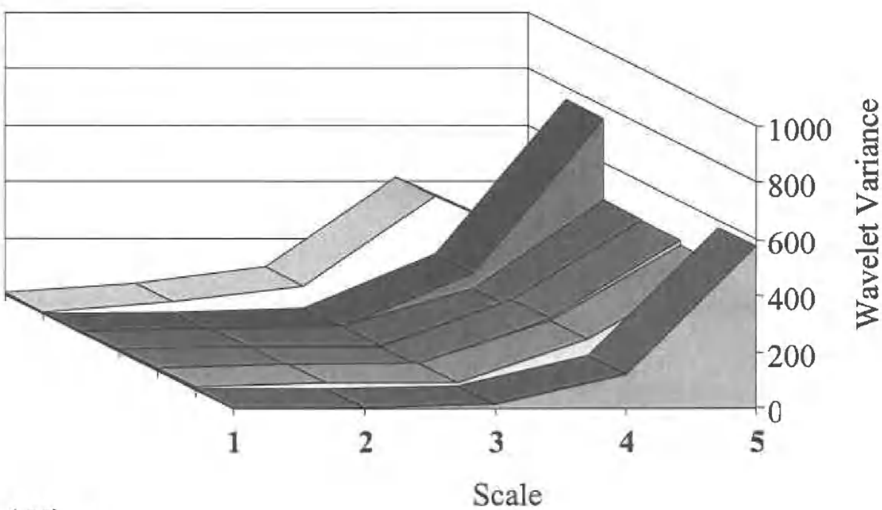
Figure 3.24b.



Field Sparrow



Brewer's Sparrow



Red-eyed Vireo

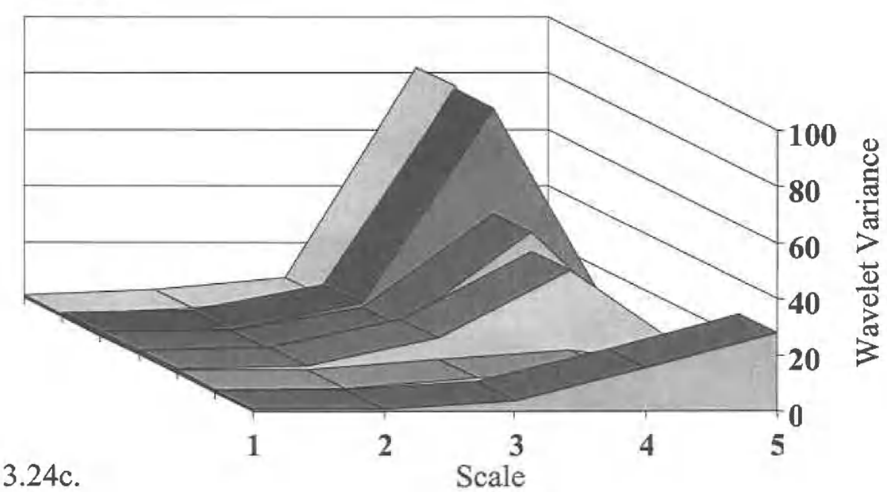


Figure 3.24c.

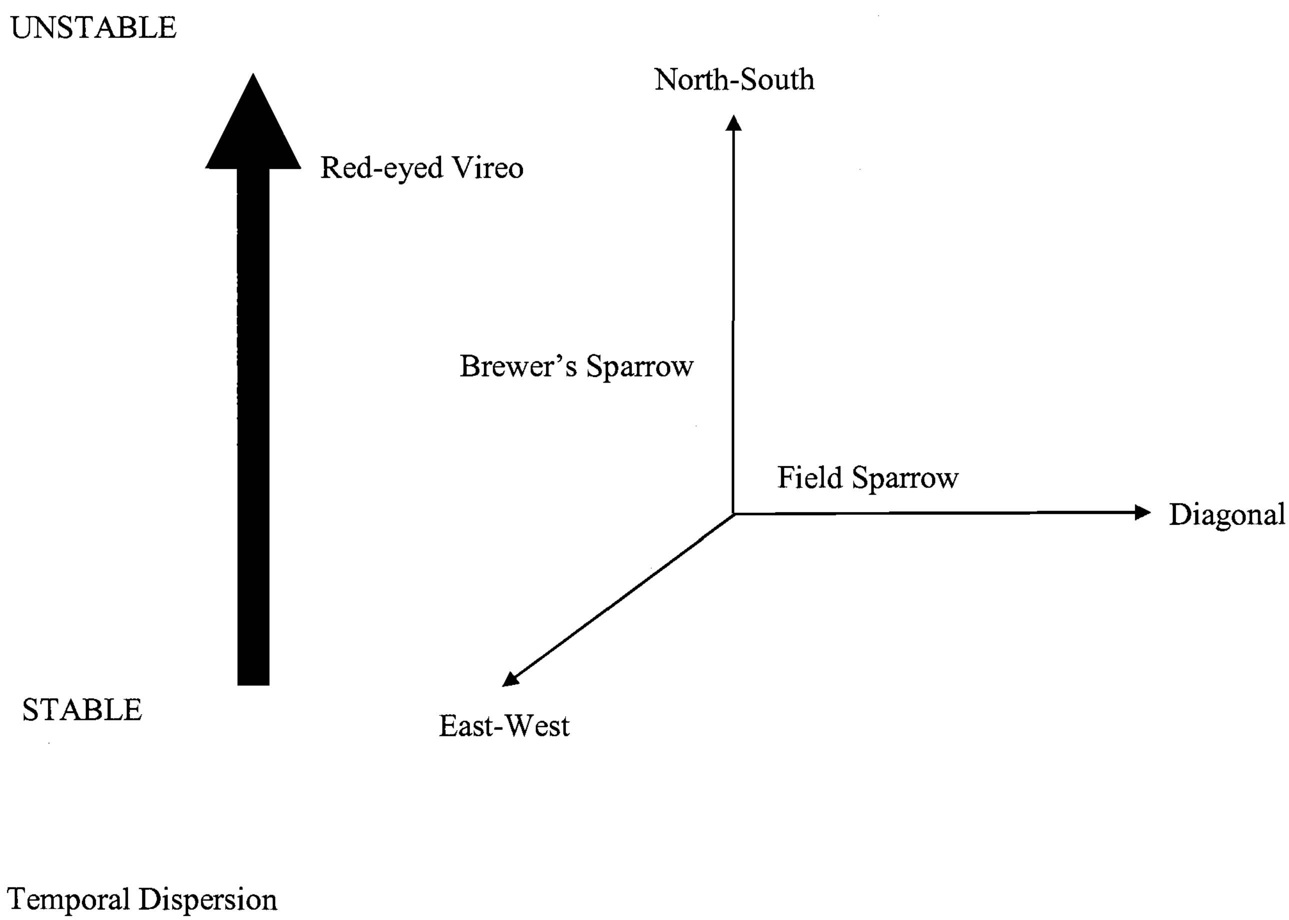

UNSTABLE
Red-eyed Vireo
North-South
Brewer's Sparrow
Field Sparrow
Diagonal
STABLE
East-West
Temporal Dispersion

Figure 3.25.

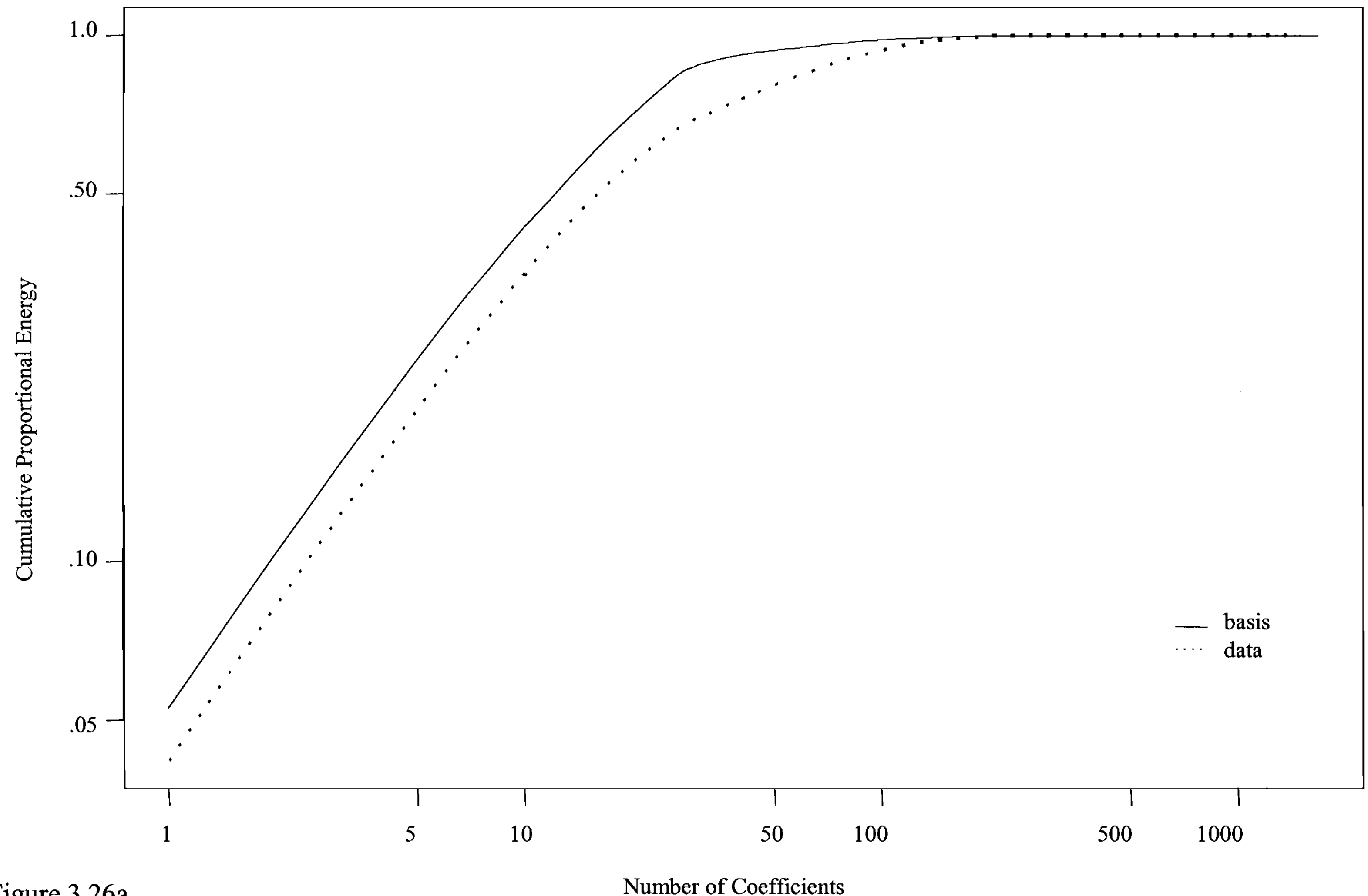

1.0
.50
.10
.05
Cumulative Proportional Energy
basis
data
1
5
10
50
100
500
1000
Number of Coefficients

Figure 3.26a.

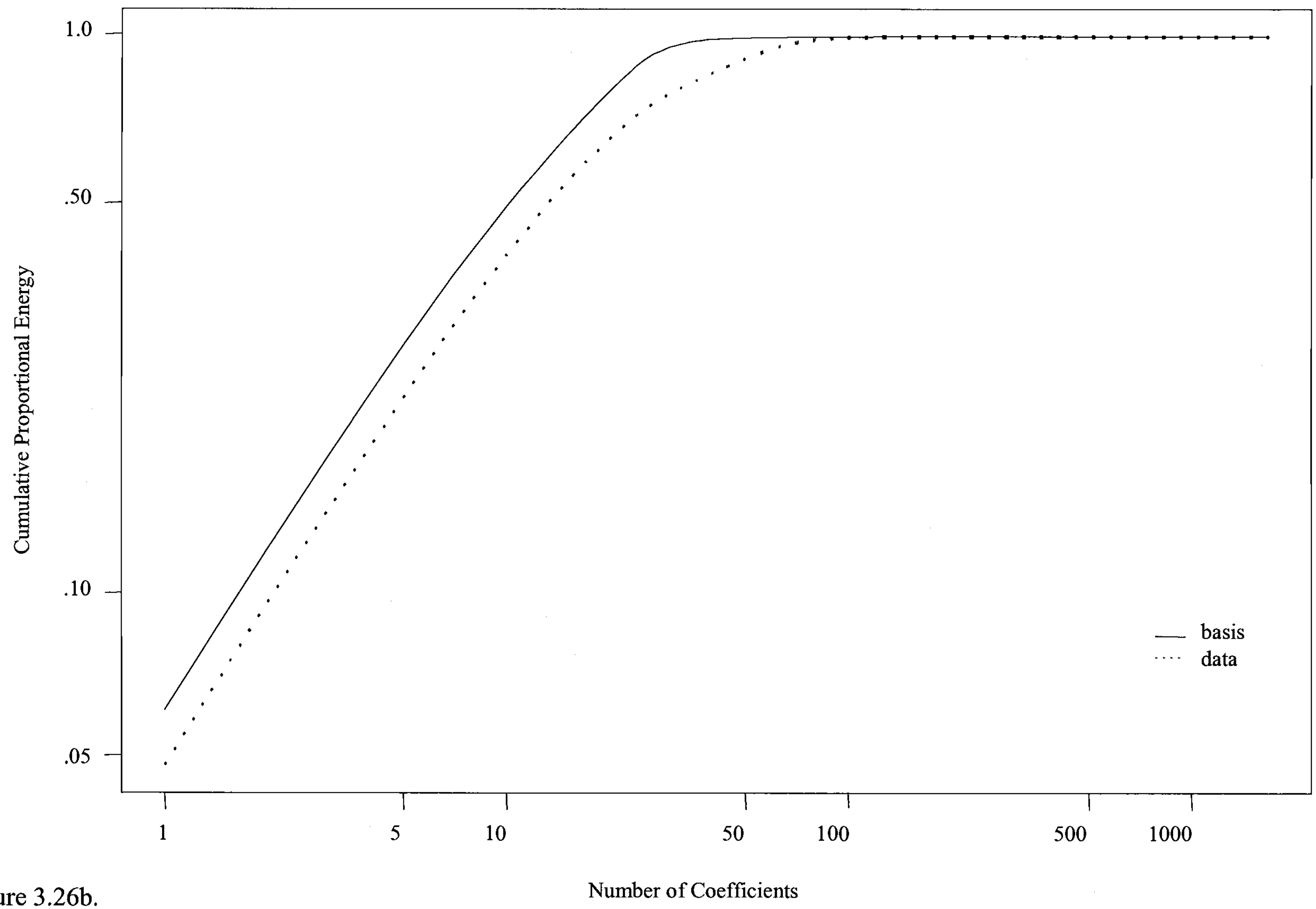

1.0
.50
.10
.05
Cumulative Proportional Energy
basis
data
1
5
10
50
100
500
1000
Number of Coefficients

Figure 3.26b.

a) North-South

b) East-West

c) Diagonal

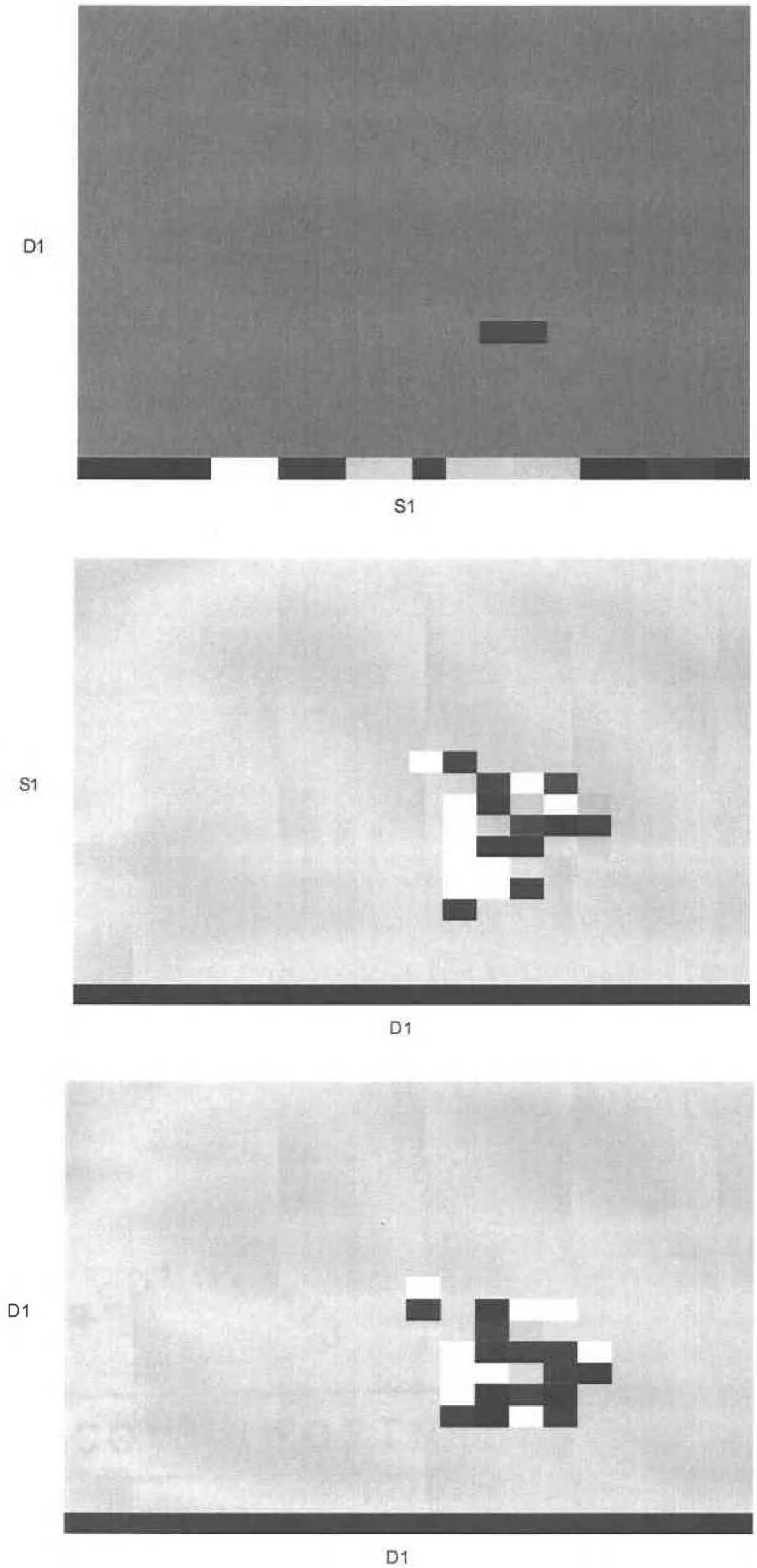
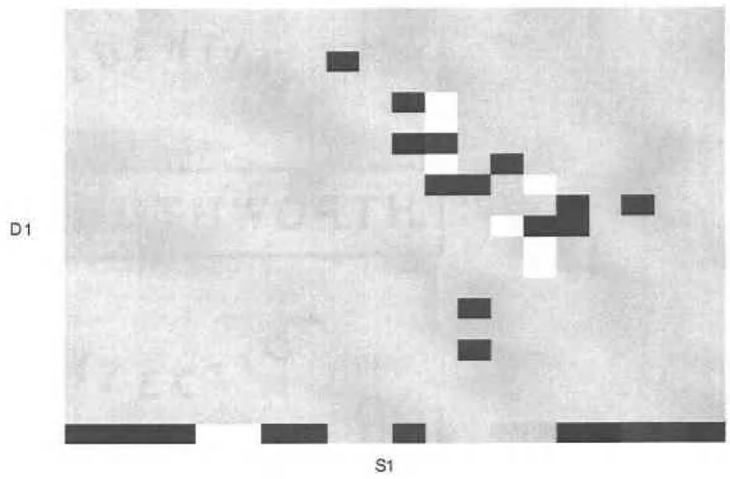
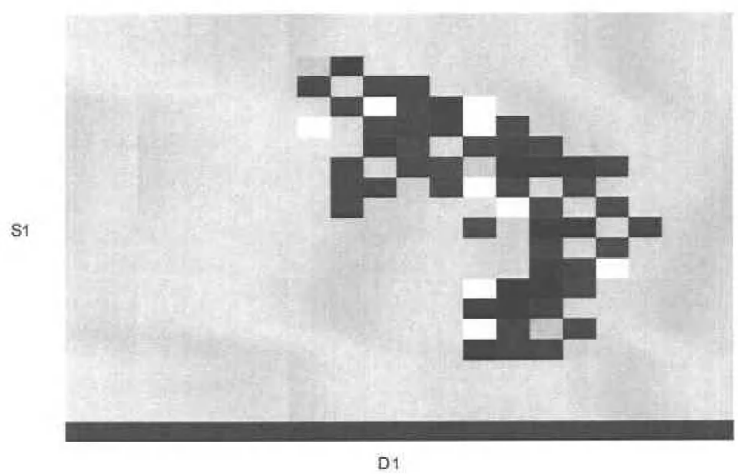


Figure 3.27.

a) North-South



b) East-West



c) Diagonal

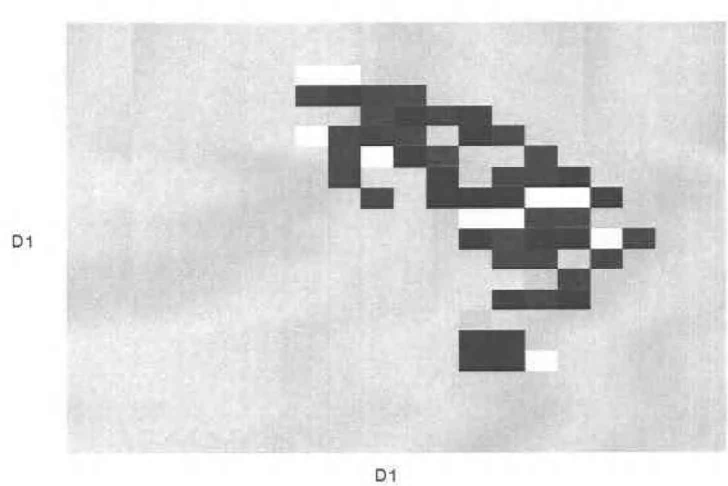
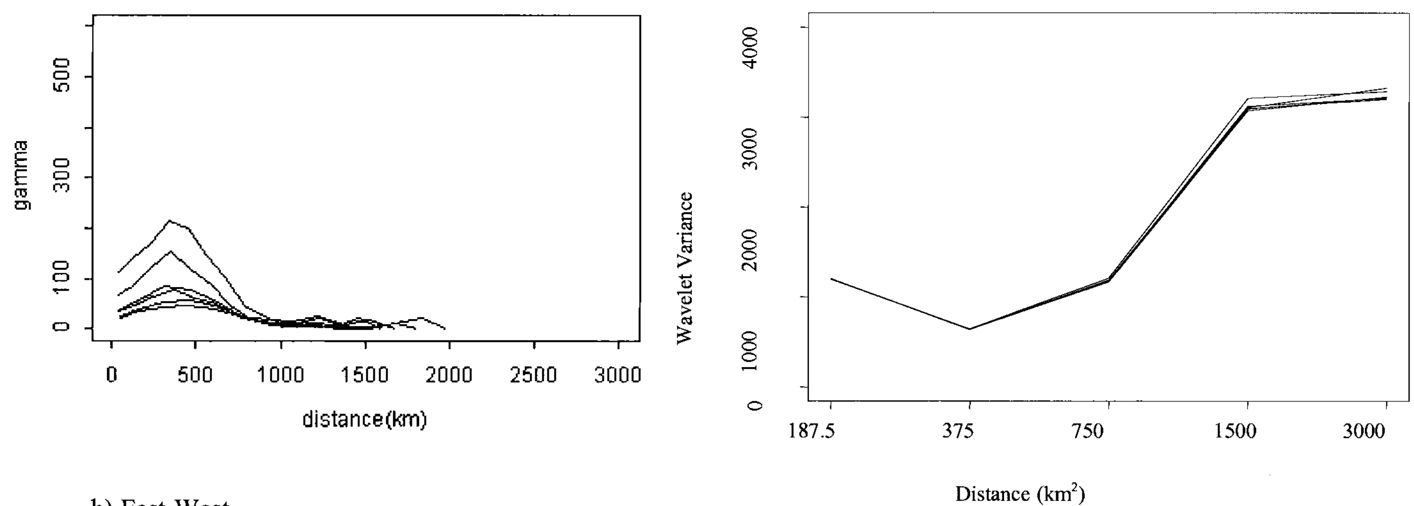


Figure 3.28.

a) North-South



b) East-West

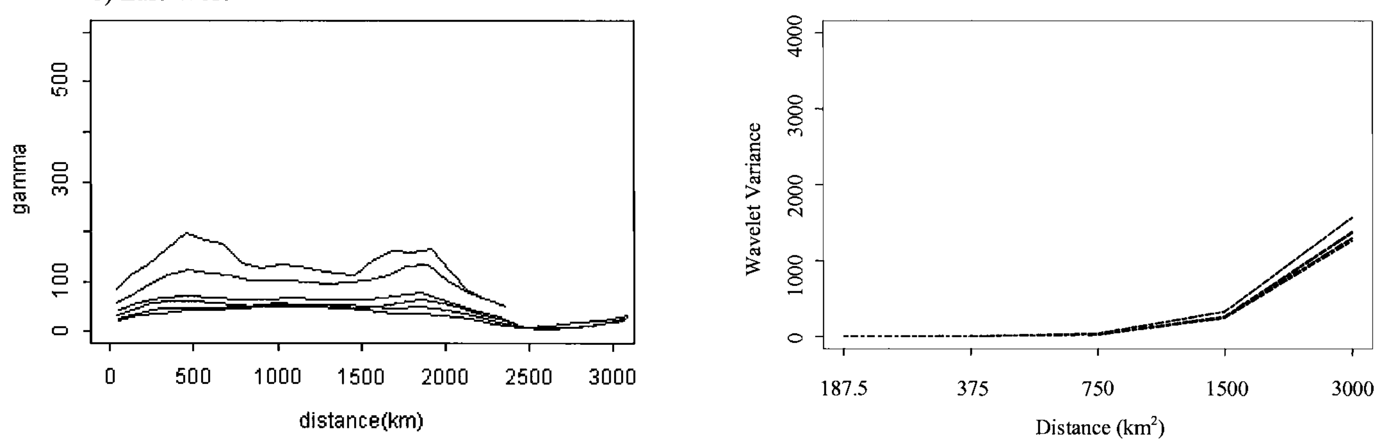


Figure 3.29a and b.

c) Diagonal

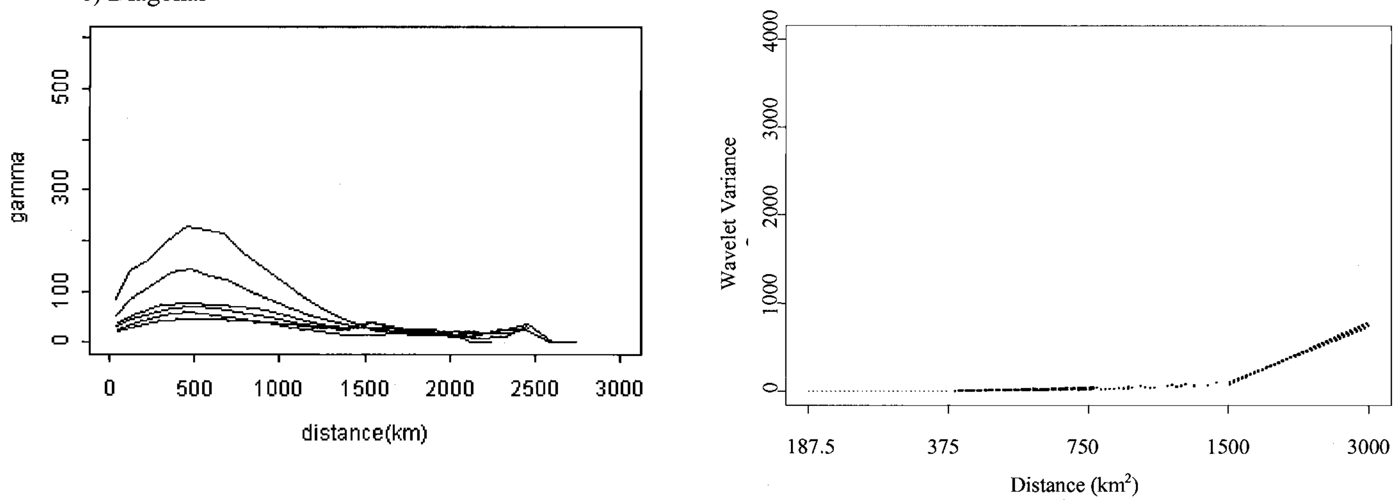


Figure 3.29c.

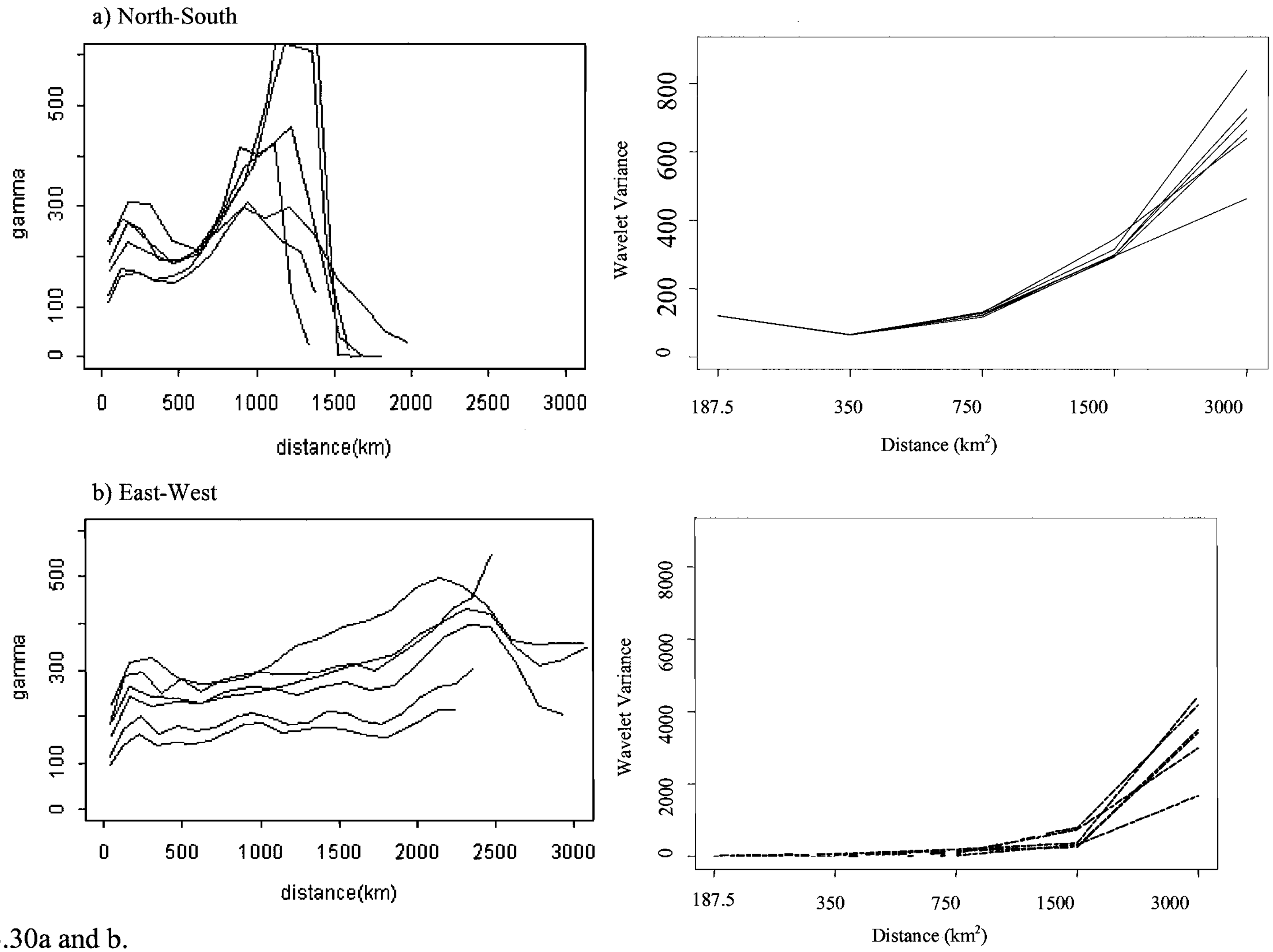


Figure 3.30a and b.

c) Diagonal

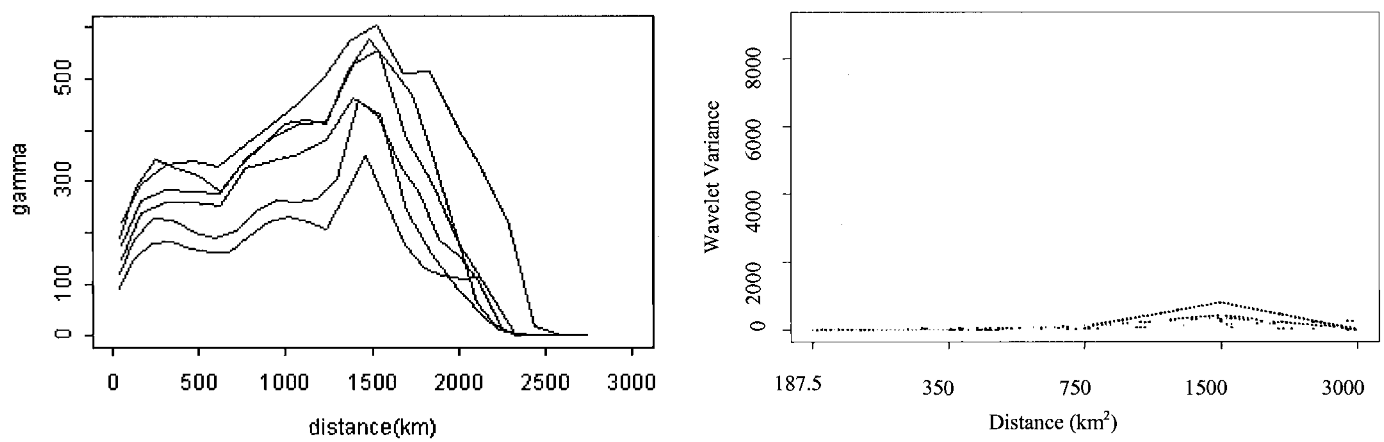


Figure 3.30c.

In this circumstance of low desired accuracy to simply provide an example, the reconstructions captured the basic forms of Field Sparrow and Red-eyed Vireo distribution. The matches for edges were not complete, requiring an adjustment of the reconstruction until the desired accuracy is achieved.

To some extent, pattern recognition is an art form. Open to some subjective interpretation, it is useful to gather information about the pattern from a number of sources. Applying multiple statistics with different strengths and weaknesses better inform the decision-making. Having explored pattern detection and reconstruction with two-dimensional wavelet analysis, we will conclude with an examination of patch size and steepness of the patch in the standard semivariogram.

Comparison of Two-dimensional wavelet analysis and Standard Semivariogram

Case Study for Field Sparrows

The low heterogeneity in Field Sparrow distribution was confirmed with standard semivariogram over the six five-year intervals (Figure 3.29). In all three directions, the dominant patch occurred at scale 1: about 350 km in the North-South, 450 km in the East-West, and 450 km in the Diagonal component. The steepness of the patch varied among intervals, but the pattern for scale 1 was consistent in all three directions. A second dominant patch at scale 3 (about 1,700 km) is possible in the East-West component, but semivariogram identified the first dominant scale best. Further analysis would be required to distinguish this feature as a nested structure versus noise.

Wavelet variance did not concur with the dominant scales suggested by semivariogram (Figure 3.29). Five scales were identified, rather than one or two. Wavelet variance was consistent within a direction. Scale 5 was dominant in all three directions. The North-South component detected low influence from scales 1 through 3 and increasing influence from scale 3 through scale 5. The only noteworthy influence in the East-West and Diagonal directions was the small influence at scale 5.

Case Study for Red-eyed Vireos

Red-eyed Vireos demonstrated high heterogeneity in the semivariogram analysis over the six five-year intervals (Figure 3.30). In all three directions, the dominant patch appeared to have a steep climb to a short, consistent, small patch at scale 1: 200 to 250 km in the North-South, 200 to 300 km in the East-West, and 150 to 250 km in the Diagonal. All three directions appeared to have a second dominant scale. The North-South component had a peak at scale 3 (1,100 and 1,200 km). The East-West had a peak at scale 4 (2,200 km). The Diagonal had a peak at scale 3 (1,500 km). Further analysis would be required to determine whether these are nested structure or noise. Overall, patterns differed among the three directions. Within a direction, the shape was similar among intervals, but steepness differed over time.

The pattern for wavelet variance differed from the semivariogram (Figure 3.30). Five scales were identified, rather than one or two. Wavelet variance was fairly consistent within a direction, but the three directions were different. The North-South component detected gradually increasing influence in scales 1 through 5 and the effect of scale 5 (3,000 km) doubled for some time intervals. The East-West component demonstrated a strong influence from scale 5 with some variation among intervals. The Diagonal component was relatively consistent with a very small peak at scale 4 (1,500 km).

DISCUSSION

Ecologists continue to seek out tools to understand the ecological significance of biotic and abiotic phenomena under broader spatial and temporal contexts. Among other more recent and sophisticated methods of pattern analysis, two-dimensional wavelet analysis offers a way to quantify spatial features in landscapes (e.g., patches, peaks, edges), while detecting and integrating this information from different spatial perspectives (e.g., scales). This method identifies individual features at one scale and integrates them as texture at another. Not only can wavelet analysis detect and quantify patterns in the data, it can identify the spatial and temporal scale of each pattern and locate it back in the original map. This enables us to find exactly what it is detecting and to interpret the individual pattern in its own biotic and abiotic context. Thus, there are two objectives to this research: (1) to investigate wavelets ability to detect pattern and (2) to provide new insights into how to understand pattern as it relates to ecological processes at multiple spatial and temporal scales.

In this manuscript we have explored the pattern detection abilities of two-dimensional wavelet analysis in long-term, large-scale ecological systems. Specifically, we compared pattern detection in the low heterogeneity of spatio-temporal patterns of Field Sparrows to the high heterogeneity of Red-eyed Vireos using data from the Breeding Bird Survey in North America as an example. We highlighted the capabilities of wavelet analysis by contrasting the corresponding capabilities of standard semivariogram. We explored pattern detection in practice and suggested how to approach the design of field experiments and monitoring programs to encompass multi-scalar data. The critical imperative is to understand the constraints of statistical inference to make realistic ecological inference.

Comparison Between Case Studies of Neotropical Migrants

Field Sparrows, Brewer's Sparrows, and Red-eyed Vireos are terrestrial birds that migrate to North America for the Summer and the tropics for the Winter. Field Sparrows represent a relatively stable distribution in North America, consistently occurring in one main cluster that expands, contracts, and moves in time without linearization. Field Sparrow distribution is more stationary in morphology of edges over time. These birds demonstrate dispersion in the East-West and Diagonal directions. Brewer's Sparrows provide an intermediate contrast between Field Sparrows and Red-eyed Vireos. Red-eyed Vireo distribution is more dynamic with the largest temporal dispersion. This species has more peaks, higher peaks, and a larger species range. The patch is large and coherent with a steep gradient and the largest amplitude. Scales 1 and 5 are North-South dominant. East-West is stationary over time.

Population Monitoring with Two-dimensional Wavelet Analysis

Effective monitoring programs are extremely important in tracking change over extended periods of time and space. The new statistical methods will improve indicator research, monitoring programs, and risk assessment to better serve a hypothesis-testing framework in ecology. Contributions of biotic and abiotic multi-scale factors to ecological patterns and processes can be considered separately, while also considering spatial, temporal, and biological organization within the landscape. For example, conditions at the community level may substantially influence the prevalence of a specific factor via mediators at an individual level that previously appeared to be independent (Legendre and Fortin 1989). Further, if we can estimate and compare aggregations at separate biological levels, then we can target our monitoring or landscape management efforts toward the appropriate levels.

In many cases of long-term monitoring to date, study designs do not encompass variables on multiple levels of scale (Cohen et al. 1990). This deficit may have occurred because ecologists were not aware of multi-scalar connections or because these connections were ignored (given that technological advances at the time could not support these analyses). Thus, historical data sets are not in a format to promote linking sub-organismal effects (e.g., individual metabolic rate, mitochondrial DNA results, corticosterone levels) to landscape-level systems. By employing these new statistics, several data sources may be analyzed simultaneously by first creating a mosaic data set. Of greater importance, however, is the ability of these analyses to influence future study designs to incorporate all appropriate variables at each scale.

Large data sets capture large- and small-scale processes, but teasing apart their temporal and spatial components can be difficult. Two-dimensional wavelet analysis is a data analytical tool that can be used to optimize monitoring efforts. By characterizing the internal structure of a species range, we can distinguish the factors that determine the distribution and abundance of organisms in space and time. Populations have important characteristics in ecological monitoring (e.g., size, density, dispersion, demographics). Wavelet analysis is useful in distinguishing biotic and abiotic processes generating large scale patterns in distribution. The detection of multi-scalar change in ecological systems requires careful monitoring with consideration to issues of precision (e.g., target areas, sample size, quadrat size, total area size, quadrat number, sampling frequency, scale), otherwise we may not collect data at the appropriate level to address our assumptions and integral associations may not be detected. We will present how wavelet analysis can be used as an analytical tool to optimize sampling design for monitoring programs and nature reserves.

CONCLUSIONS

Two-dimensional wavelet analysis characterizes complex ecological data to increase our comprehension of the reciprocal relationship between pattern and process across scales. Integrating individual features at one scale as a texture at multiple scales translates ecological patterns as a multi-dimensional volume. Visualizing complex relationships as a space-time volume captures a closer approximation of the way ecological relationships exist in nature - nonlinear, multi-scalar, and uncertain.

The adoption of newly available statistical methods would improve experimental design, analyses, and interpretation and thereby would to increase the accuracy of ecological inference. Inadequate data resolution for the scale in question and other limitations in experimental design reduce our ability to test hypotheses and verify spatially and temporally explicit models (e.g., measuring how well field observations match expectations based on computer models of metapopulation theory). Sampling properties are often under-explored (e.g., degree of aggregation, sample size, missing values, autocorrelation of multiple individuals from the same group and interdependencies among individual observations over space and time). By not taking these sampling properties into account, we limit our understanding of spatial, temporal, and organizational heterogeneity in ecological systems. Wavelet statistics provide a means to investigate previously unexamined pattern in complex databases to answer questions we have not been able to address until now.

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CHAPTER 4

DISCUSSION

Long-term, large-scale ecological monitoring programs have become increasingly important in conservation as the complex questions of sustainability become more immediate. Pattern analysis with advanced statistics will be critical for the success of conservation and restoration due to the ability of these statistical methods to detect ecological pattern, to characterize pattern change over time, to measure current levels of variability, and to identify changes in variables that require action. This approach will help us make choices about the resources to protect, the most effective level of protection, and the success of these efforts in minimizing risks to the environment. The ultimate goal is to detect appropriate ecosystem or landscape pattern, quantify this pattern, and make decisions about conservation, management, and policy based on this information.

Effective monitoring must involve sampling designs sufficiently detailed to detect ecologically significant patterns at multiple scales, yet logistically tractable and resource-efficient for sustained use. Now new methods can help optimize these objectives and contribute to the design of more realistic conceptual and empirical models that lead to more efficient sampling prior to implementation. Thus, these new methods are important for successful large-scale monitoring. Pattern detection and quantification of complex ecological data increases our comprehension of the reciprocal relationship between pattern and process across scales. Integrating individual features at one scale as a texture at multiple scales translates ecological patterns as a multi-dimensional volume. Moreover, visualizing complex relationships as a space-time volume captures a closer approximation of the way ecological relationships exist in nature: nonlinear, multi-scalar, uncertain. Success in maintaining ecological sustainability for future generations lies in the flexibility of approaching conservation efforts from both the current deterministic, linear perspective and the integrated, nonlinear perspective that encompasses Complexity Theory and uncertainty.

The goal of this dissertation was to explore the methodology of four advanced spatial and time series statistics (developed in other scientific disciplines) for applications to conservation ecology from a perspective that integrates information from the organism to the landscape. Within the framework of Complexity Theory, this study evaluated the relative abilities of semivariogram, Fourier analysis, one-dimensional-, and two-dimensional-wavelet analysis to detect and quantify multi-scale and scale-specific pattern in avian species distribution from the large-scale, long-term Breeding Bird Surveys monitoring program. In the preceding chapters, I explored Complexity Theory as a framework for pattern analysis in ecological monitoring (Chapter 1); examined the relative capabilities of semivariogram, Fourier analysis, and one-dimensional wavelet analysis to detect and classify spatio-temporal pattern in a comparison of stochastic processes, deterministic simulations, and empirical species range data for Western Meadowlarks (Chapter 2); and illustrated pattern recognition and reconstruction capabilities of two-dimensional wavelet analysis in three bird species with differing degrees of heterogeneity (Field Sparrow, Brewer's Sparrow, and Red-eyed Vireo; Chapter 3).

I found that wavelet analysis is a more sophisticated tool to investigate the reciprocal relationship between pattern and process relative to several other times series and spatial statistics used in landscape ecology. Wavelet analysis provides a way to look at different aspects of the whole pattern, and pieces of the pattern, because all the information is within the wavelet transform and retains the relationships among the constituents. Whether to use one- or two-dimensional wavelet analyses depends on the available data, question of interest, and specific parameters of the study design. Both of these forms of wavelet analysis have the flexibility to be useful in scientific research conducted under either the deterministic or the complexity framework. The usefulness of these wavelet analyses holds either when ignoring uncertainty as a nuisance, or when embracing uncertainty as a means to inform ecological research design, implementation, and interpretation. Closer statistical approximations of pattern in nature must be pursued to increase the accuracy of ecological inference.

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GLOSSARY

Directionality	The difference in a property of a system (e.g., bird distribution) as a result of changes in direction (i.e., North-South, East-West, Northeast-Southwest, Northwest-Southeast). The measure of this property has a different value when measured in different directions. This state of non-randomness is called anisotropy. The opposite is isotropy or the state of having the same properties in each direction.
Ecological pattern	The relative position of data or the relationship between multiple variables in data that relate to the interactions between the biotic and abiotic components of an ecological system. Pattern has many features, such as degree of heterogeneity and repeatability, but it's primarily described by grain and extent. Grain is the size of an individual measurement (e.g., distance, area, volume) and extent is the distance, area, or volume of the entire sample (i.e., all individual measurements).
Epistemology	Sometimes referred to as the theory of knowledge, epistemology is a branch of philosophy that involves the study of the nature and basis of human knowledge, especially its origin, limits, and validity.
Heterogeneity	Variability or differences in the distribution of data points. Most ecological data are heterogeneous due to variation in the distribution of biotic components based on other biota or abiotic resources. The opposite is homogeneity in which the data points are distributed in a regular, uniform pattern.
Non-stationarity	Change in distribution of a characteristic of a time series or spatial dataset with time or space. Non-stationarity expresses the change in statistical properties (most commonly the mean and variance) over time or space. The opposite is stationarity in which the distribution of a characteristic of a time series or spatial dataset does not change over time or space.
Scale	The length of measurement (e.g., length of a side of a pixel, grid cell, sampling window). Scale is primarily described by grain and extent. Grain (or resolution) is the size of an individual measurement (e.g., pixel, quadrat, grid cell), and often is the length measurement squared. High resolution provides greater clarity and definition. Extent is the distance, area, or volume of the entire sample, the domain of all individual measurements (i.e., study area,

GIS coverage, image). A large or coarse scale usually refers to coarse grain and large extent. A small scale refers to fine grain and small extent.

Wavelet	A mathematical function used in signal processing and image compression. A set of wavelets creates the basis of a wavelet transform that can be created in many forms (e.g., Haar, Mexican Hat, French Top Hat, Morlet, Daubechies), each transform having a different shape (e.g., rounded, squared) and different properties (e.g., orthogonal, bi-orthogonal, normalized). Orthogonality means the information captured by one portion of the wavelet is completely independent of the information captured by another portion. Other terms referring to this function are analyzing wavelet, wavelet basis, and filter.