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COMPUTER SYSTEMS AND MODELS, USE OF

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GLOSSARY

aggregation Combining several potentially separate components of a system to simplify analysis.

dynamic model Mathematical description of a system that has components that vary in time.

multimodel Single integrated model that links together models taking different approaches.

parameter Constant in a model that must be estimated from data, or assumed to be of a particular value.

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MODELS IN A VARIETY OF FORMS play a critical role in advancing our understanding of natural systems. Models abstract basic principles and derive the implications of such abstractions. This provides a method to analyze alternative hypotheses about natural system responses and the mechanisms that underlie these responses. This article presents an introduction to various modeling approaches and discusses how these have been applied to analyze species abundance and distribution.

I. WHAT IS A MODEL?

Just as storytellers can take their audience on trips to faraway places and provide a glimpse at life in different cultures, scientists tell their stories about the way the world works by making models. Such models never provide a complete view of how the world works, but do give us glimpses that help us to piece together interactions between different parts of the world and the processes that connect them. These models take many forms, some being mostly verbal, others mostly qualitative and graphical, some phrased in various mathematical forms, and still others set up as collections of rules within a computer program.

Models provide maps of varying levels of complexity to help us understand the topography of science. There are coarse road maps that provide merely the outline of major arteries for traffic, telling us nothing about buildings or other features of the landscape, but providing an overview of the linkages between key components of a system. More elaborate models show us the buildings and the infrastructure that links these buildings—the sewer and power lines. Even more complex models would indicate the humans in each building, their occupations, and the flow of money or capital

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goods between them. Similarly, models at many levels of complexity can be useful for addressing different questions in the study of biodiversity. A very coarse model might analyze the effect of land use change worldwide on total species richness. A more complex model could consider particular regions and analyze differentially the changes in land use within them and the associated changes in species numbers. A still more complex model could consider the local dynamics of individual species and from this elaborate the dynamics of species numbers.

II. THE PURPOSES OF MODELING

A. General Objectives of Models

Which type of model one constructs depends on the questions being asked and the availability of data to construct a reasonable model. Though there are many specific purposes for constructing models (Haefner, 1996), these may be grouped into a few general objectives: Description, Mechanism, Prediction, and Control. These objectives are not mutually exclusive, so that descriptive and mechanistic approaches may be used to aid prediction and control.

1. Description

Sometimes all that might be desired is a simple description of a collection of data. For example, an average provides a single value to summarize a list of numerical data. This may be sufficient for some purposes that do not require a description of how much variation is in the data. To assess variation, a dispersion measure such as the variance would be needed. These summary statistics are coarse, ignoring many of the details in the data. Yet they do allow us to easily comprehend major differences between different data sets. Extensive species lists within certain taxa from two locations may be compared by considering just the total numbers of species in the two locations and the number of species in common between them. Such a summary may be sufficient for a comparison of the two locations, while ignoring details such as the diversity within the taxa included. Descriptive approaches may be much more complex than simply providing averages and variances. Indeed the field of exploratory statistics deals with methods to analyze and summarize multidimensional data (Jambu, 1991). A typical example would be methods of time-series analysis in which the histories of species numbers might be compared between two locations or correlated with the histories of anthropogenic actions in the locations.

2. Mechanism

If the objective is to provide an understanding of how a particular system operates, then it is necessary to take account of the processes that govern the system. While all such mechanistic models are descriptive at some level, the point here is to deal with the basic physical, chemical, and biological processes operating in the system. This requires including those processes that operate at a spatial and temporal extent appropriate for the problem one is addressing, and ignoring others. Thus, analysis of how alternative global warming predictions would affect worldwide biodiversity might include the geographic variation in the temperature predictions at a spatial extent of hundreds of square kilometers, but would no doubt ignore the microclimate variation of every square meter. Even if it were possible to characterize the meter-by-meter temperature differences predicted by the alternative warming trends, the lack of available detail on the species present at this detailed spatial resolution limits the utility of including such detail. A discussion of such scaling issues is included elsewhere in these volumes.

3. Prediction

Predictive models are of two general types: those that attempt to project the behavior of the system based on certain explicit assumptions, and those that attempt to forecast the future behavior. The difference is between what might be true in the future if certain assumptions hold (projection) and what will be true in the future (forecasting) (Caswell, 1989). In many biological situations, the forecasting problem is not even attempted, as it would involved taking account of a wide variety of unpredictable abiotic phenomena (e.g., hurricanes and droughts). It is often feasible to construct a model to project the future dynamics of a system based on current observations and particular reasonable assumptions about the interactions in the system. The majority of population models (discussed elsewhere in these volumes) are of this form, in which abiotic influences are not included. These models can project the future behavior of the population based on the biotic forces of demographics, genetics, and social structure within the population. Uncertainties associated with unpredictable phenomena can be taken into account by attempting to project just the mean and variance of the variables of interest (e.g., population size).

4. Control

When a system has one or several components that are under human control, either completely or in part, then a model can be used to help determine how to apply

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such a control to meet certain objectives. Examples of controls are harvest quotas, limits on fertilization or pesticide application, flows from a dam, limiting importation of potentially harmful invasive species, and land use zoning regulations. Examples of objectives are maximizing biodiversity, minimizing population extinction probability, reducing the spread of nonnative species, and maintaining population size above some determined threshold (such as a minimum viable population size). Control models mostly focus on the dynamics of the system, with the simplest form of control being bang/bang, meaning on/off, such as allowing harvest in certain years and not allowing harvest in other years. A related objective is for control models to produce a relative comparison of alternatives in order to rank these alternatives according to some criteria (DeAngelis *et al.*, 1998). Still other control models are used to analyze the physiological responses of individual organisms to varying environments and the homeostasis that can arise through these responses.

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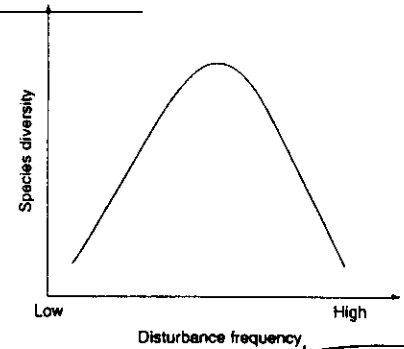

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FIGURE 1 Illustration of the intermediate disturbance hypothesis.

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III. TYPES OF MODELS

Models can be physical, such as animal models used in drug testing and airplane models used in wind tunnels. In biodiversity contexts, microcosms and mesocosms, which are limited biological systems built in a laboratory setting, play this role. These are meant to mimic the key biotic forces interacting within a natural system, but are constructed at a spatial extent that allows for easy observation and controlled experimentation. They cannot include all of the components of the real system, but do allow for projection of how the real system might respond under particular perturbations. Physical models clearly are limited, particularly to organisms that are mostly sessile or have very short distance movements.

Mathematical models come in a wide variety of forms. Some are simply graphical relations that show the qualitative relationship between certain components of a system, mainly to demonstrate the shape of response and whether one component increases or decreases with another. An example would be the increase and then decrease in species diversity along a gradient from low to high frequency of disturbance (Fig. 1). Here, there is no attempt to predict at exactly what disturbance frequency the exact peak in species diversity occurs. Rather, the objective is to illustrate the qualitative behavior of diversity, representing the "intermediate disturbance hypothesis," which posits that highest diversity occurs at intermediate disturbance frequencies.

The majority of mathematical models in ecology deal with the dynamics of populations and communities. Such models consider the basic processes of birth and death, immigration and emigration, and competition and predation to elucidate general theories of population dynamics. Described using differential or difference equations, these models allow for projection of the long-term behavior of populations, as well as provide methods to project the within-population structure (age, size, genetic, etc.).

Computer models are quite varied in structure. First, all the standard mathematical models of populations and communities, constructed using differential or difference equations, may be implemented on computers. Indeed, since it may be quite difficult to develop analytic solutions for such models, analysis of their behavior often requires the use of numerical solution methods implemented on a computer. There are many computer models that, although they may have a description that is essentially mathematical in form, are really described by the code itself rather than an explicit set of mathematical equations. An example would be cellular automata models, one type of which consists of a two-dimensional lattice, with each point on the lattice having one of a number of states (Langton, 1988). The simplest situation would be each lattice point being occupied (e.g., in the 1-state) or unoccupied (in the 0-state). The model is then described by a set of rules that determines how the state of a lattice point changes from one time step to another, based on the states of surrounding lattice points. Such a cellular automation

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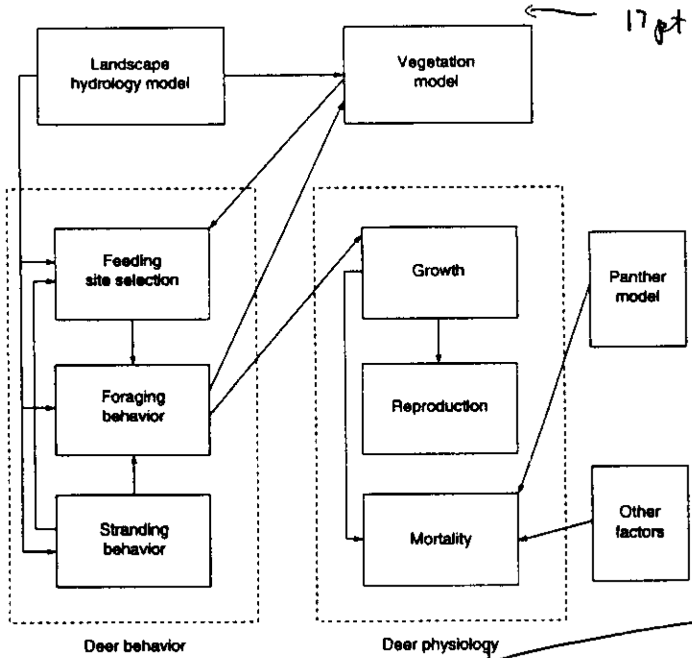

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FIGURE 2 Graphical depiction of the major components of an individual-based model for deer. (From Comiskey et al., 1997.)

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may be used to mimic the spatial dynamics of populations, in which each lattice point represents a possible location of an individual. Alternatively, each lattice point can be interpreted as a local population, and the entire lattice then can follow the collection of such populations, called the metapopulation.

System simulation models are elaborate computer models that attempt to include most of the biotic and abiotic factors that affect the system. Many agricultural system models are of this type, and include the crop, its pests, soil nutrients, and weather conditions, among other factors. Some other types of computer models are described in later sections. In all cases, though the model is in essence specified by the code itself, it is very useful to have some graphical description of the major components of the model. One example is shown in Fig. 2. There are a number of general modeling software packages designed explicitly to aid construction of computer models through the use of graphical elements.

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IV. LIMITATIONS OF MODELS

A. Trade-offs: Generality, Precision, Realism

No one model can do everything. In the process of deciding what components of a system to include, what processes to consider, and what spatial and temporal extent is appropriate, the model excludes part of reality. Modeling is a process of selective ignorance. We decide what to include and what to exclude. Part of the art of modeling is coming to grips with the issue of which details are important and which ones are not. In most cases the process is iterative, with a sequence of different models being tried until a model is arrived at that includes just the essential details necessary to address the problem of concern.

One view of the trade-offs in constructing a model is that no one model can be simultaneously general, precise, and realistic (Levins, 1968). As Fig. 3 illus-

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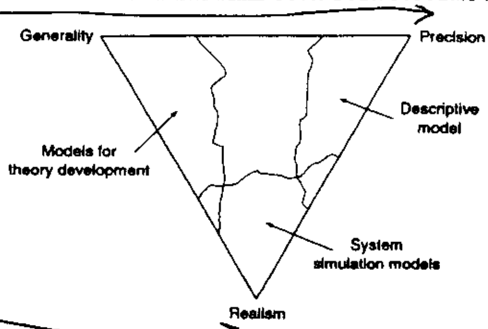

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FIGURE 3 Trade-offs in modeling.

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trates, these properties may be viewed as points of a triangle. Generality implies that the model may be useful in many different natural systems. A realistic model is one with components, parameters, and variables that are all possible to estimate from observations. A precise model is one that produces quantitative, accurate descriptions of the natural system. Models for theory development, including most of the classical population and community models, are quite general, somewhat realistic, but lacking in precision. Descriptive models designed to mimic the response of particular systems tend to be quite precise, slightly realistic, and not at all general. Most regression models are of this type. They may provide an accurate portrayal of a particular system, for example, winter wheat growth in Nebraska, but are not transferable to other situations such as winter wheat growth in eastern Russia. System simulation models tend to be quite realistic, somewhat precise, but not very general. Control models take up various positions in the figure, depending on the level of precision desired.

B. Aggregation and Loss of Detail

A major factor that affects where a particular model fits into the scheme shown in Fig. 3 is the amount of aggregation included. Natural systems consist of many components that can be lumped together or disaggregated. Population models that use a single variable to represent the whole population must inherently ignore the within-population structure (e.g., age and size). Such a model would not be able to discriminate between a population with mostly small individuals and one with mostly large individuals, unless this within-population structure was assumed to affect the population's growth characteristics in some manner. Aggregation implies a loss of detail that allows for quite general models. Often this gives model parameters that are not at all easily estimated from observations. Examples would be the growth rates in population models and the competition coefficients in community models. The less aggregation in the model, the more parameters there tend to be and more data are required in order to estimate them. (PE)

C. Uncertainties: Mechanisms, Data for Parameterization, Biotic and Abiotic Forcing Functions

The modeling process is limited by the information available. There may not be basic agreement on the mechanisms that are critical in the system of concern, so that any particular model includes only some of the mechanisms, or just partial information on these mechanisms. Many population models applied to vertebrates ignore social structure, despite evidence that it is often present in such populations. This is typically due to lack of understanding of the effect of such structure at population levels, and gives rise to another set of models designed specifically to investigate these effects.

Under situations in which the mechanisms are well understood, it may not be possible to accurately estimate model parameters because adequate data are lacking. There are a variety of statistical methods designed specifically to determine the optimal choice of parameters in such situations (Hilborn and Mangel, 1997). These methods may take account of parameters estimated either for similar species or for similar locations other than the one being considered. For example, it may be necessary to use observed clutch size distributions for one bird species in application to a similar species about which such information is lacking. Another uncertainty associated with natural system models arises due to the unpredictability of forcing functions such as weather and disturbance. If historical information is available on these functions, this may be used to estimate the stochastic effects of such forcing. These various uncertainties limit the detail at which models may be constructed, and thus limit the types of questions that may be addressed using models.

V. SOME TOOLS OF THE TRADE

A. Statistical Approaches

Statistical models usually have a descriptive objective rather than a mechanistic one. The parameters within these models are directly estimated by choosing them in a manner that best fits a certain data set. Thus any particular statistical model is typically not very general in application to different systems. The structure of such models may be useful in a wide variety of different contexts. Regression models, which assume a particular mathematical relationship between variables and assume that errors in the data take a particular form, are widely applied. Numerous regressions have been estimated for species richness as a function of latitude, altitude, and rainfall (Huston, 1994). Discussion of statistical methods applied to estimation of population sizes and densities may be found elsewhere in these volumes.

B. Dynamic Models

Although many of the traditional models for populations and communities are in the form of dynamical systems (e.g., collections of linked differential or difference equations), often the types of analyses performed for these models are based around equilibrium assumptions. The objective is to find long-term asymptotic behavior. This may be a static equilibrium (e.g., population sizes approach a constant value through time) or a dynamic equilibrium (e.g., population sizes follow repeatable patterns through time) (Murray, 1989). While these situations may arise, many models produce behavior that does not have a long-term equilibrium structure. Another key objective is to determine the stability characteristics of any equilibria that arise, in the mathematical sense of determining whether a model that is perturbed from an equilibrium condition will return to it. The dynamics arising in all these models takes account of the basic demographics of the population, as well as interactions with other populations. Adding abiotic conditions such as temperature and rainfall, or adding spatial components, often requires that the analysis be done using numerical simulations.

C. Geographical Information Systems

The advent of remote-sensing methods using airplane cameras and satellite imaging has opened new possibilities for following and modeling the responses of the earth's biota. A key tool that allows the use of such materials are Geographical Information Systems (GIS), which enable computers to graphically display the remote-sensing data as two-dimensional maps. Each image may represent one aspect of an underlying landscape, such as landcover or vegetation type. The image value at any particular location (or pixel) in the map is estimated using models that classify the output of the cameras or the multispectral scanners on satellites into types appropriate for the objective. These models require ground-truthing to ensure that the estimated value for a particular location matches what is actually present. GIS methods allow various spatially explicit components of a landscape to be combined by looking at different map layers (different images measuring different aspects of the landscape). A mathematical function is then applied that averages or applies thresholds to these various components. Estimates of regional and worldwide carbon uptake are obtained using such methods applied to vegetation maps, in which different carbon assimilation values are assigned to different vegetation types, linked with weather maps supplying temperature and rainfall patterns.

VI. APPLICATIONS

A. Habitat Suitability Indices

Habitat Suitability Evaluation Procedures (HEP) are a formalized methodology for impact assessment on wildlife habitat. These are based on Habitat Suitability Index (HSI) models, which attempt to summarize the site characteristics that affect the utilization of particular habitats by a variety of wildlife species. Numerous HSI models have been constructed, typically consisting of very simple regression-type models. The key habitat variables are often some measure of canopy cover in a variety of classes, diameter classes of trees and shrubs, tree stem densities, area of open water, and distance to forest cover, among others. The objective is to combine these variables, based on extensive field observations done in a correlative manner, to provide overall indices of suitability. HSIs are always indexes with values between zero and one, and they are assumed to be proportional to carrying capacity.

HSIs are based only on local habitat variables; they completely ignore any effects due to species interactions, except those due to indirect effects on related habitat variables. The models ignore the spatial interactions of habitat types across a landscape. This leads to difficulty in situations for which the size, shapes, edge effects, and neighborhood relationships have a greater effect on habitat preference than local forest composition and structure variables. The models also do not take account of the issue of presence/absence of a species, and thus ignore any historical influence on potential local abundance. HSIs are inherently static entities, so any dynamics they produce are driven completely by changes in habitat variables and not by the inherent dynamics and demography in the species being considered. Despite these criticisms, HSIs are perhaps the most commonly used set of ecological models, in part because users realize their limitations and view them as a simplified tool to summarize a very complicated situation by a single number. Such simplification must result in a loss of information, but a key issue regarding HSIs is whether they indeed can be used as a useful predictor for abundance. A summary of the HSI modeling approach is given in Verner *et al.* (1986).

B. GAP Analysis

The Gap Analysis Program (GAP) is a nationwide comprehensive effort in the United States to inventory plant and animal species, computerize the results, and have the capability to analyze spatially the relationships among different taxa. GAP relies heavily on GIS methods, and has as a major objective the capacity to identify "gaps" in biodiversity. Such gaps are presumed to arise in locations that are expected, from biological knowledge of species requirements, to have certain mixtures of species present, but for some reason do not. The focus of these efforts is not on rare or threatened and endangered species, but rather on the status of ordinary species and their habitats in order to inform policymakers to improve their decisions. Much of the remote-sensing information cannot determine the presence or absence of particular species, because the technology can provide information only on basic vegetation components of a landscape, and landforms such as rivers, roads, and urban areas. Thus, an extensive ground effort is under way to survey the distribution of various species, map these, and relate these mapped distributions to habitat variables, land use, and ownership, and other related species distributions. The focus is on vertebrate species, basic floristic types whose presence can be estimated from satellite image analysis, and landform information.

Gap analysis does not attempt to explicitly model biodiversity, but rather uses the preceding surrogate measures as a method to assess spatial patterns in biodiversity. There are acknowledged taxonomic biases in this approach. The objective has been to provide basic methods to assess the impacts of the rapid land use changes that have occurred in the United States over the past several decades and how these impact biodiversity. Other limitations of this approach are the lack of detailed demographic information included for the species of concern, the static nature of the project, and the reliance on mapping methodologies that require extensive ground-truthing to ensure accuracy. Full documentation on the GAP may be found on the web at http://www.gap.uidaho.edu/gap. A basic reference is Scott *et al.* (1993).

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C. Metapopulation Models

Both HEP and GAP are attempts to account for the spatial nature of biodiversity by including explicit maps of basic habitat variables. An intermediate approach between models that include all the spatial detail available from maps and those that ignore all spatial aspects of a system are metapopulation models. These models consider a landscape to be split up into a number of localized populations, called subpopulations, with the entire collection of these called a metapopulation (Gilpin and Hanski, 1997). Most of the biotic interactions driving population dynamics occur within the localized subpopulations, but there are exchanges of individuals between these subpopulations. This allows for differing environmental, demographic, genetic, and disease situations to be present in the subpopulations. Depending on the assumptions about transport of individuals between the subpopulations, these can be relatively isolated or closely coupled.

A clear advantage of metapopulation models is the ability to derive analytic results, such as equilibrium and stability behavior, as a function of the within-subpopulation characteristics and the between-subpopulation factors such as movement. The models are particularly appropriate for cases in which a landscape can be reasonably viewed as containing discrete patches of habitat suitable for the population, with the intervening regions not suitable. The level of detail in these models can be quite variable, with the simplest versions just treating subpopulations as either present of absent. More complicated models take account of demographics within each subpopulation or explicit details on the relative spatial locations of each subpopulation that affect movement between them. These can be used for a population viability analysis, in which the probability that the overall population will survive for varying time periods is estimated.

D. Individual-Based Approaches

All of the foregoing approaches include various levels of aggregation in their components in order to simplify the model. An alternative reductionist approach is to take account of differences between individuals within a population, allow the individuals to feed, grow, and interact, and from the aggregated behavior of these individuals build an understanding of population-level responses (DeAngelis and Gross, 1992). These individual-based approaches are increasingly common thanks to advances in computer science and the increasing availability of data on behavior and physiology of species of particular interest. The advantages of these approaches include the ability to consider the effect of abiotic factors on populations through their direct impact on individual behavior and growth, to take account explicitly of spatial variation in habitat factors, and to deal with small populations in which individual differences within the population can have great impacts on population-level responses. Disadvantages of individual-based approaches include the requirement for a great amount of detailed data to realistically simulate individual behaviors, and the typical necessity of making numerous simulations to evaluate any particular response that may arise because of the stochastic nature of the models.

VII. FUTURE TRENDS

A. Multimodeling and Regional Assessment

Natural systems have many interacting components operating at a variety of temporal and spatial extents and requiring differing levels of detail to describe the interactions between them. One historical approach in ecology to model such systems is to break it into a number of compartments (often for different trophic levels, and sometimes with grouping within each trophic level) and consider the dynamics of each compartment with movements of energy, biomass, or nutrients among them. It is quite difficult to make these systems analysis approaches spatially explicit or to link them to GIS. Yet it is now becoming possible to link together a variety of different modeling approaches in order to best utilize the available data, with different resolutions at different trophic levels, and carry this out in a spatially explicit manner. Such multimodels may use very simple models similar to HSIs for some trophic components, more complex dynamical systems for certain populations with mostly very localized interactions, and individual-based models for organisms that move great distances and average over the spatial heterogeneity. One example of such an approach is the ATLSS (Across Trophic Level System Simulation) Project, which is an ongoing attempt to build a multimodel for estimating the biotic impacts of alternative water management plans on the Everglades of south Florida (DeAngelis *et al.*, 1998).

Building multimodels requires extensive landscape data obtainable from remote-sensing and ground efforts. The approach is inherently dynamic, and thus requires methods to estimate the spatial dynamics of key environmental drivers, or else have available a history of this spatially that can be analyzed statistically. In the Everglades, the major driver is water, and both historical data and detailed hydrologic models are available to provide estimates for scenario evaluations. Without such data, assumptions must be made about the dynamics of the landscape. With the reduced cost of data storage and the development of standards for spatially explicit data, it is expected that future models will have available extensive time series of remotely sensed images to both calibrate multimodels and provide the opportunity to iteratively improve their predictive abilities. For problems at regional levels, such multimodels are a rational method to aid planning while taking account of the best scientific data at the variety of resolutions available.

B. Behavioral Dynamics of Species of Special Concern

Great strides are being made in improving our understanding of the conservation biology of rare, threatened, and endangered species throughout the world. In an effort to better estimate the responses of populations of these species, numerous remote-sensing methods have been employed to track the movements of individual organisms. These include radio-tracking devices implanted within sampled individuals, which allow explicit location and physiological data (e.g., body temperature) to be obtained regularly throughout the individual's life from either satellites, airplanes, or sampling locations on the ground. The technology has advanced so that implantation of such devices can be done rapidly with no determinable harm to the individual. When done for many individuals within a population, it is becoming possible to follow the behavioral dynamics of mixtures of individuals. This includes the ability to ascertain details of mating, territoriality, and aggressive interactions.

It is likely in the future that managers concerned with a particular species will be able to observe in real time the movements of many individuals within a population. Then they might apply spatially explicit modeling methods to project the response of the population to particular management alternatives. This scenario suggests that the simultaneous monitoring of other species that interact with the species of concern would allow for the regular application of adaptive management methods.

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See Also the Following Articles

ECOSYSTEM FUNCTION MEASUREMENT • MEASUREMENT AND ANALYSIS OF BIODIVERSITY • REMOTE SENSING AND IMAGE PROCESSING.

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